ZOOSYSTEMATICA ROSSICA
ISSN 2410-0226 [online] 0320-9180 [print]
Zoological Institute, Russian Academy of Sciences, St Petersburg ▪ https://www.zin.ru/journals/zsr/
Vol. 35(1): 3–19 ▪ Published online 25 March 2026 ▪ DOI 10.31610/zsr/2026.35.1.3
RESEARCH ARTICLE

A new species of *Capnea* (Actiniaria: Capneidae) from the north-west Pacific, with an overview of related taxa

Новый вид *Capnea* (Actiniaria: Capneidae) из северо-западной части Тихого океана с обзором родственных таксонов

N.P. Sanamyan, K.E. Sanamyan, A.D. Kukhlevskiy, T.B. Morozov & S.A. Gorin

Н.П. Санамян, К.Э. Санамян, А.Д. Кухлевский, Т.Б. Морозов, С.А. Горин

Nadya P. Sanamyan, Kamchatka Branch of Pacific Geographical Institute of Far-Eastern Branch of the Russian Academy of Sciences, 6 Partizanskaya St., Petropavlovsk-Kamchatskiy 683000, Russia. E-mail: actiniaria@sanamyan.com

Karen E. Sanamyan, Kamchatka Branch of Pacific Geographical Institute of Far-Eastern Branch of the Russian Academy of Sciences, 6 Partizanskaya St., Petropavlovsk-Kamchatskiy 683000, Russia. E-mail: actiniaria@sanamyan.com

Andrey D. Kukhlevskiy, A.V. Zhirmunskiy National Scientific Centre of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, 17 Palchevskogo St., Vladivostok 690041, Russia. E-mail: ad.kukhlevskiy@gmail.com

Taras B. Morozov, Kamchatka Branch of the Russian Federal Research Institute of Fisheries and Oceanography, 18 Naberezhnaya St., Petropavlovsk-Kamchatskiy 683000, Russia. E-mail: t.morozov@kamniro.vniro.ru

Sergey A. Gorin, Marine Research Centre of Lomonosov Moscow State University, 1 Ramenskiy Blvd, Moscow 119607, Russia. E-mail: serge.gorin@gmail.com

Abstract. The sea anemone *Capnea tokranovi* **sp. nov.** is described from the Sea of Okhotsk and the Pacific Ocean south of Kamchatka. This is the fourth species of this genus and the first member of *Capnea* Forbes, 1841 reported from Russian waters. Morphologically, particularly in the arrangement of the tentacles, *Capnea tokranovi* **sp. nov.** is more similar to the Antarctic *C. georgiana* (Carlgren, 1927) than to the Japanese *C. japonica* (Carlgren, 1940) or *C. sanguinea* Forbes, 1841, which is known from the waters of north-western Europe. The taxonomic position of the family Capneidae and related taxa is discussed. The genera *Chitinactis* Gusmão et Rodríguez, 2021 and *Discoactis* Izumi et al., 2025, which are grouped in the same clade as *Capnea*, are morphologically similar to *Condylanthus* Carlgren, 1899 and *Segonzactis* Riemann-Zürneck, 1979 and should be classified within Condylanthidae. The family Condylanthidae is closely related to Capneidae. *Capnea indica* (Verrill, 1869) is transferred to the genus *Actinoporus* Duchassaing, 1850. The recently established family Peachiidae is shown not to be distinct.

Резюме. Актиния *Capnea tokranovi* **sp. nov.** описана из Охотского моря и Тихого океана к югу от Камчатки. Это четвертый вид этого рода и первый представитель *Capnea* Forbes, 1841, зарегистрированный в российских водах. Морфологически, в частности по расположению щупалец, *Capnea tokranovi* **sp. nov.** ближе к антарктической *C. georgiana* (Carlgren, 1927), чем к японской *C. japonica* (Carlgren, 1940) или *C. sanguinea* Forbes, 1841, известной из вод северо-запада Европы. Обсуждается таксономическое положение семейства Capneidae и близких к нему таксонов. Роды *Chitinactis* Gusmão et Rodríguez, 2021 и *Discoactis* Izumi et al., 2025, которые в филогенетическом анализе попадают в одну кладу с *Capnea*, морфологически сходны с *Condylanthus* Carlgren, 1899 и *Segonzactis* Riemann-Zürneck, 1979, и их следует отнести к Condylanthidae. Семейство Condylanthidae филогенетически близко к Capneidae. *Capnea indica* (Verrill, 1869) перенесён в род *Actinoporus* Duchassaing, 1850. Показано, что недавно созданное семейство Peachiidae не является самостоятельным.

Key words: taxonomy, biodiversity, Sea of Okhotsk, Kamchatka, Actiniaria, Capneidae, Condylanthidae, *Capnea*, new species

Ключевые слова: таксономия, биоразнообразие, Охотское море, Камчатка, Actiniaria, Capneidae, Condylanthidae, *Capnea,* новый вид

ZooBank Article LSID: 6B09704B-F1EA-42B3-959E-1DCDF7F7C2DF

Introduction

Capnea Forbes, 1841 is a highly distinctive genus of sea anemones, well defined by its unusual morphology and external appearance: a wide, flat oral disc with short, often lobed tentacles arranged in short radial rows around its periphery, allowing for easy and unmistakable identification in the field. Preserved specimens, even when strongly contracted, can also be easily identified to genus level by several characters, especially the peculiar shape of the retractor muscles.

The first specimens of this genus, collected in the Sea of Okhotsk, were examined by us about 25 years ago. They were readily identified as *Capnea*; however, the species remained undetermined. The specimens were contracted, and the arrangement of the tentacles—particularly the number of tentacles in each endo- and exocoel, a key character distinguishing species—could not be examined without destructive sectioning. Another difficulty was that the only *Capnea* species reported from the North Pacific, *C. japonica* (Carlgren, 1940), was at that time known only from a brief and uninformative original description (Carlgren, 1940), which lacked illustrations of the internal morphology.

In 2018, one of us (K. Sanamyan) learned that our Japanese colleague, Dr Kensuke Yanagi, had collected *C. japonica* from its type locality and planned to publish a redescription. This was exciting news, as the identification of our material depended on clarifying the morphology and taxonomic position of the Japanese species.

In 2020, one of us (T. Morozov) collected a *Capnea* specimen in the Sea of Okhotsk and preserved a tissue sample for molecular analysis. Yanagi & Izumi (2021) published a redescription of *C. japonica* and provided molecular data demonstrating that the Japanese species is related to, but distinct from, our Sea of Okhotsk specimens.

Finally, in 2023, one of us (S. Gorin) collected a specimen from the Sea of Okhotsk and, for the first time, obtained photographs of a live individual with an expanded oral disc. This enabled us to confirm key morphological details and to describe the species herein.

Material and methods

The specimens were collected from the Sea of Okhotsk and the north-west Pacific between 1998 and 2023 (Fig. 1). Most were preserved in formalin, with only two specimens—collected in 2020 and 2023—accompanied by small tissue samples fixed in 96% ethanol for molecular analysis. In total, seven adult specimens and two juveniles were examined; the latter were extracted from the gastral cavity of the paratype ZIN 14231. The methods used for preparing histological sections, measuring cnidae, and the terminology employed are consistent with those in all our previous publications (Sanamyan & Sanamyan, 2019; Sanamyan et al., 2019, 2021). For the study of the cnidom, we followed the method of Hand (1954), which is the most appropriate for determining cnidae size ranges. This method involves examining all cnidae in a preparation to record the maximum and minimum dimensions of each cnida type, rather than randomly measuring a limited number of cnidae. For very rare cnidae, we indicate the number of measurements in the description; for the more frequent cnidae, specifying the number of capsules measured following Hand's method is not appropriate (see details in Sanamyan et al., 2021: 387). In this study, for the basitrich referred to as "rare" in the tentacles (Fig. 6H), 42 capsules were measured. All other cnidae types are more common, and their measurements are considerably more numerous; however, these numbers do not reflect the total count of cnidae examined and assessed in the preparations and are therefore not provided.

The phylogenetic analysis is based on a large dataset comprising approximately 240 taxa (some identified only to genus level, precluding an

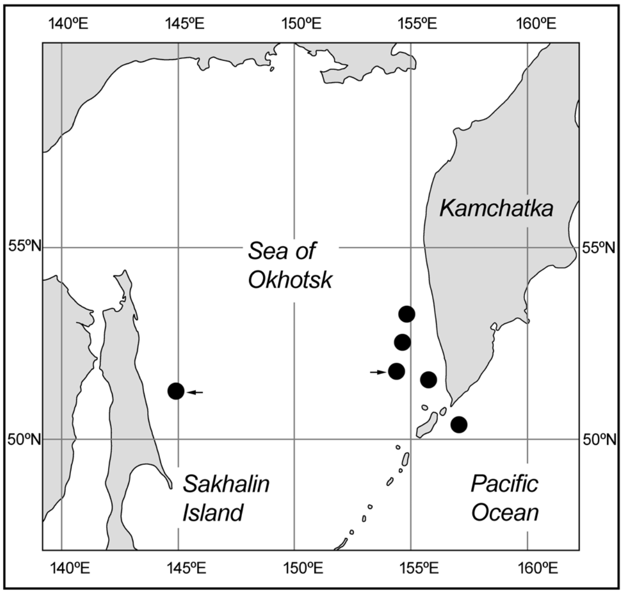

Fig. 1. Sampling locations (black circles); stations where specimens were collected for DNA analysis indicated by arrows.

exact species count) and 368 sequences in the concatenated alignment (*Electronic supplementary material 1*, Table 2; see Addenda). Three mitochondrial gene fragments (12S rRNA, 16S rRNA, and COIII) and two nuclear gene fragments (18S rRNA and 28S rRNA) were used for phylogenetic reconstruction. Sequence alignment was performed using MAFFT v7.526 (command line: “mafft --thread 16 --genafpair --maxiterate 1000”; Katoh & Standley, 2013).

Bayesian inference was conducted using the MPI version of MrBayes 3.2.7a (compiled from source code; Ronquist et al., 2012), which is considerably faster than the standard implementation. The analysis comprised two parallel runs, each with four Markov chains, run for 50 million (5×10^7) generations. We employed the option “nst=mixed” to enable sampling across substitution model space during the Bayesian MCMC analysis, thereby eliminating the need for a priori model testing (*Electronic supplementary material 2*; see Addenda).

A maximum likelihood (ML) tree was generated using IQ-TREE2 v.2.2.0 (Minh et al., 2020) with automatic model selection (Kalyaanamoorthy et al., 2017) and ultrafast bootstrap approximation (Hoang et al., 2018) (*Electronic supplementary material 2*; see Addenda).

A comparison of BI and ML tree topologies, incorporating BI posterior probabilities and ML bootstrap values, was conducted using EasyTree-Editor software (developed by K. Sanamyan; a brief description and download link are provided in the Electronic supplementary material of Sanamyan et al., 2026). The final tree was visualised and prepared for publication using the same programme.

The holotype of the new species is deposited in the collection of the Zoological Museum at Moscow Lomonosov State University, Russian Academy of Sciences (ZMMU), Moscow. The paratypes are deposited in the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN), Saint Petersburg.

Results

Order **Actiniaria** Hertwig, 1882

Family **Capneidae** Gosse, 1860

Genus ***Capnea*** Forbes, 1841

Type species: *Capnea sanguinea* Forbes, 1841, by monotypy.

Capnea tokranovi **sp. nov.**

(Figs 2–7)

Holotype. RUSSIA, Sea of Okhotsk, off east coast of Sakhalin, 51°21.5760′N, 144°27.6361′E, 340 m, 23 July 2023, Van Veen bottom grab, coll. S.A. Gorin (ZMMU SC-70620).

Paratypes. RUSSIA, Sea of Okhotsk: off western coast of Kamchatka: vessel Pogranichnik Petrov, trawl 28, 52°46′N, 154°40.8′E – 52°44.4′N, 154°42.7′E, 250 m, muddy bottom, 8 June 1992, coll. B.A. Sheiko, 1 specimen (ZIN 14226); vessel Pacific Breeze, ca. 53°N, 180–240 m, July–Aug. 1998, shrimp trawl, coll. P.S. Vasiliev, 1 specimen (ZIN 14227); vessel Professor Kaganovskiy, trawl 48, 53°20′N, 154°50′E, 150 m, sandy bottom, T –0.35 °C, 14 July 1999, coll. A.V. Chetvergov, 1 specimen (ZIN 14228); vessel Pogranichnik Petrov, trawl 149, 51°40′N, 155°58′E, 351 m, 25 Aug. 2000, coll. A.V. Chetvergov, 1 specimen (ZIN 14229); vessel TINRO, trawl 51, 52°10.26′N, 154°27.42′E – 52°11.10′N, 154°27.24′E, 10 June 2020, 305–304 m, coll. T.B. Morozov, 1 specimen (ZIN 14230); NW Pacific, at southern tip of Kamchatka: vessel Tomi-Maru-53, trawl 195, 50°19′N, 156°51′E, 220–190 m, T 1.7–1.4 °C, 28 Sept. 2000, coll. A.M. Tokranov, 1 specimen (ZIN 14231).

Description. Preserved specimens usually conical or lens-shaped, with concealed oral disc and tentacles, measuring 28–48 mm in diameter and 10–28 mm in height. Preserved holotype 47 mm in diameter, 28 mm in height (Fig. 3B). Pedal disc wide, circular. Column divisible into scapus and thinner-walled capitulum forming collar (Figs 2C, 3B). In most preserved specimens (except two), capitulum and distal scapus invaginated (Fig. 3C). Column surface smooth.

Oral disc and tentacles of freshly collected holotype orange, with scattered red stripes (Fig. 2A). Column also orange, paler proximally; ectoderm abraded in parts, revealing whitish mesogloea beneath (Fig. 2B, C). Oral disc diameter of holotype, when expanded in a seawater container, measuring between half and one-third of pedal disc diameter (Fig. 2B, C). Oral cone low, circular, with irregular mouth (Fig. 2). Tentacles very short, capitate, arranged in radial rows: each exocoel with two tentacles, each endocoel with two to four (usually three) tentacles (Fig. 2A). Tentacles divisible into marginal and discal. Two outer tentacle cycles marginal: alternating exocoelic (outer) and endocoelic (inner). These tentacles largest and lobed, usually with two capitate lobes arranged radially (one behind another). All discal tentacles smaller, usually rounded, with lobes being commonly indistinct or absent. Marginal endocoelic tentacle cycle located between two exocoelic cycles. All discal endocoelic tentacle cycles (first, second, and third) adoral (closer to mouth) to exocoelic discal cycle. Innermost discal (endocoelic) tentacle cycle incomplete. Endocoels (marked by mesenterial insertions) significantly wider than exocoels (due to more tentacles in endocoels extending closer to oral disc centre than exocoelic tentacles).

Mesogloea of pedal disc and column thin, but becoming up to ten times thicker, up to 1.0 mm thick, in contracted distal part of scapus (Fig. 3C). Arrangement of mesenteries is clearly visible on pedal disc of preserved specimens through mesentery insertions (Fig. 3A), and consistent across all specimens examined. Mesenteries at base arranged in five cycles 6+10+16+32+64, but last cycle often incomplete and its mesenteries small and located only near limbus (Figs 3C, 4C). Fourth cycle also restricted to proximal part of column (Fig. 3C). Mesenteries of three older cycles reaching distal part of column: holotype with 32 pairs of mesenteries on oral disc: 6+10+16 (Fig. 2A). Arrangement of mesenteries exhibiting bilateral symmetry due to duplication of mesenterial pairs of second cycle within four primary exocoels: lateral and ventral primary exocoels each containing two pairs of second-cycle mesenteries, whereas each of dorsal primary exocoels containing one pair of second-cycle mesenteries. Mesenteries of first, second, and at least majority of third cycle reaching actinopharynx.

Actinopharynx cylindrical and, in cross-section, featuring very small (shallow) ventral siphonoglyph, supported by a pair of directive mesenteries (Fig. 3D). Actinopharynx with five large bifurcated ridges at insertions of first cycle mesenterial pairs and two ridges on either side of siphonoglyph, corresponding to pair of ventral directives. Ridge corresponding to dorsal pair of directives deeply divided longitudinally into two equal lobes, but no siphonoglyph-like structure observed between these lobes. Ridges corresponding to four lateral pairs of first mesenterial cycle longitudinally divided into unequal lobes, where dorsal lobe larger than ventral. Between these primary ridges located six smaller ridges corresponding to insertions of pairs of second-cycle mesenteries, as well as four very small ridges located in lateral and ventral primary exocoels (one in each sector). These small ridges located at attachment lines of second pair of second-cycle mesenteries in these sectors, positioned dorsally to first pair of second-cycle mesenteries supporting larger ridges.

Mesenteries thin. Strong circumscribed retractors present on mesenteries of first and second cycles and, in two dorsal primary endocoels, on mesenteries of third cycle (Fig. 5B). Retractors usually pinnate in transverse sections, each with long, thin central lamella and typically branching lateral lamellae (Fig. 4D). Retractors on mesenteries of second cycle in ventral and lateral primary exocoels usually smaller than retractors on mesenteries of first cycle and those on mesenteries of second cycle in dorsal primary exocoels, and approximately equal in size to retractors on mesenteries of third cycle in dorsal primary endocoels (Fig. 5B). Mesenteries of third cycle in ventral and lateral primary exocoels sometimes with weak circumscribed retractors. Mesenteries of fourth and

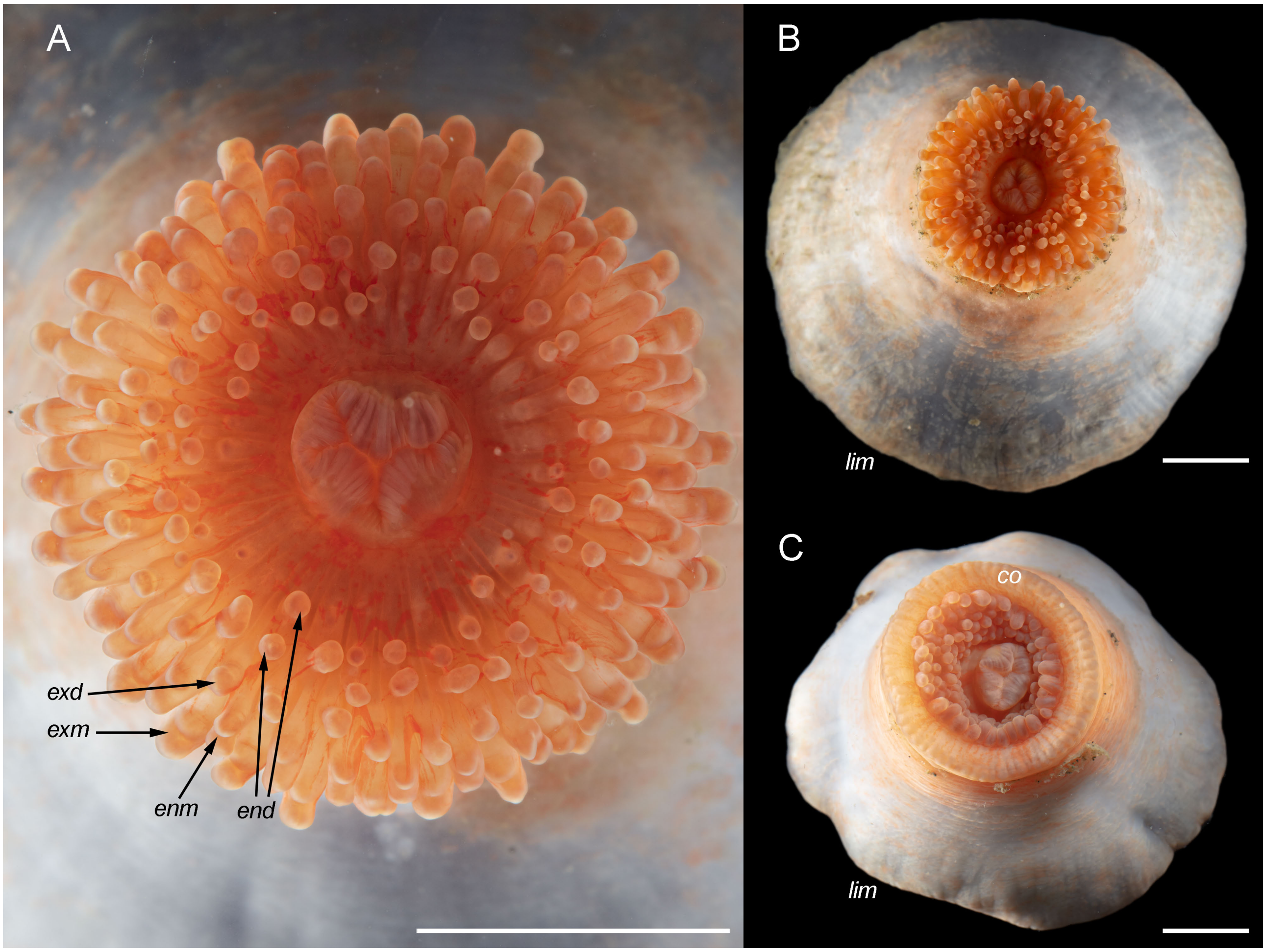

Fig. 2. *Capnea tokranovi* **sp. nov.**, live specimen, holotype. **A**, oral disc with tentacles; **B**, whole specimen with expanded oral disc; **C**, same specimen showing distinct collar. Abbreviations: *co* – collar; *end* – endocelic discal tentacles; *enm* – endocelic marginal tentacle; *exd* – exocoelic discal tentacle; *exm* – exocoelic marginal tentacle; *lim* – limbus. Scale bars: 10 mm (A–C).

fifth cycles without retractors. All mesenteries with characteristic concentrated palmate bundle of parietal muscles on side of retractor, composed of four to six mesogloeal lamellae, reaching 100–120 µm in length (to 50 µm in fifth cycle), three or four of which branched (Fig. 4E). Parieto-basilar muscles well developed along entire length of all mesenteries, and free long flap formed at retractor level in mesenteries of first, second and third cycles (Figs 4D, 5B). Mesenteries of first to third cycle with filaments and gonads; small (to 300 µm) marginal and oral stomata present. Arrangement of six primary mesenterial pairs clearly visible in centre of inner side of pedal disc (Fig. 5C), where couple I forming continuous arc (numbering according to Stephenson, 1928: fig. 35).

Marginal sphincter muscle endodermal, strong, pinnate, 1.5 mm long, 0.9 mm wide in transverse section, with thick central lamella (Figs 3C, 4A). Lateral mesogleal folds of sphincter weakly branched but strongly anastomosing, forming reticulate structure in cross-section. Endodermal circular columnar musculature well developed (Fig. 4A). Basilar muscles well developed (Fig. 4F). Longitudinal muscles of tentacles and radial muscles of oral disc mesogloeal (Fig. 4B).

Smallest paratype (28 mm in diameter, 10 mm in height, ZIN 14226) sterile; remaining paratypes (ZIN 14227–14231) and holotype females with ova up to 700 µm in diameter. Specimen ZIN 14231 contained two immature individuals in gastral cavity, with pedal discs measuring

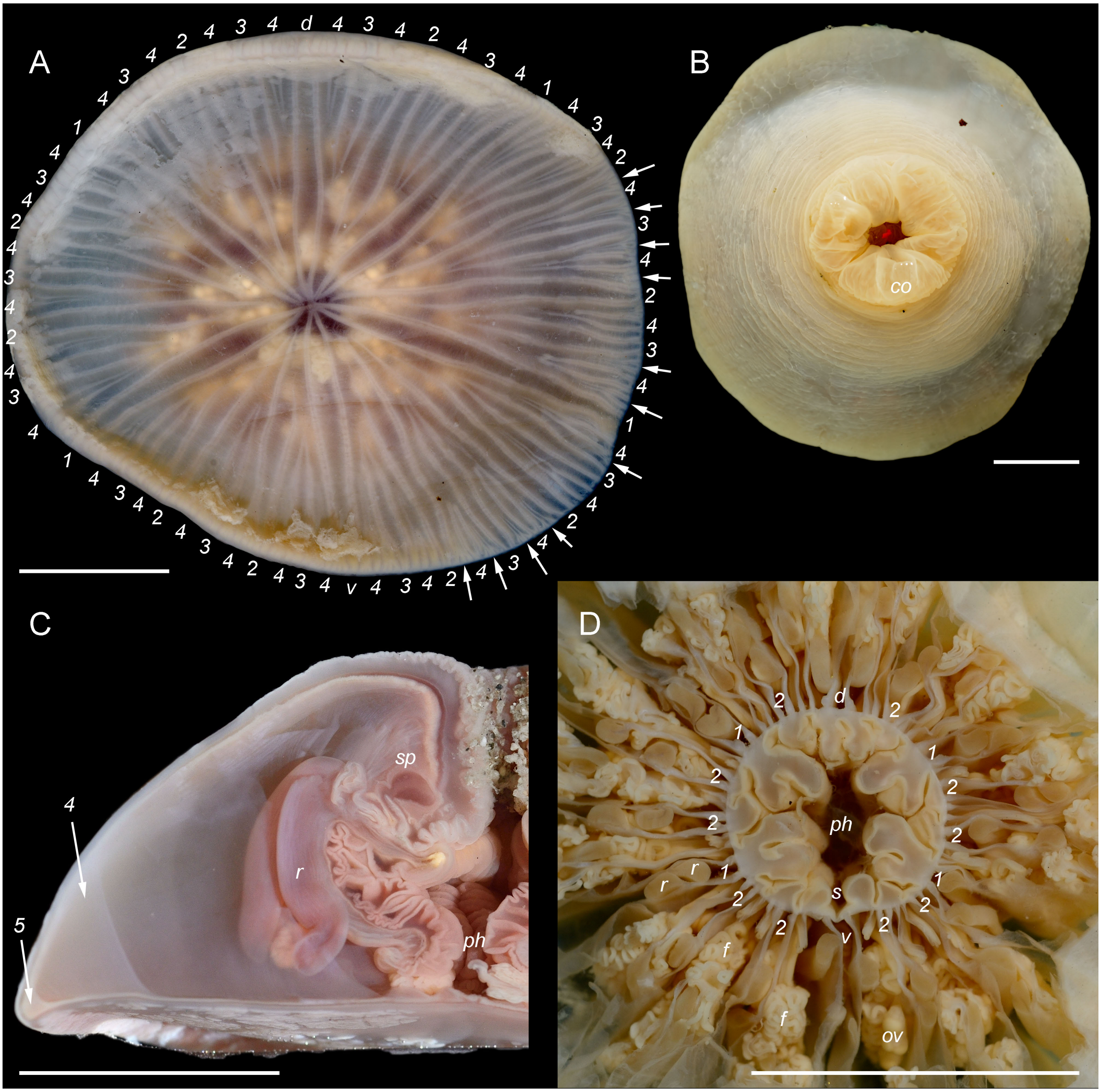

Fig. 3. *Capnea tokranovi* **sp. nov. A**, pedal disc of paratype (ZIN 14229), first four cycles of mesenteric pairs indicated by numerals, while largest pairs of fifth cycle indicated by arrows; **B**, preserved holotype, top view; **C**, longitudinal section through paratype (ZIN 14230), mesenteries of two youngest cycles developing at base indicated by arrows with numbers; **D**, transverse section of paratype (ZIN 14227) at actinopharynx level, with numbering of first two cycles of perfect mesenterial pairs. Abbreviations: *co* – colar; *d* – dorsal pair of directives; *f* – filements; *ov* – ova; *ph* – actinopharynx; *r* – retractor; *s* – siphonoglyph; *sp* – sphincter; *v* – ventral pair of directives. Scale bars: 10 mm (A–D).

20 mm in diameter and heights of 8 mm and 10 mm (Fig. 5D–G). These juveniles exhibited expanded (non-retracted) margins and tentacles, with narrowing in middle of scapus. Their sphincter (Fig. 5A) similar to that of adult specimens (pinnate, with thick central lamella) but smaller, measuring 0.6–0.7 mm in length and 0.2 mm in width in transverse section.

Cnidom composed of gracile spirocysts, basitrichs, *p*-mastigophores A, *p*-mastigophores B1

Table 1. Size ranges (length × width, in microns) and distribution of cnidae of *Capnea tokranovi* **sp. nov.**, based on seven adult specimens and two juveniles (the latter extracted from the gastral cavity of paratype ZIN 14231). "N" represents the ratio of the number of specimens in which each cnida type was found to the total number of specimens examined.

Body region	Cnidae	Size range (µm)	N
Pedal disc	(A) basitrichs (few)	19–28 × 2.5–3.8	6/6
Scapus	(B) basitrichs (common)	21.5–31 × 3–4	8/8
Capitulum and oral disc	(C) spirocysts (numerous)	33.6–48.4 × 2.7–3.8	5/5
	(D) basitrichs (common)	17–25.7 × 2.4–3.5	5/5
	(E) basitrichs (common)	27.5–37.6 × 3.5–4.6	5/5
Tentacles	(F) spirocysts (very numerous)	25–55 × 2.2–5.5	7/7
	(G) basitrichs (few)	16.4–26 × 2–3.7	7/7
	(H) basitrichs (rare)	28–37.7 × 2.8–4.5	7/7
Actinopharynx	(I) basitrichs (numerous)	35–47.5 × 4–7.4	7/7
	(J) *p*-mastigophores A (few)	34.5–43 × 5–8	7/7
Unilobate filaments	(K) basitrichs (common)	11.5–16.4 × 2.3–3.3	9/9
	(L) *p*-mastigophores B1 (few)	15–23.5 × 3.8–6.5	9/9
	(M) *p*-mastigophores A (numerous)	24.4–39.2 × 4.5–8	9/9

(Table 1, Fig. 6). Cnidoglandular tracts of filaments containing only *p*-mastigophores A (Fig. 6M) and drop-shaped *p*-mastigophores B1 (Fig. 6L), while small basitrichs (Fig. 6K) common in endoderm near cnidoglandular tracts. Small drop-shaped *p*-mastigophores B1 (Fig. 6L) often with pointed (non-bifurcated) shaft in unfired capsule. Shaft bearing spiral of five to ten spine whorls. Valve flaps visible in fired capsules. Inverted shafts of *p*-mastigophores A in filaments (Fig. 6M) exhibiting 17–22 spine whorls, while those in actinopharynx (Fig. 6J) with 23–26 whorls. Cnida composition and size in two brooded specimens corresponded to those of mature individuals, although basitrichs far more abundant (very numerous) in pedal disc and scapus of juveniles.

Molecular data. We successfully sequenced two specimens of *Capnea tokranovi* **sp. nov.** from geographically distant locations: the holotype (off eastern Sakhalin) and the paratype (off southeastern Kamchatka; ZIN 14230). All five sequenced markers (12S, 16S, 18S, 28S, and COIII) showed 100% identity between these specimens. Phylogenetic analyses demonstrate that *C. tokranovi* **sp. nov.** is genetically closer to *C. japonica* than to *C. georgiana* (Carlgren, 1927), yet represents a distinct species from both (Fig. 7). The complete tree generated in the present study is available in *Electronic supplementary material 2*, and the pairwise distances are provided in *Electronic supplementary material 1*, Table 3 (see Addenda).

Remarks. The genus *Capnea* includes only four species: *C. sanguinea*, *C. georgiana*, *C. japonica,* and *C. tokranovi* **sp. nov.**

The original description of *Capnea sanguinea* is based on a small specimen collected near the Isle of Man, England (Forbes, 1841). Gosse (1860) erected the family Capneidae for *Capnea* (recognising only one species, *C. sanguinea*, in this genus) and added the genus *Aureliania* Gosse, 1860 to this family, with two species: *A. augusta* Gosse, 1860 and *A. heterocera* (Thompson, 1853). *Aureliania augusta* and *A. heterocera* were subsequently synonymised with *C. sanguinea* (see Fautin, 2016). The geographic range of *C. sanguinea* is rather limited; the species is known from the "south-west of England, the Irish Sea, and western Ireland", as well as from "northern France, Biscay, and the Mediterranean" (Manuel, 1988: 119). It is important to note that the Mediterranean records were based only on a specimen described by Andres (1883) as *A. regalis*

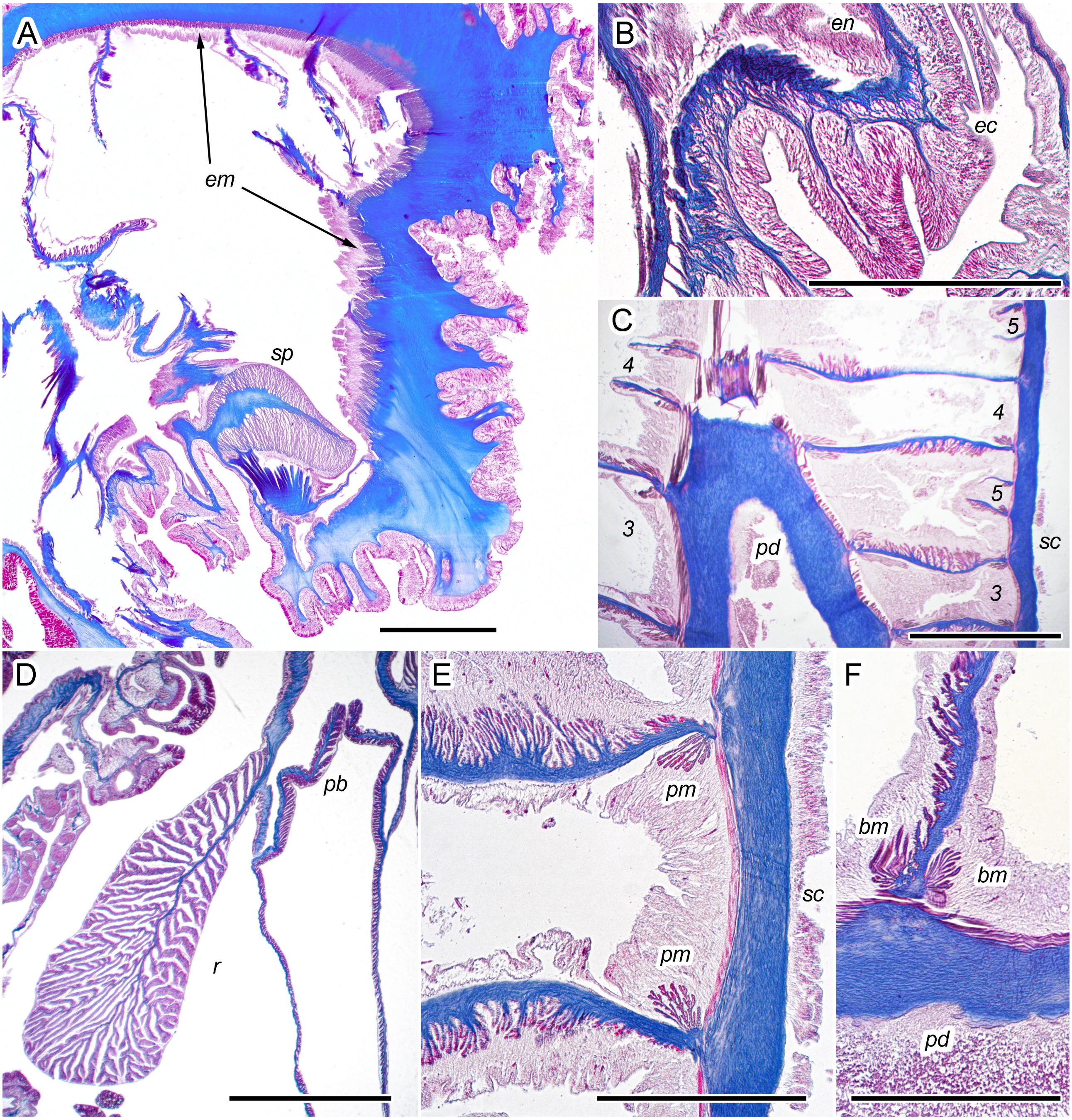

Fig. 4. *Capnea tokranovi* **sp. nov.**, histological sections of paratype (ZIN 14230). **A**, longitudinal section through distal column; **B**, radial muscles of oral disc; **C**, section through proximal column and pedal disc near limbus; **D**, transverse section through retractor of dorsal directive mesentery; **E**, transverse section through parietal portion first-cycle mesenterial pair; **F**, basilar muscles of directive mesentery. Cycle number of mesenterial pairs indicated by numerals. Abbreviations: *bm* – basilar muscles; *ec* – ectoderm; *em* – endodermal circular columnar muscles; *en* – endoderm; *pb* – parietobasilar muscle flap; *pd* – pedal disc; *pm* – parietal muscles; *r* – retractor; *sc* – scapus; *sp* – sphincter. Scale bars: 1.0 mm (A, C, D); 0.5 mm (B, E, F).

Andres, 1883 from Naples and redescribed by Carlgren (1900); its synonymy with *C. sanguinea* requires confirmation.

The arrangement of the tentacles in *C. sanguinea* is very stable and distinct from that of *C. tokranovi* **sp. nov.**: it always has two tentacles associated with each endo- and exocoel, whereas *C. tokranovi* **sp. nov.** has up to four tentacles in each endocoel. The shape of the tentacles also differs: in *C. tokranovi* **sp. nov.**, the tentacles are less lobulated and generally slenderer than in *C. sanguinea*. Furthermore, while the endocoels and exocoels in *C. sanguinea* (as delineated by mesenterial insertions on the oral disc) are approximately equal in width, in *C. tokranovi* **sp. nov.** the endocoels are several times as wide as the exocoels. This disparity in width results from both the greater number of tentacles within the endocoels of *C. tokranovi* **sp. nov.** and their extended spread towards the mouth.

Capnea georgiana (including its synonym *Aureliania tricirrata* Carlgren et Stephenson, 1929) is known only from Antarctic waters. It was redescribed by Dunn (1983) and Rodríguez & López-González (2013). This species has two to four (or more than four, according to Rodríguez & López-González, 2013) tentacles associated with each endocoel, a character shared with *C. tokranovi* **sp. nov.** However, the two species differ molecularly and occur in geographically distant regions (the Antarctic and the North Pacific), making conspecificity highly unlikely. Rodríguez & López-González (2013) report that in the Antarctic species, the first four mesenterial cycles are perfect and fertile, whereas in *C. tokranovi* **sp. nov.**, only the first three cycles may be fertile and may extend to the actinopharynx. Dunn (1983) described up to four mesenterial cycles, with all but the last being fertile, and all or all but the very last being perfect.

Capnea japonica is known from two records from Japan: Carlgren (1940) described two specimens from off Misaki, Sagami Bay, and Yanagi & Izumi (2021) provided a detailed redescription based on one specimen from near the type locality, as well as the type specimens. Unlike *C. tokranovi* **sp. nov.**, *C. japonica* has only two tentacles per endocoel, a character it shares with the European *C. sanguinea*. The parietal portion of the mesenterial longitudinal musculature appears diffuse in *C. japonica* (Yanagi & Izumi, 2021: fig. 4A), whereas in *C. tokranovi* **sp. nov.** it is more pronounced, concentrated, circumscribed, and palmate. Molecular data confirm that, although *C. japonica* and *C. tokranovi* **sp. nov.** are related, they are distinct species.

The mesenterial arrangement has not been described for these three species. However, based on other morphological evidence (e.g., the number of marginal tentacles), they likely share the same mesenterial organisation as *C. tokranovi* **sp. nov.**, with 6+10+16+... mesenterial pairs.

Another species formally assigned to this genus is *Capnea indica* (Verrill, 1869), originally described as *Stephanactis indica* Verrill, 1869 and subsequently transferred to *Aureliania* (a junior subjective synonym of *Capnea*) by Carlgren (1949). Morphologically, the single known specimen of *S. indica* more closely resembles *Actinoporus* Duchassaing, 1850 than *Capnea*: its base is narrower than the column, the oral disc is wider than the column, and the oral disc (with the tentacles) appears non-contractible. The specimen is small (approximately 15 mm in height and 10 mm in diameter) and possesses 40 radial rows of five or six tentacles (Verrill, 1869). The column was described as smooth. Notably, *Actinoporus elongatus* Carlgren, 1900 was also initially described as having a smooth column (Carlgren, 1900), though subsequent authors reported “up to 4 verrucae per endocoelic row and 1–2 per exocoelic row” (Fautin et al., 2015: 52).

The characters of the preserved specimen of *Stephanactis indica*, particularly its narrower base and wider oral disc, contradict the established observation that, in genera possessing more mesenterial cycles at the base than at the margin (such as *Capnea*), fixed specimens typically exhibit a wider base. We consider the assignment of *S. indica* to *Capnea* to be unsubstantiated and hereby transfer it to *Actinoporus*. Moreover, it is highly likely that *S. indica* may be a juvenile specimen of the widely distributed Indo-Pacific species *Actinoporus elongatus*. If this is confirmed, the name *Actinoporus indicus* (Verrill, 1869) **comb. nov.** would become a senior subjective synonym of *A. elongatus*.

Etymology. The species is named in honour of our colleague, Dr Alexey M. Tokranov, head of the laboratory where the first two authors (N. and K. Sanamyan) conduct their research. Dr Tokranov has made significant contributions to the study of marine biodiversity, collected many interesting species of sea anemones—including one of the specimens described in this study—and fostered

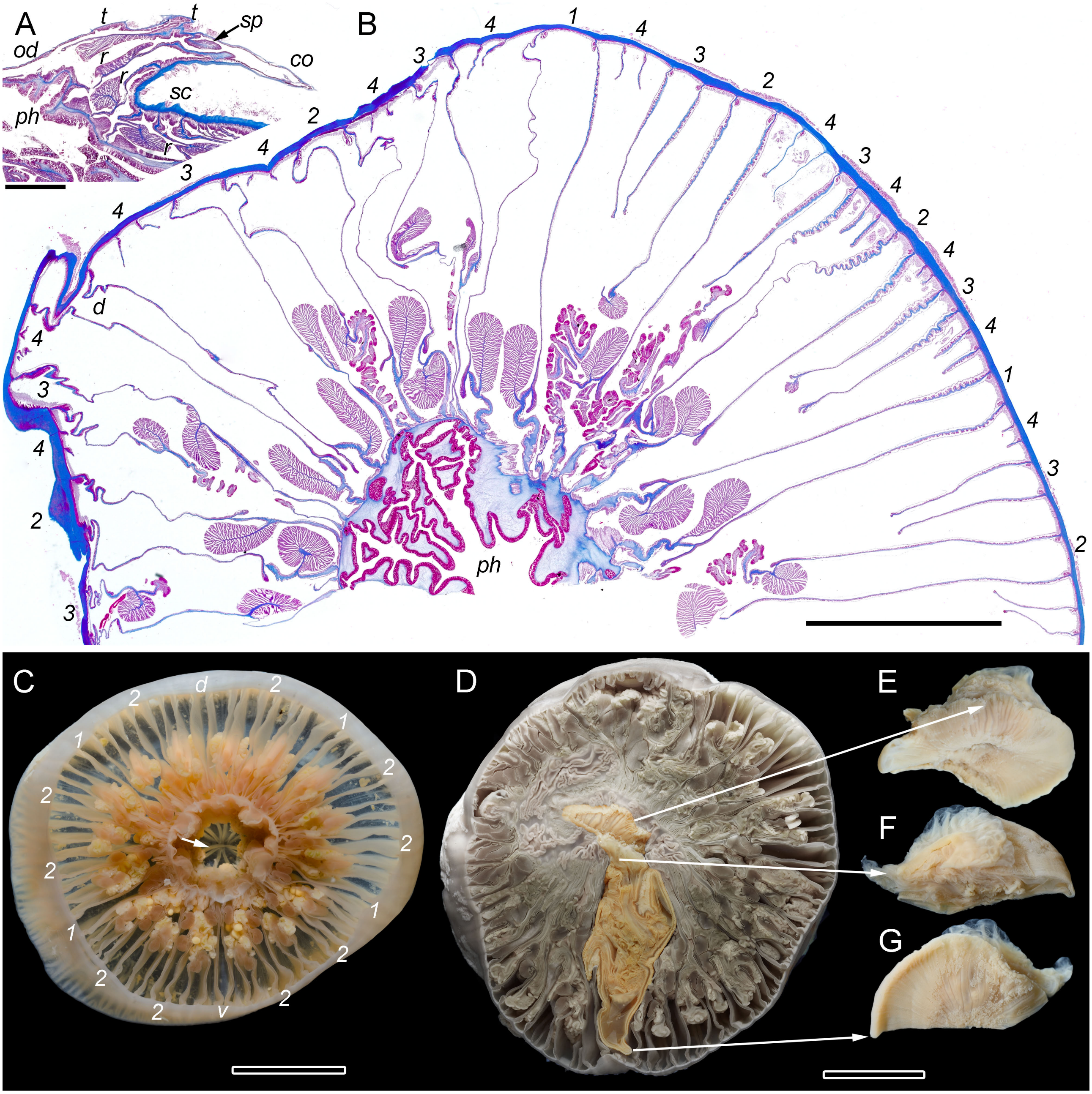

Fig. 5. *Capnea tokranovi* **sp. nov. A**, longitudinal section of distal portion of column of juvenile specimen extracted from gastral cavity of paratype (ZIN 14231); **B**, transverse section through column at actinopharynx level (paratype ZIN 14230); **C**, transverse section of paratype (ZIN 14229), couple I on inner side of pedal disc indicated by arrow; **D**, transverse section of paratype (ZIN 14231), with two juvenile specimens in gastral cavity highlighted in colour (indicated by arrows in right plane); **E–G**, two juvenile specimens extracted from gastral cavity of paratype (ZIN 14231). Cycle number of mesenterial pairs indicated by numerals. Abbreviations: *co* – collar; *d* – dorsal directive pair; *od* – oral disc; *ph* – actinopharynx; *r* – retractor; *sc* – scapus; *sp* – sphincter; *t* – tentacle; *v* – ventral directive pair. Scale bars: 1.0 mm (A); 5.0 mm (B); 10 mm (C–G).

a positive and supportive working environment, enabling us to focus entirely on our scientific research without restrictions on topic selection or unnecessary administrative burdens.

Distribution. *Capnea tokranovi* **sp. nov.** is known from the western and eastern regions of the Sea of Okhotsk, as well as from the southern tip of Kamchatka (Fig. 1). The species is rare; only

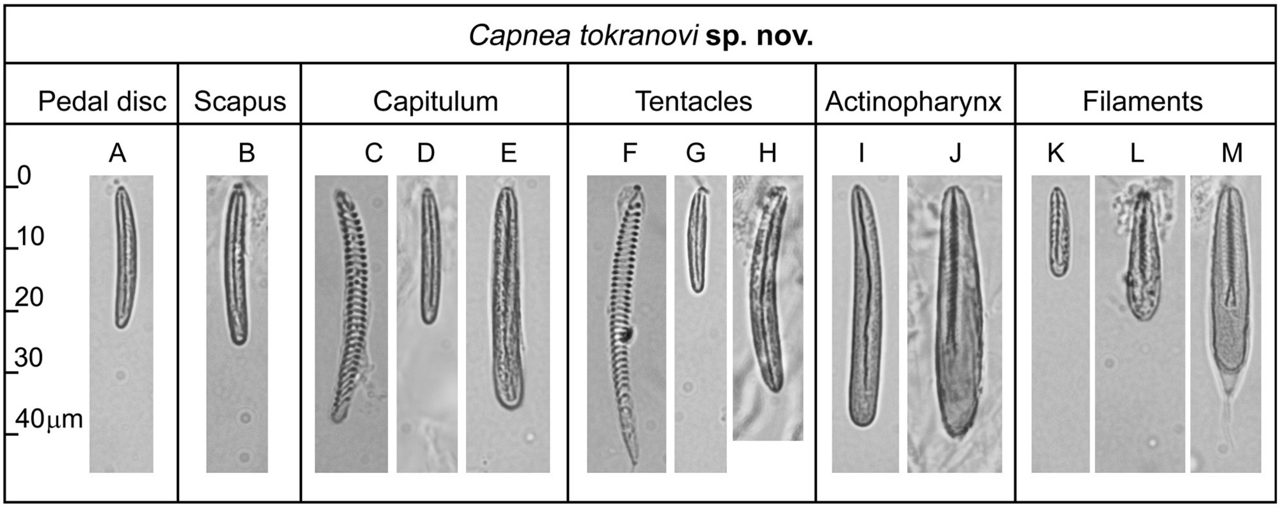

Fig. 6. *Capnea tokranovi* **sp. nov.** Cnidom (see Table 1 for size ranges).

seven specimens were collected during seven separate expeditions over an extended period (from 1998 to 2024).

Habitat. Unattached on sandy or soft muddy substrates, this species is currently known only from a relatively narrow depth range of 150–351 m. It occurs in regions where the bottom water temperature is very low, ranging from –0.35 to 1.7 °C, according to the data provided by the collectors.

Discussion

Taxonomic position of Capneidae. Carlgren (1949) considered the family Aurelianidae (a junior subjective synonym of Capneidae) to be related to a group of predominantly tropical sea anemone families possessing an endodermal marginal sphincter muscle ("Endomyaria") and characterised by the presence of more than one tentacle associated with each endocoel (Homostichanthidae, Stichodactylidae, Thalassianthidae; see Carlgren, 1949). However, in all previously published molecular analyses, and in our analysis presented here (Fig. 7), *Capnea* has been resolved within a clade containing the genera of Actinostolidae (*Actinostola* Verrill, 1883, *Stomphia* Gosse, 1859) and the genera formerly classified under Actinostolidae but now assigned to separate families: Anthosactinidae (*Anthosactis* Danielssen, 1890, *Hormosoma* Stephenson, 1918, *Tealidium* Hertwig, 1882) and Sicyonidae (*Sicyonis* Hertwig, 1882, *Ophiodiscus* Hertwig, 1882) (Gusmão et al., 2019; Gusmão & Rodríguez, 2021; Sanamyan et al., 2021; Yanagi & Izumi, 2021).

All these genera possess a strong mesogleal sphincter muscle (not separated from the circular endodermal muscles of the column) and only one tentacle associated with each endo- and exocoel—characters considered highly significant in the traditional classification of sea anemones by Carlgren (1949). Therefore, the phylogenetic position of *Capnea* among these genera, with its well-developed endodermal sphincter and several tentacles per endocoel, appears unexpected and intriguing, and still awaits morphological explanation (Yanagi & Izumi, 2021).

Yanagi & Izumi (2021) compared the unequally developed mesenteries in their specimen of *C. japonica* with the "Actinostola rule" characteristic of the Actinostolidae. However, in the provided illustrations (Yanagi & Izumi, 2021: fig. 4A, B), the mesenteries of the youngest cycle are of equal length, thus not conforming to the "Actinostola rule", which specifically describes the arrangement of mesenteries in the youngest cycles. Izumi et al. (2025) later concluded that this was a mistake caused by poor specimen condition. We found no evidence of this rule in our specimens. Therefore, the "Actinostola rule" cannot be used to support the relationship between *Capnea* and actinostolid genera.

Unequal mesentery development frequently occurs in the older cycles (second and third) in Anthosactinidae and Sicyonidae (Carlgren, 1921; Doumenc, 1975; Sanamyan et al., 2021). In *C. tokranovi* **sp. nov.**, the mesenterial pairs of the second and third cycles sometimes show somewhat unequal development in the lateral and ventral primary exocoels (Fig. 5A). The bilateral mesentery arrangement in *C. tokranovi* **sp. nov.**, formed by duplication of second-cycle pairs in the lateral and ventral primary endocoels, may suggest phylogenetic relationships with Actinostolidae and Sicyonidae. Similar duplications occur in *Stomphia* (in all or in four primary exocoels; Carlgren, 1921, 1949; Manuel, 1988) and Sicyonidae (Carlgren, 1921; Doumenc, 1975; Sanamyan et al., 2021).

Members of Sicyonidae exhibit well-developed parietal portions of the longitudinal mesenterial muscles on the retractor side (Sanamyan et al., 2021), resembling those in *C. tokranovi* **sp. nov.**, although less developed. This musculature pattern also characterises *Condylanthus magellanicus* Carlgren, 1899, Condylanthidae (see Garese et al., 2025: fig. 4e).

The endo-mesogleal nature of the sphincter muscle in Actinostolidae, Anthosactinidae, Sicyonidae, Exocoelactinidae, and Tetracoelactinidae aligns these families more closely with sea anemones that possess endodermal sphincters (Sanamyan et al., 2021). Consequently, the presence of sea anemones with endodermal sphincters (*Capnea* and *Condylanthus*) within this group is less surprising than initially presumed.

Related genera: *Chitinactis* and *Discoactis*. In our molecular analyses using both Maximum Likelihood (ML) and Bayesian Inference (BI) methods, the three *Capnea* species formed a strongly supported clade (100% bootstrap support in ML, 1.00 posterior probability in BI; Fig. 7) with two monotypic genera: *Chitinactis* Gusmão et Rodríguez, 2021 (originally classified within Actinostolidae) and *Discoactis* Izumi et al., 2025 (the sole member of Discoactinidae).

These taxa share a distinctive retractor morphology—strongly circumscribed pinnate retractors that are often connected to the mesentery by a thin lamella. Such retractors are uncommon among non-burrowing species of Actiniaria, but they also occur in *Condylanthus* Carlgren, 1899 and *Segonzactis* Riemann-Zürneck, 1979 (Condylanthidae). Although *Condylanthus* and *Segonzactis* remain unsequenced to date, their morphological characters (discussed below) strongly suggest close relationships to *Chitinactis* and *Discoactis*, respectively, and these four genera should be classified within a single family—Condylanthidae.

Condylanthus magellanicus Carlgren, 1899 (the type species of *Condylanthus*) was recently redescribed in detail by Garese et al. (2024). *Condylanthus magellanicus* and *Chitinactis marmara* Gusmão et Rodríguez, 2021 exhibit remarkable similarities in both general morphology—including a broad base, the presence of a cuticle, and the number of tentacles—and anatomical characters, notably the greater number of mesenteries at the base compared to the margin, and particularly their distinctive retractor morphology (compare Gusmão & Rodríguez, 2021: fig. 4P with Garese et al., 2025: fig. 4b).

Formally, these species differ in two reported characters: (1) gonad position (third-cycle mesenteries in *Chitinactis vs.* first-cycle in *Condylanthus*), and (2) sphincter muscle (described as a strong mesogleal in *Chitinactis vs.* a weak, diffuse endodermal in *Condylanthus*). However, the photograph of the longitudinal section through the column of *C. marmara* (see Gusmão & Rodríguez, 2021: fig. 4G) shows thickened mesoglea with a spongy texture containing scattered small voids, but no visible embedded musculature. Similar "holes" are more or less evident in the columnar mesoglea of *C. magellanicus* (see Garese et al., 2025: fig. 4a). We interpret this structure as inconsistent with a true mesogleal sphincter. Conversely, the well-developed circular endodermal musculature with prominent muscle processes in the distal column suggests the potential presence of a diffuse endodermal sphincter, as documented in *Condylanthus*. Similarly, while gametogenic tissue in *Chitinactis* is reported in third-cycle mesenteries, the illustration (Gusmão & Rodríguez, 2021: fig. 4L) ambiguously depicts gonad position. Our interpretation suggests these may actually represent gonads protruding from first-cycle mesenteries, an interpretation supported by their numerical correspondence to first-cycle mesenterial counts.

Thus, we conclude that the genus *Chitinactis* may be congeneric with *Condylanthus*; however, in the present article, we refrain from synonymising them pending clarification of the morphological details of *C. marmara* discussed above. Nevertheless, we have no doubt that it should be assigned to Condylanthidae rather than to Actinostolidae, and we hereby reassign it to this family.

Discoactis resembles *Capnea* in several characters, including its broad pedal disc, the significantly greater number of mesenteries at the base compared to the distal column, and, notably, very strong pinnate-circumscribed retractors. However, these genera differ in the structure of the sphincter muscle and the arrangement of the mesenteries and tentacles. These differences were discussed by Izumi et al. (2025).

Morphologically, *Discoactis* exhibits a striking similarity to *Segonzactis*. Both genera share a characteristic wide, non-contractile, and non-adhesive base adapted for an unattached existence on soft substrates (compare Riemann-Zürneck, 1979: fig. 4 with Izumi et al., 2025: fig. 2). They possess a small number of tentacles (eight to ten in *Segonzactis* and 14–18 in Discoactis), with longitudinal muscles distinctly better developed on one side (compare Riemann-Zürneck, 1979: figs 5, 6 with Izumi et al., 2025: fig. 3E), a similar distribution of mesenteries (significantly more numerous at the base), and comparable mesenterial musculature, including notably similar morphology of pinnate-circumscribed retractors.

In *Segonzactis*, the column is subdivided into the scapus and scapulus. In the diagnosis of *Discoactis*, the authors state that it has a capitulum (rather than a scapulus); however, in the species description, they refer to a scapulus. *Segonzactis* has a very weak, diffuse endodermal sphincter, whereas *Discoactis* is described as having a very weak mesogleal sphincter. The illustration intended to depict this (Izumi et al., 2025: fig. 3A) is difficult to interpret: although the mesogleal sphincter is listed in the figure abbreviations, it is not marked on the figure itself and is unidentifiable. In any case, distinguishing between a weak, diffuse endodermal sphincter and a very weak mesogleal sphincter is subjective and depends on whether a few muscle fibres (or traces thereof) in the mesoglea are interpreted as a mesogleal sphincter, or whether a slight concentration of circular muscles in the distal column is regarded as a weak, diffuse endodermal sphincter muscle.

The only significant difference between *Segonzactis* and *Discoactis* is that, in *Segonzactis*, the first cycle comprises eight macrocnemes and four microcnemes paired with dorsolateral and ventrolateral macrocnemes (an *Edwardsia*-like configuration), whereas in *Discoactis*, this cycle consists of ten macrocnemes and two microcnemes paired with ventrolateral macrocnemes, which were misinterpreted as dorsolateral in the original description. As illustrated by Izumi et al. (2025: fig. 3C), only the right half of the cross-section reveals traces of a very weak siphonoglyph, supported by a pair of ventral directives. Adjacent to these are the microcnemes belonging to the sixth protomesenterial couple, following Stephenson (1928: fig. 35). In *Segonzactis*, only eight macrocnemes of the first cycle reach the oral disc, whereas in *Discoactis*, two mesenterial cycles (6 + 6 = 12 pairs) extend to this level. The absence of endocoelic tentacles in the second mesenterial cycle in *Discoactis* cannot be compared with *Segonzactis*, as the latter has fewer tentacles. We consider these differences insufficient to justify separating *Discoactis* and *Segonzactis* at the family level and therefore classify *Discoactis* within Condylanthidae.

Distinctness of Condylanthidae. The striking similarities between *Capnea* and the aforementioned genera of Condylanthidae (*Condylanthus*, *Chitinactis*, *Segonzactis*, and *Discoactis*) raise the question of whether Condylanthidae should be retained as a separate family or treated as confamilial with Capneidae. *Capnea* differs from all these genera in having multiple tentacles per exo- and endocoel. However, as demonstrated by numerous phylogenetic analyses, the radial arrangement of tentacles (with multiple tentacles per endo- and exocoel) appears to be less taxonomically significant than traditionally believed. For example, *Bolocera* Gosse, 1860 (with tentacles arranged in circles) and *Liponema* Hertwig, 1882 (with tentacles in radial rows), although formally placed in different families, are phylogenetically and morphologically more closely related to each other than *Bolocera* is to other actiniid genera (*Electronic supplementary material 2*; see Addenda). Nevertheless, the radial arrangement of tentacles remains recognised as a family-level character. Thus, we refrain in this work from formally proposing synonymy between Condylanthidae and

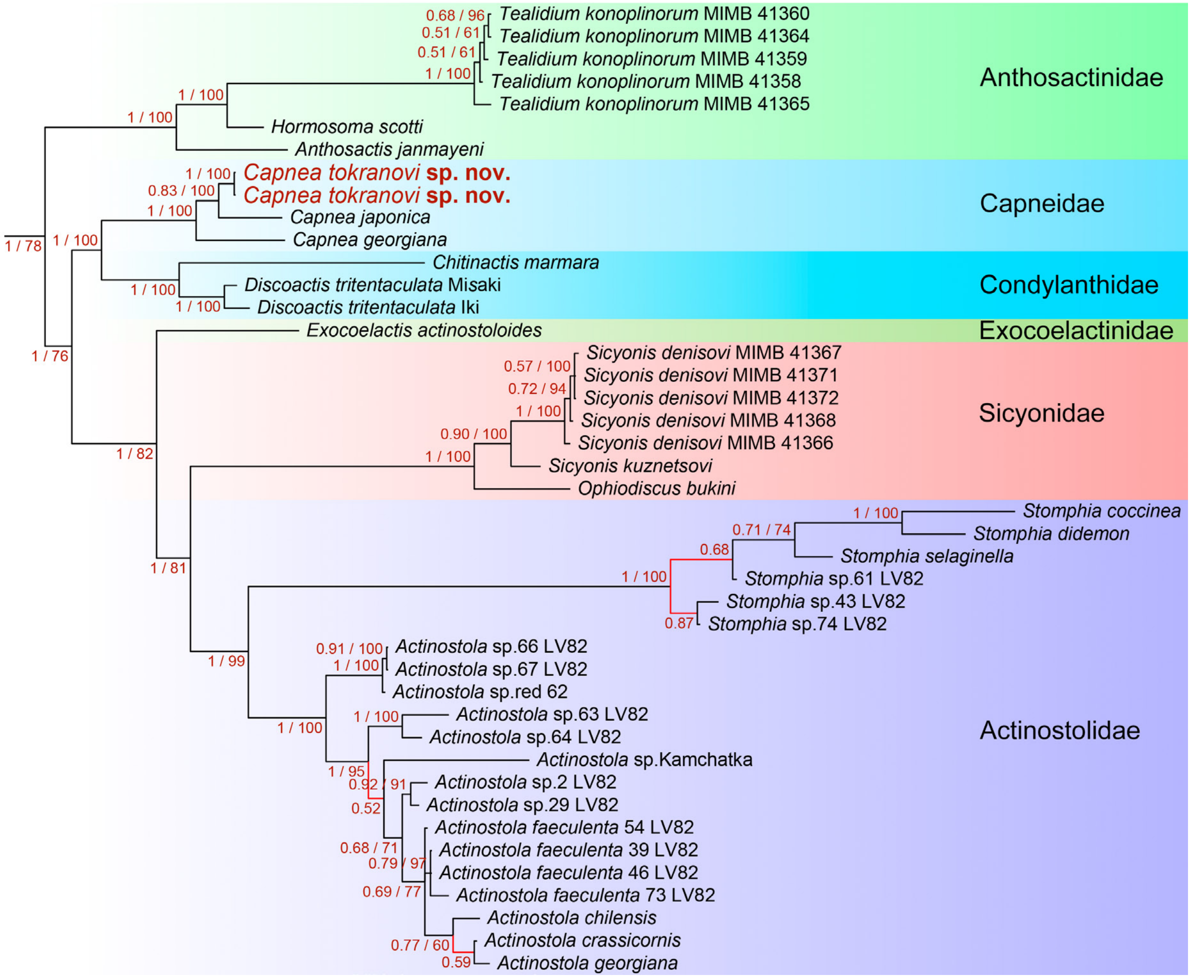

Fig. 7. Phylogenetic relationships based on a concatenated dataset of 12S, 16S, 18S, 28S, and COIII genes, inferred using Bayesian inference (BI). Numbers at the branches indicate BI posterior probabilities and ML bootstrap values (format: BI/ML). Branches with conflicting topologies between BI and ML analyses are shown in red. Only a subtree containing relevant taxa is displayed. For the full tree, see *Electronic supplementary material 2*.

Capneidae. It is noteworthy, however, that Riemann-Zürneck (1979: 236) documented one (unfortunately poorly preserved) specimen of *Segonzactis platypus* Riemann-Zürneck, 1979 with two tentacles in each endocoel of the directives, an observation demonstrating that this character (multiple tentacles per exo-/endocoel) carries less taxonomic weight than previously assumed, at least within this group of genera.

Four other monotypic genera are currently assigned to the Condylanthidae. Among these, *Charisea* Torrey, 1902 is misclassified within this family; it appears to be phylogenetically closer to *Metridium* de Blainville, 1830 and other acontiate anemones (*Electronic supplementary material 2*; see Addenda). In contrast, *Cadetactis* Fautin, 2016, *Riactis* Fautin, 2016, and *Pseudhormathia* Carlgren, 1943 are too poorly known to assess their affinities.

Phylogenetic positions of several other taxa in our analyses. Sicyonidae. The positions of Actinostolidae, Exocoelactinidae, Anthosactinidae, and the Capneidae + Condylanthidae clade are very stable in phylogenetic reconstructions, consistently resembling the topology shown in Fig. 7. In contrast, the Sicyonidae clade (represented by three species with seven concatenated sequences) demonstrates an unstable position across studies. Sanamyan et al. (2021) recovered it as sister to Exocoelactinidae + Actinostolidae, while our current analysis places it as sister to Actinostolidae. However, it is sometimes recovered in a completely different position, for example as sister to actiniid sea anemones (Durán-Fuentes et al., 2024). To evaluate this discrepancy, we conducted multiple sequential ML and BI analyses using identical and slightly varied alignments and parameters. These replicated analyses occasionally recovered Sicyonidae as either nested within or sister to actiniid anemones (as shown by Durán-Fuentes et al., 2024), albeit with consistently low support values (BI ca. 0.5–0.7). Whether this reflects true evolutionary relationships or artefacts arising from problematic sequences remains unclear. Incorrect sequences do occur in datasets used for phylogenetic analyses of sea anemones (see comments on several specific cases under Table 2 in *Electronic supplementary material 1*).

Halcampulactis solimar Gusmão et al., 2019. The position of *Halcampulactis* Gusmão et al., 2019 is also unstable in phylogenetic reconstructions. In the phylogenetic analysis presented by Gusmão et al. (2019: fig. 6), this species appears between *Capnea* and Actinostolidae (represented by *Stomphia* and *Actinostola*). Sanamyan et al. (2021: fig. 38) recovered it within a strongly supported clade with *Capnea* (97% ML bootstrap / 0.99 BI posterior probability). Our current analysis places *H. solimar* alongside *Halcampoides* Danielssen, 1890 and *Scytophorus* Hertwig, 1882, distant from the *Capnea* clade, a result consistent with the phylogeny shown by Gusmão & Rodríguez (2021: fig. 2). In the phylogenetic reconstruction published by these authors, the clade formed by *Halcampoides*, *Scytophorus*, and *Halcampulactis* is sister to: (1) a clade comprising former actinostolid genera (Actinostoloidea), and (2) a clade uniting Metridioidea and Actinioidea. Thus, this group is nested between Anenthemonae and Enthemonae but does not belong to Actinostoloidea (contrary to the authors' indication; yellow box in Gusmão & Rodríguez, 2021: fig. 2). In our analysis, the *Halcampoides* + *Scytophorus* + *Halcampulactis* clade is resolved with strong support among anemones assigned by Gusmão & Rodríguez (2021) to Enthemonae, as a sister group to the families of Metridioidea (*Electronic supplementary material 2*; also see comments on the incorrect 18S sequence of *Scytophorus* under Table 2 in *Electronic supplementary material 1*; see Addenda).

Since *Halcampoides*, *Scytophorus* and *Halcampulactis* form a well-supported clade, the taxonomic status of Halcampulactinidae (which contains only *H. solimar*) requires reevaluation—specifically, whether to maintain this family or to transfer *H. solimar* to Halcampoididae. Morphologically, these genera are similar, although *Halcampulactis* differs in having eight macrocnemes and four microcnemes, compared to the twelve macrocnemes found in *Halcampoides*. The taxonomic significance of this difference remains unclear, particularly as similar variation occurs in other families, for example, Haloclavidae. In any case, Halcampulactinidae is closely related to Halcampoididae.

Haloclavidae. In our molecular analyses using both ML and BI methods, *Haloclava* Verrill, 1899 [including *Haloclava* sp. and *H. producta* (Stimpson, 1856)], *Anemonactis* Andres, 1881, *Antennapeachia* Izumi et al., 2016, *Metapeachia* Carlgren, 1943, *Peachia* Gosse, 1855, and *Synpeachia* Yap et al., 2014, formed a well-supported clade (97% ML bootstrap / 1.00 BI posterior probability). This finding directly contradicts the results of Hamilton et al. (2022), who recovered *Antennapeachia*, *Peachia*, *Synpeachia*, and *Metapeachia* in a distinct clade separate from *Anemonactis* and *Haloclava* sp., prompting them to establish the family Peachiidae for these genera. Notably, Hamilton et al. (2022) also found *H. producta* to be phylogenetically distant from its congener *Haloclava* sp. We attribute these discrepancies to problematic sequences in certain specimens, notably the incorrectly assigned *Drosophila* sequence (AF254370) used as 18S rRNA data for *H. producta* (see comments under Table 2 in *Electronic supplementary material 1*). Our results do not support recognising Peachiidae as a separate family. In any case, both family names erected by Hamilton et al. (2022), Peachiidae Hamilton et al., 2022 and Harenactidae Hamilton et al., 2022, are unavailable, as they were published in an online-only journal without prior registration in ZooBank (ICZN, 2012: Art. 8.5.3).

Addenda

Electronic supplementary material 1. A list of taxa and sequences used for phylogenetic analysis, pairwise distances and phylogenetic tree. Tables 2 and 3. File format: PDF.

Electronic supplementary material 2. **Fig. 8.** Phylogenetic relationships inferred from a concatenated dataset (12S, 16S, 18S, 28S, and COIII) using Bayesian inference (BI). Numbers on the branches indicate BI posterior probabilities and ML bootstrap values (format: BI/ML). Branches with conflicting topologies between BI and ML analyses are shown in red. File format: JPEG.

All these materials are available from: https://doi.org/10.31610/zsr/2026.35.1.3

Acknowledgements

The authors gratefully acknowledge Pavel S. Vasiliev, Boris A. Sheiko, Aleksey M. Tokranov, and Aleksandr V. Chetvergov for their initiative in collecting the study material. We are grateful to the Faculty of Geography at M.V. Lomonosov Moscow State University and JSC "IESPA" for organising the research cruise. We thank the crew and expeditionary staff of the research vessel Professor Multanovsky, especially Dmitry V. Bokhanov and Alexey I. Starkov, for their assistance in collecting the material. The molecular component of this study was supported by funding under the state assignment to the A.V. Zhirmunskiy National Scientific Centre of Marine Biology, FEB RAS, focusing on the theme "Molecular biology, biochemistry and immunology of marine organisms" (No. 124021900010-2). This research was partially funded under the state assignment to the Kamchatka Branch of the Pacific Geographical Institute, FEB RAS, focusing on the theme "Structural and functional organisation, dynamics and productivity of terrestrial and coastal ecosystems in the Far East of Russia. Development of scientific foundations and economic tools for sustainable natural resources management" (No. 124012700496-4).

References

Andres A. 1883. Le Attinie. *Atti della Reale accademia dei Lincei. Serie terza*, **14**: 211–673.

Carlgren O. 1900. Zur Kenntnis der stichodactylinen Actiniarien. *Öfversigt af Kongliga Vetenskaps-Akademiens f*örhandlingar, **2**: 277–287.

Carlgren O. 1921. Actiniaria Part I. *Danish Ingolf-Expedition*, **5**(9): 1–241. Copenhagen: Bianco Luno.

Carlgren O. 1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa. *Kungliga fysiografiska sällskapets handlingar*, **51**: 1–62.

Carlgren O. 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. *Kungliga Svenska Vetenskapsakademiens handlingar*, **1**: 1–121.

Doumenc D.A. 1975. Actinies bathyales et abyssales de l'océan Atlantique nord familles des Hormathiidae (genres Paracalliactis et Phelliactis) et des Actinostolidae (genres Actinoscyphia et Sicyonis). *Bulletin du Muséum national d'histoire naturelle (Paris)*, **197**: 157–204. https://doi.org/10.5962/p.279151

Dunn D.F. 1983. Some Antarctic and sub-Antarctic sea anemones (Coelenterata: Ptychodactiaria and Actiniaria). *Antarctic research Series*, **39**: 1–67. https://doi.org/10.1029/AR039p0001

Durán-Fuentes J.A., González-Muñoz R., Daly M. & Stampar S.N. 2024. Antholoba fabiani sp. nov. (Actiniaria, Metridioidea, Antholobidae fam. nov.), a new species and family of sea anemone of the southwestern Atlantic, Brazil. *Marine Biodiversity*, **54**(40): 1–17. https://doi.org/10.1007/s12526-024-01433-9

Fautin D.G. 2016. Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). *Zootaxa*, **4145**(1): 1–449. https://doi.org/10.11646/zootaxa.4145.1.1

Fautin D.G., Tan R., Yap N.W.L., Tan S.H, Crowther A., Goodwill R., Sanpanich K. & Tay Y.C. 2015. Sea anemones (Cnidaria: Actiniaria) of Singapore: shallow-water species known also from the Indian subcontinent. *Raffles Bulletin of Zoology*, **31**: 44–59.

Forbes E. 1841. Contributions to British actinology. I. On Kapnea, a new helianthoid polype. *Annals and Magazine of natural History*, **7**: 81–85. https://doi.org/10.1080/03745484109442669

Garese A., Durán-Fuentes J., Martin J.P., González-Muñoz R. & Acuña F.H. 2025. Redescription of the poorly known sea anemone Condylanthus magellanicus Carlgren 1899 on the Argentine Patagonian coast. *Polar Biology*, **48**(30): 1–9. https://doi.org/10.1007/s00300-025-03350-4

Gosse P.H. 1860. *A history of the British sea-anemones and corals*. London: Van Voorst. 362 p. https://doi.org/10.5962/bhl.title.3997

Gusmão L.C., Berniker L., Van Deusen V., Harris O. & Rodríguez E. 2019. Halcampulactidae (Actiniaria, Actinostoloidea), a new family of burrowing sea anemones with external brooding from Antarctica. *Polar Biology*, **42**(7): 1271–1286. https://doi.org/10.1007/s00300-019-02516-1

Gusmão L.C. & Rodríguez E. 2021. Two sea anemones (Cnidaria: Anthozoa: Actiniaria) from the Southern Ocean with evidence of a deep-sea, polar lineage of burrowing sea anemones. *Zoological Journal of the Linnean Society*, **20**: 1–24. https://doi.org/10.1093/zoolinnean/zlaa176/6144247

Hamilton N., Gusmão L.C., Izumi T., Rodríguez E., Yap N.W.L. & Daly M. 2022. Phylogeny and taxonomy of Haloclavidae (Verrill, 1899) with a redescription of the parasitic, burrowing sea anemone, Peachia chilensis Carlgren, 1931. *PLoS ONE*, **17**(9): 1–30. https://doi.org/10.1371/journal.pone.0266283

Hand C.H. 1954. The sea anemones of central California Part I. The corallimorpharian and athenarian anemones. *Wasmann Journal of Biology*, **12**: 345–375.

Hoang D.T., Chernomor O., Haeseler A., Minh B.Q. & Vinh L.S. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, **35**: 518–522. https://doi.org/10.1093/molbev/msx281

ICZN – International Commission on Zoological Nomenclature. 2012. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Zoosystematica Rossica*, **21**(2): 323–327. https://doi.org/10.31610/zsr/2012.21.2.323

Izumi T., Yanagi K. & Kohtsuka H. 2025. Mt. Fuji in the Ocean–description of a strange new species of sea anemone, Discoactis tritentaculata fam., gen., and sp. nov. (Cnidaria; Anthozoa; Actiniaria; Actinostoloidea) from Japan, with the foundation of a new family and genus. *Diversity*, **17**(430): 1–26. https://doi.org/10.3390/d17060430

Kalyaanamoorthy S., Minh B.Q., Wong T.K.F., Haeseler A. & Jermiin L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, **14**: 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K. & Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, **30**(4): 772–80. https://doi.org/10.1093/molbev/mst010

Manuel R.L. 1988. British Anthozoa (Coelenterata: Octocorallia and Hexacorallia): keys and notes for the identification of the species. *Synopses of the British Fauna*, **18**: 1–241. https://doi.org/10.1163/9789004627543_002

Minh B.Q., Schmidt H.A., Chernomor O., Schrempf D., Woodhams M.D., von Haeseler A. & Lanfear R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, **37**(5): 1530–1534. https://doi.org/10.1093/molbev/msaa015

Riemann-Zürneck K. 1979. Two disc-shaped deep-sea Anthozoa from the Gulf of Biscay, with a survey of adaptation types in the Actiniaria. *Zoomorphologie*, **93**: 227–243. https://doi.org/10.1007/BF00994001

Rodríguez E. & López-González P.J. 2013. New records of Antarctic and Sub-Antarctic sea anemones (Cnidaria, Anthozoa, Actiniaria and Corallimorpharia) from the Weddell Sea, Antarctic Peninsula, and Scotia Arc. *Zootaxa*, **3624**(1): 1–100. https://doi.org/10.11646/zootaxa.3624.1.1

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**: 539–542. https://doi.org/10.1093/sysbio/sys029

Sanamyan N.P. & Sanamyan K.E. 2019. Tetracoelactis ioran, a new genus and species of deep-sea anemones of the family Exocoelactinidae (Cnidaria: Anthozoa: Actiniaria) from the Northwestern Pacific Ocean. *Zoosystematica Rossica*, **28**(2): 238–248. https://doi.org/10.31610/zsr/2019.28.2.238

Sanamyan N.P., Sanamyan K.E., McDaniel N., Martynov A.V., Korshunova T.A. & Bocharova E.S. 2019. A revision of sea anemones of the genus Cribrinopsis (Actiniaria: Actiniidae) from British Columbia with the description of a new species. *Marine Biodiversity*, **49**(4): 1951–1969. https://doi.org/10.1007/s12526-019-00956-w

Sanamyan N.P., Sanamyan K.E., Galkin S.V., Ivin V.V. & Bocharova E.S. 2021. Deep water Actiniaria (Cnidaria: Anthozoa) Sicyonis, Ophiodiscus, and Tealidium: re-evaluation of Actinostolidae and related families. *Invertebrate Zoology*, **18**(4): 385–449. https://doi.org/10.15298/invertzool.18.4.01

Sanamyan N.P., Sanamyan K.E., Kukhlevskiy A.D. & Savinkin O.V. 2026. A new species of Edwardsianthus (Actiniaria: Edwardsiidae), with an overview of the genus and patterns of development of tentacles and mesenteries in the family. *Invertebrate Zoology*, **23**(1): 25–50. https://doi.org/10.15298/invertzool.23.1.02

Stephenson T.A. 1928. *The British sea anemones*, **1**. London: The Ray Society. 148 p.

Verrill A.E. 1869. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N., from 1853 to 1856. Collected by Dr. Wm. Stimpson, naturalist to the Expedition. Part IV. Actiniaria [Second part]. *Proceedings of the Essex Institute*, **6**: 51–104.

Yanagi K. & Izumi T. 2021. Redescription of the sea anemone Capnea japonica (Cnidaria: Anthozoa: Actiniaria). *Species Diversity*, **26**: 153–163. https://doi.org/10.12782/specdiv.26.153

Editorial responsibility: D.A. Gapon

ZOOSYSTEMATICA ROSSICA
ISSN 2410-0226 [online] 0320-9180 [print]
Zoological Institute, Russian Academy of Sciences, St Petersburg ▪ https://www.zin.ru/journals/zsr/
Electronic supplementary material to: Vol. 35(1): 3–19, DOI 10.31610/zsr/2026.35.1.3

A list of taxa and sequences used for phylogenetic analysis, pairwise distances and phylogenetic tree

Electronic supplementary material 1 to the article:
Sanamyan N.P., Sanamyan K.E., Kukhlevskiy A.D., Morozov T.B & Gorin S. 2026. A new species of *Capnea* (Actiniaria: Capneidae) from the north-west Pacific, with an overview of related taxa. *Zoosystematica Rossica*, **35**(1): 3–19.

Table 2. A list of taxa and sequences used in the phylogenetic analysis

Note. Sequences generated during the present study are shown in bold. For many taxa, the names in GenBank include author abbreviations, which are retained here following the taxonomic names. See the comments below the table regarding taxa marked with an asterisk (*).

Taxa	12S	16S	18S	28S	COIII
Acricoactis brachyacontis	KX451131	KX451133	KX451135	-	KX451137
Actinauge richardi	EU190719	EU190761	EU190850	KJ483055	FJ489480
Actinernus elongatus	KJ482930	KJ482966	KJ483023	KJ483126	-
Actinernus robustus	LC768522	-	LC484632	LC768597	-
Actinia fragacea	EU190714	EU190756	EU190845	KJ483085	GU473334
Actinia tenebrosa	KT852045	KT852111	KT852174	-	KT852330
Actinoscyphia plebeia	EU190712	EU190754	FJ489437	KJ483067	FJ489476
Actinostola chilensis	-	GU473285	GU473302	KJ483110	GU473357
Actinostola crassicornis	-	EU190753	EU190843	KJ483098	GU473332
Actinostola faeculenta 39 LV82	MZ569933	MZ567242	MZ569908	MZ569961	MZ576864
Actinostola faeculenta 46 LV82	MZ569935	MZ567244	MZ569910	MZ569963	MZ576866
Actinostola faeculenta 54 LV82	MZ569936	MZ567245	MZ569911	-	MZ576867
Actinostola faeculenta 73 LV82	MZ569943	MZ567252	MZ569916	MZ569967	MZ576874
Actinostola georgiana	KJ482928	KJ482952	KJ483032	KJ483099	KJ482991
Actinostola sp. red 62	MZ569938	MZ567247	MZ569912	MZ569964	MZ576869
Actinostola sp. 2 LV82	MZ569931	MZ567240	MZ569907	MZ569959	MZ576862
Actinostola sp. 29 LV82	MZ569932	MZ567241	-	MZ569960	MZ576863
Actinostola sp. 63 LV82	MZ569939	MZ567248	-	-	MZ576870
Actinostola sp. 64 LV82	MZ569940	MZ567249	MZ569913	-	MZ576871
Actinostola sp. 66 LV82	MZ569941	MZ567250	MZ569915	MZ569965	MZ576872
Actinostola sp. 67 LV82	MZ569942	MZ567251	MZ569915	MZ569966	MZ576873
Actinostola sp. Kamchatka	-	MZ567255	MZ569917	MZ569970	MZ576877
Actinothoe sphyrodeta	FJ489401	FJ489421	FJ489440	KJ483111	FJ489481
Adamsia palliata	FJ489398	FJ489419	FJ489436	KJ483101	FJ489474

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
Aiptasia couchii	KP761199	KP761254	KP761301	-	KP761405
Aiptasia couchii 2	KP761200	KP761255	KP761303	-	KP761403
Aiptasia mutabilis	JF832963	FJ489418	FJ489438	KJ483115	FJ489505
Aiptasia mutabilis 2	KP761194	KP761248	KP761300	-	KP761404
Aiptasiogeton hyalinus	KR704266	KR186040	KR704268	-	-
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 boniensis	EU190717	EU190759	EU190848	KJ483053	FJ489479
Andvakia discipulorum	GU473273	GU473287	GU473316	KJ483051	-
Anemonactis minuta	MW724529	MW725091	-	-	MW735963
Anemonia erythraea	KY789302	KY789335	-	-	KY789271
Anemonia viridis	EU190718	EU190760	EU190849	EU190806	GU473335
Antennapeachia jambio	MW724530	MW725090	MW725225	-	MW735964
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 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	-	-	-

Taxa	12S	16S	18S	28S	COIII
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 1	KT310208	JQ927444	KT852173	KT852263	KT310207
Aulactinia stella 2	KT852044	KT852110	KT852173	KT852263	KT852329
Aulactinia stella Kamch	-	MW491958	-	MW491996	-
Aulactinia stella KolaP	-	MW491959	-	MW491997	-
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	PP946945	PP946952	PP946966	PP951987
Aulactinia vancouverensis L	KT852019	KT852085	KT852151	-	KT852305
Aulactinia veratra	KT852001	KT852063	KT852131	-	KT852283
Aulactinia verrucosa	EU190723	EU190766	EU190854	KT852250	FJ489484
Aulactinia vladimiri Kamch 2014 1	**PZ162585**	**PZ162577**	**PZ162602**	**PZ162594**	**PZ161652**
Aulactinia vladimiri Kamch 2014 2	**PZ162586**	**PZ162578**	**PZ162603**	**PZ162595**	**PZ161653**
Bartholomea annulata	EU190721	EU190763	EU190851	KJ483068	FJ489483
Bathyphellia australis	FJ489402	FJ489422	EF589063	EF589086	FJ489482
Bellactis ilkalyseae	-	KP761238	KP761316	-	KP761393
Bellactis Ilkalyseae 2	KR186020	KR186036	KR186051	-	-
Bolocera kerguelensis	KJ482925	KJ482965	KJ483029	KJ483133	KJ482985
Boloceroides mcmurrichi	GU473270	-	EU190852	KJ483103	KJ483002
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

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
Calliactis japonica	FJ489403	FJ489423	FJ489441	KJ483057	FJ489486
Calliactis parasitica	EU190711	EU190752	EU190842	KJ483102	FJ489475
Calliactis polypus	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 tokranovi **sp. nov.**	**PZ162587**	**PZ162579**	**PZ162604**	**PZ162596**	**PZ161654**
Capnea tokranovi **sp. nov.**	**PZ162588**	**PZ162580**	**PZ162605**	**PZ162597**	**PZ161655**
Carcinactis dolosa	MN266878	MN266877	MN266880	MN266874	MN295038
Cereus herpetodes	JF832956	JF832969	JF832983	JF832992	-
Cereus pedunculatus	EU190724	EU190767	EU190855	EU190813	FJ489471
Charisea saxicola	KT852020	KT852086	KT852152	-	KT852306
Chitinactis marmara	MT676806	MT676783	MT676785	MT676789	MT790710
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 olegi 2018	**PZ162589**	**PZ162581**	**PZ162606**	**PZ162598**	**PZ161656**
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 LV82 18 65	PP902551	PP902556	PP902561	PP902566	PP915639
Cribrinopsis sp. red LV82 7 26	PP902550	PP902555	PP902560	PP902565	PP915638
Cribrinopsis sp. white LV82 T3 78	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

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
Diadumene lineata Japan	JF832965	JF832973	JF832987	KJ483107	JF833007
Diadumene lineata USA	EU190730	EU190774	EU190860	KJ483108	FJ489506
Diadumene sp.	JF832960	JF832976	JF832980	KJ483130	JF833005
Discoactis tritentaculata Misaki	LC874807	LC875472	LC875474	LC875477	LC876766
Discoactis tritentaculata Iki	LC874806	LC875473	LC875475	-	LC876767
Edwardsia andresi	-	-	AF254374	-	-
Edwardsia elegans 1	EU190726	EU190770	AF254376	KJ483087	GU473338
Edwardsia elegans 2	-	-	-	AY345870	-
Edwardsia japonica 1	GU473274	GU473288	GU473304	KJ483048	GU473359
Edwardsia japonica 2	-	-	-	GU473321	-
Edwardsia timida 1	-	KT852113	-	KT852265	KT852332
Edwardsia timida 2	GU473281	GU473299	GU473315	-	-
Edwardsia tuberculata	-	-	AF254381	-	-
Edwardsianthus amethystus	LC649470	LC649478	LC649486	-	-
Edwardsianthus carbunculus	LC649472	LC649480	LC649488	-	-
Edwardsianthus gilbertensis 1	EU190728	EU190772	EU190859	EU190817	-
Edwardsianthus gilbertensis 2	-	LC649481	LC649489	-	-
Edwardsianthus gilbertensis 3	LC649468	LC649476	LC649484	-	-
Edwardsianthus pudicus	LC649467	LC649475	LC649483	-	-
Edwardsianthus pudicus 38	-	PX056174	PX056182	PX056190	-
Edwardsianthus pudicus 1	PX056171	PX056175	PX056183	PX056191	-
Edwardsianthus pudicus 2	-	PX056176	PX056184	PX056192	-
Edwardsianthus pudicus 3	-	PX056177	PX056185	PX056193	-
Edwardsianthus sapphirus	LC649469	LC649477	LC649485	-	-
*Edwardsianthus smaragdus **	LC649471	-	-	-	-
Edwardsianthus vostok 1	PX056172	PX056178	PX056186	PX056194	-
Edwardsianthus vostok 2	-	PX056179	PX056187	PX056195	-
Edwardsianthus vostok 3	PX056173	PX056180	PX056188	PX056196	-
Edwardsianthus vostok 4	-	PX056181	PX056189	PX056197	PX060958
Edwardsiella loveni	KX946216	KX946212	KX946218	KX946219	KX946217
Entacmaea 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	KT852009	KT852072	KT852140	KT852255	KT852292
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

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
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	EU190858	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
Exaiptasia pallida 1	KP761183	KP761270	KP761286	-	-
Exaiptasia pulchella	EU190715	EU190757	EU190846	EU190803	KJ482979
Exocoelactis actinostoloides	KP793003	KP793004	LC875476	LC875478	LC876768
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	-	KT852297
Gyractis sp. Oman	KY789325	KY789357	-	KY789390	KY789290
Halcampa duodecimcirrata	JF832966	EU190776	AF254375	-	-
Halcampa arctica 2 M4	**PZ162590**	**PZ162582**	**PZ162607**	**PZ162599**	**PZ161657**
Halcampoides purpureus	EU190735	EU190780	AF254380	EU190824	-
Halcampoides purpureus	KR051003 12S	KR051003 16S	-	-	KR051003 COIII
Halcampoides purpureus GR2021 *	MT676807	MT676782	-	-	MT790709
Halcampoides sp. Kamchatka	MZ569946	MZ567256	MZ569918	MZ569971	MZ576878
Halcampulactis solimar	MK279362	MK279363	MK279364	-	MK279366
Halcurias fragum 1	LC768536	LC768561	LC768586	LC768613	-
Halcurias fragum 2	LC768537	LC768562	LC768587	LC768614	-
Halcurias fragum 3	LC768538	LC768563	LC768588	LC768615	-
Halcurias hiroomii 1	-	LC768556	LC768581	LC768608	-
Halcurias hiroomii 2	-	LC768557	LC768582	LC768609	-
Halcurias hiroomii 3	-	LC768558	LC768583	LC768610	-
Halcurias hiroomii 4	-	LC768559	LC768584	LC768611	-

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
Halcurias hiroomii 5	LC768535	LC768560	LC768585	LC768612	-
Halcurias pilatus	KJ482931	KJ482967	KJ483020	KJ483109	KJ482997
Haloclava producta *	EU190734	EU190779	AF254379	KJ483097	JF833008
Haloclava sp. *	KJ482924	KJ482963	-	-	KJ482989
Harenactis argentina	KJ482926	KJ482964	KJ483026	KJ483047	KJ482984
Heteractis aurora	MK519414	MK519469	-	-	MK522453
Heteractis magnifica	EU190732	EU190777	EU190862	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 1	-	LC484643	LC484638	LC768598	-
Isactinernus quadrilobatus 2	KJ482932	KJ482968	KJ483024	KJ483105	KJ482998
Isactinia olivacea	-	KT852077	KT852144	-	KT852296
Isanthus capensis	JF832967	GU473291	GU473307	KJ483096	GU473362
Isohalcurias carlgreni 1	LC768539	LC768564	LC768589	LC768616	-
Isohalcurias carlgreni 2	LC768540	LC768565	LC768590	LC768617	-
Isohalcurias carlgreni 3	LC768541	LC768566	LC768591	LC768618	-
Isohalcurias carlgreni 4	-	LC768567	LC768592	LC768619	-
Isohalcurias citreum 1	LC768542	LC768569	LC768593	LC768620	-
Isohalcurias citreum 2 *	LC768543	LC768570	-	-	-
Isohalcurias citreum 3	LC768544	-	LC768595	LC768621	-
Isohalcurias malum 1	LC768545	LC768571	-	LC768622	-
Isohalcurias malum 2	LC768546	LC768572	LC768596	LC768623	-
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	EU190867	KJ483049	GU473342
Metapeachia tropica 1	MW158842	MW158859	MW725226	MW158877	MW158889
Metapeachia tropica 2	MW158845	MW158862	MW725227	MW158879	MW158892
Metapeachia tropica 3	-	MW763149	MW725228	MW763144	-
Metridium farcimen	MT893228	MT893265	-	-	MT896170
Metridium s. fibriatum (Japan)	-	JF832974	JF832988	JF832996	JF833009

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
Metridium senile	KJ482916	KJ482950	KJ483035	KJ483113	KJ482975
Metridium senile (WA, USA)	EU190740	JF832972	JF832982	KJ483076	JF833003
Metridium senile 1	KT852024	EU190786	AF052889	EU190829	FJ489494
Metridium senile 2 Argentina	JF832962	JF832971	JF832981	JF832991	JF833002
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
Paracalliactis sp.	FJ489411	FJ489429	FJ489447	KJ483061	FJ489496
Paranthus niveus	GU473277	GU473295	GU473311	KJ483072	GU473344
Paraphelliactis sp.	FJ489412	FJ489431	FJ489449	FJ489466	FJ489498
Peachia cylindrica	EU190743	EU190789	KJ483015	EU190832	MW735965
Peachia quinquecapitata	MW724531	MW725092	MW725229	MW737673	MW735966
Peronanthus sp.	KJ482917	KJ482956	KJ483014	KJ483066	KJ482976
Phellia exlex	JF832958	JF832978	JF832984	KJ483121	JF833004
Phellia gausapata	EU190744	EU190790	EU190870	KJ483054	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	EU190871	-	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	-	MT676788	MT790708
Sicyonis denisovi MIMB 41366	MZ569948	MZ567258	MZ569920	MZ569973	MZ576880
Sicyonis denisovi MIMB 41367	MZ569949	MZ567259	MZ569921	MZ569974	MZ576881

Taxa	**12S**	**16S**	**18S**	**28S**	**COIII**
Sicyonis denisovi MIMB 41368	MZ569947	MZ567257	MZ569919	MZ569972	MZ576879
Sicyonis denisovi MIMB 41371	MZ569950	MZ567260	MZ569922	MZ569975	MZ576882
Sicyonis denisovi MIMB 41372	MZ569951	MZ567261	MZ569923	MZ569976	MZ576883
Sicyonis kuznetsovi *	-	MZ567262	MZ569924	MZ569977	MZ576884
Spongiactis japonica	-	KX946214	-	-	-
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
Synactinernus churaumi 1	LC768532	LC484641	LC484636	LC768606	-
Synactinernus churaumi 2	LC768533	LC484642	LC484637	LC768607	-
Synactinernus churaumi 3	-	LC768554	LC768579	-	-
Synactinernus churaumi 4	LC768534	LC768555	LC768580	-	-
Synactinernus flavus 1	LC768525	LC484639	LC484633	LC768602	-
Synactinernus flavus 2	LC768526	LC484640	LC484634	LC768603	-
Synactinernus flavus 3	LC768527	LC768549	LC768575	LC768604	-
Synactinernus flavus 4	LC768528	LC768550	LC768576	-	-
Synactinernus flavus 5	LC768529	LC768551	LC768577	-	-
Synactinernus flavus 6	LC768530	LC768552	LC768578	-	-
Synactinernus flavus 7	LC768531	LC768553	LC484635	LC768605	-
Synhalcurias elegans	-	-	KJ483021	KJ483120	-
Synhalcurias elegans 1	-	-	LC768573	LC768599	-
Synhalcurias elegans 2	-	LC768547	LC768574	LC768600	-
Synhalcurias kahakui *	-	LC768548	-	LC768601	-
Synpeachia temasek	MW724532	MW725093	MW725230	MW737674	MW735967
Tealidium konoplinorum MIMB 41358	MZ569956	MZ567267	MZ569929	MZ569982	MZ576889
Tealidium konoplinorum MIMB 41359	MZ569957	MZ567265	MZ569928	MZ569981	MZ576888
Tealidium konoplinorum MIMB 41360	MZ569958	MZ567268	MZ569930	MZ569983	MZ576890
Tealidium konoplinorum MIMB 41364	MZ569955	MZ567265	MZ569927	MZ569980	MZ576887
Tealidium konoplinorum MIMB 41365	MZ569954	MZ567264	MZ569926	MZ569979	MZ576886
Telmatactis sp.	JF832968	JF832979	KJ483013	KJ483135	-
Tempuractis rinkai	LC649473	LC649482	LC649490	-	-

Taxa	12S	16S	18S	28S	COIII
Triactis producta	-	-	EU190876	KJ483125	-
Urtibrina clandestina 1	PP946960	PP946946	PP946953	PP946967	PP951988
Urtibrina clandestina 2	PP946961	PP946947	PP946954	PP946968	PP951989
Urtibrina rimicola 1	PP946962	PP946948	PP946955	PP946969	PP951990
Urtibrina rimicola 2	PP946963	PP946949	PP946956	PP946970	PP951991
Urtibrina rimicola 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	KT852034	KT852098	KT852163	-	KT852318
Urticina grebelnyi Kamch 2012	**PZ162591**	**PZ162583**	**PZ162608**	**PZ162600**	**PZ161658**
Urticina timuri Kamch 2012	**PZ162592**	**PZ162584**	**PZ162609**	**PZ162601**	**PZ161659**
Verrillactis paguri	FJ489414	FJ489433	-	KJ483046	FJ489503

Comments

***Edwardsianthus smaragdus* Izumi et Fujii, 2021.** The 16S (LC649479) sequence of this species markedly deviates from the 16S sequences of all other edwardsiid anemones but closely resembles those of members of other groups (99% similarity with *Andvakia* Danielssen, 1890 and several other genera). As the 16S sequences of other *Edwardsianthus* England, 1987 species do not exhibit such deviation, we suspect that this sequence is erroneous and therefore prefer to exclude it from our dataset.

The 18S (LC649487) sequence attributed to this species is incorrect and actually belongs to a symbiont, showing 99.47% similarity with *Symbiodinium* Freudenthal, 1962 (Alveolata: Dinoflagellata: Symbiodiniaceae). Consequently, it has been excluded from our dataset.

***Halcampoides purpureus* (Studer, 1879) GR2021.** The 28S (MT676790) sequence of this specimen appears to be either contaminated or of poor quality, as it contains long insertions and exhibits lower similarity than expected when compared with other sea anemone sequences. The 18S (MT676786) sequence from the same specimen shows similar issues, although to a lesser extent. To ensure data reliability, we have excluded both sequences from our dataset.

***Haloclava* sp.** Hamilton et al. (2022) used the sequences KJ483031 (18S) and KJ483138 (28S) for this taxon. These sequences exhibit relatively low similarity to other Actiniaria sequences (maximum 88.2% and 88.18%, respectively). Given that the 18S and 28S sequences of *Haloclava producta* (Stimpson, 1856) do not deviate to such an extent from those of other Actiniaria (showing 94–99% similarity with sequences from many species), we infer that this is not a characteristic of the species itself and that KJ483031 and KJ483138 are, at least in part, erroneous. Consequently, they have been excluded from our dataset.

***Haloclava producta* (Stimpson, 1856).** Hamilton et al. (2022) and numerous other authors (in at least ten publications) have incorrectly used AF254370 as the 18S sequence for *H. producta*. Izumi et al. (2025) employed the same sequence for both the 18S and 28S markers of *H. producta*. In fact, this sequence (AF254370) belongs to *Drosophila* Fallén, 1823 (Hexapoda: Diptera: Drosophilidae); the correct 18S sequence for *H. producta* is AF254379. Although this error likely originated from a typographical mistake in the original publication, its continued use has demonstrably affected phylogenetic reconstructions, as evidenced by the markedly divergent positioning of *H. producta* in many published trees.

Additionally, in our dataset, we replaced EU190823 (28S), used by Hamilton et al. (2022), with the much longer (but otherwise identical) sequence KJ483097.

***Isohalcurias citreum* Izumi et al., 2023 2.** The 18S (LC768594) sequence of this specimen appears to be incorrect, as it shows a high similarity to actiniid anemones (98.84% similarity with *Urticina* Ehrenberg, 1834), whereas the 18S sequences of the other two specimens of the same species are typical. Consequently, it has been excluded from our dataset.

***Ophiodiscus bukini* Sanamyan et al., 2021.** The 12S sequence (MZ569953) is likely mislabeled, showing 99.25% similarity with *Aulactinia incubans* Dunn, Chia et Levine, 1980 and 99.11% similarity with *Aulactinia stella* (Verrill, 1864). Consequently, this sequence was excluded from our dataset.

***Synhalcurias kahakui* Izumi et Yanagi, 2021.** The 12S (LC768524) sequence of this species shows no similarity to any sequence of Actiniaria but is highly similar to sequences of a stony coral (99.84% similarity with *Rhizotrochus* Milne Edwards et Haime, 1848). Consequently, it has been excluded from our dataset.

***Scytophorus striatus* Hertwig, 1882.** The 18S sequences of *S. striatus* (MT676784) and *Chitinactis marmara* Gusmão et Rodríguez, 2021 (MT676785) are 100% identical, have the same length, and share sequential accession numbers. We suspect that, by accident, the same sequence—most likely that of *Chitinactis* Gusmão et Rodríguez, 2021, judging from its similarity to sequences of *Capnea* Forbes, 1841 and *Actinostola* Verrill, 1883—was submitted to GenBank instead of sequences from two distinct species. Consequently, we have excluded MT676784 from our dataset.

***Sicyonis kuznetsovi* Sanamyan et al., 2021.** The 12S sequence (MZ569952) of this species appears to be incorrect, likely due to contamination, as it shows high similarity to Hormathiidae and is closely related to acontiate anemones (97.9% similarity with *Calliactis* Verrill, 1869), while exhibiting significant divergence from other species of *Sicyonis* Hertwig, 1882 and members of the Actinostolidae and Anthosactinidae 12S sequences. Other sequences of *S. kuznetsovi* do not show such deviation, suggesting contamination in the 12S data. Consequently, this sequence was excluded from our dataset.

Table 3. Pairwise genetic distances calculated between the species under consideration

		1	**2**	**3**	**4**
1	*Capnea georgiana*				
2	*Capnea japonica*	0.018			
3	*Capnea tokranovi* **sp. nov.**	0.011	0.003		
4	*Chitinactis marmara*	0.057	0.039	0.045	
5	*Discoactis tritentaculata*	0.019	0.014	0.013	0.037

Fig. 1. Phylogenetic relationships inferred from a concatenated dataset (12S + 16S + 18S + 28S + COIII) using Bayesian inference (BI). Numbers at branches indicate BI posterior probabilities and ML bootstrap values (format: BI/ML). Branches with conflicting topologies between BI and ML analyses are shown in red.