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The genera *Urticina* and *Cribrinopsis* (Anthozoa: Actiniaria) from the north-western Pacific

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(Accepted 14 March 2006)

Abstract

Three species of *Cribrinopsis* and two species of *Urticina* from Kamchatka, Commander Islands, and the Sea of Okhotsk are discussed. It is confirmed that the widely distributed north-east Pacific anemone known as *U. lofotensis* (*Tealia lofotensis*: Hand, 1955) is different from the European species of the same name (*Madoniactis lofotensis* Danielssen, 1890) but is conspecific with *Cribrinopsis albopunctata* sp. nov. from Kamchatka. *Urticina grebelnyi* sp. nov. is a large species common in East Kamchatka and recorded also from Puget Sound from where it was previously known as *U. crassicornis* (Müller, 1776). *Cribrinopsis olegi* sp. nov. is a distinctive species with short, often almost spherical tentacles known only from East Kamchatka.

Keywords: Actiniaria, Anthozoa, Cribrinopsis, Urticina

Introduction

Two closely related genera of sea anemones, *Cribrinopsis* and *Urticina* (the senior synonym of *Tealia*), contain several common species from the cold and temperate coastal waters of the northern hemisphere. The genus *Urticina*, well defined by several features including cnidom, contains only decamerous species or species with more irregular, often 11-, 12-, 13- or 14-merous arrangement of the mesenteries. *Cribrinopsis*, clearly distinguished from *Urticina* by its cnidom, currently contains decamerous and hexamerous species, although the position of the hexamerous species in this genus is not well established.

Despite the fact that *Urticina* species are often recorded and are the subject of various biological studies, the taxonomic status of some common Pacific species is confused. The Pacific fauna includes several species all of which, with the probable exception of *U. crassicornis* (Müller, 1776), are distinct from the European species. The differences between European and Pacific species were discussed by several authors (Carlgren 1921; Manuel 1981; Wedi and Dunn 1983; Hartog 1986). Hartog (1986) maintained that Pacific *T. lofotensis*: Hand, 1955 and *T. coriacea*: Hand, 1955 are not conspecific with the European species and require new names. Nevertheless, the names originally applied to European

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species are persistently and incorrectly used for several of the most common and distinctive Pacific species.

The present study is based on many specimens collected and photographed in the north-west Pacific and on material from European localities. Of three *Cribrinopsis* and two *Urticina* species recorded in the East Kamchatka, Commander Islands, and the Sea of Okhotsk, three species are new. The species from Kamchatka resembling *T. lofotensis*: Hand, 1955 and conspecific with *T. lofotensis*: Sebens and Laakso, 1977 is described as *C. albopunctata* sp. nov. A large verrucose species, *U. grebelnyi* sp. nov., previously known from the north Pacific where it was erroneously assigned to *U. crassicornis* (see Chia and Spaulding 1972; Sebens and Laakso 1977) is newly recorded and described from Kamchatka. In addition, two European species of *Urticina* have been examined and described, including the specimens of *U. eques* (Gosse, 1860) collected in Lofoten, Norway, the type locality of *Madoniactis lofotensis* (Danielssen, 1890) (junior synonym of *U. eques*).

Cnidae were measured according to the method of Hand (1954). This method is more suitable for establishing accurate size ranges than the method described by Williams (1996), although the obtained measurements are not random and therefore are not suitable for statistical analysis. However, accurate size ranges are much more important for taxonomic purposes than statistical data such as mean and standard deviation. Actually this is indirectly confirmed by Williams (1996, p 339) who stated: 'statistically significant differences may occur between the mean lengths of cnida samples from the same specimen and from different specimens of the same species'. Cnidae terminology follows England (1991).

All specimens are deposited in the Kamchatka Branch of the Pacific Institute of Geography (KBPIG). Some underwater photographs of discussed species are on the website http://actiniaria.com/urticina/.

Description of species

Genus Cribrinopsis

Diagnosis (modified from Carlgren 1949)

Actiniidae with well-developed pedal disc. Column with adhesive verrucae or without these. Pseudospherules absent or present. Fosse distinct. Sphincter strong, circumscribed. Tentacles short, thick, their longitudinal muscles principally mesogloeal. Radial muscles of oral disc meso-ectodermal to mesogloeal. Numerous perfect mesenteries usually decamerously arranged. Well-developed mesenterial muscles. Gonads on mesenteries of the first cycle and on the other stronger mesenteries. Same number of mesenteries proximally and distally, or mesenteries slightly more numerous proximally. Size ranges (lengths) of large basitrichs in actinopharynx and tentacles always overlap. Cnidom: spirocysts, basitrichs, microbasic p-mastigophores A, and microbasic p-mastigophores B.

Cribrinopsis albopunctata sp. nov.

(Figures 1, 2, 12)

Tealia lofotensis: Hand 1955, p 80; Sebens and Laakso 1977, p 162. Not Madoniactis lofotensis Danielssen 1890, p 47.

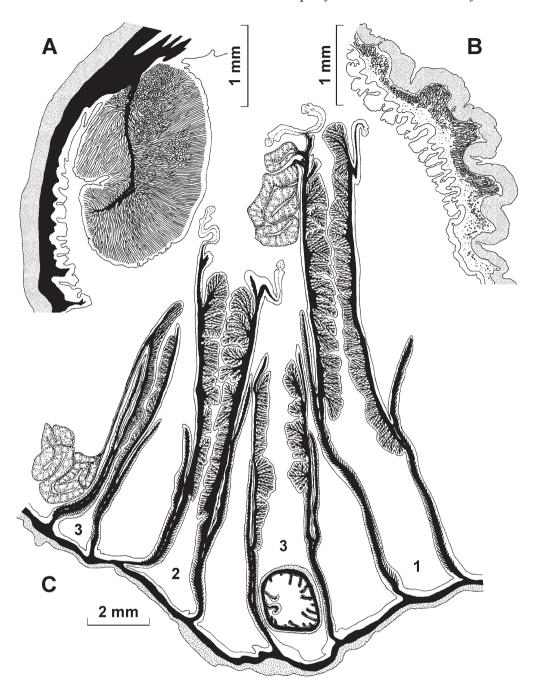


Figure 1. Cribrinopsis albopunctata sp. nov. (A) Cross-sections of the marginal sphincter; (B) cross-section of the tentacle; (C) mesenteries of the first, second and third orders, gonads on one mesentery of the first and one mesentery of the third order, large larva is between the mesenteries of the third order.

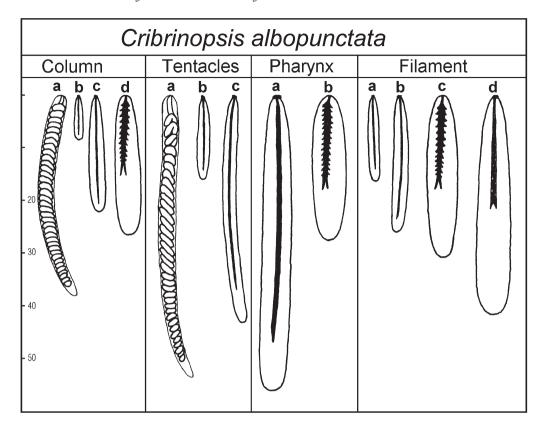


Figure 2. Cribrinopsis albopunctata sp. nov., cnidome.

Material examined

Holotype: East Kamchatka: Avacha Bay, Starichkov Island, 13 m, 5 June 2003 (KBPIG 261/3). Paratypes: East Kamchatka: Avacha Bay, Starichkov Island, 13 m, 5 June 2003, one specimen (KBPIG 262/4); 11 m, 18 June 2003, four specimens (KBPIG 263/5).

Other specimens. East Kamchatka: Avacha Bay, Starichkov Island, 20 m, 9 September 2003, two specimens (KBPIG 267/9); Bezymyannaya Bay, 10 m, 1 October 2004, four specimens (KBPIG 264/6); November 2004, one specimen (KBPIG 265/7); Tri Brata Islands, 21 September 2002, 12–13 m, two specimens (KBPIG 266/8). Commander Islands: Medny Island, intertidal, 4 August 1995, one specimen (KBPIG 11/1).

Description

External structure. Known living specimens are not large, the height of the column and the diameter of the base rarely exceeding 7 cm. The largest contracted formalin-preserved specimen is about 4.5 cm in diameter, and 3 cm in height. The pedal disk is wide and strongly adhesive. In most specimens the cylindrical column is dark red or vermilion, sometimes paler, rose coloured or white, becoming paler toward the base. White adhesive verrucae are arranged in longitudinal rows corresponding to the exocoels and endocoels from the margin to the limbus, they become smaller toward the base. The most distal verrucae are larger,

sometimes partly fused together. Verrucae over the endocoels may be larger and form longer rows than those over the exocoels, and in smaller specimens exocoel verrucae may appear only near the margin (Figure 12A). Verrucae are not strongly adhesive, but may attach particles of gravel and broken shells. Occasionally marginal verrucae have a shallow dark depression in the centre, giving an impression of a perforation, but true perforated pseudospherules are not present. There is a deep fosse and short capitulum.

The oral disk is flat and circular, commonly of the same ground colour as the column, or sometimes differently coloured, greenish or olive. Dark red radial bands running from the middle of the oral disk to the fosse, outline the tentacle bases and form a characteristic colour pattern (Figure 12B, D). In the pale or white specimens the disk may be uniformly coloured.

The tentacles, arranged decamerously in four cycles on the outer half of the oral disk, are not numerous, the largest examined specimen had 72 tentacles and another smaller specimen had 76 tentacles. They are conical, pointed and slightly longer than the radius of the oral disk, and in preserved specimens longitudinally striated, thick, and short. In life the tentacles are uniformly coloured red, rose, or white along most of their length, usually with the white patch on the bases.

Internal structure. Circumscribed marginal endodermal sphincter is strong, circular to oval in transverse section, with one short and thin central lamella (Figure 1A). Radial muscles of the oral disk and longitudinal muscles of the tentacles are strong, mesogloeal to ectomesogloeal (Figure 1B). There are two deep siphonoglyphs supported by directives. Mesenteries usually are arranged decamerously and regularly, in three cycles (10+10+20 pairs), the last cycle may be incomplete. Two of the examined specimens had 9+9+18 pairs. The largest specimen had an additional pair of the fourth cycle (10+10+16+1). Some of the small mesenteries of the last cycle do not reach the margin and therefore the number of tentacles is slightly smaller than the total number of mesenteries. Mesenteries of the first, the second, and some of the third order may be perfect. The gonads in most examined specimens are poorly developed, detected mostly on mesenteries of the second and third orders, but also on the proximal part of some mesenteries of the first order. Spermatic vesicles to 0.3 mm in diameter. Retractor muscles are strong and restricted, up to reniform on the mesenteries of the youngest cycles. Strong parietobasilar muscles form a long free flap. Parietal muscles on transverse sections extend from the column wall to the retractor muscle (Figure 1C).

Numerous large (to 9 mm long and 6 mm diameter) larvae are in one specimen (holotype) collected early in summer. Larvae have numerous tentacles, 23 being found in one expanded larva. It is interesting that this specimen has only male gonads.

Size and distribution of cnidae (letters in parentheses refer to Figure 2, all measurements in μm ; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae is confirmed in sections):

Column

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spirocysts (a): 25-45 \times 2.5-4 (common), N=14/14 basitrichs (b): 7-16 \times 1.5-2 (rare), N=12/14 basitrichs (c): 18-30 \times 2.5-3.5 (common), N=14/14 p-mastigophores A (d): 19-30 \times 4.5-6 (very rare), N=12/14 Tentacles spirocysts (a): 22-62 \times 2-4 (numerous), N=13/13 basitrichs (b): 10-19 \times 1.5-2.5 (rare), N=5/13 basitrichs (c): 25-53 \times 2-3 (numerous), N=12/13
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Actinopharynx basitrichs (a): 36-60\times4-6 (numerous), N=14/14 p-mastigophores A (b): 26-35\times5-7 (very rare), N=10/14 Filaments basitrichs (a): 11-18\times1.5-2.5 (common), N=11/12
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basitrichs (a): $11-18 \times 1.5-2.5$ (common), N=11/12 basitrichs (b): $20-30 \times 2.5-3.5$ (numerous), N=12/12 p-mastigophores A (c): $24-36 \times 5-7$ (common), N=11/12 p-mastigophores B (d): $29-47 \times 4.5-7$ (common), N=12/12

Presence of numerous spirocysts in columnar ectoderm (confirmed in sections) is one of the characteristic features of the species.

Habitat

Records from East Kamchatka are from 9 to 26 m depth and the species apparently is absent from the intertidal zone here. One specimen was found in a tide pool on the Commander Islands. Specimens always are attached to the sides or upper surfaces of stones and are never buried in sand. The column may or may not have a few attached gravel particles or broken shells.

Remarks

The present species is related to *Cribrinopsis olegi* sp. nov. which differs mainly in its short tentacles with spherical expanded ends, absence of spirocysts in the columnar ectoderm, and habitat (*C. olegi* sp. nov. is always buried in sand). It differs distinctly from *C. williamsi* Carlgren, 1940 and *C. fernaldi* Siebert and Spaulding, 1976 which are hexamerous. *Cribrinopsis similis* Carlgren 1921 has a smooth column. Insufficiently described *C. asiatica* (Averincev, 1967) differs in its long blunt-tipped tentacles, colour of column (yellow-white, greenish with red mosaic, brownish yellow), and colour of veruccae (brown or rose-red).

Cribrinopsis albopunctata sp. nov. is very similar and appears to be conspecific with Pacific anemones identified by Hand (1955) as *Tealia lofotensis* (Danielssen, 1890). However, the present specimens, as well as the other Pacific specimens recorded as *T. lofotensis* (see Hand 1955; Sebens and Laakso 1977) differ distinctly from the European *T. lofotensis* (see Remarks under *Urticina eques*).

The present specimens have similar sets of nematocysts, in all parts of the body studied, to those reported by Sebens and Laakso (1977) for the large specimens from Puget Sound, although the sizes of the nematocysts are slightly different and size ranges may be wider in the present specimens. The set of nematocysts reported by Hand (1955) for Californian specimens differs in more details from ours and from those of Sebens and Laakso (1977), the latter authors considered these differences to be within the expected intraspecific variation. The enidom of the Pacific specimens is characteristic of *Cribrinopsis*, but not of *Urticina*. In the latter genus, unlike *Cribrinopsis*, the sizes of the larger basitrichs in the tentacles and in the actinopharynx differ significantly and the size ranges do not overlap (Figure 11). The attribution of the present specimens to *Cribrinopsis* is confirmed by occasional presence of the gonad on some mesenteries of the first cycle, although this has not been reported for the east Pacific specimens and the enidom appears to be a more reliable feature to distinguish *Cribrinopsis* from *Urticina* than the distribution of gonads.

The specimens from Puget Sound are much larger than the present specimens, with the column in full extension reaching 22×18 cm and with more tentacles, 103-135 (Sebens and Laakso 1977). The specimens from California are a similar size to the present specimens but have more tentacles, up to 160 (Hand 1955) and from about 94 to 154 (Wedi and Dunn 1983). Brooding has not been observed in American specimens although large larvae were found in one of the present specimens. Despite the differences referred to above, the present specimens appear to be conspecific with the Puget Sound *T. lofotensis*: Sebens and Laakso, 1977, and probably also with the Californian *T. lofotensis*: Hand, 1955.

Cribrinopsis olegi sp. nov. (Figures 3, 4, 13)

Material examined

Holotype: East Kamchatka: Avacha Bay, Starichkov Island, 13 m, 5 June 2003 (KBPIG 246/8). Paratypes: East Kamchatka: Avacha Bay, Starichkov Island, 6 m, 31 August 2004, one specimen (KBPIG 248/10); 13 m, 5 June 2003, one specimen (KBPIG 247/9); 20 m, 9 September 2003, two specimens (KBPIG 243/5); Bezymyannaya Bay, 10 m, 1 October 2004, three specimens (KBPIG 244/6, 245/7, 252/14); 9–12 m, one specimen (KBPIG 249/11); 15 m, 21 September 2004, three specimens (KBPIG 250/12, 251/13). Kronotsky Bay, Morzhovaya Bay, 12 m, 18 May 2003, seven specimens (KBPIG 239/1, 240/2, 241/3, 242/4).

Other specimens. East Kamchatka: Avacha Bay, Bezymyannaya Bay, 9–12 m, 1 October 2004, one specimen (KBPIG 254/16); 10 m, one specimen (KBPIG 255/17). Commander Islands: Medny Island, Drovenskoy Point, 15 m, 23 June 1995, one specimen (KBPIG 59/21); Gladky Point, 32 m, 24 July 1992, one specimen (KBPIG 66/18). North Kurile Islands: Shumshu Island, 30 m, 8 July 1985, one specimen (KBPIG 127/19).

Description

External structure. This large species reaches 10 cm in diameter and height when fully expanded and the largest formalin-preserved specimens are about 6.5 cm diameter and 4 cm high. The base is circular and strongly adhesive. In most specimens the column is rose-coloured or red, with white spots of the verrucae. The colour becomes paler toward the base. Some specimens are entirely white. The adhesive verrucae are arranged in longitudinal rows corresponding to exocoels and endocoels and they are larger and carry larger particles of gravel and broken shell in the distal part of the column. Toward the base they gradually become smaller, less adhesive and disappear completely in the proximal half of the column. Verrucae form a distinct annulus on the margin. Externally, marginal verrucae are similar to columnar verrucae, but they are slightly larger, sometimes elongated longitudinally, and usually have a darker depression, with a thinner wall, in the centre. Enlarged verrucae on the margin have the same nematocysts as the rest of the column. There is a deep fosse and short capitulum.

The oral disk is flat and circular, always paler than the column, pale rose or yellowish, greyish, whitish, sometimes with irregular light dirty-green patches. Mesenterial insertions are marked by thin white lines radiating from the mouth.

From 100 to 140 tentacles are arranged decamerously in five cycles on the outer half of the oral disk, the inner tentacles larger than the outer. In smaller specimens there are fewer

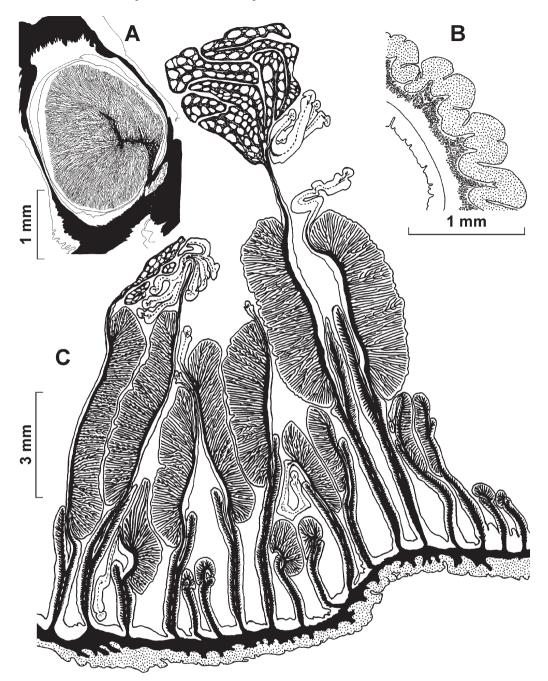


Figure 3. Cribrinopsis olegi sp. nov. (A) Cross-sections of the marginal sphincter; (B) cross-section of the tentacle; (C) mesenteries of the first to fifth orders, gonads on one directive and one mesentery of the second order.

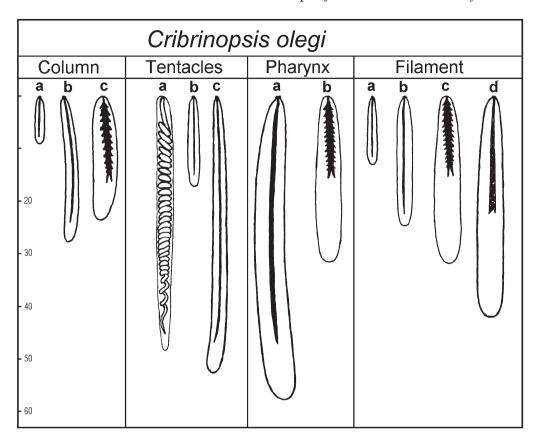


Figure 4. Cribrinopsis olegi sp. nov., cnidome.

tentacles: 64 and 78 tentacles were counted in the preserved specimens with diameter 24 and 33 mm, respectively. The tentacles are short (up to 1.5 cm long) and thick, usually with a large, almost spherical expansion up to 1 cm diameter on the distal end (Figure 13). Each tentacle has a large slit-like terminal pore. In the preserved specimens the tentacles are longitudinally folded, short, and almost spherical. The shape of the tentacles is the most conspicuous distinguishing character for the species. The ground colour of the tentacles is white or yellowish with numerous short longitudinal red stripes on the expanded distal half. The border between the expanded distal and cylindrical proximal half of each tentacle is marked by a wide white transverse band. In white specimens the tentacles and oral disk are pure white, without the colour stripes.

Internal structure. The marginal endodermal sphincter is strong, circumscribed, with one short, not always pronounced central lamella (Figure 3A). Radial muscles of the oral disk and longitudinal muscles of the tentacles are mesogloeal, sometimes to ecto-mesogloeal (Figure 3B). Transverse sections of the tentacles show the muscle meshes closer to the outer (ectodermal) side of the mesogloea. The pharynx has two deep thick-walled siphonoglyphs supported by directives.

Mesenteries are arranged decamerously, in larger specimens in four cycles, the fourth cycle usually incomplete: $10+10+20+(0\sim40)$. In some specimens regular decamerous

symmetry is violated by additional pairs of mesenteries of the second, third, and fourth orders. If only one pair of the mesenteries of the fourth cycle is present in the exocoels of the second order (between the mesenteries of the first and the second cycles) this pair usually is placed between the mesenteries of the second and third cycles. Some specimens may have a few small mesenteries of the fifth cycle. The number of mesenteries appears to be a little greater than the number of the tentacles. The mesenteries of the first, the second, some of the third, and even the fourth order may be perfect. The mesenteries from the first to the fourth cycles including the directives, and sometimes mesenteries of the fifth cycle are fertile. Gonads are better developed on the proximal parts of the mesenteries; this is especially evident on the first cycle, which may appear as sterile on the transverse sections in the middle of the column. Oocytes to 1 mm and spermatic vesicles to 0.5 mm in diameter. The retractor muscles are strong, restricted, and almost reniform on younger cycles, with numerous branched lamellae (Figure 3C). Well-developed parietobasilar muscles form a long free flap.

One examined specimen was hermaphrodite, with well-developed male and female gonads and numerous embryos; all other specimens have gonads of one sex only. Young, brooded internally, are large and especially numerous in the specimens collected in autumn. Embryos are up to 2 mm in length in the specimen collected at the beginning of September, and up to 10 mm in the specimen collected on 1 October. Larger embryos have well-developed filaments and tentacles.

Size and distribution of cnidae (letters in brackets refer to Figure 4, all measurements in μ m; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae is confirmed on sections):

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Column
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basitrichs (a): 6-12 \times 1-2 (rare), N=13/15
basitrichs (b): 13-31 \times 2-3.5 (common), N=15/15
p-mastigophores A (c): 18-29 \times 4-6 (very rare), N=8/15
Tentacles
spirocysts (a): 26-62 \times 2-3.5 (numerous), N=15/15
basitrichs (b): 12-26 \times 2-2.5 (very rare), N=7/15
basitrichs (c): 32-60 \times 2.5-3.5 (numerous), N=15/15
Actinopharynx
basitrichs (a): 35-70 \times 4.5-7 (numerous), N=15/15
p-mastigophores A (b): 22-38 \times 5.5-6.5 (very rare), N=9/15
Filaments
basitrichs (a): 11-20 \times 1.5-2.5 (common), N=12/14
basitrichs (b): 21-37 \times 2.5-4 (numerous), N=14/14
p-mastigophores A (c): 23-36 \times 4.5-6 (common), N=14/14
p-mastigophores B (d): 34-55 \times 4.5-7 (common), N=14/14
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Habitat

Several specimens of *C. olegi* sp. nov. were found at 6 m depth, but the majority of the specimens are from 10 to 32 m. The species is always buried in sand, gravel, or broken shell with the pedal disk always attached to buried stones so only the oral disk with the tentacles is visible on the surface. Contracted specimens are buried completely in sand. Symbiotic shrimps [probably *Lebbeus grandimanus* (Brazhnikov)] were found on many specimens.

Etymology

The species is named after Oleg Vlasenko, the captain of the boat *Chaika*, who helped in our field work.

Remarks

Cribrinopsis olegi sp. nov. differs from all known species of Urticina and Cribrinopsis by its short thick tentacles with almost spherical expanded ends. Bunodes crassus Andres, 1884, wrongly assigned to Cribrinopsis by Schmidt (1972), also has thick tentacles with rounded ends, but their shape is clearly different, and this warm-water Mediterranean species differs from C. olegi sp. nov. in many features, including the hexamerous arrangement of the mesenteries. Cribrinopsis albopunctata sp. nov. resembles the present species in the presence of the white verrucae on the usually red or pink column. Living specimens of C. olegi sp. nov. and C. albopunctata sp. nov. are very different in appearance and are readily distinguished by the shape and colour of the tentacles (the latter species lacking the red stripes characteristic of C. olegi sp. nov.), and by habitat (C. olegi sp. nov., unlike C. albopunctata sp. nov., always being buried in the sand). Preserved specimens of the two species often are similar, especially when the tentacles are strongly contracted and their real shape obscured. The presence of the spirocysts in the columnar ectoderm in C. albopunctata sp. nov. and their absence in the same tissue in C. olegi sp. nov. is a good distinguishing feature confirmed in cross-sections.

Cribrinopsis similis Carlgren, 1921

(Figure 5)

Cribrinopsis similis Carlgren 1921, p 156; 1928, p 279 (synonymy); Zhiubikas 1977, p 108.

Material examined

Vessel *Pogranichnik Pertov*, Sea of Okhotsk, trawl 97, 53°41.4′N, 154°32.9′E–53°39.7′N, 154°33.2′E, 200 m, globigerina ooze, 18 July 2001, seven specimens, collector A. V. Chetvergov (KBPIG 268/1, 269/2).

Description

External appearance. Preserved specimens are large, cylindrical, up to 7 cm diameter and 8 cm high. Size and colour of living specimens are not known, although the specimens examined shortly after fixation showed remnants of red colour in some parts of the column and tentacles. The column is smooth, without columnar verrucae or marginal pseudospherules. The circular base is the same diameter as the column. Remnants of mud on the lower part of the column and an undamaged intact base in all specimens suggests that the specimens live unattached on soft bottoms with the lower part of the column immersed in the mud. The specimens have about 80–90 conical or cylindrical tentacles, wrinkled transversely and with pointed tips.

Internal structure. The marginal endodermal sphincter is strong, circumscribed, with not always pronounced central lamella. Longitudinal muscles of the tentacles are mesogloeal and strong.

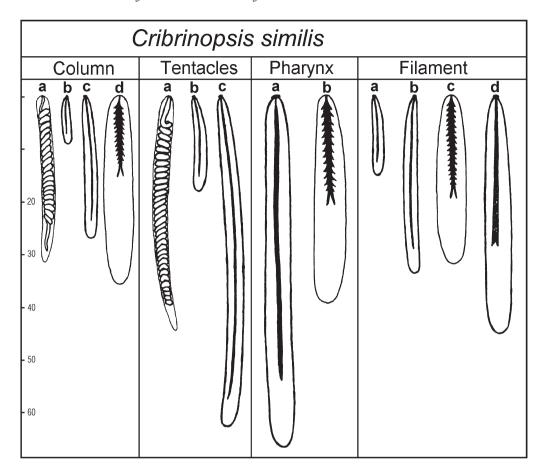


Figure 5. Cribrinopsis similis Carlgren, 1921, cnidome.

The mesenteries are arranged decamerously in three cycles, with a few additional small mesenterial pairs in some exocoels. The number of mesenteries is the same distally and proximally, and small and large specimens have about the same number. Well-developed gonads are present on all cycles. On the younger cycles gonads are developed in the distal part of the mesenteries, while in older cycles the gonads are situated proximally, near the base.

The retractor muscles are strong, restricted, and almost reniform on younger cycles. Well-developed parietobasilar muscles form a long free pennon.

Size and distribution of cnidae (letters in brackets refer to Figure 5, all measurements in μm ; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae is confirmed on sections):

Column

spirocysts (a): $30-70 \times 3-4.5$ (common), N=3/3 basitrichs (b): $9-12 \times 1.5-2$ (common), N=3/3 basitrichs (c): $21-32 \times 2-3$ (common), N=3/3 p-mastigophores A (d): $30-39 \times 5.5-6$ (rare), N=3/3

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Tentacles
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spirocysts (a): 27-76\times3-5 (numerous), N=2/2 basitrichs (b): 14-19\times2.5 (very rare), N=2/2 basitrichs (c): 42-73\times2.5-3.5 (numerous), N=2/2 Actinopharynx basitrichs (a): 39-72\times3.5-5.5 (numerous), N=2/2 p-mastigophores A (b): 35-43\times6-7 (common), N=2/2 Filaments basitrichs (a): 11-16\times2 (common), N=2/2 basitrichs (b): 23-41\times2-3 (numerous), N=2/2 p-mastigophores A (c): 25-39\times5-6.5 (common), N=2/2 p-mastigophores B (d): 25-52\times4-5.5 (common), N=2/2
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Remarks

The present specimens from the Sea of Okhotsk agree well with the original description of *C. similis*. This large species is characterised by the relatively small and more or less constant number of the mesenteries and tentacles. As in all species of *Cribrinopsis* and *Urticina*, the number of tentacles is the same or slightly smaller than the number of mesenteries in the middle of the column. Carlgren's (1921, p 159) statement that "the number of mesenteries seems sometimes to be a little smaller than that of tentacles" is an obvious mistake, as appears from his definition of the genus and the statement that the mesenteries grow from the base upward. The colour of the living specimens of this species was recorded only by Zhiubikas (1977), who reported the body wall to be carmine-red, or yellowish with dark green or red patches. The oral disk and lips are pink. The tentacles near their bases are pale red and become dark red toward the tips. Light bands run from the lips to the tentacle bases. The mesenteries are probably always arranged decamerously, the two hexamerous specimens reported by Carlgren (1921) from the Bering Sea and Ikamiut, Greenland, being either abnormal, or, especially in the case of the Bering Sea specimen, belonging to another species.

The species is known from numerous Arctic locations including Greenland, Iceland, Faroe Islands, Spitsbergen, Barents Sea and, probably, the Bering Sea. Carlgren (1921) reported also a specimen from the Korea Strait, a location too distant from the known range. The record may be based on incorrect identification.

Genus Urticina

Diagnosis (modified from Carlgren 1949)

Actiniidae with well-developed pedal disc. Column with adhesive or non-adhesive verrucae or without these. Fosse well developed. Sphincter strong, circumscribed. Tentacles short, stout, their longitudinal muscles ectodermal to mesogloeal. Radial muscles of oral disc ectodermal to mesogloeal. Numerous perfect mesenteries arranged as a rule decamerously or more irregularly 11-, 12-, 13-, or 14-merously. Usually 10–20 oldest pairs sterile, rarely only six pairs. Basitrichs of the actinopharynx much larger than those of the tentacles and size ranges do not overlap. Same number of mesenteries proximally and distally. Cnidom: spirocysts, basitrichs, microbasic p-mastigophores A, and microbasic p-mastigophores B.

Urticina crassicornis (Müller, 1776)

(Figures 6, 15A, B)

Actinia crassicornis Müller 1776, p 231. Urticina felina: McMurrich 1911, p 65.

Urticina felina crassicomis: Carlgren 1921, p 170 (synonymy).

Tealia felina var. crassicornis: Stephenson 1935, p 150.

? Tealia crassicornis: Hand 1955, p 72 (part).

Not Tealia crassicornis: Chia and Spaulding 1972, p 206; Sebens and Laakso 1977, p 165;

Widersten 1976, p 865.

Material examined

East Kamchatka: Avacha Bay, Starichkov Island, 14 m, 21 September 2004, one specimen (KBPIG 271/12); Kekkurny Point, 12 m, 14 July 2003, three specimens (KBPIG 274/18); Bezymyannaya Bay, 9–12 m, 1 October 2004, three specimens (KBPIG 272/16, 273/17); November 2004, one specimen (KBPIG 275/19). Commander Islands, Medny Island: Drovenskoy Point, intertidal pool, 4 August 1995, three specimens (5/1, 62/8); 5 m, 23 July 1995, two specimens (KBPIG 58/5); 15 m, one specimen (KBPIG 61/7); Glinka Bay, 6 m, 8 August 1995, six specimens (KBPIG 8/2, 56/3, 57/4, 60/6); 5 m, 1 August 1995, one specimen (KBPIG 64/10); Sivuchi Kamen Kliff, 10 m, 23 July 1992, one specimen (KBPIG 65/11); Gladky Point, 5 m, 21 June 1992, one specimen (KBPIG 163/13); Gavrilovskaya Bay, 15 m, 9 July 1992, one specimen (KBPIG 165/14); Matvea Point, 5–7 m, 5 July 1992, two specimens (KBPIG 168/15).

Description

External appearance. The typical living specimens are up to 10 cm high and with a tentacular crown up to 10 cm diameter and the column about 6–7 cm diameter. The largest formalin-preserved specimen is 4 cm in diameter and 3 cm high. The circular base is wider than the column and strongly adhesive. The colour is variable, although most specimens range from plain reddish brown to pale orange. Some specimens from the Commander Islands are deep red with irregular longitudinal green patches or strips. The column is smooth, without traces of verrucae or vesicles, and is always clear, without attached sand or other foreign particles. The margin is smooth. There is a deep fosse and a short capitulum.

The oral disk is flat and circular, much paler than the column, usually yellowish or whitish. Short thin red radial bands outline the tentacle bases; the region around the mouth may be reddish, and otherwise the colour of the oral disk is plain.

The tentacles, arranged decamerously up to five cycles, number from 74 in the smallest specimen to 163 in large specimens. Conical tentacles, of the same colour as the disk, are plain-coloured, without bands or other markings. In preserved specimens the tentacles are longitudinally folded, cylindrical, up to 2 mm in diameter and up to 7 mm long. Some may be bifurcated, or even have up to four tips.

Internal structure. A strong circumscribed endodermal sphincter with one central lamella is typical for the genus. Radial muscles of the oral disk and longitudinal muscles of the tentacles are mesogloeal, sometimes ectomesogloeal, and strong. The mesenteries are arranged decamerously and regularly in four cycles, 10+10+20+40, although the last cycle may be incomplete in smaller specimens. Two specimens (KBPIG 274/18, 275/19) have, in

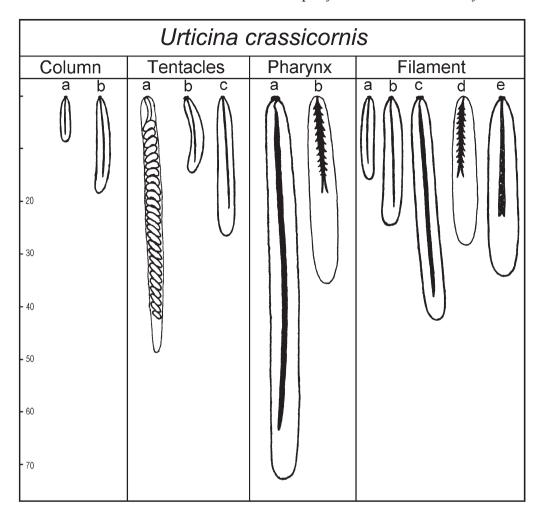


Figure 6. Urticina crassicornis (Müller, 1776), cnidome.

addition, several mesenterial pairs of almost the same size as mesenteries of the fourth cycle. The mesenteries of the first, second and some of the third cycle are perfect. In most specimens only third and fourth cycles of the mesenteries are fertile, although the gonads may be present in the mesenteries of the second cycle in small specimens. The retractor muscles on the oldest cycles are long, weak and diffuse, but restricted on the fourth cycle. The parietobasilar muscles are well developed and form a clear pennon.

The sexes are separate. Embryos were not found in any specimen.

Size and distribution of cnidae (letters in brackets refer to Figure 6, all measurements in μm ; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae excepting the smallest basitrichs in column is confirmed on sections):

Column

basitrichs (a): $7-10 \times 1.5-2$ (very rare), N=4/13 basitrichs (b): $14-23 \times 2-3$ (common), N=13/13

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Tentacles spirocysts (a): 18-55\times2-3.5 (numerous), N=11/11 basitrichs (b): 9-17\times1.5-2.5 (common, mostly crescent-shaped), N=10/11 basitrichs (c): 17-31\times2-3 (common), N=11/11 Actinopharynx basitrichs (a): 54-86\times5-7 (numerous), N=13/13 p-mastigophores A (b): 24-40\times5-6 (rare), N=12/13 Filaments basitrichs (a): 12-17\times1.5-2.5 (numerous), N=9/10 basitrichs (b): 15-25\times2.5-3.5 (common), N=8/10 basitrichs (c): 40-66\times4-6.5 (very rare), N=8/10 p-mastigophores A (d): 20-30\times4-5.5 (numerous), N=10/10 p-mastigophores B (e): 28-40\times5-6.5 (numerous), N=10/10
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Habitat

The specimens were recorded from the intertidal zone to 20 m depth, attached to stones or rocks, never buried in sand.

Remarks

Carlgren (1921) examined numerous specimens of this species from many localities in the Arctic seas, and distinguished it by the complete absence of any traces of verrucae on the column. In addition to the northern specimens Carlgren (1921, 1934) assigned several specimens from the north Pacific (the Bering Sea and Bering Island) to this species. Hand (1955) described *Tealia crassicornis* from California. This is the only record of the species from the Pacific published after Carlgren's works provided with a description and, in general, corresponding to the species. Hand (1955), however, reported that the Californian specimens occasionally have weakly adhesive verrucae to which small particles of gravel may adhere. This feature never occurs in *U. crassicornis* (confirmed in the present study by examining many living and preserved specimens). This, associated with its southern location, makes the record from California doubtful. More recent records are confused and deal with one or more other distinct species. For instance, Widersten (1976) described smooth and verrucose specimens, some with 48 marginal verrucae (which never occur in U. crassicornis), and some with only 68 mesenteries (too few for U. crassicornis). The species discussed as T. crassicornis by Chia and Spaulding (1972) has non-adhesive vesicles on column and parapet and differs in this feature from *U. crassicornis* and, probably, from the California species described by Hand (1955).

Although the present specimens are morphologically identical to the northern specimens of *U. crassicornis*, and have similar nematocysts to those reported by Carlgren (1921), there is still some doubt about the north Pacific specimens belonging to *U. crassicornis*. Although northern specimens are viviparous (Carlgren 1921; Stephenson 1935), embryos have not been found in the present specimens. Chia and Spaulding (1972) reported *U. crassicornis* being oviparous in the northeastern Pacific (San Juan Island). The species they studied, however, is not conspecific with *U. crassicornis*; it is similar to and probably conspecific with *U. grebelnyi* sp. nov. Chia and Spaulding (1972: 206) compared their findings with the data of Appellöf (1900) "who reported that in Europe this species releases its gametes freely into

the sea". However, the species studied by Appellöf (1900) is not conspecific with U. crassicornis and was synonymised with T. felina lofotensis (= U. eques) by Carlgren (1921).

Urticina eques (Gosse, 1860) (Figures 7, 15C, D)

Bolocera eques Gosse 1860, p 351.

Madoniactis lofotensis Danielssen 1890, p 47 (part).

Tealia lofotensis: Carlgren 1902, p 42.

Urticina felina lofotensis: Carlgren 1921, p 168 (synonymy).

Tealia felina var. lofotensis: Stephenson 1935, p 147.

Urticina eques: Manuel 1981, p 109.

Not Tealia lofotensis: Hand 1955, p 80; Sebens and Laakso 1977, p 162 (=Cribrinopsis

albopunctata sp. nov.).

Material examined

Lofoten, Norway, 12 specimens, coll. Dr D. Schories (KBPIG 256/1, 257/2).

This species has not been recorded from the Pacific. Specimens collected in Lofoten, Norway (type locality of *Madoniactis lofotensis*) are briefly described for comparison with the Pacific species of the genus.

Description

External appearance. Available formalin-preserved specimens are dome-shaped, strongly contracted, with completely retracted tentacles, 28–46 mm diameter and 17–23 mm high. On underwater photos the same specimens have whitish or yellowish ground colour with wide or narrow, irregular, mainly longitudinal red patches. In some specimens the prevailing colour is red. Small non-adhesive verrucae are distinctly visible on the living specimens, especially on the contracted anemones (Figure 15C). The verrucae are of the same colour as the column or paler, and they probably do not become as inflated and blister-like as in *U. grebelnyi* sp. nov. In preserved specimens the verrucae are difficult to recognize. The oral disk and the tentacles are yellow-whitish, transparent, with the red longitudinal bands outlining tentacle bases on the disk; the tentacles are encircled with the wide white and red bands in the middle. Tentacles are arranged decamerously in five cycles.

Internal structure. The sphincter is strong, circumscribed and circular in cross-section. Radial muscles of the oral disk and longitudinal muscles of the tentacles are mesogloeal. Mesenteries are arranged decamerously, 10+10+20+40, although in the smaller specimens the last cycle may be incomplete. The largest specimen has the following arrangement of the mesenteries: 12+10+22+43+1. Mesenteries from the first to the third cycles may be perfect. The mesenteries of the third and fourth cycles are fertile; in one small specimen a gonad is present also on one mesentery of the second cycle. The retractor muscles are long and diffuse.

The sexes are separate. No embryos were found in any specimen.

Size and distribution of cnidae (letters in brackets refer to Figure 7, all measurements in μ m; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae is confirmed on sections):

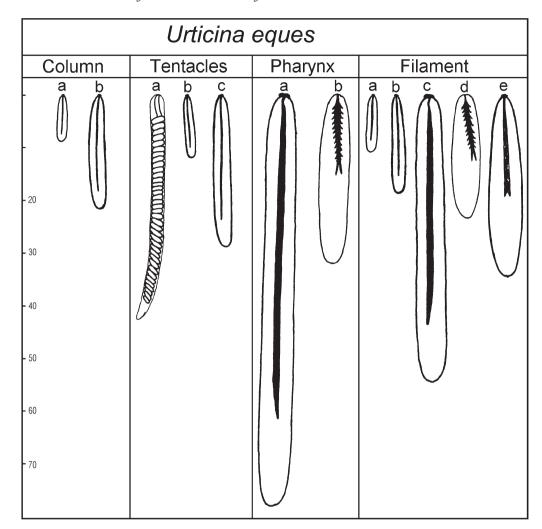


Figure 7. Urticina eques (Gosse, 1860), cnidome.

Column

basitrichs (a): $8-11 \times 1.5-2$ (rare), N=4/4 basitrichs (b): $17-25 \times 2-3$ (common), N=4/4

Tentacles

spirocysts (a): $20-60 \times 2-4$ (numerous), N=3/3 basitrichs (b): $9-12 \times 1.5-2$ (rare), N=2/3 basitrichs (c): $24-30 \times 2-3$ (numerous), N=3/3

Actinopharynx

basitrichs (a): $63-95 \times 5-6.5$ (numerous), N=4/4

p-mastigophores A (b): $22-28 \times 4.5-5.5$ (very rare), N=2/4

Filaments

basitrichs (a): $10-14 \times 2$ (common), N=4/4 basitrichs (b): $15-24 \times 2-3.5$ (common), N=4/4

basitrichs (c): $54-80 \times 5.5-7$ (very rare), N=4/4

p-mastigophores A (d): $22-28 \times 4.5-5.5$ (common), N=4/4 p-mastigophores B (e): $20-39 \times 4.5-7$ (common), N=4/4

Remarks

For a long time this northern species was attributed to *Madoniactis lofotensis* Danielssen, 1890 (recorded under the generic names *Urticina* or *Tealia*, or as a variety or subspecies of *U. felina*). The possible conspecificity of Danielssen's species with *Bolocera eques* Gosse, 1860 was first suggested by Carlgren (1921) who questionably synonymised these species, but used *U. felina lofotensis* as a valid name. Stephenson (1935, p 143) had no doubt that *B. eques* is conspecific, but also used Danielssen's name (as *T. felina* var. *lofotensis*). Finally, Manuel (1981) formally synonymised *M. lofotensis* with *Urticina eques* and in the present paper we fully support his conclusion.

Manuel (1981, p 110) supposed that *T. lofotensis* described by Hand (1955) from California may be not conspecific with the present species: "Although this anemone [*T. lofotensis*: Hand, 1955] bears strong external resemblance to the present species, measurement of its nematocysts do not wholly agree". Hartog (1986, p 87) found this to be an "understatement". Based on his own (unpublished) studies of the northern species he considered the Californian species distinct and indicated that it requires a new name. Actually, the Pacific species widely known as *U. lofotensis* and described in detail by Hand (1955) and Sebens and Laakso (1977) does not resemble the European species externally. The Pacific species has white, always well-visible verrucae on the usually uniformly coloured crimson column. In European specimens the verrucae are smaller, usually inconspicuous, they may be whitish, but often of the same colour as the column and the species look completely different (Figure 15C, D). Further, the nematocyst data clearly distinguish the two species: the lectotype of *Madoniactis lofotensis* (see Carlgren 1921), as well as the present specimens of *U. eques* have cnidom typical for *Urticina*, while the cnidom of Pacific specimens is typical for *Cribrinopsis* (Figure 11).

Urticina felina (Linnaeus, 1761) (Figure 8)

Priapus felinus Linnaeus 1761, p 510. Actinia coriacea Cuvier 1798, p 653.

Actinia tuberculata Cocks 1850, p 94.

Urticina felina coriacea and tuberculata: Carlgren 1921, p 163 (synonymy).

Tealia felina var. coriacea: Stephenson 1935, p 140.

Urticina felina: Manuel 1981, p 106. Not Tealia coriacea: Hand 1955, p 76.

Material examined

Great Britain, Swansea, the Mumbles Point, intertidal zone, 18 June 1993, three specimens, coll. Dr A. Rzhavsky (KBPIG 69/1).

This species is not present in our material from the northwestern Pacific. We give brief morphological information and nematocysts data of the examined specimens from the British Isles for comparison with other *Urticina* species.

Description

Preserved specimens, 27–49 mm in diameter and 13–32 mm high, are highly verrucose, covered by gravel and shell particles. They are in agreement with the previous description of this species from northern waters (see synonymy). Mesenteries are arranged decamerously, in four cycles, the last cycle incomplete. The gonads are on the mesenteries from the second to fourth cycles. In one specimen a gonad is present also on one mesentery of the first cycle. The longitudinal muscles of the tentacles and oral disk are from mesoectodermal to mesogloeal.

Size and distribution of cnidae (letters in brackets refer to Figure 8, all measurements in μ m; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae is confirmed on sections):

Column

basitrichs (a): $7-12 \times 1.5-2$ (very rare), N=3/3 basitrichs (b): $15-19 \times 2-2.5$ (common), N=3/3

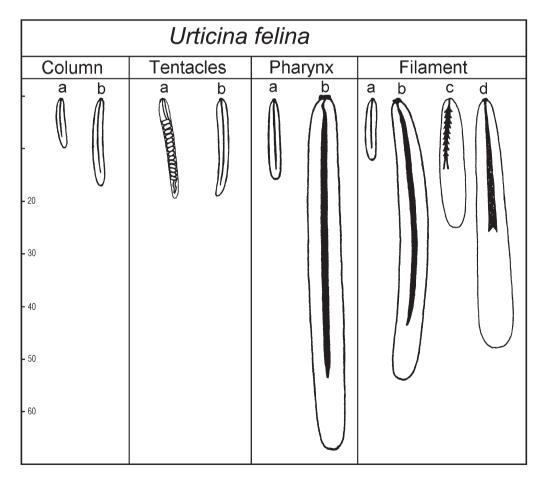


Figure 8. Urticina felina (Linnaeus, 1761), cnidome.

Tentacles

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spirocysts (a): 16-32 \times 2-2.5 (numerous), N=2/2 basitrichs (b): 16-22 \times 2-2.5 (common), N=2/2
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Actinopharynx

basitrichs (a): $13-18\times 2-2.5$ (very rare), N=2/3 basitrichs (b): $54-77\times 5-6.5$ (common), N=3/3

Filaments

basitrichs (a): $11-13 \times 2$ (common), N=3/3

basitrichs (b): $55-61 \times 5.5-6$ (very rare), N=1/3

p-mastigophores A (c): $20-27 \times 3-5$ (common), N=3/3 p-mastigophores B (d): $29-52 \times 5-7.5$ (common), N=3/3

Remarks

This is the best defined and well-known species. Although in one specimen we detected a gonad in one mesentery of the first cycle, a feature previously considered as not occurring in *Urticina*, there is no doubt about its identity. The specimens agree with all descriptions of this species from Europe and have been collected on British shores, where the species is very common (Stephenson 1935). We agree with Hartog (1986) who had no doubt that Californian *Tealia coriacea*: Hand, 1955 is a distinct species and requires a new name. Not one of the recorded species in the studied area in the north-west Pacific is similar to *U. felina*.

Urticina grebelnyi sp. nov.

(Figures 9, 10, 14)

Tealia crassicornis: Chia and Spaulding 1972, p 206; Sebens and Laakso 1977, p 165.

Not Actinia crassicornis Müller 1776, p 231.

Urticina tuberculata: Zamponi and Acuna 1996, p 3.

Not Actinia tuberculata Cocks 1850, p 94.

Material examined

Holotype: East Kamchatka: Avacha Bay, Starichkov Island, 7.5 m, 25 July 2002 (KBPIG 223/6). Paratypes: East Kamchatka: Avacha Bay, Bezymyannaya Bay, 10 m, 22 August 2000, one specimen (KBPIG 193/3); Kekkurny Point, 12 m, 14 July 2003, one specimen (KBPIG 259/13); Zhirovaya Bay, 12–13 m, 15 July 2003, one specimen (KBPIG 260/14); Starichkov Island, 10 m, 15 September 2002, one specimen (KBPIG 229/7); 20 m, 9 September 2003, one specimen (KBPIG 238/10). Kronotsky Bay, Morzhovaya Bay, 12 m, 18 May 2003, two specimens (KBPIG 231/8).

Other specimens. East Kamchatka: Avacha Bay, Kazak Point, 6 m, 25 July 2000, one specimen (KBPIG 191/1); 3 m, 10 July 2002, two specimens (KBPIG 214/4); 10 August 1983, one specimen (KBPIG 258/11); Bezymyannaya Bay, 4 m, 22 August 2000, two specimens (KBPIG 192/2); Starichkov Island, 10 m, 26 June 2002, one specimen (KBPIG 215/5). Kronotsky Bay, Morzhovaya Bay, 8.5 m, 18 May 2003, one specimen (KBPIG 235/9). Commander Islands: Bering Island, Podutesnaya Bay, 20 m, 22 July 1991, two specimens (KBPIG 67/12); Tundrovaya Bay, 20 m, 18 August 1986, one specimen (KBPIG 68/15).

Description

External appearance. The typical living specimens are large, about 20 cm high, with the cylindrical column about 15 cm diameter, and the extended crown of the tentacles up to 25 cm diameter. Large formalin-preserved specimens are up to 15 cm diameter and up to 10 cm high. In living specimens the strongly adhesive circular pedal disk is always wider than the column, but in the preserved specimens the pedal disk contracts and often becomes narrower than the column. The colour pattern is almost constant and shows only a little variation. The column of all specimens is covered by large irregular patches of green and red, the size of these patches varying; in some specimens the prevailing colour is red, in others green. The pedal disk is the same colour as the column. The whole column is covered by numerous non-adhesive verrucae (sensu Hartog 1987). In fully expanded living specimens verrucae do not protrude over the surface of the column, and since they often are not marked by their colour, they may be inconspicuous. When the specimen contracts verrucae become large, inflated and thin-walled (Figure 14C, F). Strongly inflated verrucae may be lobed, especially on the margin. The verrucae on the margin are somewhat larger than the columnar verrucae and have white markings on the tops; each marginal verruca corresponds to one exoor endocoel. Verrucae may be arranged into longitudinal or transverse rows depending on the contraction of the specimen. Marginal and columnar verrucae have the same nematocysts as the rest of the column. There is a deep fosse, up to 1.5 cm, and a capitulum the same height. The fosse has a bright red band running along the parapet, 5–7 mm wide, becoming green toward the bottom. The capitulum is the same colour as the disk.

The oral disk is flat and circular, pale yellow-green, pale lilac, or brownish. Short thin red radial bands outline the tentacle bases; otherwise the colour of the oral disk is plain.

Tentacles are arranged 12-merously or irregularly in five cycles, up to 200 tentacles in large specimens. Usually they are shorter than the radius of the oral disk (up to 4–5 cm long), up to 1 cm diameter near the base, cone-shaped, longitudinally folded in contraction. Rarely some of the tentacles may have bifurcated tips. The tentacles are the same colour as the disk or paler, and are always encircled by a wide lilac, reddish, or brownish band in the middle. Tentacle tips are often the same colour.

Internal structure. The mesogloea of the column is thick, up to 4 mm in large specimens. The columnar verrucae on the transverse sections appear as places with thin mesogloea between the deep tubular evagination of the endoderm and invagination of the ectoderm. Although the presence of the verrucae may not be evident on the contracted specimens, their presence can be always detected in sections.

The marginal endodermal sphincter is strong, circumscribed, with one short main lamella (Figure 9A). Radial muscles of the oral disk and longitudinal muscles of the tentacles are mesogloeal (Figure 9B). Two deep siphonoglyphs are supported by directives.

The first 12 pairs of mesenteries are equally developed as belonging to the same cycle. Accordingly, distribution of the mesenterial pairs may be described as 12+12+24+49 (specimen 238/10). Some specimens may be perfectly 11-merous (11+11+22+45, specimen 231/8) or 13-merous (13+12+26+50, specimen 260/14), 14-merous (14+14+28+52, specimen 67/12) or, often, the arrangement of the mesenteries may be irregular with a different number of mesenterial pairs on the left and right sides of the directive plane. The number of mesenteries appears to be somewhat greater than the number of tentacles (e.g. 186 tentacles and 202 mesenteries in specimen 260/14, or 174 tentacles and 216 mesenteries in specimen 67/12). Gonads are present only on the two last cycles of the mesenteries, the first two cycles (24 pairs) are always sterile. Oocytes to 0.8 mm and spermatic vesicles to

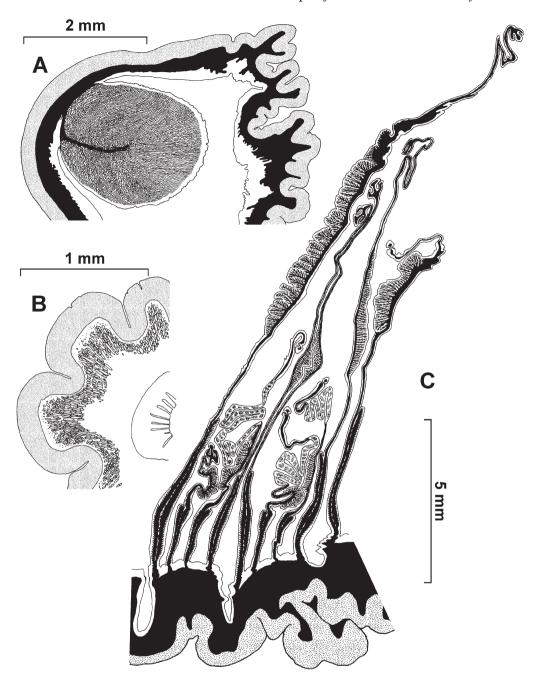


Figure 9. *Urticina grebelnyi* sp. nov. (A) Cross-sections of the marginal sphincter; (B) cross-section of the tentacle; (C) mesenteries of the first to fourth orders, gonads on mesenteries of the fourth order.

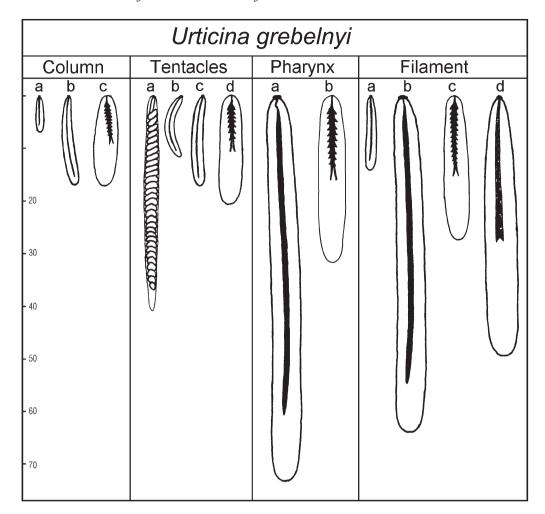


Figure 10. Urticina grebelnyi sp. nov., cnidome.

0.15 mm in diameter. The retractor muscles are rather weak and diffuse to restricted. Well-developed parietobasilar muscles form a free flap. Parietal muscles on transverse sections extend from the column wall to halfway to retractors (Figure 9C).

The sexes are separate, no embryos were found in any specimen.

Size and distribution of cnidae (letters in brackets refer to Figure 10, all measurements in μm ; N is the proportion of examined specimens that had a particular type of cnida; distribution of all cnidae is confirmed on sections):

Column

basitrichs (a): $6-12 \times 1.5-2.5$ (common), N=4/7 basitrichs (b): $14-29 \times 2-3.5$ (numerous), N=7/7 p-mastigophores A (c): $16-24 \times 5-6$ (very rare), N=4/7

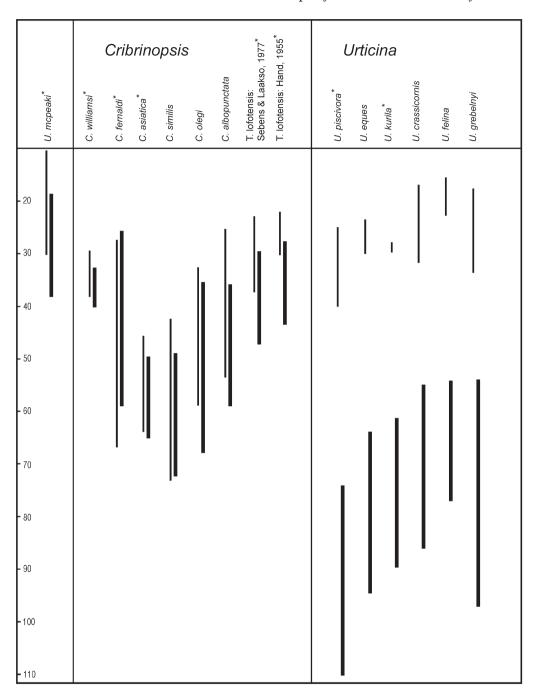


Figure 11. Comparison of size ranges of large basitrichs in tentacles (thin lines) and in actinopharynx (thick lines) of some species assigned to *Urticina* and *Cribrinopsis* (*literature data).



Figure 12. Cribrinopsis albopunctata n. sp.



Figure 13. Cribrinopsis olegi sp. nov.

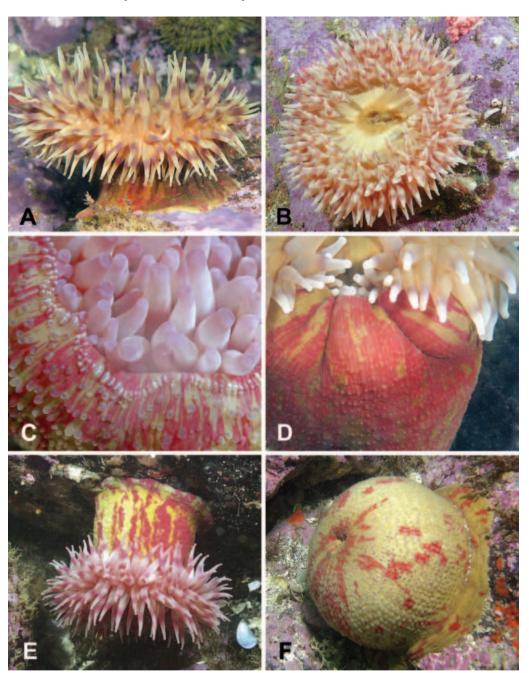


Figure 14. Urticina grebelnyi sp. nov.

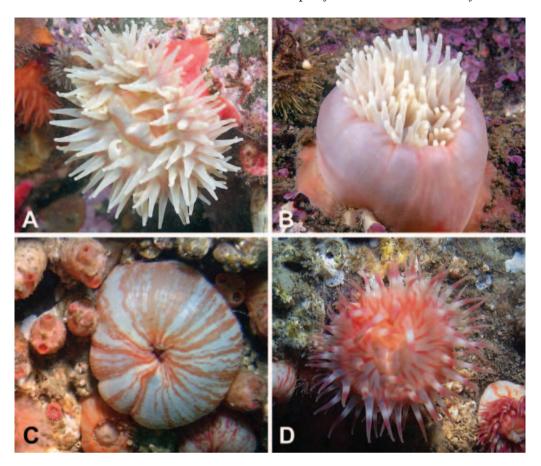


Figure 15. (A, B) Urticina crassicornis (Müller, 1776); (C, D) Urticina eques (Gosse, 1860).

Tentacles

spirocysts (a): $21-55 \times 2-4$ (numerous), N=6/6

basitrichs (b): $8-14 \times 1.5-2.5$ (common, mostly crescent-shaped), N=6/6

basitrichs (c): $18-32\times2-3.5$ (numerous), N=6/6 p-mastigophores A (d): $19-22\times5$ (very rare), N=5/6

Actinopharynx

basitrichs (a): $52-97 \times 4.5-7$ (numerous), N=8/8

p-mastigophores A (b): $27-38 \times 5-6$ (very rare), N=5/8

Filaments

basitrichs (a): $12-21 \times 2-2.5$ (common), N=9/10

basitrichs (b): $51-81 \times 5-6.5$ (common), N=10/10

p-mastigophores A (c): $21-38 \times 5-6$ (common), N=10/10

p-mastigophores B (d): $29-51 \times 5-8$ (numerous), N=10/10

Presence of rare p-mastigophores A in the ectoderm of the tentacles appears to be a characteristic feature of the species (these cells were not detected in the tentacles of the other examined species of *Urticina* and *Cribrinopsis*).

Habitat

The specimens were found from 3 to 25 m depth, and never in the intertidal zone in the studied area. They are always attached to large boulders or rock, and are never buried in sand. The column is always clear from gravel particles or other foreign matter. Several large specimens were recorded attached around the den of a large octopus.

Etymology

The species is named after Dr Sergey Grebelnyi who first recognised this species in 1983.

Remarks

The species is characterised by its large size and numerous non-adhesive ampullaceous verrucae spread over the whole column. They form a distinct annulus on the margin and may become large and inflated when the specimen contracts. The species is most closely related to the northern *U. eques*. Verrucae in the latter species are weakly developed, and usually the mesenteries are arranged decamerously (Stephenson 1935), while not one of the numerous dissected specimens of the present material has decamerously arranged mesenteries. Also, there are some differences in the cnidom, which seem to be real rather than apparent. In particular, *U. grebelnyi* sp. nov., unlike *U. eques*, has p-mastigophores A in the ectoderm of the column and tentacles and crescent-shaped basitrichs in the tentacles, and appears to have only one type of small basitrich in the filaments, while *U. eques* has two types of small basitrichs in the filaments. This distinction, however, needs to be confirmed on material from different locations.

The present species is not related to *U. felina* and *U. crassicornis*, the former having strongly adhesive verrucae (very different from the non-adhesive verrucae of *U. grebelnyi* sp. nov.) and the latter always has a smooth column. However, it is certainly conspecific with the specimens from Puget Sound identified as *Tealia crassicornis* by Chia and Spaulding (1972) and Sebens and Laakso (1977) (see Remarks, *U. crassicornis*).

Urticina tuberculata: Zamponi and Acuna, 1996 from Vancouver Island appears to be conspecific with the present species. Most authors who studied *U. tuberculata* in Europe considered it to be very similar to *U. felina* and "perhaps hardly worthy of varietal rank" (Stephenson 1935, p143), and Manuel (1981) finally synonymised them. Indeed, according to the original description of *Actinia tuberculata* cited by Gosse (1860, p217), the body is "densely covered with large grayish-white tubercles, the apex of each tubercle is depressed". The depressions in these tubercles suggest that they are true adhesive verrucae similar to those of *U. felina*. Non-adhesive verrucae of *U. grebelnyi* sp. nov. may appear as depressed, but only on the preserved specimens, while the original description of *A. tuberculata* was made from a living specimen.

Urticina piscivora (Sebens and Laakso 1977) differs in possessing verrucae only in the upper portion of the column where they are arranged in about five rows and, in addition, the colour is different. Urticina columbiana Verrill, 1922 and U. kurila Averincev, 1967, unlike the present species, have well-developed adhesive verrucae and live buried in sand.

This spectacular species is very abundant in some localities in the vicinity of the Petropavlovsk-Kamchatsky and is the largest actiniid species recorded on the depths accessible for divers in the studied area. It certainly is present in Puget Sound.

General remarks on Cribrinopsis and Urticina

Some features distinguishing examined species of *Urticina* and *Cribrinopsis* are summarised in Table I.

Carlgren (1921) distinguished *Cribrinopsis* from *Urticina* by the distribution of the gonads (which are present in all mesenterial cycles in *Cribrinopsis* but absent in the first cycle in *Urticina*), and by differences in the size ranges of the nematocysts in the tentacles and actinopharynx. He proposed that if in the future the gonads are found in the first cycle of the mesenteries in *Urticina*, then the only significant difference remaining is in the size of the nematocysts, and in this case the genera possibly should be united. A comparison of the size ranges of the large basitrichs in the tentacles and actinopharynx in the different species referred to these genera clearly shows two distinct groups of species. In *Urticina*, basitrichs in the actinopharynx are larger than large basitrichs in the tentacles, and the size ranges do not overlap. In the species referred to *Cribrinopsis* (as in closely related *Aulactinia* and many other actiiniid genera), the size ranges of the basitrichs in the actinopharynx and the tentacles do not differ so considerably as in *Urticina*, and always overlap (Figure 11).

The second feature, the distribution of the gonads, is a more ambiguous generic feature. The record of the gonad in the first cycle of *U. felina* shows that the gonads may occur in the first cycle of mesenteries in *Urticina* (although commonly they are not present there). On the other hand, in many specimens of *Cribrinopsis* the gonads may be poorly developed on the mesenteries of the older cycles, where they occur mainly in the proximal part of some mesenteries (near the base), while the gonads on younger cycles are better developed and occur more distally.

The significance of the arrangement of the mesenteries in Actiniidae is discussed by Carlgren (1921, p 147) who concluded that "decamerism, octomerism and hexamerism principally may be used as genus character" at least in certain genera including *Urticina*. Indeed, all species referable to *Urticina* according to nematocysts data have a strong tendency to be either decamerous (*U. felina*, *U. eques*, *U. crassicornis*), or more irregular 11-, 12-, 13-, or 14-merous (*U. grebelnyi* and possibly *U. piscivora*). *Cribrinopsis* currently contains four regularly decamerous species (*C. similis*, *C. asiatica*, *C. olegi* sp. nov., and *C. albopunctata* sp. nov.) and three regularly hexamerous (*C. crassa*, *C. williamsi*, and *C. fernaldi*). Of the three latter species, *C. crassa* is certainly wrongly assigned to *Cribrinopsis* (see below), and the assignment of *C. williamsi* and *C. fernaldi* also needs to be confirmed.

One of the important features of *Urticina* and *Cribrinopsis* is the large microbasic p-mastigophores B in filaments, which are present in large quantity in all specimens and species of the genera we examined. Hauswaldt and Pearson (1999) reported these cells as "p-mastigophore type II" and found them in all the *Urticina* species they studied from the northeastern Pacific. According to Schmidt (1974), microbasic p-mastigophores B ("p-rhabdoids B" according to his terminology) are commonly absent in Endomyaria and occur only in small forms in some species of *Actinia*, *Anthopleura*, and *Gyrostoma*. In addition, Hartog (1987) mentioned the presence of small and rare p-mastigophores B (as "penicilli B1") in filaments of *Bunodactis sensu lato*, *Pseudactinia*, *Phymactis*, and *Bunodosoma*.

Brief comments on other related species

Cribrinopsis williamsi Carlgren, 1940 is known from only one small sterile specimen from Humpback Bay, Alaska (56°11′N, 131°54′W). It differs from the type species of

Table I. Some features distinguishing Urticina and Cribrinopsis species examined.

	Length of large basitrichs in tentacles/pharynx (μm)	Veruccae	Arrangement of the mesenteries	Habitat	Other features
Cribrinopsis albopunctata	25–53/36–60	Adhesive	Usually decamerous	On stones or rocks, never buried in sand	Numerous spirocysts in columnar ectoderm
Cribrinopsis olegi	32–60/35–70	Adhesive, disappear toward the base	Decamerous	Always buried in sand	Short thick tentacles with almost spherical expanded ends
Cribrinopsis similis	42-73/39-72	Absent	Decamerous	Soft bottom?	Numerous spirocysts in columnar ectoderm
Urticina crassicornis	17–31/54–86	Absent	Decamerous	On stones or rocks, never buried in sand	
Urticina eques	24–30/63–95	Small, non-adhesive	Usually decamerous	On stones or rocks, never buried in sand	d
Urticina felina	16-22/54-77	Large, strongly adhesive	Usually decamerous	Always buried in sand	
Urticina grebelnyi	18–32/52–97	Large, numerous, non-adhesive	Usually 12-merous, but may be 11-, 13-, 14- merous or irregular	On stones or rocks, never buried in sand	p-Mastigophores in tentacles

Cribrinopsis in being hexamerous and in possessing fairly well-developed perforated marginal pseudospherules and Carlgren (1940) was not certain if this species should be assigned to Cribrinopsis.

Cribrinopsis fernaldi Siebert and Spaulding, 1976 from San Juan Island, Washington, appears to be similar to *C. williamsi*. Like the latter species it is hexamerous and has well-developed marginal pseudospherules. In the original description Siebert and Spaulding (1976) figured only one type of p-mastigophores in the filament, and either they combined p-mastigophores A and B into a single category, or p-mastigophores B are not present in filaments of this species. In the latter case the species should be excluded from *Cribrinopsis*.

Cribrinopsis asiatica (Averincev, 1967) was originally described from Kurile Islands as *Tealia* and transferred to *Cribrinopsis* by Grebelnyi (1982). The mesenteries are arranged decamerously and the first cycle is fertile (Grebelnyi 1982).

Bunodes crassus Andres, 1884 is a Mediterranean species assigned to Cribrinopsis by Schmidt (1972). This hexamerous species lacks p-mastigophores B in the filament, excluding it from Cribrinopsis. The species possibly should be assigned to Bunodactis sensulato.

Urticina piscivora (Sebens and Laakso, 1977) is a large species described from Puget Sound. The arrangement of the mesenteries appears to be similar to the mesenteries of *U. grebelnyi* sp. nov. The distribution of tentacles is described as "probably decamerous but irregular with the two first cycles containing up to 12 tentacles each" (Sebens and Laakso 1977, p 156). Non-adhesive verrucae in this species are only on the upper part of the column where they arranged in one to five rows.

Urticina kurila (Averincev, 1967) was originally described as Tealia coriacea kurila from Kunashir and Shikotan Islands (South Kurile Islands). Although the original description (Averincev 1967) lacks information about the arrangement of the mesenteries, the cnidom is typical of Urticina. The species is covered by adhesive verrucae and lives buried in sand. These features distinguish it from all Urticina species recorded from East Kamchatka.

Urticina columbiana Verrill, 1922 is a large species originally reported from Puget Sound. Its internal structure is insufficiently known and its assignment to *Urticina* requires confirmation. The species is covered by crowded crusty (adhesive?) verrucae and lives buried in sand.

Urticina mcpeaki Hauswaldt and Pearson, 1999 described from Baja California is certainly not an Urticina. The nematocysts in the actinopharynx are much smaller than in any Urticina species. Although the photographs in the original description give the impression that the sizes of basitrichs in the actinopharynx and tentacles differ considerably (Hauswaldt and Pearson 1999, Figure 5), they show the smallest basitrich in the tentacles and the largest basitrich in the actinopharynx and actually the size ranges of the nematocysts in the tentacles and actinopharynx greatly overlap (Figure 11). Regularly hexamerous arrangement of the mesenteries is another difference from Urticina.

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