Invertebrate Zoology, 2025, 22(2): 219–236

A new genus and species of sea anemone (Cnidaria: Actiniaria) related to *Urticina*, with the reinstated family Tealidae Hertwig, 1882 and keys to genera and species

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ABSTRACT: The family Tealidae Hertwig, 1882 is reinstated to include the genera *Urticina* and *Cribrinopsis*, formerly assigned to Actiniidae, and *Urtibrina* gen.n. Members of this family have mesenteries with a strong tendency toward decamerous arrangement. Sequences of 16S rRNA of all included species have long insertion termed here as “Tealidae-insertion”, which is unique to the family. The new genus *Urtibrina* gen.n. is created for *Urticina clandestina* and a new species *Urtibrina rimicola* sp.n., both recorded from British Columbia, Canada and Washington State, USA. The genus *Urtibrina* gen.n. has all the features of *Urticina* but differs from it in possessing gonads on the mesenteries of all cycles and is supported by molecular analysis.
How to cite this article: Sanamyan N.P., Sanamyan K.E., McDaniel N.G., Kukhlevskiy A.D., Bocharova E.S. 2025. A new genus and species of sea anemone (Cnidaria: Actiniaria) related to *Urticina*, with the reinstated family Tealidae Hertwig, 1882 and keys to genera and species // Invert.Zool. Vol.21. No.2. P.219–236, Suppl. data. doi: 10.15298/invertzool.22.2.01

KEY WORDS: Sea anemones, synapomorphy, North East Pacific, family Tealidae, Cnidaria, Anthozoa, Actiniaria, *Urtibrina* gen.n., *Urtibrina rimicola* sp.n.

Описание нового рода и вида морских анемон (Cnidaria: Actiniaria), родственного роду *Urticina*, с восстановлением семейства Tealidae Hertwig, 1882 и ключами до родов и видов

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РЕЗЮМЕ: Восстановлено семейство Tealidae Hertwig, 1882. В его состав включены *Urticina* и *Cribrinopsis*, которые ранее относили в Actiniidae, и *Urtibrina* gen.n. Виды этого семейства характеризуются сильной тенденцией к декамерной организации мезентериев. Сиквенсы 16S rRNA всех входящих в состав семейства видов имеют длинную и уникальную для семейства вставку, которую мы назвали «теалидной вставкой». Новый род *Urtibrina* gen.n. создан для ранее известного вида *Urticina clandestina* и для нового вида *Urtibrina rimicola* sp.n. Оба вида известны из Британской Колумбии, Канада, и штата Вашингтон, США. Род *Urtibrina* gen.n. характеризуется всеми признаками рода *Urticina,* но отличается от него наличием гонад на мезентериях всех циклов и поддержан молекулярными данными.

Как цитировать эту статью: Sanamyan N.P., Sanamyan K.E., McDaniel N.G., Kukhlevskiy A.D., Bocharova E.S. 2025. A new genus and species of sea anemone (Cnidaria: Actiniaria) related to *Urticina*, with the reinstated family Tealidae Hertwig, 1882 and keys to genera and species // Invert.Zool. Vol.21. No.2. P.219–236, Suppl. data. doi: 10.15298/invertzool.22.2.01

КЛЮЧЕВЫЕ СЛОВА: актинии, молекулярная синапоморфия, Северо-Восточная Пацифика, семейство Tealidae, Cnidaria, Anthozoa, Actiniaria, *Urtibrina* gen.n., *Urtibrina rimicola* sp.n.

Introduction

This work expands upon our publications on sea anemones of the genera *Urticina* and *Cribrinopsis* in general, and on sea anemones of British Columbia in particular (Sanamyan, Sanamyan, 2006; Sanamyan *et al*., 2013, 2019, 2020). Members of these genera received much attention during recent decades, especially following the publication of Sanamyan & Sanamyan (2006) who demonstrated that *Urticina* and *Cribrinopsis* species inhabiting North Pacific waters differ specifically from the species originally described from North Atlantic and European waters. Later it became clear that the diversity of this very interesting group of species is strongly underestimated. Underwater in-situ photographs of collected specimens proved to be especially useful in revealing diversity among these anemones. In the introduction of Sanamyan *et al*. (2013) we wrote that numerous underwater photographs of sea anemones taken by one of us (N. McDaniel) in British Columbia revealed that sea anemones in this region are more diverse than was thought previously, with several species which have not been assigned to any known species. Descriptions of some of these species were published (Sanamyan *et al*., 2013, 2018, 2019) and in the present work we describe another new species, *Urtibrina rimicola* sp.n., erect a new genus *Urtibrina* gen.n. for it and for *Urticina clandestina*, previously described from the same region, and reinstate the family Tealidae for *Urticina*, *Cribrinopsis* and *Urtibrina* gen.n.

Material and methods

The specimens of *Urtibrina rimicola* sp.n. described in the present paper were photographed in-situ underwater to record color, external appearance, position on the substrate and to assess the degree of variation in these features. Clippings of tissue of each freshly collected specimen were fixed in 95% etOH for molecular study. Collected specimens were fixed in seawater formalin and one specimen (KBPGI 510/2), in Davidson's solution. Later they were transferred to 70% ethanol for long term storage. In addition, the following material was examined: *Urtibrina clandestina* (holotype ZIN 11328 and paratypes KBPGI 415/1, 416/2 (cnidae of the tentacles reexamined) and specimens KBPGI 503/3, 504/4 (sequenced); *Aulactinia vancouverensis* (KBPGI 505/4, sequenced). The histological methods and terminology are the same as in our previous papers (see, e.g. Sanamyan *et al*., 2021).

The mitochondrial and nuclear gene fragments were amplified using published primers and protocols for 16S rRNA and COIII (Geller, Walton 2001), 12S rRNA (Bocharova, 2015), 18S rRNA and 28S rRNA

(Sanamyan *et al*., 2018). A dataset containing 197 taxa (270 sequences in final concatenated datasheet, Supplementary Table 1) was used. It is based largely on datasets published by previous authors (in particular Daly *et al*., 2008, 2017; Larson, Daly, 2016; Sanamyan *et al*., 2021) and some newly generated sequences. The sequences were aligned using the Mafft v7.409 with E–INS–i algorithm and "–maxiterate 1000" option (Katoh, Standley, 2013). Alignments were inspected and edited manually in AliView v.1.24 (Larsson, 2014). A ML tree was generated by IQ-TREE v.1.6.12 (Nguyen *et al*., 2015) using automatic model selection (Kalyaanamoorthy *et al*., 2017) and ultrafast bootstrap approximation (Hoang *et al*., 2018). Bayesian estimation of posterior probability was performed in MPI (fast multithread) version of MrBayes 3.2.7a compiled from source code (Ronquist *et al*., 2012). Two parallel runs each comprising six Markov chains were run for 10^7 generations and sampled at intervals of 500 generations. To view, edit and print final trees MEGA7 (Kumar *et al*., 2016) was used.

The holotype is deposited in the Zoological Institute (St. Petersburg, ZIN), a paratype, in Kamchatka Branch of Pacific Geographical Institute (Petropavlovsk-Kamchatsky, KBPGI).

Taxonomy

Order Actiniaria
Family Tealidae Hertwig, 1882

DIAGNOSIS. Actiniaria with well developed pedal disc. No acontia. Mesenteries not divisible in macro- and microcnemes. Sphincter muscle endodermal, strong, circumscribed. Tentacles arranged in circles with no more than one tentacle communicating with each endo- and exocoel. Column with adhesive to non-adhesive verrucae or smooth. Acrorhagi not present. Mesenteries have strong tendency to decamerous arrangement. Cnidom includes spirocysts, holotrichs, basitrichs, b-mastigophores, p-mastigophores A, and p-mastigophores B1. Sequences of 16S rRNA of all included species have long (25bp) and unique for the family "Tealidae-insertion" CGTCCTCAGGGTCGACCCTTAGGGC (see *Molecular data* section below).

Type genus: *Tealia* Gosse, 1858.

Included genera: *Urticina* Ehrenberg, 1834 (senior objective synonym of *Tealia* Gosse, 1858), *Cribrinopsis* Carlgren, 1921 and *Urtibrina* gen.n.

Accumulated information on the diversity of species of *Urticina*, *Cribrinopsis* and, now, *Urtibrina* gen.n., is extensive and the morphology of a large proportion of species has been well studied by modern authors. The morphology of these species, especially a strong tendency to acquire decamerous symmetry (with some variations; formation of decamerous symmetry is discussed in Sanamyan *et al*., 2019), suggests that these genera deserve separation from Actiniidae into their own family. Many species of this group were sequenced and molecular data also show that they are closely related and form a monophyletic clade. Based on the morphological and molecular data, in the present work we remove *Urticina* and *Cribrinopsis* from Actiniidae and reinstate the family Tealidae Hertwig, 1882 for them.

Hertwig (1882: 35) created the family Tealidae and stated that he takes "the structure of *Tealia crassicornis* as the paradigm for its definition". He also wrote: "the most important feature of the family is, I consider, the extremely characteristic circular muscle, which can be recognised with the naked eye, as a thick swelling on the inner side of the wall. In transverse section it shows a circular or oval figure, fastened on one side to the wall [...]". Actually he described what is now termed "strong endodermal circumscribed sphincter muscle". He also stated that he "entirely disregarded the nature of the surface of the body, so that forms both with smooth and with warty walls may find their place in the family". Although both features indeed are characteristic for the family Tealidae in its current sense, Hertwig's definition has only historical interest. The only important fact is that he created the new family name Tealidae for *Tealia*.

Nomenclatural notes on family name. (International Code of Zoological Nomenclature, ICZN, 1999 is referred below as "Code", its articles as "Article ..."). The first family created for the genus currently known as *Urticina* was Bunodidae Gosse, 1858. Its type genus, *Bunodes* Gosse, 1855, is the senior objective synonym of *Urticina*. However, *Bunodes* Gosse, 1855 is preoccupied by *Bunodes* Eichwald, 1854 (order Xiphosura) and therefore, Bunodidae Gosse, 1858 is invalid (see Article 39) and cannot be used. The next available family is Tealidae Hertwig, 1882, type genus *Tealia* Gosse, 1858, the junior objective synonym of *Urticina*. This family name is available and, as shown below, is valid.

McMurrich (1901) created the family Cribrinidae McMurrich, 1901 with the type genus *Cribrina* Ehrenberg, 1834, a subjective (and treated as junior) synonym of *Urticina*. He recognized that Tealidae Hertwig, 1882 has priority but considered "the name Tealiidae for the family is inadmissible since *Tealia* is a nomen delendum" (McMurrich, 1901: 15). There is no term "nomen delendum" in the current Code. In fact, McMurrich (1901) replaced Tealidae with Cribrinidae because he considered the name *Tealia* to be a junior synonym. According to Article 40.1, when the name of a type genus is considered to be a junior synonym, the family-group name is not to be replaced. Article 40.2 gives an exception for family names replaced before 1961 if they are in prevailing usage, but since Cribrinidae currently is not in usage (it was synonymized with Actiniidae Rafinesque, 1815 by Stephenson, 1922 and not recognized as valid since that time) this article could not be applied to validate Cribrinidae. Thus, the valid family name is Tealidae, not Cribrinidae.

Finally, it is necessary to discuss the spelling of the family name. Originally it was spelled as Tealidae (stem *Teal*- and suffix -*idae*), but subsequently sometimes as Tealiidae (stem *Teali*- and suffix -*idae*, e.g. by McMurrich, 1901). The genus *Tealia* is named after a person (Mr. Thomas Pridgin Teale, see Gosse, 1860: 207). When the name is derived from the name of person and is not a Latin or Greek word the stem is determined according to Article 29.3.3. It states that in such cases the stem "is that adopted by the author who establishes the new family-group taxon". Thus, the original spelling Tealidae, with one "i", is valid and should not be replaced with Tealiidae.

Genus *Urtibrina* **gen.n.**

Type species: *Urticina clandestina* Sanamyan, Sanamyan et McDaniel, 2013, designated herein. Other species included: *Urtibrina rimicola* sp.n.

DIAGNOSIS. Tealidae. Mesenteries decamerously arranged. Mesenteries of all orders fertile. Basitrichs in actinopharynx much larger than those in tentacles and size ranges do not overlap. About the same number of mesenteries proximally and distally. Cnidom: spirocysts, holotrichs, basitrichs, p-mastigophores A, and p-mastigophores B1.

DIFFERENTIAL DIAGNOSIS. *Urtibrina* gen.n. differs from *Urticina* in the presence of gonads on the mesenteries of the first cycle; in *Urticina* the first cycle is sterile. *Urtibrina* gen.n. differs from *Cribrinopsis* in relative size ranges of large basitrichs in the tentacles and actinopharynx: basitrichs in actinopharynx of *Urtibrina* gen.n. are much larger than basitrichs in the tentacles, a feature not characteristic for *Cribrinopsis*.

ETYMOLOGY. The generic name is derived from *Urticina* and *Cribrinopsis* to reflect morphological similarity with these two genera. The gender is feminine.

The genus *Urtibrina* gen.n. has been created to accommodate *Urtibrina rimicola* sp.n. and a species described previously as *Urticina clandestina*. The uncertain taxonomic position of *Urticina clandestina*, which shares features of *Urticina* (relative size ranges of large basitrichs in the actinopharynx and the tentacles) and *Cribrinopsis* (fertile mesenteries of the first cycle) was recognized in its original description (Sanamyan *et al*., 2013). After discussion the authors of this species decided to assign it to *Urticina* because in rare cases some mesenteries of the first cycle in some species of *Urticina* may be fertile (e.g. Sanamyan, Sanamyan, 2006 detected one fertile mesentery of the first cycle in one specimen of *Urticina felina*). Now, the discovery of the second species which also has all mesenteries of the first cycle fertile, prompts us to remove *Urticina clandestina* from the genus *Urticina* and place it, together with the species described in the present paper, in the new genus *Urtibrina* gen.n. According to molecular data these two species are closely related to each other and form a clade sister to a clade comprising all *Urticina* and *Cribrinopsis* species (Figs 6, 7), being basal (with 100% support) among three groups.

Urtibrina rimicola **sp.n.**
Table 1; Figs 1–5.

MATERIAL EXAMINED. Holotype: ZIN 13512 (female), Canada, British Columbia, Barkley Sound, Ohiat Islet, 48°51.335′N, 125°11.074′W, shallow subtidal, September 28, 2017, collectors Neil McDaniel and Andy Lamb. Paratype: KBPGI 509/1 (female) same locality, one specimen. Additional specimen: KBPGI 510/2 (female) Canada, British Columbia, Strait of Juan de Fuca, 49°24.944'N, 124°02.111'W, shallow subtidal, September 2, 2017, collector Douglas Swanston, one specimen.

DESCRIPTION. *External structure*. Live specimens have an oral disc up to 15 cm in diameter. The holotype was at least 12 cm in longest dimension, and the paratype slightly larger (Fig. 1A, E). The preserved holotype is about 20 mm in height and up to 50 mm in diameter (Fig. 2A, C), the paratype is about 22 mm high and to 63 mm in diameter (Fig. 2D), and the third specimen, not included in type series, 22×38 mm (Fig. 2B).

The pedal disc is about the same diameter as column, strongly adhesive, and covered with brown (in preservative) cuticle.

The cylindrical column is covered by numerous prominent adhesive verrucae, crowded in most parts of column but slightly sparser in its most proximal part. Gravel and broken shell particles are firmly attached to some verrucae but are rather sparse. In live specimens the column is bright red, the tops of the verrucae whitish (Fig. 1C, D). Near the margin the verrucae are thin-walled and convex, while proximally, in preserved specimens, they have concave apices (Fig. 3B). There is a deep fossa and a very short and sometimes hardly noticeable (in specimen KBPGI 510/2) capitulum. The circular oral disc is slightly wider or about the same diameter as the column in live specimens. The oral disc is almost completely red (Fig. 1C) or, often, only in its central part around the mouth (Fig. 1A, E). In other parts the oral disc is yellow-greenish or bluish-grey. (Fig. 1B). The actinopharynx and siphonoglyphs are beige or grey (but not red). The oral cone is raised in live specimens in such a way that the whole oral disc has somewhat conical shape. The tentacles are short, not longer than a half of the radius of the oral disc, all of about the same length, conical, pointed at tips, and arranged

Table 1. Size ranges (length × width, in microns) and distribution of cnidae of *Urtibrina rimicola* sp.n. Letters in brackets correspond to letters in Fig. 5. “N” — ratio of number of specimens in which each cnidae was found to number of specimens examined.

Таблица 1. Размеры (длина × ширина, в микронах) и распределение стрекательных капсул *Urtibrina rimicola* sp.n. Буквы в скобках соответствуют буквам на рис. 5. «N» — отношение количества экземпляров, в которых данный тип книд был найден, к количеству исследованных экземпляров.

Body region	Cnidae	Size ranges (μm)	N
Pedal disc	(A) basitrichs (very rare)	8–12.5 × 1.5–1.8	2/2
	(B) basitrichs (few–common)	18–24 × 2–3	2/2
Column	(C) basitrichs (very rare–common)	9–13 × 1.5–2.4	3/3
	(D) basitrichs (common)	15.5–24 × 1.9–3	3/3
	(E) basitrichs (common)	18.8–20 × 3.5–4	1/3
	(F) p-mastigophores A (common)	18.5–34.4 × 4–7.8	3/3
Tentacles	(G) spirocysts (very numerous)	13–41 × 1.3–3	3/3
	(H) holotrichs (few, see text)	18–24.5 × 2.5–3.5	3/3
	(I) holotrichs (rare, see text)	17–26 × 5.5–6.5	2/3
	(J) basitrichs (very rare)	10–13 × 1.6–1.7	2/3
	(K) basitrichs (common)	17–29 × 2–3	3/3
	(L) p-mastigophores A (rare–common)	25–33 × 4.5–7.5	3/3
Actinopharynx	(M) basitrichs (very rare)	16–25 × 2–2.7	3/3
	(N) basitrichs (numerous)	42–62 × 5.1–7.9	3/3
	(O) p-mastigophores A (common)	21.5–34 × 4–6.5	3/3
Filaments	(P) basitrichs (rare)	11–15 × 1.6–2.5	3/3
	(Q) basitrichs (common)	17.5–27 × 2.1–3	3/3
	(R) p-mastigophores A (common)	24–33 × 4.5–8.5	3/3
	(S) p-mastigophores B1 (common)	(28) 46–63 × 5.5–8.5	3/3

decamerously in five cycles (Fig. 1A). In underwater photographs we counted 155 visible tentacles (perhaps there are a few more) in the holotype (Fig. 1A) and 174 in the paratype (Fig. 1E). In the preserved specimens the tentacles have longitudinal folds (Fig. 2A, D). The tentacles have a white or whitish patch at the base of their oral side which is usually brighter on the tentacles of the last (younger) cycle (Fig. 1B, E). A wide lilac or red band, wider on the oral side and narrower on the aboral, completely encircles the middle part of the tentacles. Tentacle tips are always light-grey, without red pigment. Mesenterial insertions on the disc between the tentacles are always dark-red to purple. Whitish radial lines extend between the mesenterial insertions on the peripheral part of the disc to the bases of the tentacles where they merge with a white spot on the oral side of the bases of the tentacles. The longest white lines run to the outer tentacles (Fig. 1A, E).

Internal structure. The marginal endodermal sphincter muscle is strong, circumscribed, pinnate, with one asymmetrically lying main mesogloeal lamella: the mesogloeal branches on its side facing toward the margin are about three times shorter than the branches on its opposite side (Fig. 3B). In the holotype the sphincter is 2×1 mm in cross sections. The longitudinal muscles of the tentacles and radial muscles of the oral disc are mesogloeal (Fig. 3C, D). The circular endodermal columnar muscles are well developed in all parts of column except verrucae (Fig. 3B). The actinopharynx has two deep siphonoglyphs supported by the directives.

The mesenteries are arranged decamerously in four cycles (Fig. 2B). Decamerous symmetry is not quite perfect and may be violated by the development of additional pairs of mesenteries of the second to fourth orders, occasional absence of mesenteries of the fourth cycle in some compartments or by occasional presence of small mesenteries of the fifth cycle (Fig. 4). In the holotype the mesenteries are arranged as 10+11+22+44=87 pairs; the paratype has 10+12+22+43=87 pairs (it has symmetrical duplication of the mesenteries of the second cycle in two compartments near one pair of directives); the third (smaller) specimen (KBPGI 510/2) has 10+10+21+38=79 pairs (Fig. 2B). The number of the mesenteries is the same distally and proximally and almost the same as the number of the tentacles. The mesenteries have oral stomata about 2 mm diameter and marginal stomata about 1 mm diameter. The retractor muscles are long and diffuse, in contraction they may form small flaps and lobes (Fig. 4). The parietobasilar muscles are well developed and form a long free flap. The mesogloea of the mesenteries in the

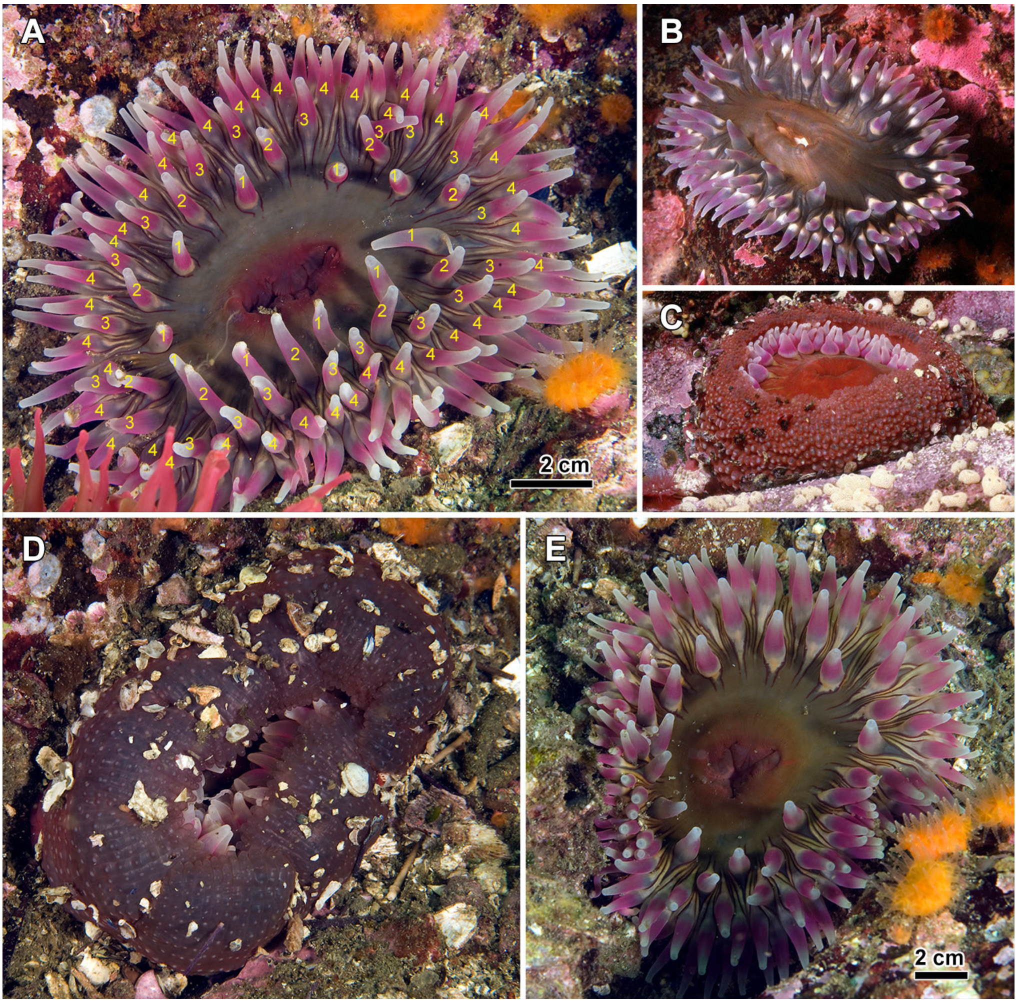

Fig. 1. *Urtibrina rimicola* sp.n. in natural habitat. A — holotype, numbers indicate four cycles of endocoelic tentacles, fifth cycle (exocoelic tentacles) not labelled; B — another specimen; C — partly contracted specimen from the west coast of Graham Island, Canada; D — contracted holotype; E — paratype.

Рис. 1. *Urtibrina rimicola* sp.n. в естественной среде обитания. A — голотип, цифрами обозначены четыре цикла эндоцельных щупалец, пятый (экзоцельный) цикл щупалец не подписан; B — другой экземпляр; C — частично сокращенный экземпляр; D — сокращенный голотип; E — паратип.

region of the parietobasilar muscles contains a chain of lacunae lined with fibers of transverse mesenterial muscles which are immersed into the mesogloea (Fig. 4). The basilar muscles are well developed. Mesenteries of all orders (first to fourth) are fertile. All examined specimens are female. The oocytes usually are 100–200 µm in diameter. No embryos were found in the coelenteron of the examined specimens.

Cnidom. Gracile spirocysts, holotrichs, basitrichs, p-mastigophores A and p-mastigophores B1 (see Fig. 5 and Table 1 for size ranges and distribution). Thick basitrichs (Fig. 5E) were found in only one specimen (KBPGI 510/2) in the proximal part of the column near the limbus. Nematocysts differ in different parts of the tentacles. Only two types of cnida were found in the tips of the inner tentacles: very numerous spirocysts (Fig. 5G) and common basitrichs (Fig. 5K). The tips of the outer tentacles, in addition, have also few thin holotrichs (Fig. 5H). The bases of the outer tentacles contain common typical basitrichs (which are common also in the column and other parts of the tentacles, Fig. 5K), rare spirocysts, thin holotrichs here are replaced by rare thick holotrichs (Fig. 5 I), and, in addition, there are p-mastigophores A (Fig. 5L) and

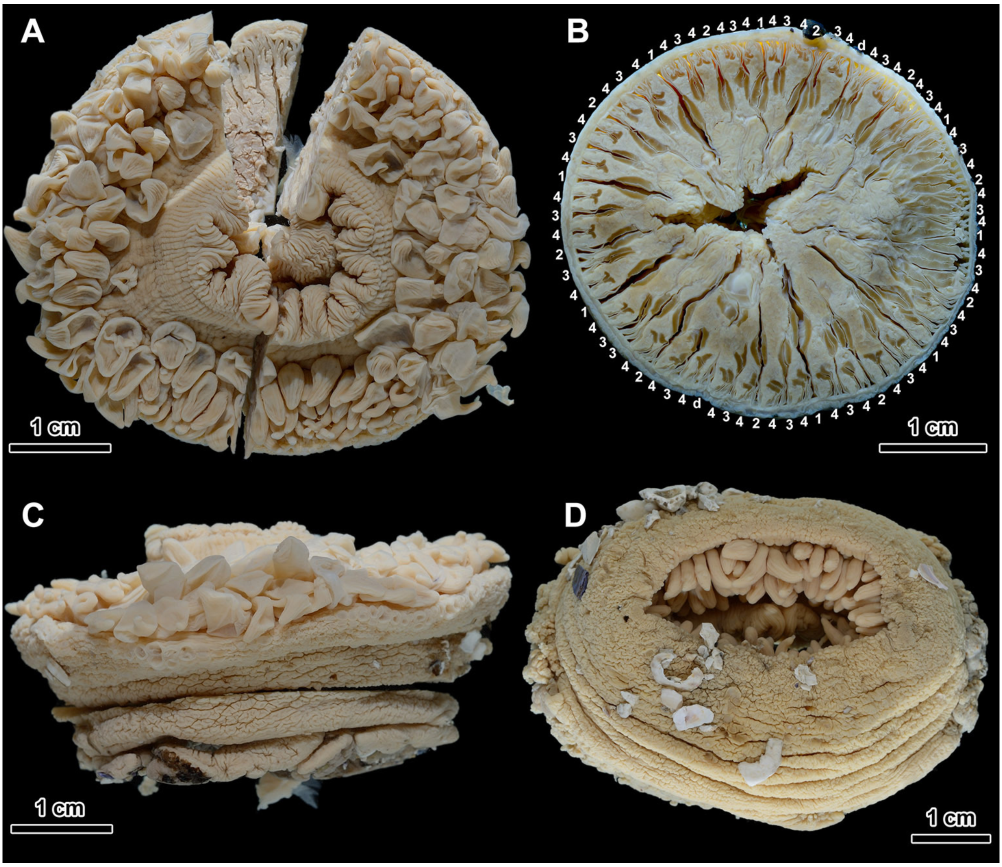

Fig. 2. *Urtibrina rimicola* sp.n., preserved specimens. A — holotype, from the top; B — sectioned specimen (KBPGI 510/2) to show general appearance of mesenteries, numbers indicate pairs of four cycles; C — holotype, from the side; D — paratype.
Abbreviations: *d* — directives.

Рис. 2. *Urtibrina rimicola* sp.n., фиксированные экземпляры. A — голотип, вид сверху; B — поперечный срез через колюмн (экземпляр KBPGI 510/2), показывающий организацию мезентериев, цифрами обозначены пары четырех циклов; C — голотип, вид сбоку; D — паратип.
Сокращения: d — направляющие пары.

sometimes small basitrichs (of the same type as in the column, Fig. 5J). In the column small basitrichs (Fig. 5C) are rare in the margin and limbus but more common in the remaining parts of the column. Similar small basitrichs (to 13×2 μm) are sparsely distributed in the endoderm of various parts of the body. The endoderm of the digestive region of the filaments (near the cnidoglandular tracts) contains basitrichs of two size ranges (Fig. 5P, Q); both are common. The cnidoglandular tracts of unilobate filaments have three types of nematocysts: common basitrichs (Fig. 5Q), thin-walled p-mastigophores A (Fig. 5R) and large thick-walled nematocysts having three-lobed flaps which are termed here as p-mastigophores B1 (Fig. 5S). The largest basitrichs (Fig. 5N) form nematocyst batteries in the ectoderm on the folds of actinopharynx (Fig. 3A). All basitrichs and *p*-mastigophores B1 are stained by basic dyes (toluidine blue) in contrast with spirocysts and *p*-mastigophores A.

HABITAT. Specimens attach to rocky substrates, usually with the pedal disc inserted tightly into a crack or crevice in the rocky bottom and with only the oral disc with the tentacles visible on the surface. When expanded the oral disc does not stand proud of the bottom, instead it spreads out near the surface of the substrate. The holotype and paratype were found living in narrow rocky crevices in bedrock in shallow, surge-swept habitat. The third specimen was excavated from sand with cobbles and pebbles attached to the pedal disc.

The species was observed from the low intertidal and shallow subtidal zones to a depth of at least 5

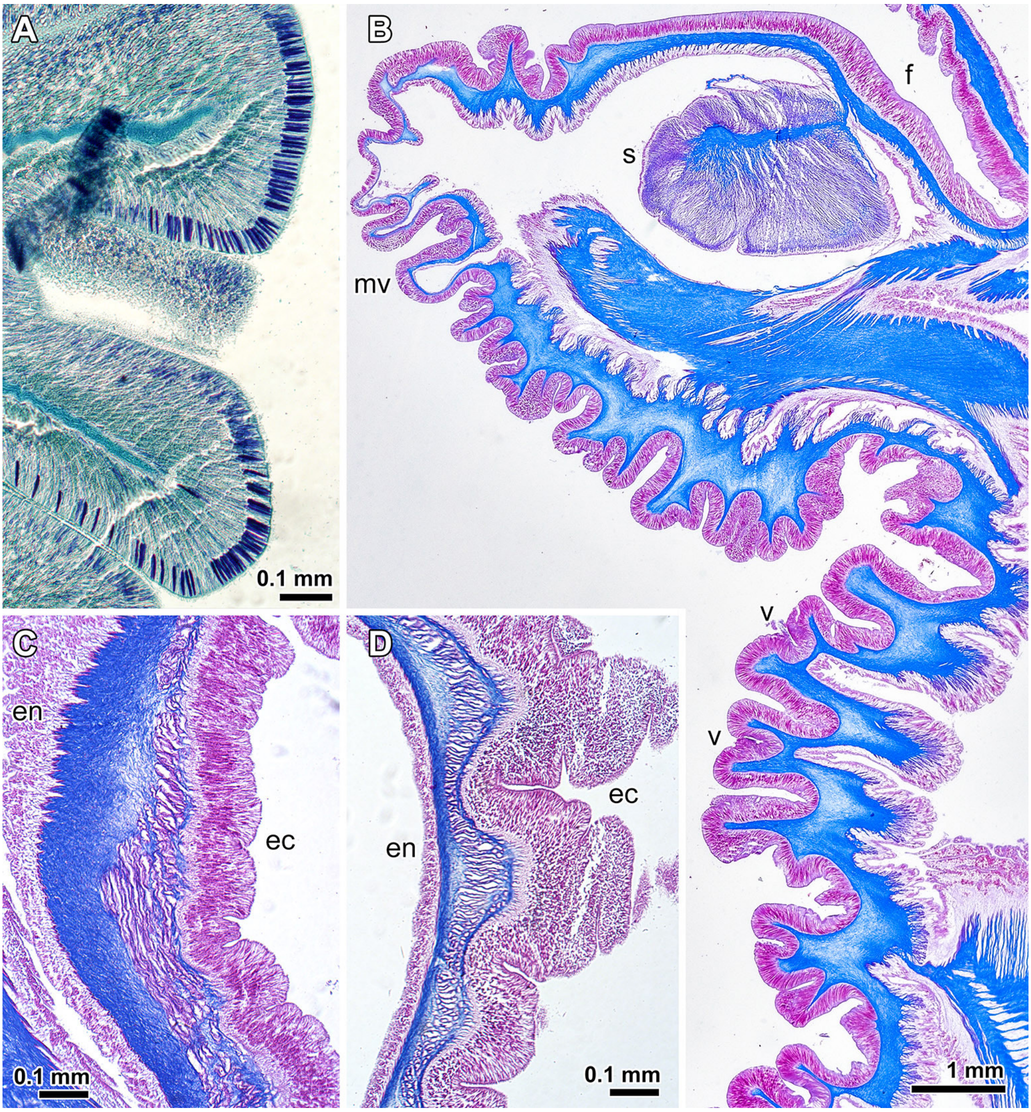

Fig. 3. *Urtibrina rimicola* sp.n., cross sections of the holotype. A — transverse section of the wall of the actinopharynx to show palisade of large basitrichs stained with toluidine blue; B — longitudinal section through distal column; C — radial mesogloeal muscles of the oral disc; D — longitudinal mesogloeal muscles of the tentacle.

Abbreviations: ec — ectoderm; en — endoderm; f — fosse; mv — marginal verrucae; s — marginal sphincter; v — verrucae.

Рис. 3. *Urtibrina rimicola* sp.n., гистологические срезы, голотип. А — поперечный срез через стенку глотки, видна батарея из больших базитрих, окрашенных толуидиновым синим; В — продольный срез через дистальную часть колюмна; С —радиальная мезоглеальная мускулатура орального диска; D — продольная мезоглеальная мускулатура щупальца.

Сокращения: ec — эктодерма; en — энтодерма; f — фосса; mv — краевые бородавки; s — маргинальный сфинктер; v — бородавки.

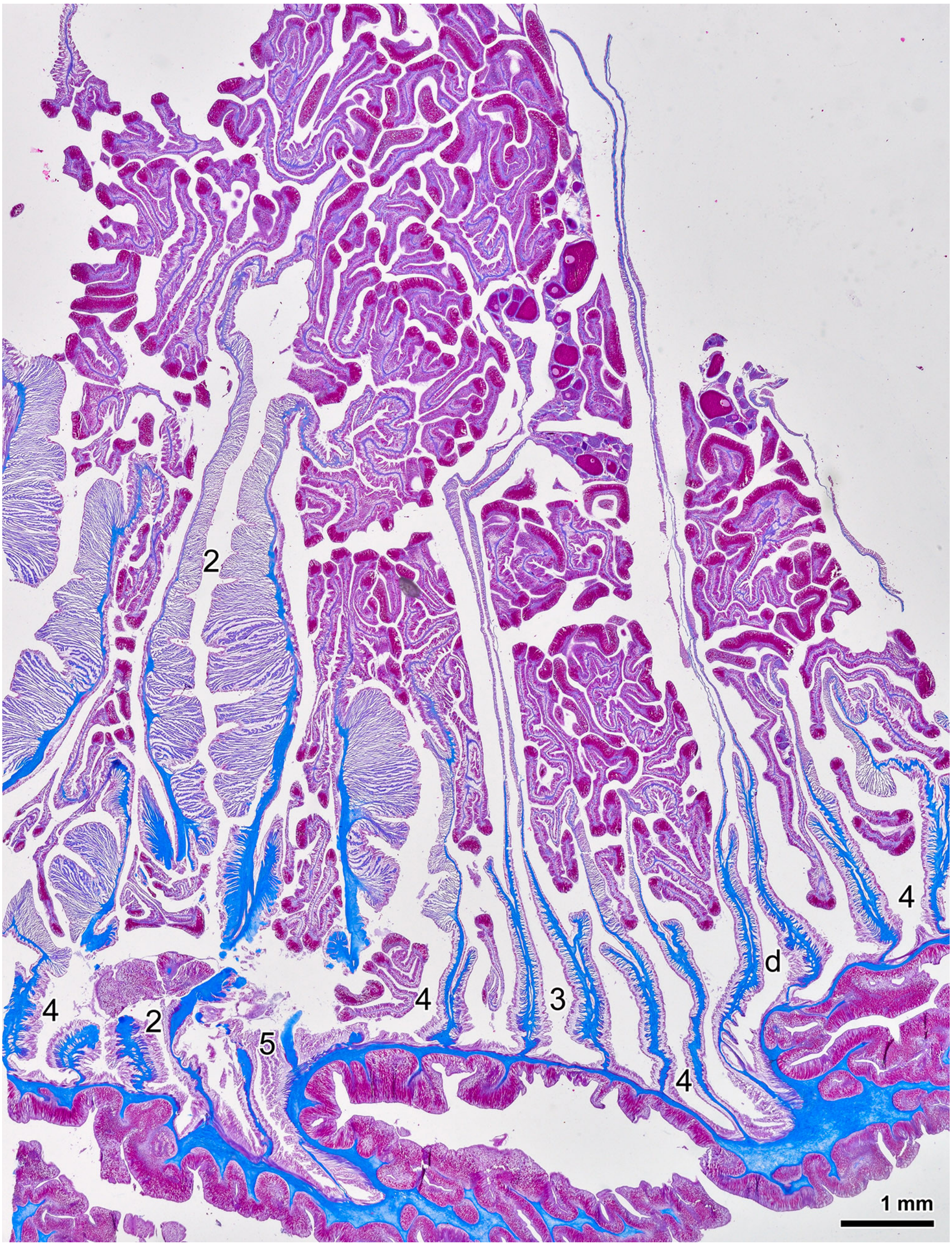

Fig. 4. *Urtibrina rimicola* sp.n., holotype, transverse section of column to show mesenteries. Numbers indicate cycles of the mesenterial pairs.
Abbreviations: d — directives.

Рис. 4. *Urtibrina rimicola* sp.n., голотип, поперечный срез через колюмн, показывающий строение мезентериев, цифрами обозначены номера циклов пар мезентериев.
Сокращения: d — направляющая пара.

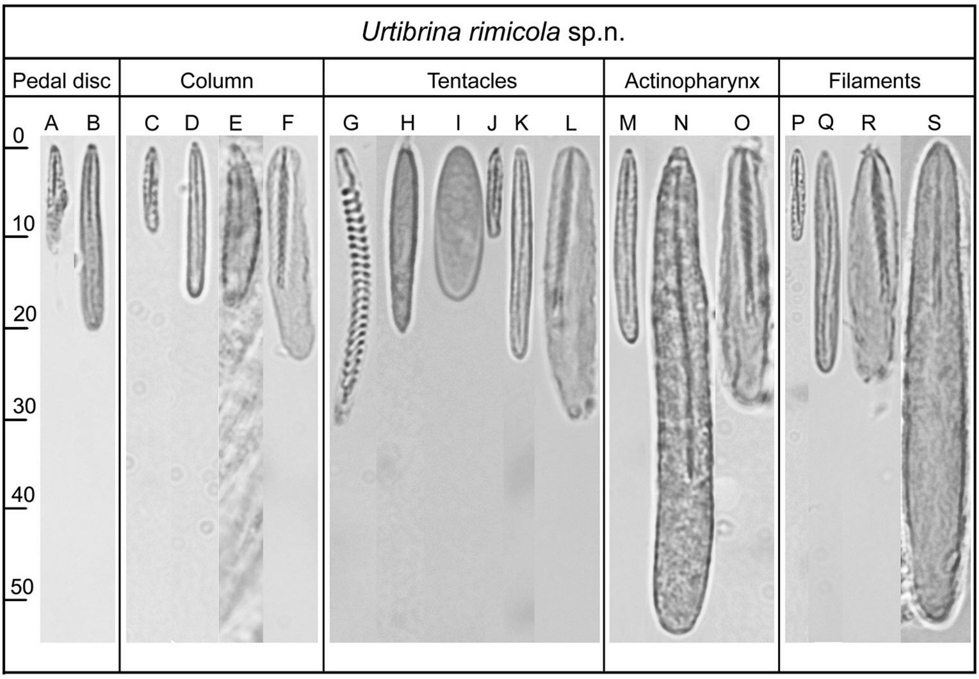

Fig. 5. *Urtibrina rimicola* sp.n., cnidom (see Table 1 for size ranges).
Рис. 5. *Urtibrina rimicola* sp.n., книдом (размерны указаны в табл. 1).

metres. In general, it appears to be an "open-coast" species, found along the outer rocky shores. It appears to thrive in surge or wave-swept habitats.

DISTRIBUTION. Known only from the North East Pacific, and currently known to occur from Cape Flattery, Washington State, USA north to the west coast of Graham Island, Haida Gwaii, British Columbia, Canada. There have been many sightings along the west coast of Vancouver Island (in Barkley Sound and Quatsino Sound, British Columbia, Canada).

ETYMOLOGY. The species name is derived from the Latin *rima* (crevice) and *cola* (inhabiting); describing the habit of this anemone to live in cracks and crevices on rocky shores.

REMARKS. The new species is closely related to *Urtibrina clandestina* (originally described in *Urticina*) in which all mesenteries of the first cycle are fertile. In all other *Urticina* species the mesenteries of one or two of the oldest cycles are sterile and the present species cannot be conspecific with any of them. Similarly, it cannot be conspecific with any species of *Cribrinopsis* because in the present species basitrichs in the actinopharynx are much larger than those in the tentacles, a feature not characteristic for *Cribrinopsis*.

Urtibrina clandestina has been described from the same region as the new species, however *U. clandestina* is usually found in protected bays where it attaches to small cobbles and the column is mostly embedded in sand or mud substrates with only the oral disc exposed. *Urticina clandestina* is common in the protected waters of the Salish Sea and is also found in protected bays on the west coast of Vancouver Island. By comparison, *Urtibrina rimicola* sp.n. is restricted to surge-swept open-coast habitats. It has not been found within the protected waters of the Salish Sea (Puget Sound and the Strait of Georgia). Although in underwater photographs these two species display some similarity, they can be readily separated from each other. Both have a relatively short verrucose red column hidden in gravel or rocky crevices, with only the disc and tentacles visible on the surface. In *U. rimicola* sp.n. the verrucae are whitish, in *U. clandestina* they are of the same color as column. In *U. rimicola* sp.n. gravel particles are not abundant and may be attached to verrucae on any parts of column; in *U. clandestina* gravel particles and broken shell form a dense belt around the middle part of column leaving the margin almost free of foreign particles. *Urtibrina clandestina* has short and thick, blunt, cylindrical tentacles giving this species a very characteristic appearance allowing unmistakable identification of live specimens. *Urtibrina rimicola* sp.n. also has short tentacles, but they are conical and pointed at the tips. Details of the color pattern of the disc and tentacles also differ: *U. clandestina* has no white lines on the oral disc which are usually present in *U. rimicola* sp.n. on the periphery

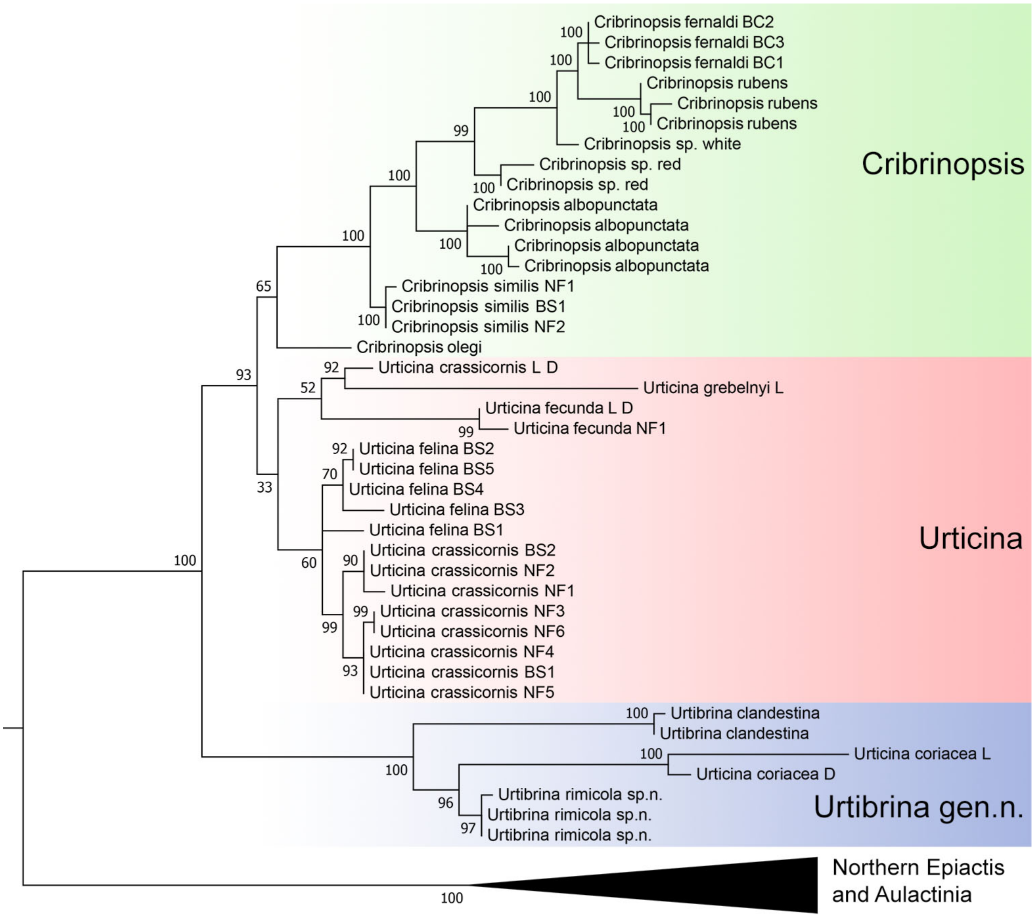

Fig. 6. Phylogenetic ML tree based on 12S + 16S + 18S + 28S + COIII concatenated dataset. Numbers above branches indicate bootstrap values for Maximum Likelihood. Only a sub-tree containing relevant taxa is shown. For full tree see Supplement Fig. 1.

Рис. 6. Филогенетическое ML дерево, основанное на объединенном наборе сиквенсов 12S + 16S + 18S + 28S + COIII. Числа показывают бутстреп значения. Показана только часть дерева с релевантными таксонами. Полное дерево см. рис. 1 в приложении.

of the disc where they run to the bases of the tentacles and merge with white spot on their oral side; the actinopharynx is red in *U. clandestina* and whitish in *U. rimicola* sp.n.; the tentacles in *U. clandestina* have two light-colored transverse bands which are absent in *U. rimicola* sp.n. The longitudinal muscles of the tentacles and radial muscles of the oral disc are mesogloeal in *U. rimicola* sp.n. but mainly mesoectodermal in *U. clandestina* (they vary from ectomesogloeal to ectodermal). Holotrichs found in the outer tentacles in *U. rimicola* sp.n. (Fig 5H, I), have not been found in repeated study of *U. clandestina*. Molecular data confirm that *U. clandestina* and *U. rimicola* sp.n. are related but specifically distinct (Figs 6, 7).

Molecular data

In our phylograms (Figs 6, 7; Supplement Figs 1, 2) two species of *Urtibrina* gen.n., *U. clandestina* and *U. rimicola* sp.n., form a clade (with 100% support) sister to the clade comprising all *Urticina* and *Cribrinopsis* species. In addition, the *Urtibrina* clade contains two specimens labelled as *Urticina coriacea* (sequences of one of them were published by Daly *et al*., 2008, another by Larson, Daly, 2016). The morphology of these two specimens was not described and exact taxonomic identity is not possible to reveal. The

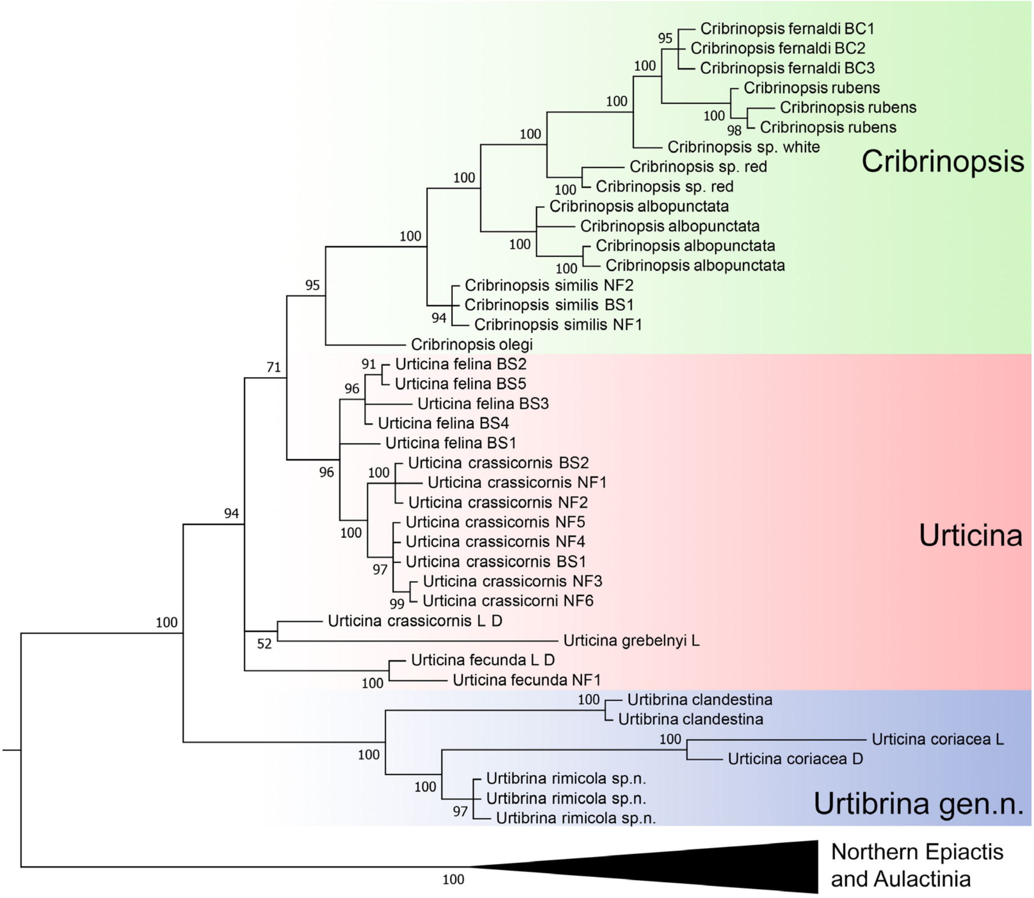

Fig. 7. Phylogenetic relationships based on 12S + 16S +18S + 28S + COIII concatenated dataset inferred by Bayesian inference (BI), numbers represent posterior probabilities (x100). Only a sub-tree containing relevant taxa is shown. For full tree see Supplement Fig. 2.
Рис. 7. Филогенетическое дерево, основанное на объединенном наборе сиквенсов 12S + 16S +18S+ 28S + COIII, представленное Байесовой вероятностью (BI). Числа показывают апостериорные вероятности для BI дерева. Показана только часть дерева с релевантными таксонами. Полное дерево см. рис. 2 в приложении.

European *Urticina coriacea* is a junior synonym of *Urticina felina* (see Sanamyan, Sanamyan, 2006), which is resolved in a different place in our tree. We suggest that the name *U. coriacea* was used in these works *sensu* Hand (1955). Hand's (1955) species is not conspecific with northern *Urticina felina* but certainly is related to *Urtibrina rimicola* sp.n. and *U. clandestina* (the similarity of *U. coriacea*: Hand, 1955 and *U. clandestina* was discussed by Sanamyan *et al*., 2013: 207). Unfortunately, both specimens of *U. coriacea* are represented by only three markers (16S, 18S and 28S) and some sequences are not quite perfect (many unclearly read nucleotides in sequence KT852266 and obviously wrong "tail", about 30 nucleotides, in KT852114, hence a long branch) so it is hard to say whether this species is conspecific with *Urtibrina rimicola* sp.n. or belongs to another (still unnamed) species of *Urtibrina* gen.n.

Species of *Urticina* (*sensu stricto*, without species transferred here in *Urtibrina* gen.n.) in our analysis are represented by specimens of *U. felina* from the Barents Sea, *U. crassicornis* from the Barents Sea and Newfoundland, *U. fecunda* from Newfoundland and *U. grebelnyi* from the North Pacific. One specimen labelled *U. crassicornis* (sequences published by Lar-

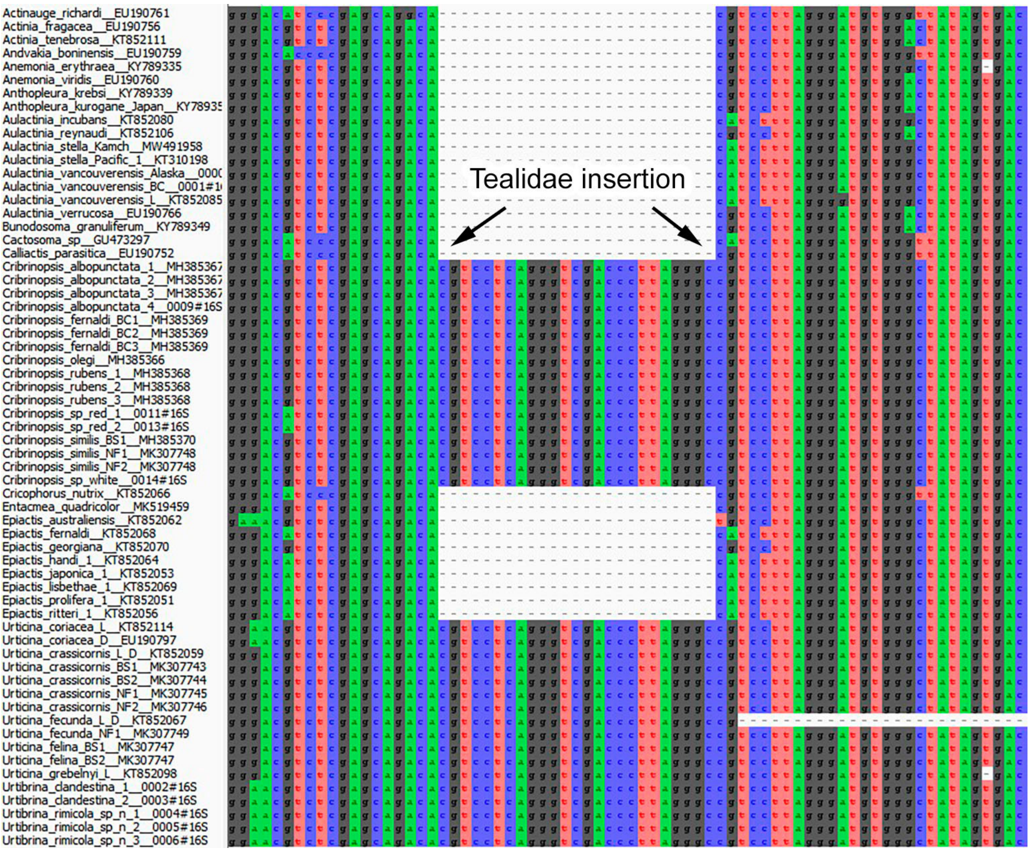

Fig. 8. A part of alignment of 16S sequences used for phylogenetic analysis in the present work (see Supplement Table 1) visualizing "Tealidae insertion" (indicated by arrows).
Рис. 8. Часть выравнивания 16S сиквенсов, использованных для филогенетического анализа в настоящей работе (см. дополнительную таблицу 1), визуализирующая «теалидную вставку» (показана стрелками).

son, Daly, 2016) is resolved separately from all other specimens of *U. crassicornis* and is likely a misidentified *U. grebelnyi* (the name *U. crassicornis* has been incorrectly applied to *U. grebelnyi* in the North East Pacific in the past, see Sanamyan, Sanamyan, 2006, 2009). *Urticina* species formed a very poorly supported clade in ML and show polytomies in BI analysis with *U. fecunda* and *U. grebelnyi* (including a possibly misidentified specimen labelled *U. crassicornis*) resolved separately from remaining *Urticina* species. At present, it is difficult to say whether the resulting trees reflect a real lack of monophyly of the genus *Urticina*, or if this is the result of other reasons (including not quite perfect sequences). In the present work, and until additional molecular data are obtained, we prefer to follow the morphological concept of this genus and do not question the generic assignment of mentioned species of this genus.

Species of *Cribrinopsis* in our dataset are represented by specimens of *C. fernaldi* and *C. rubens* from British Columbia, *C. albopunctata* and *C. olegi* from the east coasts of Kamchatka, *C. similis* from Newfoundland and the Barents Sea and two unidentified (putatively undescribed) species labelled as *Cribrinopsis* sp. "white" and "red" from the Bering Sea. They all form a separate *Cribrinopsis* clade (Figs 6, 7) with *C. olegi*, which differs from all other species in the analysis in the unusual shape of its tentacles (almost round), being basal in relation to all other species of this genus.

Taken together, all species of *Urtibrina* gen.n., *Urticina* and *Cribrinopsis* included in our dataset resolved in a highly supported monophyletic clade (100% bootstrap value) sister to a clade comprising northern species of *Aulactinia* and *Epiactis* (Supplement Figs 1, 2). It is interesting to note that 16S sequences of all species of *Urtibrina* gen.n., *Urticina* and *Cribrinopsis* have rather long (25bp) unique insertion "CGTCCTCAGGGTCGACCCTTAGGGC" which is easy to see in alignments (Fig. 8). This insertion (termed here "Tealidae-insertion") is not present in any other species of sea anemones or other organisms and can be used as an unmistakable marker that a species belongs to *Urtibrina* gen.n, *Urticina* or *Cribrinopsis*. The only exception is *Aulactinia vladimiri*. Its 16S sequence KT310197 (Sanamyan et. al., 2015) contains the above mentioned insertion, but this species will need to be sequenced again before any conclusions can be drawn. [New data obtained since this paper was accepted for publication show that this species is related to *Urticina fecunda*].

Overview of species of Tealidae and keys

Three genera of Tealidae: *Cribrinopsis*, *Urtibrina* gen.n. and *Urticina* contain together 18 species which we currently regard as valid. All are known only from the northern Hemisphere and mostly confined to cold or temperate waters. The distribution of most of them is restricted to one major geographic region. North Atlantic and Arctic waters are inhabited by five species: *Urticina felina*, *U. crassicornis*, *U. eques*, *U. fecunda* and *Cribrinopsis similis*, of which *U. fecunda* occurs only in the North East Atlantic while *U. felina* and *U. eques* only in northern seas of Europe and the Arctic. All other species inhabit North Pacific waters, from which only *Cribrinopsis olegi* has also been reported from the Arctic (Sanamyan, Sanamyan, 2009). The small number of Atlantic and Arctic species allows their rather easy identification. In the Pacific the situation is opposite and is complicated by persistent incorrect identifications in older and relatively recent scientific literature on sea anemones. Below we present a set of keys intended to help identify species in this group of sea anemones. However, it is necessary to note that 1) several undescribed species still exist in the North Pacific, and 2) many species inhabiting the Pacific coast of North America are poorly known and their positive identification will not be possible until they are reexamined (in particular the affinity of the species known from the North East Pacific under the incorrect names *U. lofotensis* and *U. coriacea* is still not quite clear).

KEY TO GENERA OF TEALIDAE

1. Large basitrichs in the actinopharynx significantly larger than large basitrichs in the tentacles.....2
– Large basitrichs in the actinopharynx of comparable size or only slightly larger than large basitrichs in the tentacles, their size ranges overlap .... *Cribrinopsis*
2. Gonads on all or on most mesenteries of the first cycle....................................... *Urtibrina* gen.n.
– First cycle of mesenteries sterile or, in exceptional cases, one or two mesenteries of the first cycle may be fertile .... *Urticina*

KEY TO SPECIES OF *CRIBRINOPSIS*

1. Column with non-adhesive verrucae, not capable of attaching any solid particles such as gravel or broken shell..2
– Verrucae adhesive or weakly adhesive...............5
2. Usually on soft bottom with column partially buried in mud. Column whitish; verrucae inconspicuous, of the same color as column 3
– On open surfaces of stones and rock. Column usually red but occasionally pale or even white; verrucae usually marked by white pigment spot 4
3. Pseudospherules present ....*C. fernaldi*
– Pseudospherules not present. Known only from the Sea of Japan .... *C. japonica*
4. North East Pacific .... *C. rubens*
– North Atlantic, northern European and Arctic seas *C. similis*
5. Tentacles very short, cylindrical or almost spherical... *C. olegi*
– Tentacles of usual shape...................................6
6. Verrucae very prominent and firm, dark colored (brown or red). Southern Kuril Islands............... ....*C. asiatica*
– Verrucae low, weakly adhesive, marked by distinct white spot contrasting with often red column 7
7. North West Pacific .... *C. albopunctata*
– North East Pacific ....*Cribrinopsis* sp. ("*Urticina lofotensis*")

Cribrinopsis similis Carlgren, 1921. This species is known from the North Atlantic and Arctic where it is rather common. Most records from the Pacific (including Carlgren, 1921 and Sanamyan, Sanamyan, 2006) are misidentifications (see Sanamyan *et al*., 2020). However, the species probably occurs in the most northern part of the Bering Sea, on the Chukotka coast of the Bering Strait (underwater photos we received from Victor Lyagushkin certainly show this species). The species lives attached to open rocky surfaces (the column is not buried in sand or hidden in crevices). Verrucae are small, not adhesive, and present over the whole column.

Cribrinopsis asiatica (Averincev, 1967). Originally described as *Tealia asiatica*, this species is known from the original description based on specimens from the southern group of the Kuril Islands (North West Pacific), where it is said to be common at depths of 30–60 m (Averincev, 1967). It also was reported from Japanese waters by Uchida, Soyama, 2001: 83 as *Urticina asiatica* and according to our data (based on material and photographs of Andrey Taratukhin) it occurs near Sakhalin Island at a depth of 20 m. Verrucae are distributed over the whole column and are described as large, firm, flattened, and, as may be judged from the text and provided figure, are adhesive. Such prominent verrucae are not common in *Cribrinopsis* and constitute a distinctive feature of this species. The species is insufficiently described but certainly distinct from all other known species of *Cribrinopsis*.

Cribrinopsis fernaldi Siebert et Spaulding, 1976. Currently known with confidence from the North East Pacific only. A large, pale-colored species with rather long tentacles which occurs mostly on soft bottom with the column partially buried in mud (see photographs in Sanamyan *et al*., 2019). Medium-sized non-adhesive verrucae occur over the whole column. A ring of prominent pseudospherules is found on the margin.

Cribrinopsis albopunctata Sanamyan et Sanamyan, 2006. Originally described from East Kamchatka (North West Pacific) and known with confidence from the Commander and Kuril Islands (Sanamyan, Sanamyan, 2006, 2020) where it is common at shallow depths. This species lives attached to the sides or upper surfaces of stones and not buried in sand. White weakly-adhesive verrucae usually are very distinctive on the red column. There are many photographs of a similar looking (red column with white verrucae) species from the North East Pacific, but its identification needs confirmation. Sometimes these specimens are labelled as *Urticina lofotensis*, but *U. lofotensis* is invalid — it is a junior synonym of the European *U. eques*, a very different species.

Cribrinopsis olegi Sanamyan et Sanamyan, 2006. This species was described from the North West Pacific and reported also from the White Sea, Sea of Okhotsk and from the coast of California (Sanamyan, Sanamyan, 2009, 2020). This is probably the most distinctive *Cribrinopsis* with unusual, almost spherical or pear-shaped tentacles. The column is always completely buried in gravel and covered with white adhesive verrucae.

Cribrinopsis japonica Tsutsui *et al*., 2014. Described from Japanese coasts of the Sea of Japan. A large species with whitish column and pinkish tentacles. Weak non-adhesive verrucae are present over the whole column. Externally this species closely resembles *C. fernaldi* and lives in the same habitat (soft bottom). Tsutsui *et al*. (2014: 201) recognized the similarity of their species with *C. fernaldi* but considered it distinct because *C. japonica* has "40 pairs of decamerously arranged mesenteries in three cycles, while *C. fernaldi* has 96 pairs arranged hexamerously." The latter statement is based on a mistake in the original description of *C. fernaldi*. Siebert & Spaulding (1976) indeed reported 96 pairs of mesenteries in their species but in reality, it only has about 48 pairs and the arrangement of the mesenteries in *C. japonica* and *C. fernaldi* (described in detail by Sanamyan *et al*., 2019) is more or less similar. Another possible feature distinguishing *C. japonica* from *C. fernaldi* is the claimed absence of pseudospherules in the Japanese species (Tsutsui *et al*., 2014).

Cribrinopsis rubens Sanamyan *et al*., 2019. This species was recently described from British Columbia where it is common. Externally it is similar to European-Arctic *C. similis* and North West Pacific *C. albopunctata*, but differs from the former in the presence of internal brooding up to the polypoid stage, and from the latter by smaller non-adhesive verrucae on the column, and from both in minor anatomical details. It is also rather distant from them molecularly (see Sanamyan *et al*., 2019).

All other species assigned in older literature to *Cribrinopsis*, including *C. williamsi* Carlgren, 1940, *C. robertii* Parulekar, 1971 and *C. crassa* (Andres, 1881) do not belong to this genus (see discussion in Sanamyan, Sanamyan, 2006 and Sanamyan *et al*., 2019).

KEY TO SPECIES OF *URTIBRINA* GEN.N.

1. Tentacles cylindrical, blunt, with two white or pale transverse bands (around the base and in the middle).......................... *Urtibrina clandestina*
– Tentacles conical, pointed, with white patch on the oral side of the base ... *Urtibrina rimicola* sp.n.

Both species are currently known with confidence only from British Columbia, Canada and Washington State, USA. Species often identified as "*Urticina coriacea*" in the North East Pacific may be conspecific with either of them or belong to another, closely related species of this genus.

KEY TO SPECIES OF *URTICINA*

1. Column perfectly smooth, without verrucae.....2
– Verrucae present..3
2. Oviparous. North West Pacific............. *U. timuri*
– Viviparous (embryos up to polypoid stage often present in the coelenteron). North Atlantic and Arctic seas............................... *U. crassicornis*
3. Verrucae adhesive 4
– Verrucae non-adhesive, vesicle-like...................7
4. Verrucae in more or less longitudinal rows or irregularly distributed. North Atlantic and Arctic seas..5
– Verrucae in distinct transverse rows, especially in partially contracted specimens. North Pacific. 6
5. Oviparous (non brooding). North European seas . ... *U. felina*

– Larvae brooded in the coelenteron, juveniles brooded externally (attached to column). North Atlantic coasts of North America .... *U. fecunda*
6. North East Pacific .... *U. columbiana*
– North West Pacific (Sakhalin and the southern group of the Kuril Islands and northern part of the Sea of Japan) .... *U. kurila*
7. Verrucae weak, barely discernible. North Europe and Arctic seas .... *U. eques*
– Verrucae well developed at least in distal column on and below margin, vesicle-like. North Pacific.... 8
8. Verrucae present over whole column. Column with patches of green and red .... *U. grebelnyi*
– Verrucae only in distal column on and just below the margin. Column usually monotone red......... .... *U. piscivora*.

Urticina felina (Linnaeus, 1761). Known only from northern seas of Europe (records from Atlantic coast of America are erroneous). The column with crowded strongly adhesive verrucae to which a large amount of foreign particles are attached, always buried in gravel or hidden in crevices. It is easy to identify because no other *Urticina* or *Cribrinopsis* species with adhesive verrucae occurs in the northern seas of Europe.

Urticina crassicornis (O.F. Müller, 1776). Known from the North East and North West Atlantic and Arctic seas. All records from the Pacific are based on misidentifications. Characterized by a perfectly smooth column, without verrucae. Sometimes small pigment spots are present on the column but they are not associated with any structures. Viviparous; juveniles are often present in the coelenteron and this feature, in combination with smooth column, allows easy differentiation from other *Urticina* species.

Urticina eques (Gosse, 1860). Known only from northern European seas. The column has small non-adhesive verrucae which are usually visible in live specimens but may be very hard or impossible to detect in preserved ones. Oviparous (embryos never present in coelenteron).

Urticina fecunda (Verrill, 1899). Known from North West Atlantic. The column has numerous adhesive verrucae arranged more or less in longitudinal rows. A brooding species, the embryos may be present in the coelenteron and juveniles are brooded externally attached to column.

Urticina columbiana (Verrill, 1922). Known from the North East Pacific only. The column is completely buried in sand with only oral disc and tentacles visible on surface. Column with very prominent verrucae arranged, especially in partially contracted specimens, in district transverse rows. Surprisingly, this very large and conspicuous species is poorly known, neither its inner anatomy, nor nematocyst data have been described. In underwater photographs (see Sanamyan *et al*., 2024) it appears to be hexamerous which casts some doubt on its assignment to *Urticina*. A sequence of 16S mRNA of *U. columbiana* downloaded from GenBank (U91753) contains "Tealidae-insertion" but there is no evidence that the source organism from which this sequence was obtained was identified correctly. *Urticina columbiana* certainly requires additional study to be properly classified.

Urticina kurila (Averincev, 1967). This species is known from the original description based on the specimens described as *Tealia coriacea kurila* Averincev, 1967 from the southern group of the Kuril Islands. It also occurs near Sakhalin Island and in the north part of the Sea of Japan (reported by Uchida, Soyama, 2001: 82 as *Urticina felina kurila*; our data is based on the material and photographs of Andrey Taratukhin, Alexander Martynov and Alexander Semenov). The column is buried in sand. It bears rather prominent adhesive verrucae arranged in short transverse series. The latter feature is somewhat similar to the arrangement of verrucae in *U. columbiana*, but in *U. columbiana* they appear to be much more numerous and more prominent.

Urticina piscivora (Sebens et Laakso, 1987). Known from the North East Pacific only. Very large, usually with brick red column and with verrucae present only in its very distal part. It attaches to surfaces of boulders and bedrock. We have not examined any specimens of this species.

Urticina grebelnyi Sanamyan et Sanamyan, 2006. Widely distributed in the North Pacific. A large species with the column covered with numerous non-adhesive verrucae which are capable of swelling into thin-walled bubbles and sometimes are lobulated, especially near the margin. In the North East Pacific, it has often been misidentified as *Urticina crassicornis*, but morphologically it is a very different species which does not occur in the Pacific.

Urticina timuri Sanamyan et Sanamyan, 2020. Known from the North West Pacific only. Distinguished from all other Pacific species of *Urticina* by a smooth column without any traces of verrucae. When this species was first discovered it was misidentified as *Urticina crassicornis* and described under this name by Sanamyan, Sanamyan (2006). However, later it was shown that the Pacific species, in contrast with the European, is oviparous, and it was redescribed as a separate species.

All other nominal species, assigned in older literature to *Urticina* (or its junior synonym *Tealia*), either do not belong to this genus, or are synonyms of species listed above. In particular, *Urticina lofotensis* (Danielssen, 1890) is a junior synonym of *U. eques*, but *U. lofotensis*: Hand, 1955 (a species from Pacific coast of North America) is closely related to *Cribrinopsis albopunctata* or is an undescribed species. *Urticina coriacea* (Cuvier, 1798) is a junior synonym of *U. felina* but *Urticina coriacea*: Hand, 1955 from the Pacific coast of North America is a member of *Urtibrina* gen.n. possibly conspecific with *Urtibrina clandestina* or *Urtibrina rimicola* sp.n., or an unnamed closely related species.

Supplementary data

The following supplementary data are available online:

Suppl. Table 1. List of taxa and sequences used for phylogenetic analysis.

Suppl. Fig. 1. ML phylogenetic tree based on contacenated datasheet, see text for details.

Suppl. Fig. 2. Phylogenetic tree represented by Bayesian Inference.

Conflict of interest

The authors declare no conflicts of interest.

Acknowledgements. The authors are grateful to Douglas Swanston who collected additional specimens used in the present study. We are grateful to two anonymous reviewers who made valuable comments and suggestions. English language was checked by Neil McDaniel (Canada). A part of this work was performed in the framework of state research project "Molecular biology, biochemistry and immunology of marine species", registration No 124021900010-2. A part of this work was carried out within the framework of the state assignment of the KF TIG FEB RAS on the topic "Structural and functional organization, dynamics and productivity of terrestrial and coastal ecosystems in the Russian Far East. Development of scientific foundations and economic instruments for sustainable nature management" (No. 124012700496-4) and "Research and conservation of the unique marine biodiversity of Kamchatka" (No. 124093000049-8). A part of this work was carried out within the framework of the state assignment of the VIGG RAS No. 125040404872-7.

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Responsible editors A.V. Chernyshev and E.N. Temereva