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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.

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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.

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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

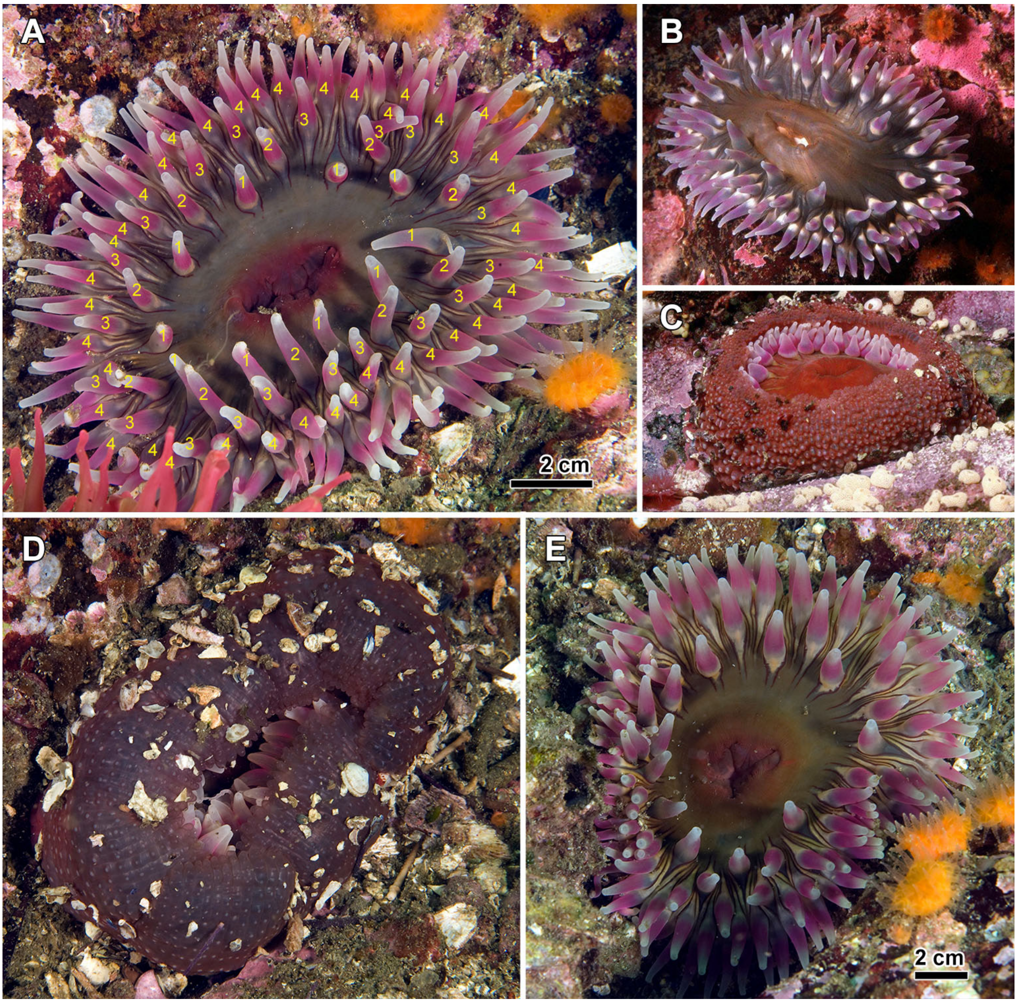

Fig. 1. *Urtibrina rimicola* sp.n. in natural habitat. A — holotype, numbers indicate four cycles of endocoelic tentacles, fifth cycle (exocoelic tentacles) not labelled; B — another specimen; C — partly contracted specimen from the west coast of Graham Island, Canada; D — contracted holotype; E — paratype.

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

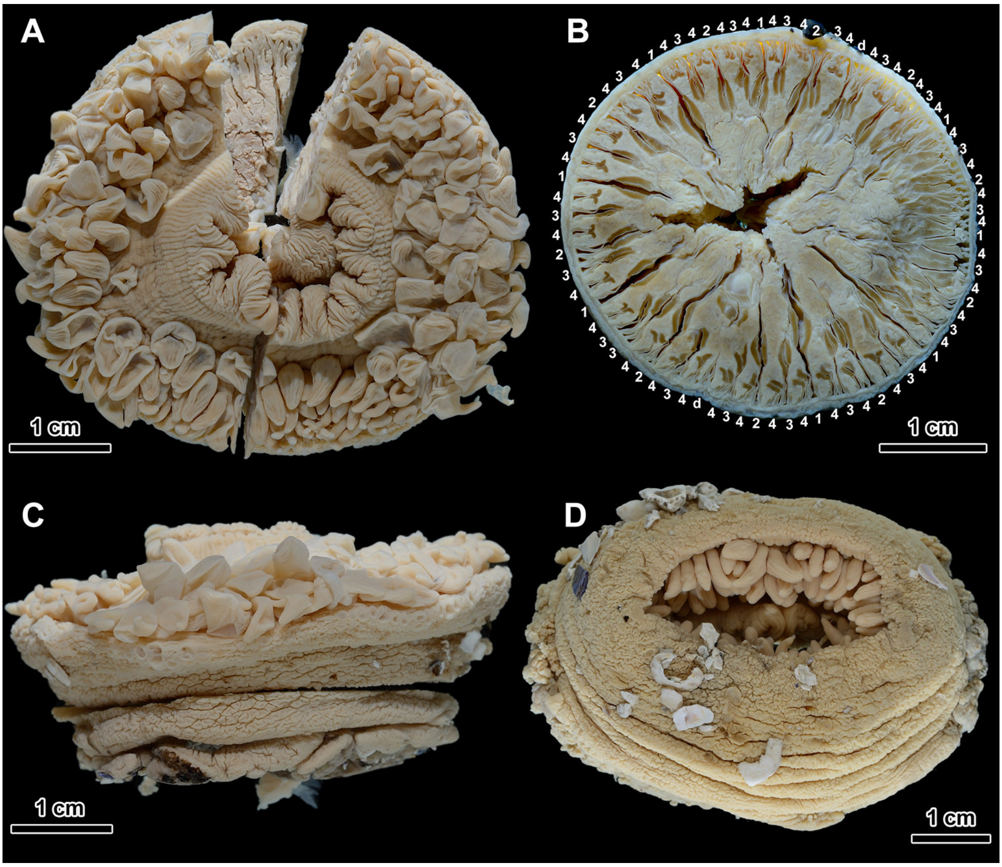

Fig. 2. *Urtibrina rimicola* sp.n., preserved specimens. A — holotype, from the top; B — sectioned specimen (KBPGI 510/2) to show general appearance of mesenteries, numbers indicate pairs of four cycles; C — holotype, from the side; D — paratype.
Abbreviations: *d* — directives.

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

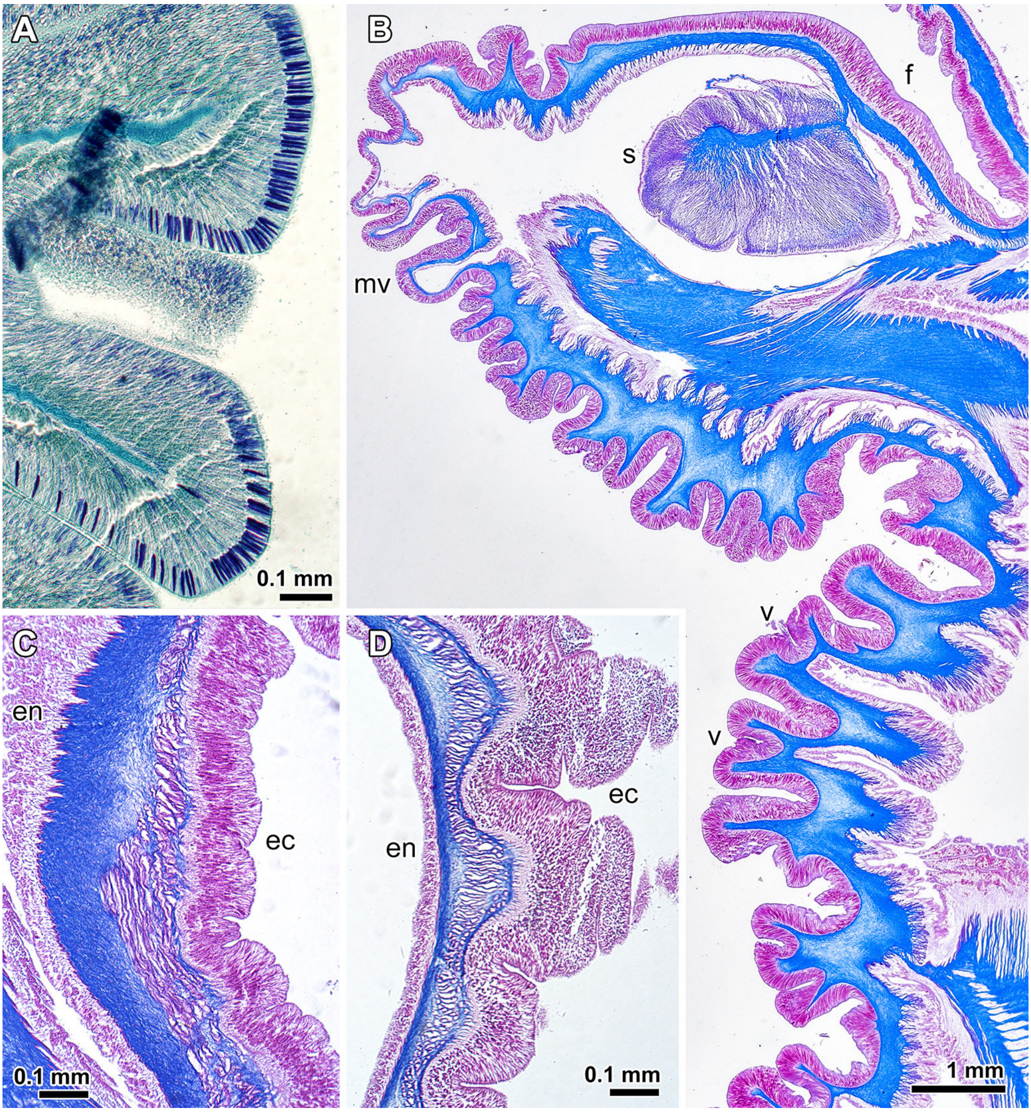

Fig. 3. *Urtibrina rimicola* sp.n., cross sections of the holotype. A — transverse section of the wall of the actinopharynx to show palisade of large basitrichs stained with toluidine blue; B — longitudinal section through distal column; C — radial mesogloeal muscles of the oral disc; D — longitudinal 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. A — поперечный срез через стенку глотки, видна батарея из больших базитрих, окрашенных толуидиновым синим; B — продольный срез через дистальную часть колюмна; C —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.

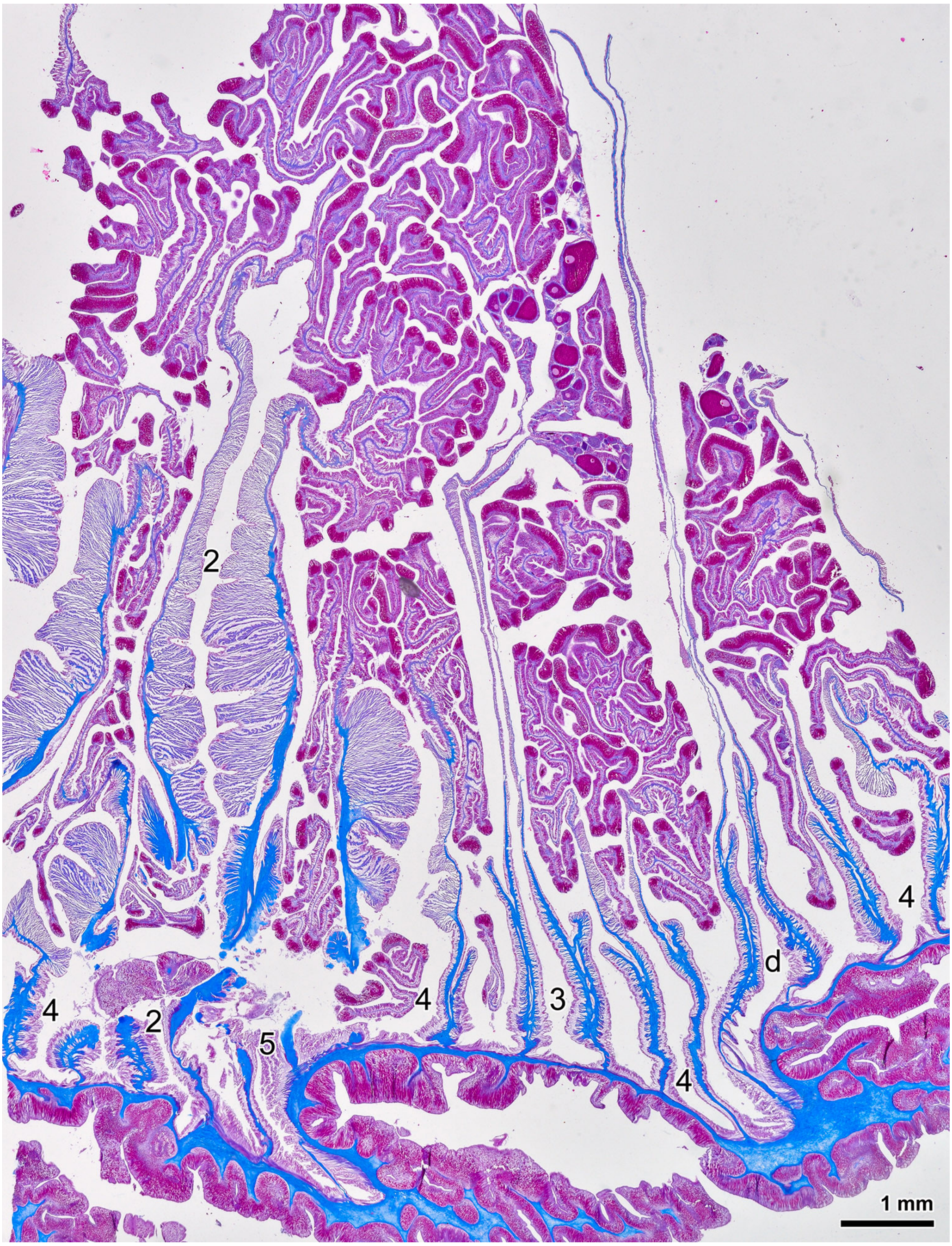

Fig. 4. *Urtibrina rimicola* sp.n., holotype, transverse section of column to show mesenteries. Numbers indicate cycles of the mesenterial pairs.
Abbreviations: d — directives.

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

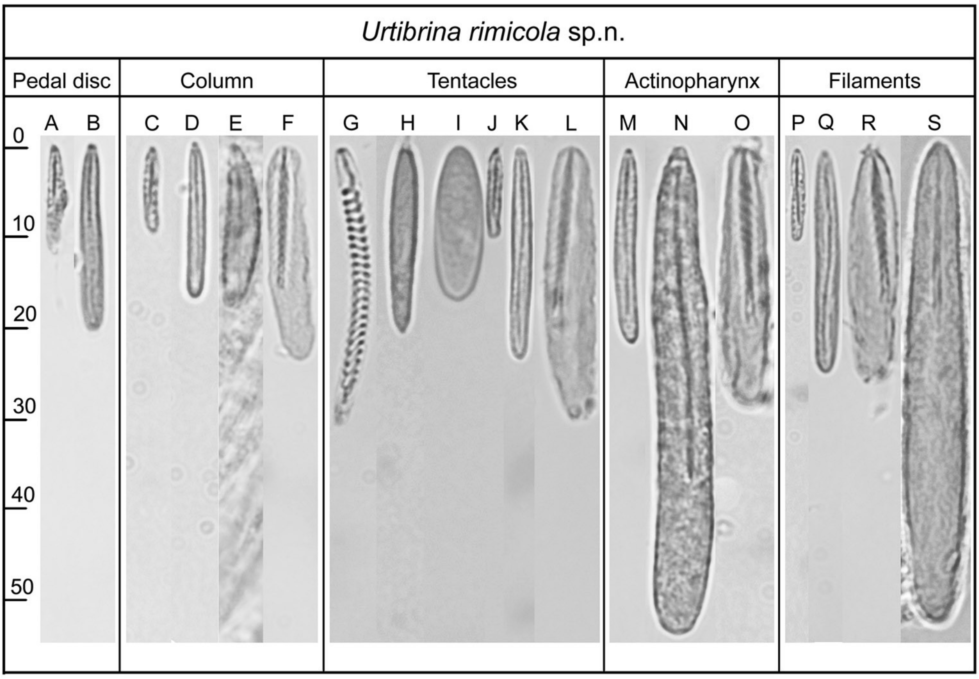

Fig. 5. *Urtibrina rimicola* sp.n., cnidom (see Table 1 for size ranges).
Рис. 5. *Urtibrina rimicola* sp.n., книдом (размерны указаны в табл. 1).

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

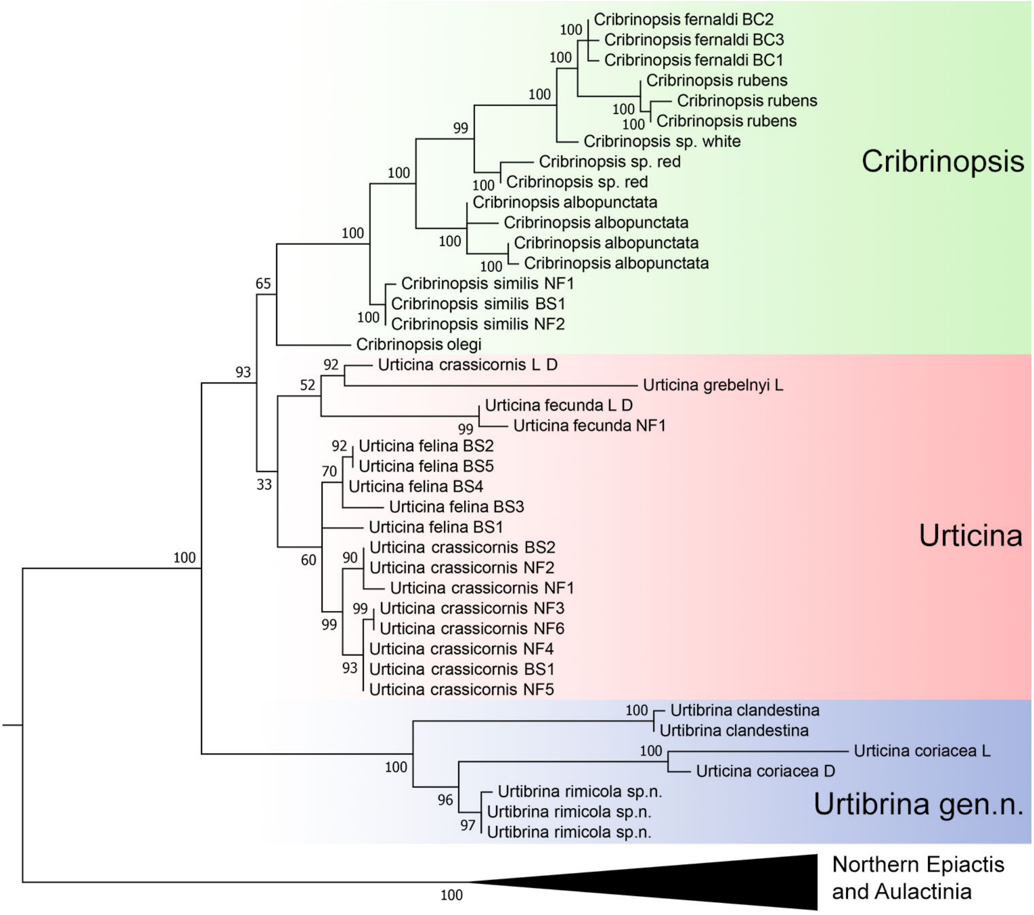

Fig. 6. Phylogenetic ML tree based on 12S + 16S + 18S + 28S + COIII concatenated dataset. Numbers above branches indicate bootstrap values for Maximum Likelihood. Only a sub-tree containing relevant taxa is shown. For full tree see Supplement Fig. 1.

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

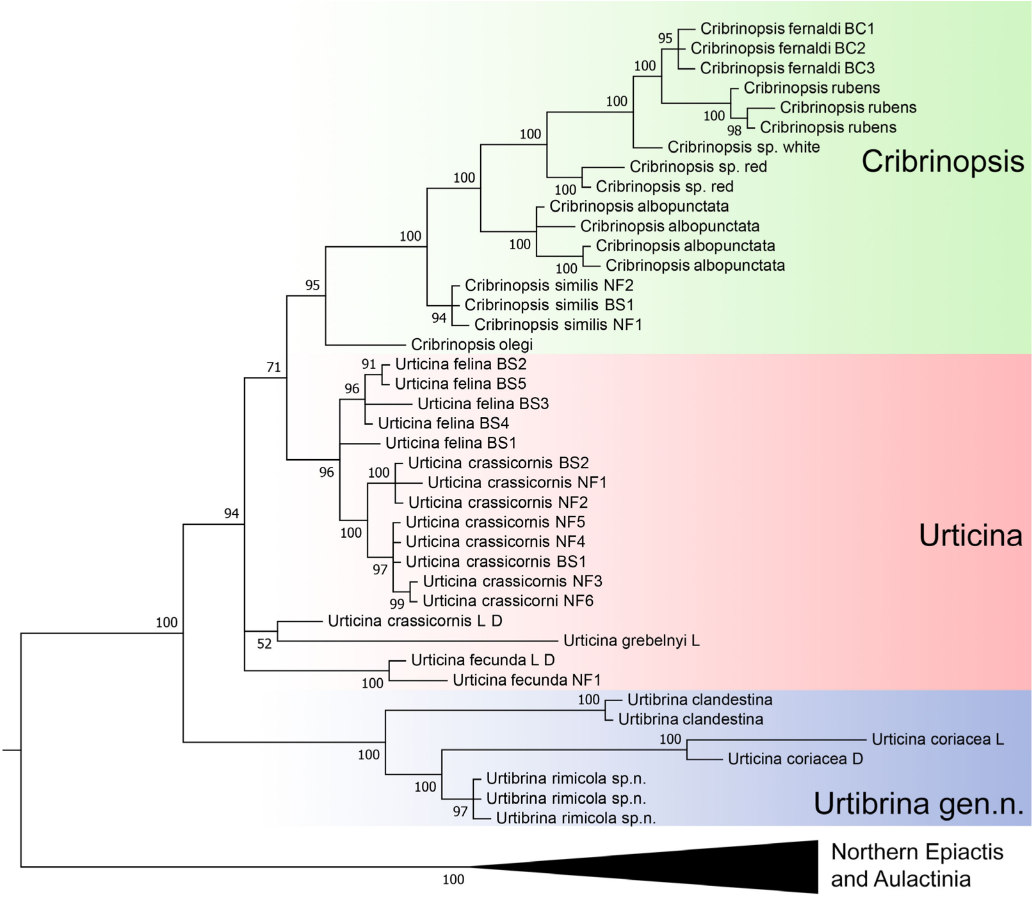

Fig. 7. Phylogenetic relationships based on 12S + 16S +18S + 28S + COIII concatenated dataset inferred by Bayesian inference (BI), numbers represent posterior probabilities (x100). Only a sub-tree containing relevant taxa is shown. For full tree see Supplement Fig. 2.
Рис. 7. Филогенетическое дерево, 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-

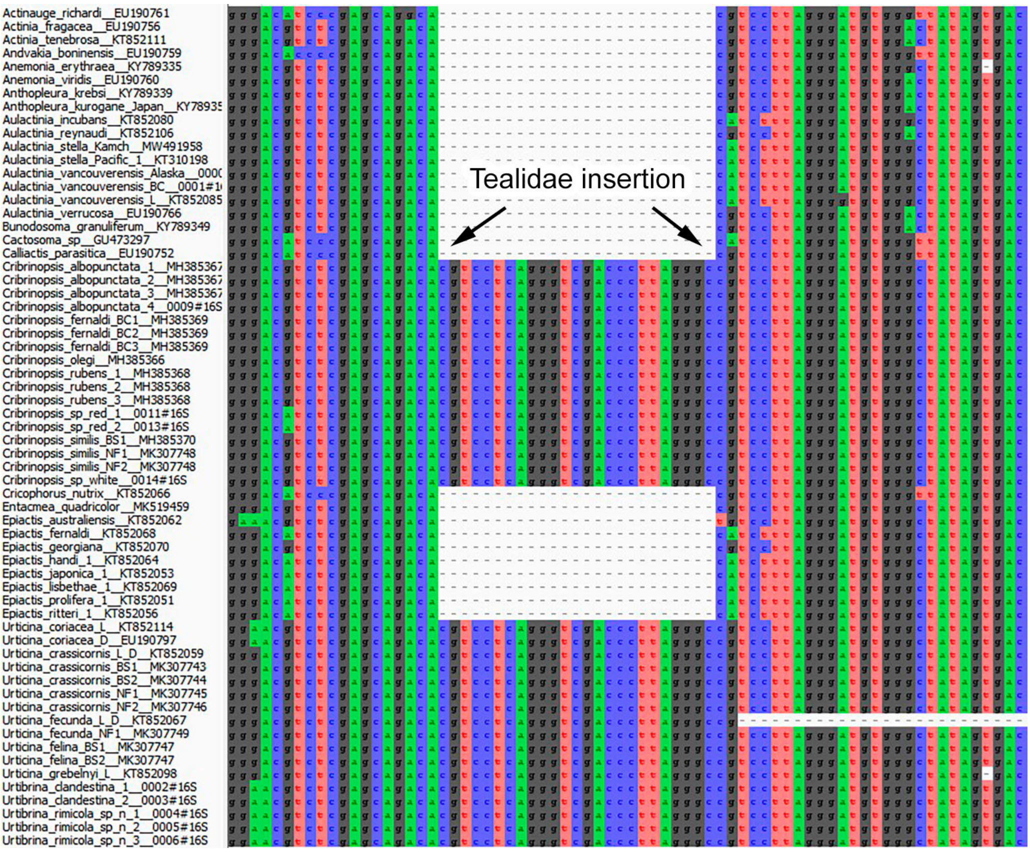

Fig. 8. A part of alignment of 16S sequences used for phylogenetic analysis in the present work (see Supplement Table 1) visualizing “Tealidae insertion” (indicated by arrows).
Рис. 8. Часть выравнивания 16S сиквенсов, использованных для филогенетического анализа в настоящей работе (см. дополнительную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

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Supplement Table 1. List of taxa and sequences used for phylogenetic analysis. Sequences generated during the present study are in bold.

Дополнительная Таблица 1. Список таксонов и сиквенсов, использованных для филогенетического анализа. Сиквенсы, полученные в ходе настоящей работы, показаны жирным шрифтом.

	12S	16S	18S	28S	COIII
Actinauge richardi	EU190719	EU190761	EU190850	KJ483055	FJ489480
Actinernus elongatus	KJ482930	KJ482966	KJ483023	KJ483126	
Actinia fragacea	EU190714	EU190756	EU190845	KJ483085	GU473334
Actinia tenebrosa	KT852045	KT852111	KT852174		KT852330
Actinostola chilensis		GU473285	GU473302	KJ483110	GU473357
Actinostola crassicornis		EU190753	EU190843	KJ483098	GU473332
Actinostola faeculenta 1	MZ569933	MZ567242	MZ569908	MZ569961	MZ576864
Actinostola faeculenta 2	MZ569935	MZ567244	MZ569910	MZ569963	MZ576866
Actinostola faeculenta 3	MZ569936	MZ567245	MZ569911		MZ576867
Actinostola faeculenta 4	MZ569943	MZ567252	MZ569916	MZ569967	MZ576874
Actinostola georgiana	KJ482928	KJ482952	KJ483032	KJ483099	KJ482991
Actinostola sp. 2 LV82	MZ569931	MZ567240	MZ569907	MZ569959	MZ576862
Actinostola sp. 29 LV82	MZ569932	MZ567241		MZ569960	MZ576863
Actinostola sp. 62 LV82	MZ569938	MZ567247	MZ569912	MZ569964	MZ576869
Actinostola sp. 63 LV82	MZ569939	MZ567248			MZ576870
Actinostola sp. 64 LV82	MZ569940	MZ567249	MZ569913		MZ576871
Actinostola sp. 66 LV82	MZ569941	MZ567250	MZ569914	MZ569965	MZ576872
Actinostola sp. 67 LV82	MZ569942	MZ567251	MZ569915	MZ569966	MZ576873
Actinostola sp. Kamchatka		MZ567255	MZ569917	MZ569970	MZ576877
Actinothoe sphyrodeta	FJ489401	FJ489421	FJ489440	FJ489455	FJ489481
Adamsia palliata	FJ489398	FJ489419	FJ489436	KJ483101	FJ489474
Aiptasia couchii	KP761199	KP761254	KP761301		KP761405
Aiptasia mutabilis	JF832963	FJ489418	FJ489438	KJ483115	FJ489505
Alicia mirabilis	KP761213		KP761310	KP761329	KP761410
Alicia sansibarensis	KJ482933	KJ482953	KJ483016	KJ483116	KJ483000
Allantactis parasitica	FJ489399	FJ489420	FJ489439	KJ483056	FJ489478
Alvinactis chessi	GU473278	GU473296	GU473312	KJ483052	GU473352
Amphianthus sp.	FJ489413	FJ489432	FJ489450	FJ489467	FJ489502
Andvakia boninensis	EU190717	EU190759	EU190848	KJ483053	FJ489479
Anemonia erythraea	KY789302	KY789335			KY789271
Anemonia viridis	EU190718	EU190760	EU190849	EU190806	GU473335
Antholoba achates Argentina	GU473269	GU473284	GU473301	KJ483128	GU473356
Antholoba achates Chile	KR051002_12S	KR051002_16S			KR051002_COIII
Antholoba fabiani Brazil	OR014502	OR000444	OR470688	OR001827	OR069378
Anthopleura anjunae	KY789324			KY789388	KY789289
Anthopleura anneae	KY789327	KY789360		KY789392	KY789293
Anthopleura artemisia	KT852015	KT852081	KT852148		KT852300
Anthopleura atodai	KT851993	KT852055	KT852123	KT852247	KT852275
Anthopleura ballii	KY789311	KY789346		KY789376	KY789281
Anthopleura biscayensis	KY789315	KY789350			KY789284
Anthopleura buddemeieri	KY789316	KY789351		KY789381	
Anthopleura dixoniana	KY789307	KY789341			KY789276

Anthopleura dowii	KY789318	KY789353		KY789383	KY789286
Anthopleura elegantissima	EU190713	EU190755	EU190844	KT852248	GU473333
Anthopleura fuscoviridis	KY789303	KY789336		KY789369	KY789272
Anthopleura handi	KT852013	KT852079	KT852146	KY789387	KT852298
Anthopleura insignis	KY789331	KY789364		KY789395	KY789297
Anthopleura japonica	KY789310	KY789345			KY789280
Anthopleura krebsi	KY789305	KY789339		KY789372	KY789275
Anthopleura kurogane Japan	KY789323	KY789356			
Anthopleura kurogane Korea	KY789321	KY789355		KY789385	KY789288
Anthopleura nigrescens	KY789309	KY789344		KY789375	KY789279
Anthopleura nigrescens Galapagos		KY789343		KY789373	KY789278
Anthopleura pallida	KY789308	KY789342			KY789277
Anthopleura rosea	KT852039	KT852104	KT852168		KT852324
Anthopleura sola		KY789365			
Anthopleura sp. Green		KY789337		KY789370	KY789273
Anthopleura sp. *inornata*	KY789304	KY789338		KY789371	KY789274
Anthopleura sp. South Africa	KY789329	KY789362		KY789393	KY789295
Anthopleura thallia	KY789333	KY789366		KY789397	KY789300
Anthopleura variata	OR882882	OR882857	OR882861	OR882865	OR865724
Anthopleura waridi	KY789301	KY789334		KY789368	KY789270
Anthopleura xanthogrammica		KY789367		KY789398	
Anthosactis janmayeni	KJ482938	GU473292	GU473308	KJ483091	GU473363
Anthostella stephensoni	JQ810719	JQ810721	JQ810723	KJ483132	JQ810726
Anthothoe chilensis	FJ489397	FJ489416	FJ489434	FJ489453	FJ489470
Aulactinia incubans	KT852014	KT852080	KT852147	KT852256	KT852299
Aulactinia reynaudi	KT852041	KT852106	KT852170	KT852260	KT852326
Aulactinia stella Barents	KT310208	JQ927444			KT310207
Aulactinia stella Kamch		MW491958		MW491996	
Aulactinia stella KolaP		MW491959		MW491997	
Aulactinia stella L D	KT852044	KT852110	KT852173	KT852263	KT852329
Aulactinia stella Pacific 1	KT310188	KT310198			KT310210
Aulactinia stella Pacific 2	KT310189	KT310199			KT310211
Aulactinia stella Pacific 5	KT310192	KT310202			KT310214
Aulactinia vancouverensis Alaska	**PP946958**	**PP946944**	**PP946951**	**PP946965**	**PP951986**
Aulactinia vancouverensis BC	**PP946959**	**PP946959**	**PP946952**	**PP946966**	**PP951987**
Aulactinia vancouverensis L	KT852019	KT852085	KT852151		KT852305
Aulactinia verrucosa	EU190723	EU190766	EU190854	KT852250	FJ489484
Bartholomea annulata	EU190721	EU190763	EU190851	KJ483068	FJ489483
Bathyphellia australis	FJ489402	FJ489422	EF589063	EF589086	FJ489482
Bellactis ilkalyseae		KP761238	KP761316		KP761393
Bolocera kerguelensis	KJ482925	KJ482965	KJ483029		KJ482985
Bunodeopsis globulifera	KJ482940	KJ482949	KJ483025	KJ483122	KJ482992
Bunodosoma californicum	KY789312	KY789347		KY789377	
Bunodosoma capense	KY789332			KY789396	KY789298
Bunodosoma cavernatum	KY789313	KY789348		KY789378	KY789282
Bunodosoma grande	EU190722	EU190765	EU190853	KJ483083	GU473336
Bunodosoma granuliferum	KY789314	KY789349		KY789379	KY789283

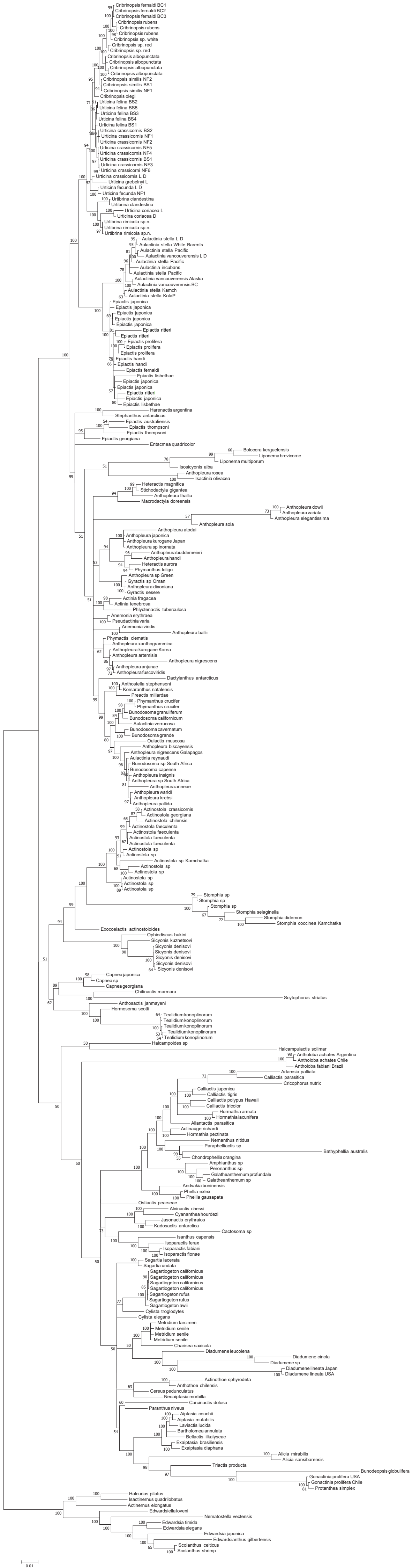
Bunodosoma sp. South Africa	KY789330	KY789363		KY789394	KY789296
Cactosoma sp.	GU473279	GU473297	GU473313	GU473329	GU473346
Calliactis japonica	FJ489403	FJ489423	FJ489441	KJ483057	FJ489486
Calliactis parasitica	EU190711	EU190752	EU190842	KJ483102	FJ489475
Calliactis polypus Hawaii	FJ489407	FJ489427	FJ489445	KJ483058	FJ489485
Calliactis tigris	MK801512	MK801514	MK801510	MK801516	MK801561
Calliactis tricolor	FJ489405	FJ489425	FJ489443	KJ483059	FJ489488
Capnea georgiana		KJ482951	KJ483022	KJ483050	KJ482990
Capnea japonica	LC602145	LC602146	LC602147	LC602148	LC602149
Capnea sp.	**PP902548**	**PP902553**	**PP902558**	**PP902563**	**PP915636**
Carcinactis dolosa	MN266878	MN266877	MN266880	MN266874	MN295038
Cereus pedunculatus	EU190724	EU190767	EU190855	EU190813	FJ489471
Charisea saxicola	KT852020	KT852086	KT852152		KT852306
Chitinactis marmara	MT676806	MT676783	MT676785	MT676789	
Chondrophellia orangina	FJ489406	FJ489426	FJ489444	KJ483060	FJ489489
Cribrinopsis albopunctata 1	MH385362	MH385367	MH376912	MH380005	MK304506
Cribrinopsis albopunctata 2	MH385362	MH385367	MH376912	MH380006	MK304506
Cribrinopsis albopunctata 3	MH385362	MH385367	MH376913	MH380006	MK304506
Cribrinopsis albopunctata 4	**PP902549**	**PP902554**	**PP902559**	**PP902564**	**PP915637**
Cribrinopsis fernaldi BC1	MH385364	MH385369	MH376917	MH380009	MK304508
Cribrinopsis fernaldi BC2	MH385364	MH385369	MH376918	MH380010	MK304508
Cribrinopsis fernaldi BC3	MH385364	MH385369	MH376918	MH380011	MK304508
Cribrinopsis olegi	MH385361	MH385366	MH376911	MH380004	MK304505
Cribrinopsis rubens 1	MH385363	MH385368	MH376914	MH380007	MK304507
Cribrinopsis rubens 2	MH385363	MH385368	MH376915	MH380008	MK304507
Cribrinopsis rubens 3	MH385363	MH385368	MH376916	MH380008	MK304507
Cribrinopsis similis BS1	MH385365	MH385370	MH376919	MH380012	MK304509
Cribrinopsis similis NF1	MK287981	MK307748	MK307728	MK307740	MK304514
Cribrinopsis similis NF2	MK287981	MK307748	MK307729	MK307741	MK304514
Cribrinopsis sp. red 1	**PP902550**	**PP902555**	**PP902560**	**PP902565**	**PP915638**
Cribrinopsis sp. red 2	**PP902551**	**PP902556**	**PP902561**	**PP902566**	**PP915639**
Cribrinopsis sp. white	**PP902552**	**PP902557**	**PP902562**	**PP902567**	**PP915640**
Cricophorus nutrix		KT852066	KT852134		KT852286
Cyananthea hourdezi	GU473275	GU473293	GU473309	KJ483081	GU473364
Cylista elegans		JF832970	JF832989	JF832994	JF833012
Cylista troglodytes	EU190746	KT852107	EU190872	KT852261	FJ489499
Dactylanthus antarcticus	GU473272	AY345877	AF052896	KJ483086	GU473358
Diadumene cincta	EU190725	EU190769	EU190856	KJ483106	FJ489490
Diadumene leucolena	JF832957	JF832977	JF832986	KJ483123	JF833006
Diadumene lineata Japan	JF832965	JF832973	JF832987	KJ483107	JF833007
Diadumene lineata USA	EU190730	EU190774	EU190860	KJ483108	FJ489506
Diadumene sp.	JF832960	JF832976	JF832980	KJ483130	JF833005
Edwardsia elegans	EU190726	EU190770		KJ483087	GU473338
Edwardsia japonica	GU473274	GU473288	GU473304	KJ483048	GU473359
Edwardsia timida	GU473281	KT852113	GU473315	KT852265	KT852332
Edwardsianthus gilbertensis	EU190728	EU190772	EU190859	EU190817	
Edwardsiella loveni	KX946216	KX946212	KX946218	KX946219	KX946217
Entacmea quadricolor	MK519405	MK519459	MK519568	MK519643	MK522443

Epiactis australiensis	KT852000	KT852062	KT852130		KT852282
Epiactis fernaldi	KT852005	KT852068	KT852136	KT852252	KT852288
Epiactis georgiana	KT852007	KT852070	KT852138	KT852254	KT852290
Epiactis handi	KT851988	KT852050	KT852118	KT852245	KT852269
Epiactis handi 1	KT852002	KT852064	KT852132	KT852251	KT852284
Epiactis japonica 1	KT851991	KT852053	KT852121		KT852272
Epiactis japonica 2	KT852025	KT852090	KT852155		KT852310
Epiactis japonica 3	KY789317	KY789352		KY789382	KY789285
Epiactis japonica 4	KT852048	KT852116	KT852178		KT852333
Epiactis japonica Pacific 1	KT310193	KT310203			KT310215
Epiactis japonica Pacific 2	KT310194	KT310204			KT310215
Epiactis japonica Pacific 3	KT310195	KT310205			KT310215
Epiactis japonica Pacific 4	KT310196	KT310206			KT310215
Epiactis lisbethae 1	KT852006	KT852069	KT852137	KT852253	KT852289
Epiactis lisbethae 2	EU190727	EU190771		EU190816	GU473360
Epiactis prolifera 1	KT851989	KT852051	KT852119	KT852246	KT852270
Epiactis prolifera 2	KT852003	KT852065	KT852133		KT852285
Epiactis prolifera 3	KY789320	KY789354		KY789384	KY789287
Epiactis ritteri 1	KT851994	KT852056	KT852124		KT852276
Epiactis ritteri 2	KT851995	KT852057	KT852125		KT852277
Epiactis ritteri 3	KT852022	KT852088	KT852154		KT852308
Epiactis thompsoni 1	KT852010	KT852073	KT852141		KT852293
Epiactis thompsoni 2	KT852011	KT852074	KT852142		KT852294
Exaiptasia brasiliensis	KP761188	KP761239	KP761312		KP761386
Exaiptasia diaphana	KP761176	KP761226	KP761280	KP761327	KP761376
Exocoelactis actinostoloides	KP793003	KP793004			
Galatheanthemum profundale	KJ482919	KJ482954	KJ483011	KJ483119	KJ482978
Galatheanthemum sp	KJ482918	KJ482955	KJ483012	KJ483065	KJ482977
Gonactinia prolifera Chile	KJ482935		KJ483008	KJ483112	KJ482994
Gonactinia prolifera USA	KJ482937	KJ482969	KJ483009	KJ483077	KJ482995
Gyractis sesere	KT852012	KT852078	KT852145	KY789386	KT852297
Gyractis sp. Oman	KY789325	KY789357		KY789390	KY789290
Halcampoides sp.	MZ569946	MZ567256	MZ569918	MZ569971	MZ576878
Halcampulactis solimar	MK279362	MK279363	MK279364		MK279366
Halcurias pilatus	KJ482931	KJ482967	KJ483020	KJ483109	KJ482997
Harenactis argentina	KJ482926	KJ482964	KJ483026	KJ483047	KJ482984
Heteractis aurora	MK519414	MK519469			MK522453
Heteractis magnifica	EU190732	EU190777		KJ483093	KJ482988
Hormathia armata	EU190731	EU190775	EU190861	KJ483062	FJ489491
Hormathia lacunifera	FJ489409	FJ489428	FJ489446	KJ483063	FJ489492
Hormathia pectinata	FJ489415	FJ489430	FJ489448	FJ489465	FJ489497
Hormosoma scotti	EU190733	EU190778	EU190863	KJ483090	GU473366
Isactinernus quadrilobatus	KJ482932	KJ482968	KJ483024	KJ483105	KJ482998
Isactinia olivacea		KT852077	KT852144		KT852296
Isanthus capensis	JF832967	GU473291	GU473307	KJ483096	GU473362
Isoparactis fabiani	JF832964	GU473283	GU473300	KJ483124	GU473355
Isoparactis ferax	KC700002		KC700005	KC700006	KC700008
Isoparactis fionae	KC700001	KC700003	KC700004		KC700007

Isosicyonis alba		KJ482959			KJ482981
Jasonactis erythraios		GU473289	GU473305	KJ483079	GU473339
Kadosactis antarctica	FJ489410	EU190782	EU190865	KJ483080	FJ489504
Korsaranthus natalensis	KJ482920	KJ482958	KJ483017	KJ483117	KJ482987
Laviactis lucida	KP761192	KP761243	KP761296		KP761402
Liponema brevicorne	EU190738	EU190784	EU190866	KJ483139	KJ483001
Liponema multiporum	KJ482922	KJ482962			
Macrodactyla doreensis	EU190739	EU190785			GU473342
Metridium farcimen	MT893228	MT893265			MT896170
Metridium senile 1	KT852024	EU190786	AF052889	EU190829	FJ489494
Metridium senile 2	JF832962	JF832971	JF832981	JF832991	JF833002
Metridium senile 3	KJ482916	KJ482950		KJ483113	KT852309
Nemanthus nitidus	EU190741	EU190787	EU190868	KJ483064	FJ489495
Nematostella vectensis	EU190750	AY169370	AF254382	KJ483089	FJ489501
Neoaiptasia morbilla	EU190742	EU190788		KJ483075	JF833010
Ophiodiscus bukini		MZ567263	MZ569925	MZ569978	MZ576885
Ostiactis pearseae	EU190751	EU190798	EU190878	KJ483082	GU473365
Oulactis muscosa	KT852033	KT852097	KT852162	KY789391	KT852317
Paranthus niveus	GU473277	GU473295	GU473311	KJ483072	
Paraphelliactis sp.	FJ489412	FJ489431	FJ489449	FJ489466	FJ489498
Peronanthus sp.	KJ482917	KJ482956	KJ483014	KJ483066	KJ482976
Phellia exlex	JF832958	JF832978	JF832984	KJ483121	JF833004
Phellia gausapata	EU190744	EU190790	EU190870	EU190833	FJ489473
Phlyctenactis tuberculosa	KY789326	KY789359			KY789292
Phymactis clematis		KY789358			KY789291
Phymanthus crucifer 1	KJ910343	KJ910345	MH670399	MH670928	KJ910346
Phymanthus crucifer 2	KJ910344	KJ910345	MH670402		KJ910346
Phymanthus loligo	EU190745	EU190791			GU473345
Preactis millardae	KJ482921	KJ482957	KJ483018	KJ483118	KJ482986
Protanthea simplex	KJ482939	KJ482970	KJ483010	KJ483078	KJ482993
Pseudactinia varia	KY789328	KY789361			KY789294
Sagartia lacerata	EU190748	EU190794	EU190874	KJ483071	FJ489500
Sagartia undata	FJ489400	FJ489417	FJ489435	KJ483070	FJ489472
Sagartiogeton awii	GU473271	GU473286	GU473303	KJ483074	GU473337
Sagartiogeton californicus 1	OP766354	OP766348	OP766366	OP766360	OP750423
Sagartiogeton californicus 2	OP766355	OP766349	OP766367	OP766361	OP750424
Sagartiogeton californicus 3	OP766356	OP766350	OP766368	OP766362	OP750425
Sagartiogeton californicus 4	OP766357	OP766351	OP766369	OP766363	OP750426
Sagartiogeton rufus 1	OP766352	OP766346	OP766364	OP766358	OP750421
Sagartiogeton rufus 2	OP766353	OP766347	OP766365	OP766359	OP750422
Scolanthus celticus	MN200251	MN200244	MN200240	MN200243	MN196672
Scolanthus shrimp	MN200242	MN200264	MN200245	MN200241	MN196671
Scytophorus striatus	MT737290	MT676781	MT676784	MT676788	
Sicyonis denisovi 1	MZ569947	MZ567257	MZ569919	MZ569972	MZ576879
Sicyonis denisovi 2	MZ569948	MZ567258	MZ569920	MZ569973	MZ576880
Sicyonis denisovi 3	MZ569949	MZ567259	MZ569921	MZ569974	MZ576881
Sicyonis denisovi 4	MZ569950	MZ567260	MZ569922	MZ569975	MZ576882
Sicyonis denisovi 5	MZ569951	MZ567261	MZ569923	MZ569976	MZ576883

Sicyonis kuznetsovi	MZ569952	MZ567262	MZ569924	MZ569977	MZ576884
Stephanthus antarcticus	KJ482927	KJ482960	KJ483019	KJ483092	KJ482983
Stichodactyla gigantea	EU190747	EU190793		EU190835	KY789299
Stomphia coccinea Kamchatka	MZ569945	MZ567254		MZ569969	MZ576876
Stomphia didemon	KJ482929	EU190795	EU190875	KJ483127	GU473348
Stomphia selaginella	GU473280	GU473298	GU473314	GU473331	GU473349
Stomphia sp. 43 LV82	MZ569934	MZ567243	MZ569909	MZ569962	MZ576865
Stomphia sp. 61 LV82	MZ569937	MZ567246			MZ576868
Stomphia sp. 74 LV82	MZ569944	MZ567253		MZ569968	MZ576875
Tealidium konoplinorum 1	MZ569954	MZ567264	MZ569926	MZ569979	MZ576886
Tealidium konoplinorum 2	MZ569955	MZ567265	MZ569927	MZ569980	MZ576887
Tealidium konoplinorum 3	MZ569956	MZ567266	MZ569929	MZ569982	MZ576889
Tealidium konoplinorum 4	MZ569957	MZ567267	MZ569928	MZ569981	MZ576888
Tealidium konoplinorum 5	MZ569958	MZ567268	MZ569930	MZ569983	MZ576890
Triactis producta			EU190876	KJ483125	
Urtibrina clandestina 1	**PP946960**	**PP946946**	**PP946953**	**PP946967**	**PP951988**
Urtibrina clandestina 2	**PP946961**	**PP946947**	**PP946954**	**PP946968**	**PP951989**
Urtibrina rimicola sp.n. 1	**PP946962**	**PP946948**	**PP946955**	**PP946969**	**PP951990**
Urtibrina rimicola sp.n. 2	**PP946963**	**PP946949**	**PP946956**	**PP946970**	**PP951991**
Urtibrina rimicola sp.n. 3	**PP946964**	**PP946950**	**PP946957**	**PP946971**	**PP951992**
Urticina coriacea D		EU190797	EU190877	EU190840	
Urticina coriacea L		KT852114	KT852176	KT852266	
Urticina crassicornis BS1	MK287979	MK307743	MK307724	MK307731	MK304511
Urticina crassicornis BS2	MK287979	MK307744	MK307724	MK307732	MK304511
Urticina crassicornis L D	KT851997	KT852059	KT852127		KT852279
Urticina crassicornis NF1	MK287979	MK307745	MK307725	MK307733	MK304512
Urticina crassicornis NF2	MK287979	MK307746	MK307726	MK307733	MK304512
Urticina crassicornis NF3	MK287979	MK307745	MK307725	MK307734	MK304512
Urticina crassicornis NF4	MK287979	MK307745	MK307726	MK307734	MK304512
Urticina crassicornis NF5	MK287979	MK307743	MK307726	MK307734	MK304512
Urticina crassicornis NF6	MK287979	MK307743	MK307725	MK307734	MK304512
Urticina fecunda L D	KT852004	KT852067	KT852135		KT852287
Urticina fecunda NF1		MK307749	MK307730	MK307742	
Urticina felina BS1	MK287980	MK307747	MK307727	MK307735	MK304513
Urticina felina BS2	MK287980	MK307747	MK307727	MK307736	MK304513
Urticina felina BS3	MK287980	MK307747	MK307727	MK307737	MK304513
Urticina felina BS4	MK287980	MK307747	MK307727	MK307738	MK304513
Urticina felina BS5	MK287980	MK307747	MK307727	MK307739	MK304513
Urticina grebelnyi L	KT852034	KT852098	KT852163		KT852318

Supplement Fig. 1. ML phylogenetic tree based on contacenated datasheet, see text for details. Numbers indicate bootstrap values for Maximum Likelihood.



Supplement Fig. 2. Phylogenetic tree represented by Bayesian Inference. Numbers represent posterior probabilities (x100).