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A new species of *Edwardsianthus* (Actiniaria: Edwardsiidae), with an overview of the genus and patterns of development of tentacles and mesenteries in the family

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ABSTRACT: The burrowing sea anemone *Edwardsianthus vostok* sp.n. is described from the shallow waters of Vostok Bay, Peter the Great Gulf, Sea of Japan, where it commonly inhabits dense aggregations of phoronids. It is the first record of the genus *Edwardsianthus* for Russian waters. Previously, *Edwardsianthus* species were known only from tropical and subtropical waters of the Pacific and Indian Oceans. *Edwardsianthus vostok* sp.n. is most closely related to *E. gilbertensis* but has much larger nematocysts in the nemathybomes, a different arrangement of the tentacles, lacks zooxanthellae, and is distinguished on the basis of molecular data. An overview of all nominal species assignable to *Edwardsianthus* is presented; the specimens of its type species, *E. pudicus*, collected in Vietnam, are examined. Patterns of development of tentacles and mesenteries in the family Edwardsiidae are discussed. It has been shown that secondary micronemes form not only exocoelically but also endocoelically, and not just in pairs but also bilaterally.
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KEY WORDS: taxonomy, biodiversity, Sea of Japan, Actiniaria, Edwardsiidae, *Edwardsianthus*.

Описание нового вида рода *Edwardsianthus* (Actiniaria: Edwardsiidae) с обзором рода и вариантов развития щупалец и мезентериев в семействе Edwardsiidae

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РЕЗЮМЕ: Роющая актиния *Edwardsianthus vostok* sp.n. описана из мелководья бухты Восток залива Петра Великого Японского моря, где она встречается в больших количествах на полях форонид. Это первая находка представителя рода *Edwardsianthus* в российских водах. Ранее виды рода *Edwardsianthus* были известны только из тропических и субтропических вод Тихого и Индийского океанов. *Edwardsianthus vostok* sp.n. наиболее близок к *Edwardsianthus gilbertensis*, от которого отличается значительно более крупными нематоцистами в нематобомах, расположением щупалец, отсутствием зооксантелл и по молекулярным данным. Представлен обзор всех номинальных видов, относящихся к роду *Edwardsianthus*; изучены экземпляры типового вида *E. pudicus*, собранные во Вьетнаме. Обсуждаются варианты развития мезентериев и организации щупалец в семействе Edwardsiidae. Показано, что вторичные микронемы формируются не только в экзоцелях, но и в эндоцелях, причём не только парно, но и билатерально.
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КЛЮЧЕВЫЕ СЛОВА: таксономия, биоразнообразие, Японское море, Actiniaria, Edwardsiidae, *Edwardsianthus*.

Introduction

Edwardsiidae is a large family comprising more than 100 species of sea anemones widely distributed in all regions of the world's oceans. Most are known from shallow or moderate depths, although several species inhabit the abyssal and ultra-abyssal zones (the deepest record for the family is *Paraedwardsia hadalis* Sanamyan et Sanamyan, 2018 collected from 7250 m). Very few edwardsiid species are known from the Far Eastern seas of Russia: *Edwardsia sojabio* Sanamyan et Sanamyan, 2013 is common at abyssal depths in the Sea of Japan (Sanamyan, Sanamyan, 2013); *Edwardsia japonica* Carlgren, 1931 is considered a common species in Amur Bay (Peter the Great Gulf, Sea of Japan) (Kostina, 2009); and *Paraedwardsia malakhovi* Sanamyan et Sanamyan, 2021 is a shallow-water species described from off the Kuril Islands and East Kamchatka (Sanamyan, Sanamyan, 2021).

Unlike many other Edwardsiidae, individuals of most species of *Edwardsianthus* England, 1987 are relatively large in size and have beautifully and often brightly colored tentacles (vivid red, blue, green, etc., see Rowlett, 2020, Izumi, Fujii, 2021). In general, live specimens can be easily identified as members of *Edwardsianthus* by the peculiar arrangement of their tentacles: in most cases, the five shorter tentacles are directed upward and the 15 longer ones are horizontal. Previously, *Edwardsianthus* species were known only from tropical or subtropical waters. Therefore, the discovery of *Edwardsianthus* specimens in the Sea of Japan, specifically at the Marine Biological Station "Vostok" (A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences), was unexpected, because this locality is significantly remote from their known distribution range (more than 1100 km north of the northernmost Japanese record). In 2024, we obtained many live specimens of this species which allowed us to keep them in captivity and study in detail the arrangement of their tentacles and understand the sequence of formation of the mesenteries — important features difficult to examine in fixed material, but clearly observable in live specimens and underwater photographs. Underwater photography has enabled the study of features of live species, while advancements in diving and resources like iNaturalist (2025) allow (through documented, georeferenced images) assessing species distributions and identifying novel synapomorphies crucial for understanding phylogenetic relationships.

Material and methods

The specimens examined in the present study were collected in Vostok Bay, Peter the Great Gulf, Sea of Japan. More than 20 of them were kept alive in captivity for several days. Subsequently, most specimens were fixed in 4% formalin solution in seawater, and some in 96% ethanol for molecular study. Formalin-fixed specimens were used for histological sections using the isopropanol-mineral oil method (Sanamyan *et al.*, 2019). For general histology, 7–10 μm sections were stained using a method derived from the Masson trichrome (see Sanamyan, Sanamyan, 2019). The arrangement of the microcnemes was examined in series of 10 μm sections of the distal end of the body and in photographs of live specimens in seawater containers. In addition, four specimens of the type species of the genus, *Edwardsianthus pudicus* (Klunzinger, 1877), collected in Vietnam (12°11′ N, 109°17′ E, depths of 2.5 and 3 m, July 2024, collector O.V. Savinkin), were studied and sequenced. The terminology and the method used to measure the cnidae are the same as in our previous papers (e.g., Sanamyan *et al.*, 2021). In the present study, the term "macrocoel" refers to a space between two adjacent macrocnemes in Edwardsiidae.

The formulae that show the number of tentacles in each cycle are not highlighted (e.g., "5+15" indicates that there are five tentacles in the inner cycle and 15 in the outer). The formulae in italics show how many outer tentacles are located between the two adjacent tentacles of the inner cycle, starting from the ventral directive tentacle (e.g., nine outer tentacles are arranged between three inner tentacles in 12-tentacular *Edwardsia* species as "*3+3+3*").

Three mitochondrial gene fragments (12S rRNA, 16S rRNA, and COIII) and two nuclear gene fragments (18S rRNA and 28S rRNA) were used for phylogenetic analysis. The dataset consisted of newly generated sequences and those accessed from GenBank of about 230 species of Actiniaria (with a total of 360 sequences in the concatenated datasheet) (Supplementary Table 1). A maximum likelohood (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). Final tree was viewed and prepared for publication in our own software EasyTreeEditor software (developed by K. Sanamyan) (Supplement Fig. 1).

The type specimens of the new species are deposited at the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, Vladivostok (MIMB).

Results

Order Actiniaria Hertwig, 1882
Family Edwardsiidae Andres, 1881
Genus *Edwardsianthus* England, 1987

Type species: *Edwardsia pudica* Klunzinger, 1877, by original designation.

The genus *Edwardsianthus* was erected to include species resembling *Edwardsia* by the presence of nemathybomes and a well-developed physa but having an unusual arrangement of mesenteries that "does not follow the usual development to the simple *Edwardsia* stage" (England, 1987: 228). In all edwardsiid genera (except *Edwardsianthus*), the first four microcnemes (corresponding to the fifth and sixth couples, see Stephenson, 1928: 77, text-fig. 35) are paired with the non-directive macrocnemes. In contrast, the microcnemes in *Edwardsianthus* are present in pairs in six non-directive macrocoels. Most of the known specimens of all *Edwardsianthus* species have 20 mesenteries: 8 macrocnemes + 12 microcnemes, and, therefore, 20 tentacles, a feature that allows identification of members of this genus in the field. Sometimes additional pairs of microcnemes are developed, and more than 20 tentacles are present. Smaller specimens may have fewer than 20 tentacles.

Fautin (2016), in her catalog of Actiniaria, incorrectly states that only one species was originally included in *Edwardsianthus*. England (1987) originally included two species in his genus: *E. pudicus* (Klunzinger, 1877) and *E. gilbertensis* (Carlgren, 1931). The former species was redescribed by him and designated as the type, and the latter was mentioned in the discussion as a distinct species of *Edwardsianthus*.

Edwardsianthus vostok **sp.n.**
Figs 1–5, Table 1.

MATERIAL EXAMINED. Holotype: Sea of Japan, Peter the Great Gulf, Vostok Bay, ~ 42°53.6′ N, 132°44.1′ E, depth 4 m, 21 May 2024, collected by A. Maiorova (MIMB 51732). Paratypes: Same data as for holotype, 20 specimens (MIMB 51733); 8 m, 10 June 2023, five specimens (MIMB 51734).

DESCRIPTION. Live specimens (observed in tanks) are up to about 40 mm in length and 2–4 mm in width. The tentacular crown is less than 8 mm in diameter, with tentacles measuring 2–3 mm in length and approximately 0.2 mm in diameter at their base. The fixed holotype is 23 mm in length and 5 mm in width in its widest part, located at some distance from the proximal end (Fig. 1A, left specimen). Paratypes range from 5 to 30 mm in length and from 1.5 to 5 mm in width.

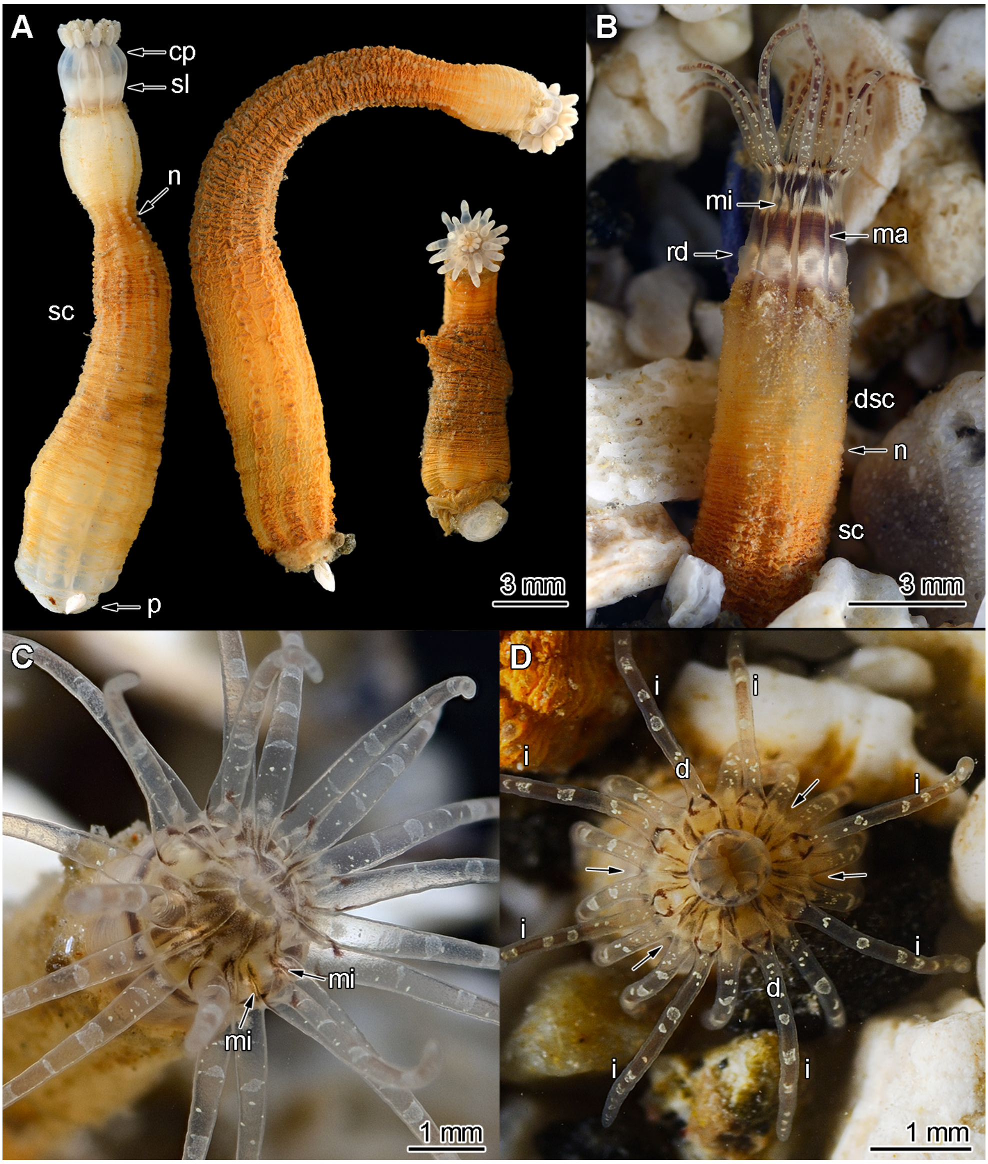

Fig. 1. *Edwardsianthus vostok* sp.n. A — fixed holotype (left) and two paratypes; B — lateral view of the upper part of a live specimen, showing scapus, scapulus, capitulum, and tentacles (the most distal ring of nemathybomes is indicated, which separates the main scapus from its distal portion, having a thin cuticle and lacks nemathybomes); C — oral disc of a live specimen; D — top view of a live specimen (arrows indicate the position of non-directive macrocnemes).
Abbreviations: cp — capitulum; d — directive tentacle; dsc — distal scapus; i — inner tentacle; ma — insertion of macrocneme; mi — insertion of microcneme; n — nemathybome; p — physa; rd — scapular ridges; sc — scapus; sl — scapulus.

The body is divisible into physa, scapus, scapulus, and capitulum. The physa is distinct but small, whitish, and thin-walled. It is clearly demarcated from the scapus and is well-visible in many specimens, though sometimes invaginated (and, therefore, not visible without dissection).

The scapus is covered with an orange-brown or yellow-brown periderm being relatively thin and free from attached solid particles. The nemathybomes are small, approximately 200 µm in diameter (Figs 1A, B; 3C), and typically appear larger and more prominent in the middle region of the scapus. They are arranged

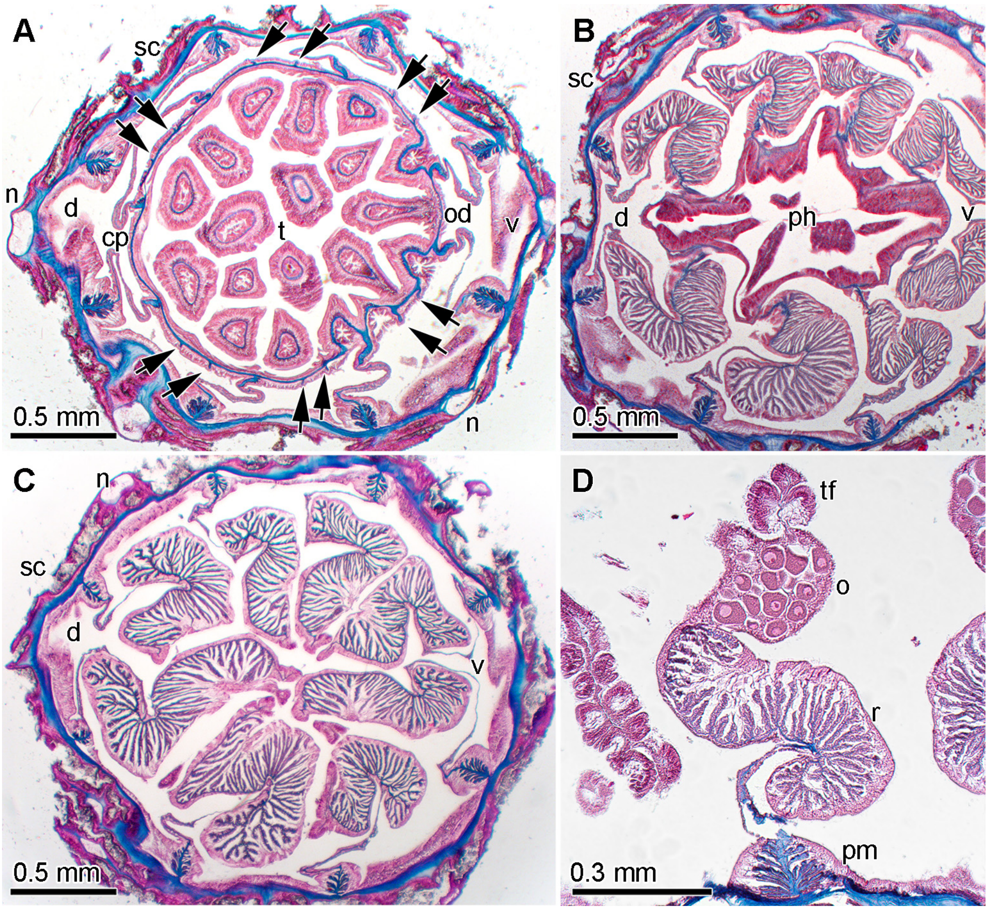

Fig. 2. *Edwardsianthus vostok* sp.n., transverse sections: A — through distal part of column at level of capitulum and oral disc (arrows indicate six pairs of microcnemes); B — through scapus at level of actinopharynx; C — through scapus below actinopharynx; D — through proximal part of scapus.
Abbreviations: cp — capitulum; d — dorsal macrocoel (directives); n — nemathybome; o — ova; od — oral disc; ph — actinopharynx; pm — parietal muscles; r — retractor; sc — scapus; t — tentacles; tf — trilobate filament; v — ventral macrocoel (directives).

into eight distinct rows along the midline of each macrocoel (Figs 1A; 2A, C). The most distal portion of the scapus (up to 3 mm long) has a thinner cuticle and lacks nemathybomes. (Fig. 1B).

The scapulus is up to 2 mm in live specimens, with eight well-visible insertions of macrocnemes and eight whitish ridges between them (Figs 1B; 3D); these ridges become progressively lower distally. A transverse brownish band marks the boundary between the scapulus and the capitulum (Fig. 1B).

The capitulum is about 1 mm in length, with white and brown pigment marks and clearly visible insertions of microcnemes between the insertions of macrocnemes (Fig. 1B). The oral disc is not wider than the column and has a raised oral cone. Brown pigment often present on the oral cone along the mesenterial insertions (Fig. 1C, D).

The tentacles of live specimens are transparent, typically showing blotches of brown pigment in the endoderm, and sprinkled with small, whitish or yellowish spots all along their entire length (Fig. 1B–D). A white patch is present on the base of the aboral side of the outer tentacles (with a total of 12 such patches in fully developed specimens). Brown markings are present on the lateral sides of the bases of the eight tentacles in the inner cycle (Fig. 1B–D).

Many specimens (including the holotype) have 20 tentacles approximately equal in length. Several smaller specimens have 16, 17, 18, or 19 tentacles. The fully developed tentacular crown exhibits two planes of symmetry: one ("directive plane") along directive axis and the other ("transverse plane") perpendicular to it (along the transverse axis). The tentacles are arranged into two cycles: eight in the inner and 12 in the outer cycle (Fig. 1D).

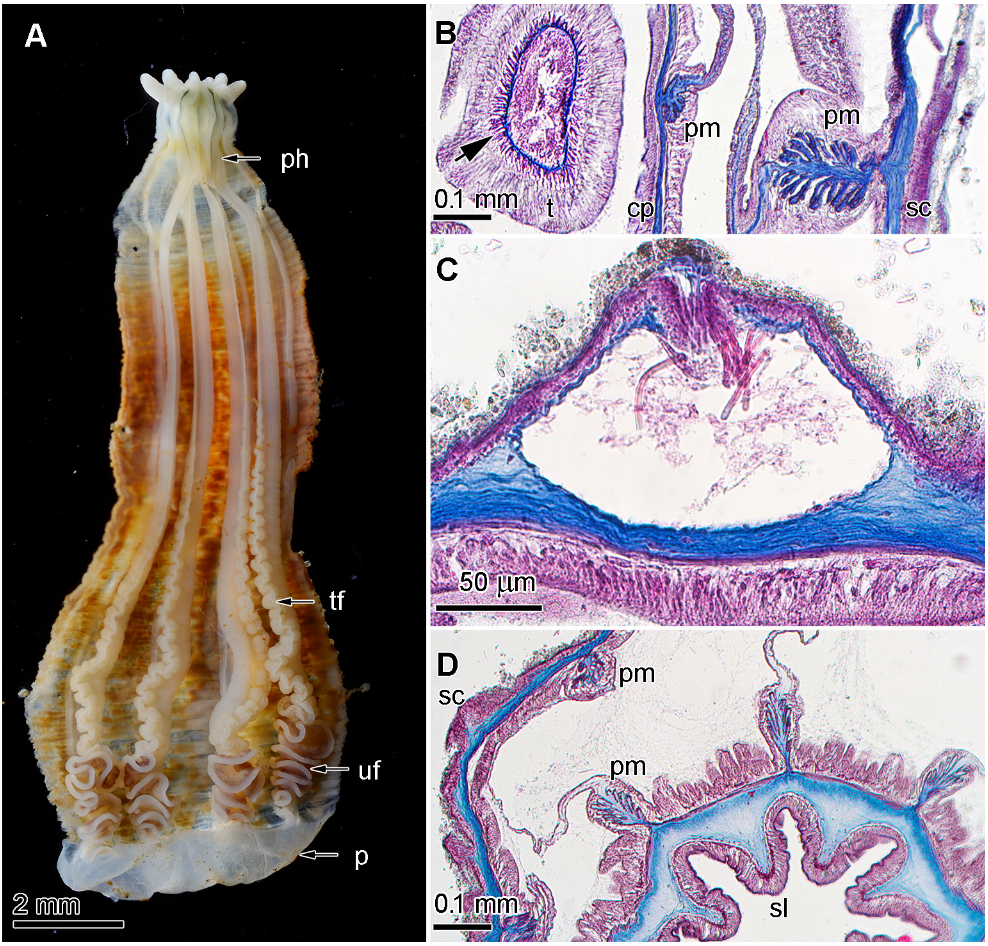

Fig. 3. *Edwardsianthus vostok* sp.n. A — longitudinal section through whole specimen; B — transverse section through the distal part of column, showing parietal musculature of macrocnemes in scapus and capitulum and longitudinal muscles of tentacle (arrow); C — nemathybome; D — transverse section through scapulus with scapular ridges.

Abbreviations: cp — capitulum; p — physa; ph — actinopharynx; pm — parietal muscle; sc — scapus; sl — scapulus; t — tentacle; tf — trilobate filament; uf — unilobate filament.

In specimens with fewer than 20 tentacles, the inner cycle invariably contains eight tentacles, while the outer cycle may contain eight to 11 tentacles. In specimens with 16 tentacles, those of the inner and outer cycles alternate (8+8); such specimens show either bilateral symmetry with a plane of symmetry along the directive axis or radial 8-merous symmetry (except the internal structure and slit-like mouth) (Fig. 4A). When the number of tentacles increases, new tentacles in the outer cycle are added exclusively in the four sectors adjacent to the transverse axis (Fig. 4B, C).

In fully developed specimens with 20 tentacles (arranged as 8+12), the four sectors adjacent to the directive axis contain only one tentacle of the outer cycle between adjacent tentacles of the inner cycle, while each of the four sectors adjacent to the transverse axis contains two outer tentacles between adjacent inner tentacles: *1+2+2+1+1+2+2+1* (Figs 1D; 4D). In fully developed specimens, the eight tentacles of the inner cycle communicate with endocoels (with two endocoels formed by directives and six endocoels formed by six pairs of microcnemes), while the outer cycle consists of exocoelic tentacles.

Eight macrocnemes run all along the column and are arranged as those in all edwardsiids (Fig. 2B, C). They form three pairs of lateral (non-directive) macrocoels: dorso-lateral, lateral, and ventro-lateral. In fully developed specimens with 20 tentacles, six pairs of microcnemes are present: one pair in each of the six non-directive macrocoels (Fig. 2A). These

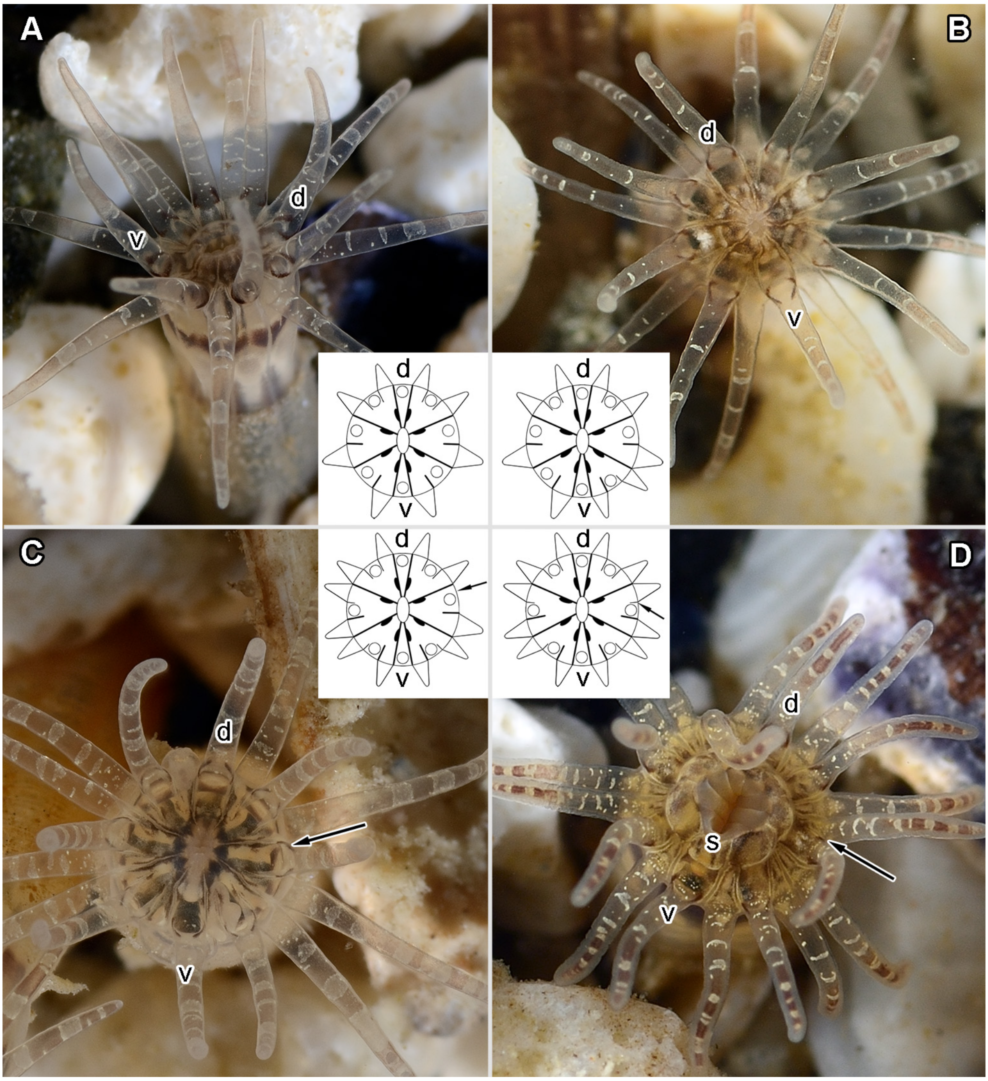

Fig. 4. *Edwardsianthus vostok* sp.n., arrangement of tentacles and mesenteries. A — 16 tentacles, 8+8; B — 17 tentacles, 8+9; C — 19 tentacles, 8+11 (arrow indicates the position where the last microcneme is missing); D — 20 tentacles, 8+12 (arrow indicates the last microcneme, which is smaller than the others). Abbreviations: d — dorsal directive tentacle; s — siphonoglyph; v — ventral directive tentacle. Tentacles of inner cycle indicated by circles in diagrams; primary mesenteries (eight macrocnemes and four microcnemes) are indicated as thicker lines, and secondary microcnemes as thinner lines.

microcnemes extend from the distal end of the scapulus all along the capitulum length (Fig. 1B) and reach the middle of the oral disc (Fig. 1C).

In specimens with 16 tentacles, the microcnemes are arranged similarly to those in 16-tentaculate species of *Edwardsia*: (1) one primary microcneme in each lateral and ventro-lateral macrocoel is paired with dorso-lateral and ventro-lateral macrocnemes forming four primary non-directive endocoels that communicate with four tentacles of the inner cycle; (2) one pair of secondary microcnemes forms an endocoel in each dorso-lateral macrocoel that communicates with a tentacle of the inner cycle (Fig. 4A).

In specimens with 17–20 tentacles, a secondary microcneme appears within the primary non-directive endocoels formed by a macrocneme and a primary microcneme. These first appear in the ventro-lateral macrocoels (in specimens with 17 and 18 tentacles (Fig. 4B), the secondary microcneme indicated by a thinner line), and subsequently in the lateral mac-

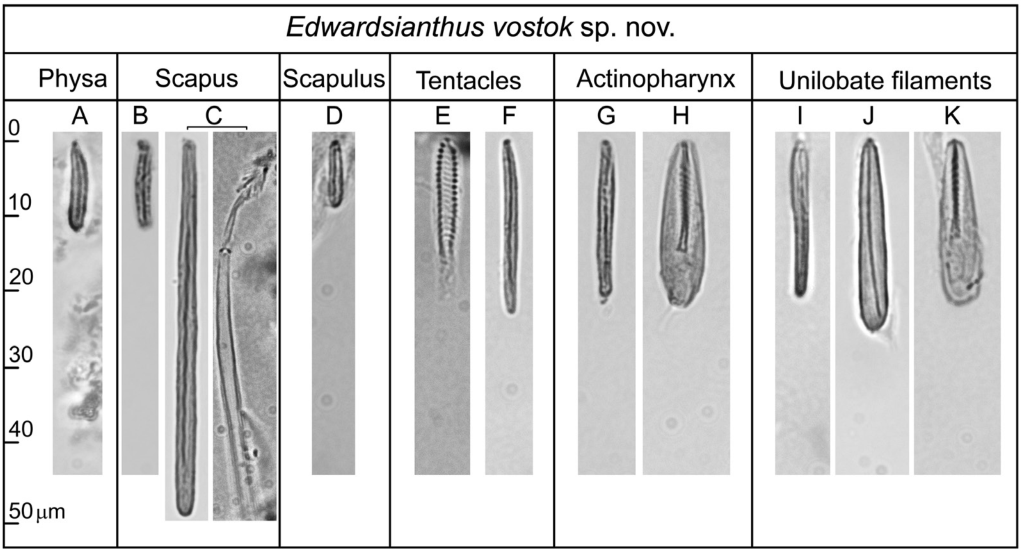

Fig. 5. *Edwardsianthus vostok* sp.n., cnidom.

Table 1. Size ranges (length × width, in µm) and distribution of cnidae in *Edwardsianthus vostok* sp.n. (inferred from examination of five specimens; letters in brackets correspond to letters in Fig. 5).

Body region	Cnidae	Size range (µm)
Physa	(A) basitrichs (common)	10–14 × 1.7–2.5
Scapus	(B) basitrichs (rare)	8–11.5 × 1.5–2
	(C) basitrichs (in nemathybomes)	(28) 46–87 × 2.5–4.8
Scapulus	(D) basitrichs (common)	8–12 × 1.5–2
Tentacles	(E) spirocysts (very numerous)	11–23 × 1.5–3.2
	(F) basitrichs (common)	19–27 × 2–2.8
Actinopharynx	(G) basitrichs (common)	18–31 × 1.7–2.9
	(H) *p*-mastigophores A (common)	18–25 × 5–6.2
Unilobate filaments	(I) basitrichs (few)	17.5–22 × 1.7–2.3
	(J) basitrichs (numerous)	24–34 × 3.5–5
	(K) *p*-mastigophores A (numerous)	18–25 × 4.9–6

rocoels (in specimens with 19 and 20 tentacles, Fig. 4C, D). The secondary microcneme, thus, forms a pair with the primary microcneme within the primary non-directive endocoels, creating a new endocoel associated with a tentacle of the inner cycle, as they develop dorsally to this tentacle (Fig. 4C, arrow). An exocoelic tentacle of the outer cycle is added between the macrocneme and secondary microcneme (where a new exocoel is formed). Secondary microcnemes are often shorter than primary ones (Fig. 4D, arrow) — this difference is clearly visible in photographs of live specimens but difficult (or impossible) to confidently interpret in histological sections of contracted fixed specimens.

All microcnemes are very small, without retractors, filaments, or gonads (Fig. 2A). The macrocnemes have strongly developed retractors, parietal muscles, gonads, trilobate and unilobate filaments. The retractor muscles are restricted, with a long diffuse part located closer to the adaxial margin of the mesenteries and with a pennon on the opposite, abaxial side (closer to the column wall), being better developed in the region below the actinopharynx (Fig. 2C). The retractor muscles are composed of 20–40 muscle processes, which are more heavily branched in the abaxial half of the retractor.

The parietal muscles in the scapus and scapulus are symmetrically developed on both sides of the mesentery, being oval, triangular, or rhombus-shaped in transverse sections, and have five to eight, often branched, mesogloeal folds (muscle processes) (Figs 2; 3B, D). The parietal muscles in the capitulum are much weaker (Fig. 3B), not symmetrical, and better developed on the side of the retractor. The parietal muscles extend for 15–20 µm onto the column wall on both sides of the mesentery (in all its parts: in the physa, scapus, scapulus, and capitulum).

The ectoderm of the physa is clearly thicker than that in the scapus. The radial muscles of the oral disc and the longitudinal muscles of the tentacles are ectodermal (Fig. 3B). The actinopharynx is very short, being twofold longer than contracted scapulus, less than 2 mm in 1.5-cm long specimen (Fig. 3A). The ventral siphonoglyph is usually not recognizable, being sometimes discernible only in the most distal part of the actinopharynx (Fig. 4D).

The distal parts of the mesenteries (immediately below the actinopharynx) lack filaments. The trilobate filaments appear on the mesenteries in the middle part of the column and become larger (thicker) proximally. In the proximal part of the column, they pass into unilobate filaments that reach the physa (Fig. 3A). The gonads are located on the level of the trilobate filaments (Fig. 2D) but are absent on the level of the unilobate filaments. The ova are up to 80 µm in diameter.

Cnidom: spirocysts, basitrichs, and *p*-mastigophores A (Table 1, Fig. 5). The nemathybomes contain numerous (about 100) large basitrichs of a single type (Fig. 5C). These basitrichs have a characteristic feature: the most basal part of the inverted stinging tube (10–12 µm, with the total stick length of 40–75 µm) is very thin, implying weaker or no spine armament. The stinging tube in exploded capsules (Fig. 5C) has an unarmed basal part of the same length (about 11 µm), with large spines located behind, as in typical basitrichs. These basitrichs are smaller (28–55 µm) in the nemathybomes of the proximal part of the scapus and larger (46–87 µm) in its middle part, where the nemathybomes are better developed. Smallest of them (only three found: 28 × 2.6; 36.5 × 2.5; 41.5 × 2.6 µm), have the same structure as larger capsules and belong to the same type. The marginal parts of the mesenteries, between the actinopharynx and trilobate filaments, contain basitrichs 26–30 × 2.6–3 µm. The trilobate filaments also contain basitrichs: 30–35.6 × 2.5–3.5 µm and, rarely, about 15 × 1.6 µm. Similar but more numerous basitrichs are present in the unilobate filaments (Fig. 5 I and 5J), but the latter additionally contain *p*-mastigophores A (Fig. 5K).

ETYMOLOGY. The specific epithet is a noun in apposition based on the name of the geographic locality of the type material, Vostok Bay at the Marine Biological Station "Vostok" (see comments in Dubois, Raffaëlli, 2009: 21 on such names).

GENERIC ASSIGNMENT AND COMPARISON WITH RELATED SPECIES. The arrangement of the mesenteries suggests that the species should be assigned to *Edwardsianthus*. As evident from the description above, up to the 16-tentacle stage, these sea anemones exhibit the mesenterial arrangement typical of edwardsiids, shared by all members of the family. However, the subsequent appearance of secondary microcnemes within the primary non-directive endocoels distinguishes this species, along with other *Edwardsianthus* species, from all remaining edwardsiids in which arrangement of the microcnemes is known. Other features, including the presence of nemathybomes (known only in *Edwardsia*, *Scolanthus*, and *Edwardsianthus*), are also consistent with those of *Edwardsianthus*. In *E. vostok* sp.n., the nemathybomes are arranged into eight rows, a feature characteristic in this genus only of *E. gilbertensis*, vs. scattered nemathybomes in all other *Edwardsianthus* species. *Edwardsianthus vostok* sp.n. differs from *E. gilbertensis* in significantly larger nematocysts in the nemathybomes: the reported length of the basitrichs in the nemathybomes in *E. gilbertensis* is 31–41 µm (Carlgren, 1931) or 34–45 µm (Izumi, Fujii, 2021) vs. mostly 46–87 µm in *E. vostok* sp.n. Moreover, *p*-mastigophores A in the actinopharynx and filaments in *E. vostok* sp.n. are significantly smaller (18–25 µm) than in *E. gilbertensis* (25.4–46.5 µm according to Carlgren, 1931 and Izumi, Fujii, 2021); the filaments of *E. gilbertensis* lack large basitrichs, and spirocysts in the tentacles are somewhat shorter than in *E. vostok* sp.n. (8.5–14.3 µm according to Izumi, Fujii, 2021 vs. 11–23 µm in *E. vostok* sp.n.) Furthermore, *E. gilbertensis* contains zooxanthellae in the endoderm (Carlgren, 1931; Izumi, Fujii, 2021) vs. the lack of zooxanthellae in *E. vostok* sp.n.. The arrangement of the tentacles in *E. gilbertensis* (5+15) also distinguishes it from *E. vostok* sp.n. (in which they are arranged into 8+12). Molecular data show these two species as related (located near each other in the phylogenetic tree) but specifically distinct (Fig. 6).

In the external appearance and color pattern, *E. vostok* sp.n. closely resembles *Scolanthus callimorphus* (see Manuel, 1981) and *S. isei* (see Izumi, Fujita, 2018: fig. 4B), but *Scolanthus* species lack the physa which is very distinct in *E. vostok* sp.n.

HABITAT. The species is reported from shallow depths (4–8 m), where it was found in so-called "phoronid beds" (dense aggregations of phoronids). In the tanks, the specimens burrowed into the gravel sediment within a few hours, and only the most distal part of the column with the crown of tentacles remained protruding above the sediment surface (Fig. 1B–D). However, the specimens were unable to burrow into a muddy substrate.

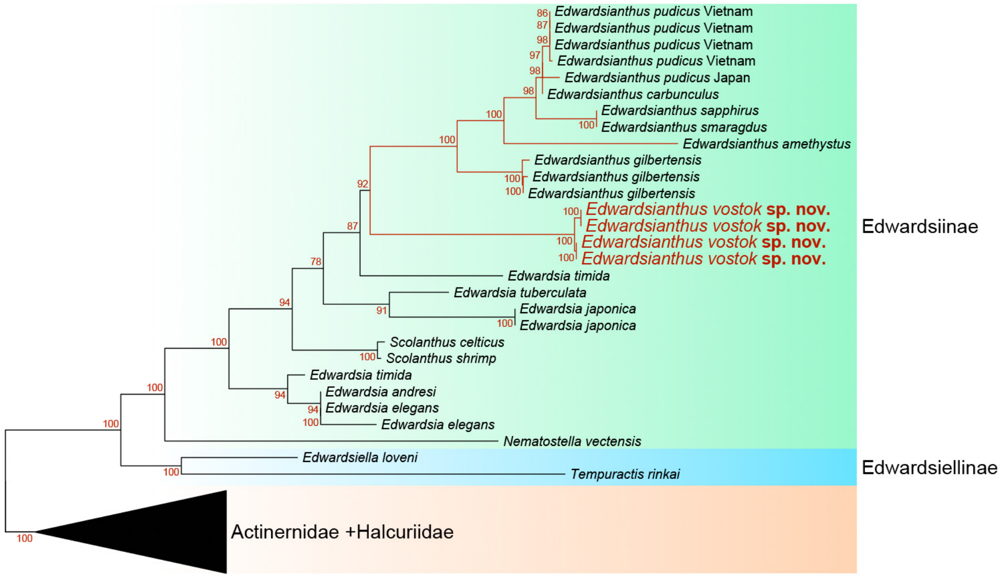

Fig. 6. Maximum Likelihood tree inferred from 12S + 16S + 18S + 28S + COIII concatenated dataset sequences; numerals are bootstrap values. Only a sub-tree containing edwardsiid taxa is shown. For full phylogenetic tree generated during the present study, see Supplement Fig. 1.

DISTRIBUTION. The species is known only from the type locality, Vostok Bay, Peter the Great Gulf, Sea of Japan.

MOLECULAR DATA. In general, the obtained results (Fig. 6) are in agreement with those reported by Izumi, Fujii (2021, fig. 10): the species of *Edwardsianthus* form a separate clade. In our analysis, *Edwardsianthus vostok* sp.n. is resolved as basal to all other *Edwardsianthus* species, with the bootstrap support being, however, not high, while *E. gilbertensis* is basal to all remaining species of the genus.

In the analysis by Izumi, Fujii (2021), *E. smaragdus* was resolved on a very long branch. This is an artifact caused by two (18S and 16S) incorrect sequences of *E. smaragdus*. The BLAST tool has shown that the 18S sequence (LC649487) of *E. smaragdus* has 99.47% identity with *Symbiodinium* sp., while 16S sequence (LC649479) is very similar to the sequences of many acontiate sea anemones but distant from those of any species of Edwardsiidae. In our dataset, we have not used these putatively incorrect sequences, and *E. smaragdus* and *E. sapphirus* are grouped together. The remaining sequences (12S) of these two species are completely identical (but differ from other *Edwardsianthus* species).

Molecular data show that *E. carbunculus* is conspecific with *E. pudicus*: the 16S and 18S sequences of *E. carbunculus* (one specimen) and *E. pudicus* (one specimen sequenced by Izumi, Fujii, 2021, and four specimens from Vietnam sequenced in the present study) are completely identical, while the 12S sequence of our specimen from Vietnam differs by only one nucleotide from the 12S of *E. carbunculus* and also by one nucleotide from the 12S of *E. pudicus* from Japan.

To date, only a few species of Edwardsiidae have been sequenced, and it is impossible to draw any conclusion on the phylogeny of this family based solely on the molecular data. However, it is noteworthy that in our tree, *Edwardsiella loveni* (Carlgren, 1892) (together with *Tempuractis rinkai* Izumi, Ise et Yanagi, 2017) forms a clade sister to all other edwardsiids. This result is in agreement with that published by Carlgren (1892) who segregated *Edwardsiella loveni* (known at that time as *Milneedwardsia loveni* Carlgren, 1892) into a separate family and then subfamily Milneedwardsiinae Carlgren, 1892 (its current valid name is Edwardsiellinae Sanamyan et Sanamyan, 2021; see Sanamyan, Sanamyan, 2021 for further information).

General remarks on the genus *Edwardsianthus* and included species

Edwardsianthus was established by England (1987), who examined many specimens from widely distant localities, including Singapore, Madagascar, Aden, the Maldives, and the Great Barrier Reef, and discussed available descriptions of several nominal *Edwardsia* species assignable to *Edwardsianthus* (*Edwardsia adenensis* Faurot, 1895, *E. rakaivae* Bourne, 1916, *E. vermiformis* Bourne, 1916, *E. bocki* Carlgren, 1931, *E. gilbertensis*, and *E. stephensoni* Carlgren, 1950). England (1987) recognized only two valid species of *Edwardsianthus*. All the specimens having scattered nemathybomes and strong retractors, collected or described from many distant tropical localities, were identified by him as *E. pudicus*, and all nominal species having these characters were synonymized with *E. pudicus*. He concluded that the specimens with the nemathybomes arranged into rows and weaker retractors belong to a separate species, *E. gilbertensis*. However, as it has now become clear, *Edwardsianthus* is represented by more than two species. Many morphotypes, evidently representing different species, may be recognized in the numerous available underwater photographs (see Rowlett, 2020, iNaturalist, 2025). Indeed, some of these morphotypes have recently been described as distinct species (Izumi, Fujii, 2021). Several of these species have strong retractors and scattered nemathybomes, and, therefore, the similarity in these two features cannot be used as a sole argument supporting the synonymy of the species. In view of the above facts, it would be useful to discuss the taxonomic history and available information on the nominal and taxonomic species assignable to *Edwardsianthus*. The nominal taxa assignable to *Edwardsianthus* are listed below in a chronological order of their original descriptions.

Edwardsia pudica Klunzinger, 1877

This species was originally described from the Red Sea. The original description (Klunzinger, 1877) contains a very informative description of the color pattern of live specimens: the body is white to grey-blue when the cuticle is scraped off; the tentacles are grey, grey-green, or brown, with light green spots and bright vermilion dots, lines, or spots on them; the disc is green, and the edge of the mouth is brown. The color pattern of the tentacles (in particular, the red dots or lines on the green spots) is remarkable and allows unmistakable identification of live specimens of this originally described color variety in photographs of live specimens (Figs 7A, B; 8E; 9B). Also, Klunzinger (1877) reported that the tentacles of the inner cycle, five or six in number, were much shorter than the outer tentacles. This feature is clearly seen in the underwater photograph of the specimen from the Red Sea (Fig. 7A). The photograph also shows that the dorsal tentacle may be somewhat bent upward. The specimens of the originally described color variety are also known from the coasts of Oman, where they are quite commonly found according to reports (Sven Kahlbrock, personal communication, 2009), and Vietnam (our data; Fig. 8E).

The iNaturalist (2025) platform hosts numerous photographs of tropical and subtropical Edwardsiidae, primarily of the genus *Edwardsianthus*, including about a hundred specimens of *E. pudicus* displaying various color morphs while retaining a recognizable color pattern. These records confirm the species' broad distribution across the Indian and Pacific Oceans: from South Africa (reaching 28°S, see iNaturalist, 2025, observation 11130532) along the eastern African coast (Mozambique, Tanzania, Kenya, and Madagascar; see iNaturalist, 2025, observations 21420427, 188906381, 18751654, 122159684), the northern Indian Ocean (iNaturalist, 2025, observations 111295436, 180906199), Southeast Asia (Indo-Pacific, e.g. see iNaturalist, 2025, observations 40300250, 50981565, 246775352, 196420942, 1861394, 207372205), northern and eastern Australia (to 30°S, see iNaturalist, 2025, observations 246725289, 251584108), New Caledonia (iNaturalist, 2025, observations 202785932, 240070043, 65068745), Fiji (iNaturalist, 2025, observations 126307233, 152479201, 194244148), the Marshall Islands (iNaturalist, 2025, observations 161090067, 161090075, 161090079), Midway Atoll on the Hawaiian Ridge (iNaturalist, 2025, observation 185182626), and as far north as Japan (32°N; see iNaturalist, 2025 observation 240100309 and Izumi, Fujii, 2021).

Carlgren (1900) recorded this species as *Edwardsiella pudica* from East Africa (Zanzibar), based on 15 specimens. He described the tentacle coloration as highly variable: grass-green, green, white-speckled, orange-red, brown, pale green with white spots and dark gray-striped aborally. The oral disc was reported as pale flesh-colored. Notably, iNaturalist (2025) currently hosts no records of *Edwardsianthus pudicus* from Zanzibar (although has records from continental coast of Tanzania), but hosts records of specimens of several putatively distinct *Edwardsianthus* species displaying color patterns that differ them markedly from *E. pudicus* while closely matching the Carlgren's (1900) descriptions (e.g. see iNaturalist, 2025 observations 39413470, 150251764, 7447429, 265270601, 185677526, 187793387). The most interesting character mentioned by Carlgren (1900: 47) was the fact that "Nesselhöckerkapseln" (=nemathybomes) in his specimens had very few nematocysts or almost completely lacked them. In further descriptions of *E. pudicus*, the absence of nematocysts in the nemathybomes was not mentioned. In the specimens from Vietnam we have examined, the nemathybomes contain numerous (hundreds) basitrichs (our data on the cnidom of *E. pudicus* from Vietnam are provided in Table 2).

Fig. 7. A — *Edwardsianthus pudicus* (Red Sea, photo by Sven Kahlbrock); B — *Edwardsianthus pudicus*, white arrows indicate insertions of secondary microcnemes (Singapore, photo by budak / CC BY-NC 4.0, iNaturalist, 2025, observation 202264465); C — *Edwardsia vivipara* with 12 tentacles, 2+10 (Edithburgh, Australia; photo by Ron Greer / CC BY-NC 4.0, iNaturalist, 2025, observation 32884764); D — *Edwardsia vivipara* with 19 tentacles, 4+15 (Kangaroo Island, Australia; photo by David Spencer Muirhead / CC BY-NC 4.0, iNaturalist,2025, observation 15711714); E, F — *Edwardsianthus gilbertensis* (Hainan, China; photo by ayegege/ CC BY-NC 4.0, iNaturalist, 2025, observation 192037145).
Abbreviations: d — dorsal directive tentacle; v — ventral directive tentacle.

England (1987: 226) identified many specimens from several distant localities as *Edwardsianthus pudicus*. He reported two color varieties of the tentacles in his specimens: "(a) delicate magenta-pink with thin purple line running from the white tip to the disk; (b) light-green with thin orange line". England (1987) stated that in *E. pudicus*, the tentacles are arranged into 8+12. He presumably assigned all endocoelic tentacles to the first cycle and all exocoelic tentacles to the second. This interpretation likely results from

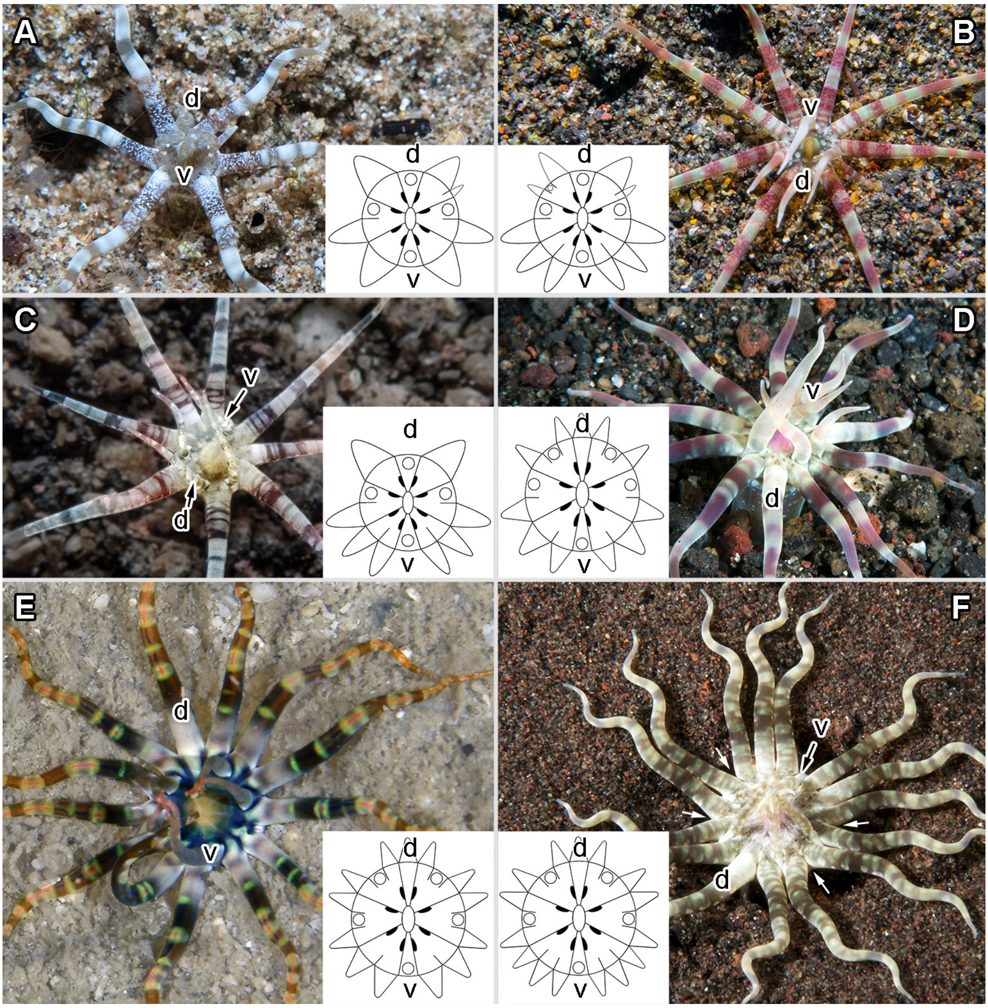

Fig. 8. A — *Edwardsianthus* sp. with 11 tentacles, 4+7 (Batangas, Philippines; photo by Georgina Jones / CC BY-SA 4.0, iNaturalist, 2025, observation 21935549); B — *Edwardsianthus* sp. with 15 tentacles, 5+10 (Indonesia, Bali Island; photo by Scott and Jeanette Johnson / CC BY-NC 4.0, iNaturalist, 2025, observation 253788715); C — *Edwardsianthus* sp. with 12 tentacles, 4+8 (Indonesia, Bali Island; photo by Glenn Biscop / CC BY-NC 4.0, iNaturalist, 2025, observation 155728358); D — *Edwardsianthus* sp. with 16 tentacles, 5+11 (Indonesia; photo by Andrey Ryanskiy); E — *Edwardsianthus pudicus* with 18 tentacles, 5+13 (Vietnam; photo by Oleg Savinkin); F — *Edwardsianthus* sp. with 20 tentacles, 5+15 (Indonesia; photo by Andrey Ryanskiy; white arrows indicate insertions of nondirective macrocnemes).
Abbreviations: d — dorsal directive tentacle; v — ventral directive tentacle. Tentacles of inner cycle in diagrams are indicated by circles.

the challenge of determining tentacle arrangement in fixed material. As Carlgren (1931: 23) emphasized, accurate determination of tentacle arrangement requires examination of either live specimens or fixed specimens in which the oral disc remains fully expanded. In the original description, Klunzinger (1877) reported five or six shorter tentacles in the inner cycle, but not eight. The photographs of live specimens from the type locality (the Red Sea) show five short, upward-directed tentacles of the inner cycle and a stable arrangement of the tentacles of the outer cycle between the tentacles of the inner cycle: *4+2+3+2+4* in specimens with 20 tentacles (Fig. 7A).

Izumi, Fujii (2021) reported *E. pudicus* from Kagoshima, southern Japan. They stated, apparently following England (1987), that the tentacles were arranged as 8+12 (Izumi, Fujii, 2021: 158). However, the photograph of the *E. pudicus* specimen examined

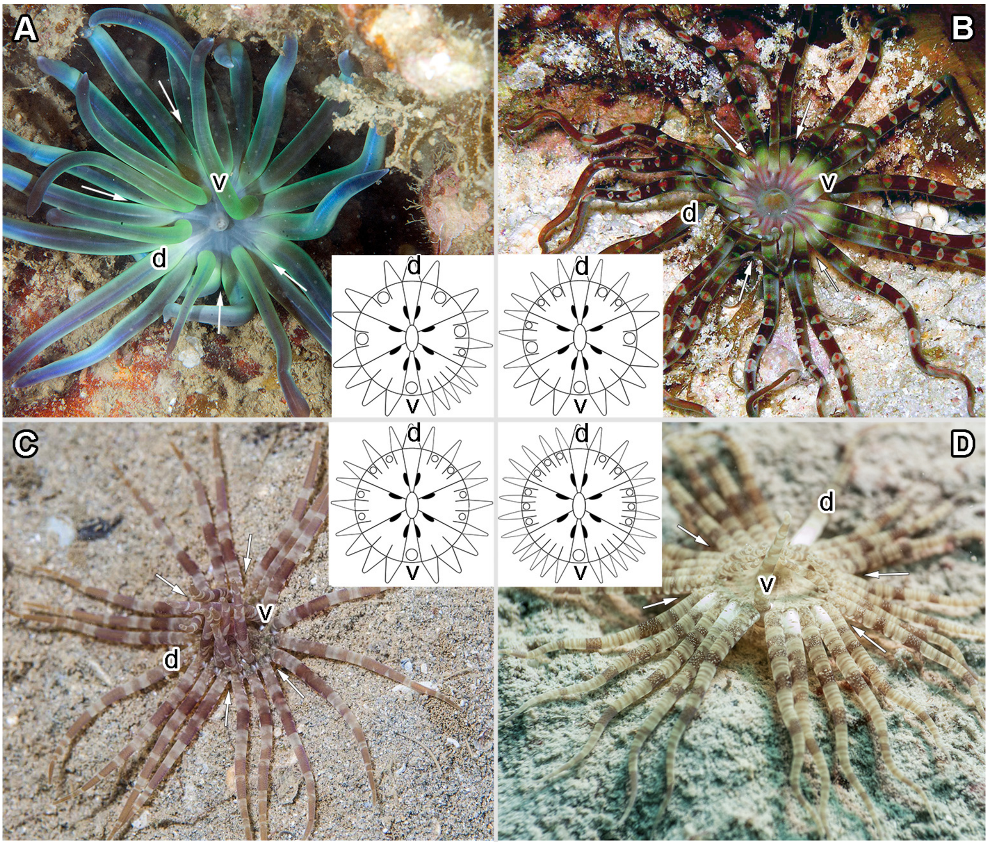

Fig. 9. A — *Edwardsianthus sapphirus* with 24 tentacles, 6+18 (Indonesia; photo by Andrey Ryanskiy); B — *Edwardsianthus pudicus* with 26 tentacles, 8+18 (Red Sea; photo by Sven Kahlbrock); C — *Edwardsianthus* sp. with 28 tentacles, 9+19 (New Caledonia; photo by juju98/ CC BY-NC 4.0, iNaturalist, 2025, observation 98965310); D — *Edwardsianthus* sp. with 38 tentacles, 12+26 (Middle Island, Queensland, Australia; photo by Terry Farr / CC BY-NC 4.0, iNaturalist, 2025, observation 200232656).

Abbreviations: d — dorsal directive tentacle; v — ventral directive tentacle. Tentacles of inner cycle in diagrams are indicated by circles. White arrows indicate insertions of non-directive macrocnemes.

in their study (see Izumi, Fujii, 2021: 159, Fig. 2B) clearly shows a tentacle arrangement of 5+15, i.e., the inner cycle consists of only five distinctly shorter and thinner tentacles, while the outer cycle consists of 15 longer and thicker ones.

The presence of zooxanthellae was not mentioned by Izumi, Fujii (2021), but they were most probably present at least in the endoderm of the tentacles (see Izumi, Fujii, 2021, Fig. 2D). The specimens described by Carlgren (1900, 1931) and England (1987) contained zooxanthellae in the endoderm, as well as our specimens from Vietnam.

Edwardsia adenensis Faurot, 1895

This species was described from a single specimen collected off Aden. While the specimen had only 15 or 16 brown-spotted tentacles (fewer than typically reported for *Edwardsianthus*), the Faurot's (1895) description of the microcneme arrangement (20 mesenteries: 8 muscular and 12 microcnemes arranged into pairs) unequivocally placed it within *Edwardsianthus*. Faurot (1895) repeatedly mentioned that his specimen had a cone-shaped aboral end (with no physa). It is likely that its physa was invaginated and overlooked, especially if it was small. Despite the Faurot's statement that his species was distinct from *Edwardsia pudica*, Carlgren (1900, 1931) later synonymized them. To support his opinion, Carlgren (1931) indicated the almost total lack of nematocysts in the nemathybomes in *E. adenensis* mentioned by Faurot (1895), a feature that Carlgren (1900) observed in the East African material identified by him as *E. pudica*. For the same specimens, Carlgren (1900: 46) reported the weak development of the physa. This is corroborated by his illustration (Carlgren, 1900: Table

Table 2. Size ranges (length × width, in μm) and distribution of cnidae in *Edwardsianthus pudicus* (inferred from examination of two specimens).

Body region	Cnidae	Size range (μm)
Physa	Basitrichs (common)	13–16.8 × 2.3–3
Scapus	Basitrichs (common)	13–14 × 2.2–2.8
	Basitrichs (in nemathybomes)	41.5–51.5 × 2.8–3.6
Scapulus	Basitrichs (common)	11–14.5 × 2–3
	Basitrichs (few)	33–39 × 2.3–3.3
Tentacles	Spirocysts (numerous)	9–20 × 1.8–3.4
	Basitrichs (numerous)	19–28 × 2–3
Actinopharynx	Basitrichs (common)	11–17.5 × 2.1–3.2
	Basitrichs (common)	30–37.5 × 3–4.2
	P-mastigophores A (very rare)	35–35.2 × 4.8–6
Unilobate filaments	Basitrichs (common)	17.3–28.6 × 2.4–3.2
	Basitrichs (numerous)	30.5–39 × 3.3–4.8
	P-mastigophores A (few)	22.5–32 × 3.6–5.5

I, Fig. 5), where no physa is visible, and the aboral end of the body appears tapered. England (1987) also synonymized these two species, basically because he found the retractor muscles of *E. adenensis* similar to those of *E. pudicus*.

However, other *Edwardsianthus* species possess similarly strong retractors (Izumi, Fujii, 2021). Moreover, Izumi, Fujii (2021) described a new species, *Edwardsianthus amethystus* Izumi et Fujii, 2021, characterized primarily by “nemathybome-like structures protruding from the mesoglea, but without any nematocysts”, for which they indicated “quite small physa” (Izumi, Fujii, 2021: 175). The specimens described from off Aden and waters of Zanzibar and Japan are characterized not only by the absence of nematocysts in the nemathybomes but also by a similar spotted color pattern: tentacles with brown spots (Faurot, 1895), white spots (Carlgren, 1900), and light (“pale purple”) and dark (“dark purple”) spots, as described in the text and visible in lifetime photographs of the holotype of *E. amethystus* (see Izumi, Fujii, 2021: 175–176, Fig. 9A). iNaturalist (2025) also hosts numerous photographs of a distinct *Edwardsianthus* species that differs from *E. pudicus* in its spotted color pattern and having similarly wide geographic distribution: the eastern African coast (reaching 22°S, Mozambique, Zanzibar, Kenya; see iNaturalist, 2025, observations 26519647, 194505324, 166892725, 270210024), the Red Sea (e.g. iNaturalist, 2025, observations 147335348, 137297912), Persian Gulf (iNaturalist, 2025, observations 145170710, 60825186), the Maldives (iNaturalist, 2025, observations 171945748, 166556258, 200173806), Southeast Asia (Indo-Pacific, e.g. iNaturalist, 2025, observations 148351098, 38092518, 37270141, 35783939, 103409366, 198572005, 251272097), northern and eastern Australia (to 27°S, iNaturalist, 2025, observations 214308769, 249723949, 31825146), New Caledonia (iNaturalist, 2025, observations 97308400, 66797152), Fiji (iNaturalist, 2025, observation 149017361), the Marshall Islands (iNaturalist, 2025, observations 161090074, 181990807, 220968768), French Polynesia (iNaturalist, 2025, observation 61642309), and Northern Mariana Islands (iNaturalist, 2025, observation 225625031). All the facts above provide evidence that the synonymization of *E. adenensis* with *E. pudicus* was unjustified, and the East African specimens studied by Carlgren were misidentified by him and should be assigned to another species, possibly to *E. adenensis*. At the same time, *E. amethystus* may also be conspecific with *E. adenensis*.

Edwardsia rakaiyae Bourne, 1916

This species is based on three specimens from Papua New Guinea described by Bourne (1916). The presence of 20 tentacles and the arrangement of the microcnemes (“twelve in number, two in each sulco-lateral, lateral, or sulculo-lateral intermesenterial interspace”, Bourne, 1916: 518) undoubtedly indicates that it belongs to *Edwardsianthus*, but the taxonomic affinity of the species cannot be determined. The original description is based on specimens kept in alcohol for a long time (see introduction in the paper of Bourne, 1916) which completely lost their original color. Bourne (1916: 518) indicated that the tentacles were arranged in two cycles, 8+12 (“The tentacles in two circlets: the inner comprising eight, the outer twelve tentacles”), but, since the distal part of the column was invaginated, it was impossible to determine how the tentacles were actually arranged in live specimens. The retractors, described as “enormously developed”, the scattered “papillae” on the scapus, and the larger size exclude conspecificity with *E. gilbertensis*. England (1987) synonymized *E. rakaiyae* with *E. pudicus*, but it may equally be conspecific with any other *Edwardsianthus* species having similar strong retractors (*E. sapphirus* and *E. amethystus*). On iNaturalist (2025), there are photos of only two specimens of *Edwardsianthus* from Papua New Guinea, both apparently belonging to the same species with spotted tentacles (iNaturalist, 2025, observations 251272097, 154146096). Thus, *E. rakaiyae* may be conspecific with *E. adenensis*, but currently we prefer to follow Williams (1981), who considered *Edwardsia rakaiyae* a *nomen dubium* and exclude it from the synonymy of *E. pudicus*.

Edwardsia vermiformis Bourne, 1916

This species is based on a single, severely damaged, and poorly fixed specimen described by Bourne (1916) from New Caledonia. England (1987) stated that “the presence of much-branched mesogloeal folds of the retractors and the nemathybomes scattered over the column indicate that *E. vermiformis* might be referred to *E. pudica*”. As discussed above, these two features are not sufficient for species identification because they are characteristic of several distinct species. iNaturalist (2025) hosts 36 photographs of *Edwardsianthus* specimens from New Caledonia, among which, besides *E. pudicus*, at least three other *Edwardsianthus* species have been documented. Moreover, the specimen *E. vermiformis* was so damaged that Bourne (1916) failed to see the tentacles or microcnemes, therefore, their arrangement remains unknown, and there is no certainty in assigning it to *Edwardsianthus*. We see no reason to synonymize *E. vermiformis* with *E. pudicus* and prefer to follow Williams (1981), who considered it a *nomen dubium*.

Edwardsia bocki Carlgren, 1931

The species has been described from many specimens from Fiji by Carlgren (1931) and synonymized with *E. pudicus* by England (1987). The color pattern of the tentacles is unknown. It has scattered nemathybomes and very strong retractors and, therefore, may be conspecific with any of the *Edwardsianthus* species having these features. Based on the cnida sizes provided by Carlgren, this specimen cannot be confidently assigned to any species with published cnida measurements. The nematocyst sizes in nemathybomes (27–43 × 2.5–3 μm) were, on average, slightly smaller (Carlgren reported a length of 36.2 μm) than in other species. However, as we demonstrated above in the description of cnidome for *Edwardsianthus vostok* sp.v., size ranges of basitrichs in nemathybomes may vary significantly across different scapus regions. iNaturalist (2025) contains six photographs of *Edwardsianthus* from Fiji: four of *E. pudicus* and two images of another *Edwardsianthus* species with spotted tentacles. Thus, *Edwardsia bocki* may be conspecific with *E. pudicus* or represent a distinct species — this can only be determined by examining new material from the type locality.

Edwardsianthus gilbertensis (Carlgren, 1931)

This species was originally described by Carlgren (1931) as *Edwardsia gilbertensis* from numerous specimens collected in the waters of the Gilbert Islands (Kiribati) and the Kai Islands (Indonesia). It is distinguished from most other *Edwardsianthus* species by its nemathybomes arranged into rows and moderate-sized retractors. The Japanese specimens reported by Uchida, Soyama (2001) and Izumi, Fujii (2021) have an inconspicuous whitish-gray coloration. It is the smallest known tropical/subtropical species in the genus, whose fixed specimens have a uniformly thin column (2–4 mm wide and 20–65 mm long) (Carlgren, 1931, 1950; Izumi, Fujii, 2021). Live specimens possess remarkably small tentacles: five inner tentacles about 1 mm long, and outer tentacles 2–3 mm long (Izumi, Fujii, 2021: 164).

Rowlett (2020: 248) published several photographs of specimens identified as *E. gilbertensis* from Indonesia. Unfortunately, no anatomical description was provided for these specimens, but their bright coloration, significantly larger size, and longer tentacles suggest that they likely represent a species different from true *E. gilbertensis*. Carlgren (1931: 10) and Izumi, Fujii (2021: 165) reported that *E. gilbertensis* forms beds of large numbers of individuals, a feature not observed in other *Edwardsianthus* species. Rowlett (2020: 248) stated that up to 4800 specimens per square meter were “reported from a Hawaiian mud flat”. At iNaturalist (2025), there are photographs of small sea anemones in dense populations (from Hainan, China) that match the descriptions of *E. gilbertensis* by Carlgren (1931, 1950) and Izumi, Fujii (2021) in terms of the size and arrangement of the tentacles (16–20 tentacles in two cycles: five very small tentacles of the inner cycle, and the outer tentacles approximately equal in length to the oral disc radius), the body shape, and the nemathybomes arranged into eight rows (Fig. 7E, F).

Edwardsia stephensoni Carlgren, 1950

This species was described from eight specimens from the Great Barrier Reef by Carlgren (1950) and synonymized with *E. pudicus* by England (1987). The tentacles of one fixed specimen retained a green coloration. Green tentacles were described for *E. sapphirus*. In addition, Rowlett (2020: 249) mentioned *Edwardsianthus* sp., which also had green color on the tentacles, as endemic to New South Wales. Any of these species may be conspecific with *E. stephensoni*, and there is no reason to consider it a synonym of *E. pudicus*. Carlgren (1950: 42, fig. 1) stated that the tentacles in *E. stephensoni* were arranged into three cycles: 5+3+12, where the first two cycles (eight tentacles) were endocoelic, and all tentacles of the third cycle were exocoelic (he illustrated this with a drawing made by Stephenson). He stated that "the ventral directive tentacle belongs to the first cycle, the dorsal directive tentacle to the second cycle". This arrangement appears intermediate between that of *Edwardsianthus vostok* sp.n. (8+12) and other *Edwardsianthus* species (5+15) which typically show two distinct cycles of tentacles. However, the examination of the extensive photographic records at iNaturalist (2025) has not revealed any *Edwardsianthus* specimens displaying this particular tentacle arrangement in three cycles. It is possible that Stephenson's illustration reproduced in Carlgren (1950) merely schematically emphasized the endocoelic nature of the three tentacles in the outer cycle, while all the remaining tentacles were exocoelic. Of the 12 *Edwardsianthus* specimens documented on iNaturalist (2025) from the Great Barrier Reef, half exhibit the colour pattern typical of *E. pudicus*, while the remainder display spotted tentacles in grey or brown shades.

Edwardsianthus carbunculus Izumi et Fujii, 2021, *E. sapphirus* Izumi et Fujii, 2021, *E. smaragdus* Izumi et Fujii, 2021, and *E. amethystus* Izumi et Fujii, 2021

These four species were described by Izumi, Fujii (2021) from southern Japanese islands. For three species (*E. carbunculus*, *E. sapphirus*, and *E. smaragdus*), the authors reported a previously undocumented feature for this genus: the presence of two distinct size classes of basitrichs (small and large) in the nemathybomes. However, the small basitrichs (about 16–20 × 3–4 μm in all three species) were rare (only four, eight, and two capsules observed in each species, respectively) and likely represented contaminants from surrounding epithelia. Conversely, the numerous large basitrichs reported in the column epithelium of *E. carbunculus* appear to be contaminants from nemathybomes (with their sizes matching exactly).

Edwardsianthus carbunculus, described from a single specimen, shows no distinction from *E. pudicus* in molecular features (see the Molecular Data section) and is almost certainly conspecific with it. We see no significant morphological differences between them, except for the excess red pigmentation in coloration of *E. carbunculus*, which may represent intraspecific variation. The differentiation in habitat ("*E. pudicus* inhabits tropical/subtropical waters vs. *E. carbunculus* lives only in temperate seas", Izumi, Fujii, 2021: 167) based on a single specimen, as the authors propose, is also inaccurate. Rowlett (2020: 249) published a photograph of an identical color morph of *E. pudicus* from Singapore (tropical waters). Furthermore, the type locality for *E. carbunculus* (Nishidomari, Kochi Prefecture, Japan, about 32°46.7′ N 132°43.9′ E) cannot be definitively classified as temperate due to the influence of the Kuroshio Current, which forms subtropical mode water in the Shikoku Basin (Sugimoto, Hanawa, 2014; Nishikawa *et al.*, 2023). This locality, thus, represents the northernmost record of *E. pudicus*.

Edwardsianthus sapphirus and *E. smaragdus*, described from a single specimen each, cannot be distinguished on the basis of molecular data (see the Molecular Data section above) (Fig. 6). They are similar in coloration of the tentacles (metallic greenish-blue and brilliant green with pale purplish tips, in both cases without any color spots, patches, etc.) The size ranges of nematocysts in these species are similar and in most cases overlap (see table 5 in Izumi, Fujii, 2021: 171). The only difference is that *p*-mastigophores in the actinopharynx were not reported for *E. sapphirus*, while rare capsules of this type were mentioned for *E. smaragdus* (only five capsules found), and two spirocysts (probably contaminants from the tentacles) were found in the filaments of *E. smaragdus* only. If further study shows that the differences in the musculature development are related to the differences in size or age, these two species should be considered conspecific. iNaturalist (2025) lists 13 records labeled "*Edwardsianthus sapphirus*" with identical spotless blue-green coloration, distributed exclusively in the Asia-Pacific region: Indonesia, Malaysia, the Philippines, and the Solomon Islands (e.g., iNaturalist, 2025, observations 83833186, 224123492, 58413829, 16262769). The records from Japan from Okinawa Island and Amami-Oshima Island (26°N and 28°N; Izumi & Fujii, 2021) represent the northernmost known occurrences of this species.

In total, on iNaturalist (2025), we found almost 300 observations of *Edwardsianthus*, which can be divided by color pattern into at least six species, possibly up to eight or more (allowing for the possibility of significant color variability in some species). Thus, the taxonomy of *Edwardsianthus* is unresolved and requires further revision, because several nominal species, which were synonymized in the past with *E. pudicus*, may appear distinct valid species, while the statuses of several recently described species remain unclear.

The arrangement of tentacles and mesenteries as a potentially important taxonomic character

England (1987, Fig. 4) used the arrangement of mesenteries as a key character to differentiate *Edwardsianthus* from *Edwardsia*. However, as now becomes clear, the diagram he published is oversimplified, and the development and arrangement of the mesenteries in Edwardsiidae exhibit significantly greater variability and complexity. The mesentery arrangement in *Edwardsianthus* should not be derived from an 8-mesenterial "*Edwardsia*"-stage, as proposed by England (1987, Fig. 4), but rather from the typical 16-tentacle (16-mesenterial) stage, observed in many *Edwardsia* and *Scolanthus* species, by the addition of four secondary microcnemes within the primary non-directive endocoels. Moreover, the process continues beyond this stage: further addition of microcnemes is possible, either exocoelically in pairs or bilaterally within secondary endocoels. Below, we describe several variants of the arrangement of mesenteries and tentacles, with these data combined into a summary diagram (Fig. 12) that shows also the early developmental stages adapted from the descriptions of tentacle formation in *Nematostella vectensis* Stephenson, 1935 (see Ikmi *et al.,* 2020).

Edwardsianthus specimens with 20 or fewer than 20 tentacles

Edwardsianthus vostok sp.n. differs from other *Edwardsianthus* species by the arrangement of the tentacles. Typically, it has eight tentacles in the inner cycle and 12 in the outer cycle, with two planes of symmetry. In other species of this genus, the inner cycle is usually composed of five shorter vertical tentacles, and the outer cycle of 15 longer and thicker horizontal ones. The latter are arranged as *4+2+3+2+4* between the tentacles of the inner cycle, with the bilateral symmetry (Fig. 8F, diagram).

In *E. vostok* sp.n., all eight endocoelic tentacles are located in the inner cycle, while in the other *Edwardsianthus* species, three of them are in the outer cycle of horizontal tentacles: two tentacles between the microcnemes in the ventro-lateral macrocoels and one in the dorsal directive endocoel. The tentacle originating from the dorsal directive endocoel is often lighter near its base (Figs 7B; 8D–F; 9A, D) and occasionally curved upward (Fig. 7A). In live specimens (observed in underwater photographs), the tentacles frequently form distinct groupings: the horizontal tentacles of each macrocoel, separated by macronemes, lie closer to one another (Figs 8F; 9; 10). In young, not fully formed specimens of these species, which have a smaller number of tentacles (16 or 18), the inner cycle usually contains five short vertical tentacles, while the outer cycle contains a variable number of tentacles arranged as *3+1+3+1+3* in specimens with 16 (Fig. 8D) or as *3+2+3+2+3* in specimens with 18 tentacles (Fig. 8E). In younger specimens at pre-16-tentacle stages, when both pairs of microcnemes have not yet developed in the dorso-lateral macrocoels (between which tentacles of the inner cycle emerge), the dorsal tentacle in tropical *Edwardsianthus* species points upward (Fig. 8A–C). At these stages, the inner cycle consists of four tentacles, resulting in the following arrangements: 4+6 in 10-tentacled specimens, 4+8 in 12-tentacled specimens, and 4+10 in 14-tentacled specimens (Figs 8C, 12). The lability of the dorsal tentacle and its tendency to curve upward persists in some adult specimens (Fig. 7A).

In specimens with 11 tentacles (Fig. 8A) and 15 tentacles (Fig. 8B), the developmental sequence in the dorso-lateral macrocoels is as follows: a small, outer-cycle tentacle, located ventrally to the large outer-cycle tentacle, is first to form (separated by one microcneme), then a vertical inner-cycle tentacle appears between them (separated from the large tentacle by the second microcneme). Examination of mesenterial insertions on the oral disc occasionally reveal paired microcnemes differing slightly in length, with the shorter secondary microcneme positioned dorsally to the primary one (Fig. 7B).

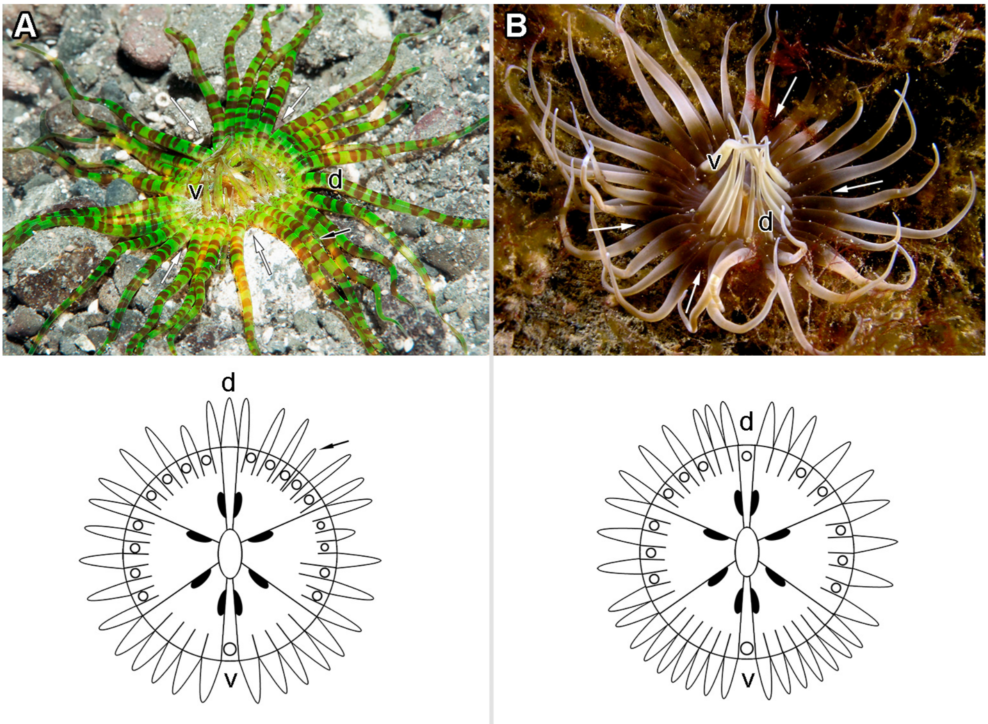

Fig. 10. Edwardsiidae sp. (reconstruction of mesenterial arrangement). A — specimen with 50 tentacles, 18+32 (Papua New Guinea, Milne Bay; photo by Andrey Ryanskiy; black arrow indicates the most slender tentacle of the outer cycle); B — specimen with 47 tentacles, 13+34 (East Timor; photo by Nick Hobgood / CC BY-SA 3.0).
Abbreviations: d — dorsal directive tentacle; v — ventral directive tentacle. Tentacles of inner cycle in diagrams are indicated by circles. White arrows indicate positions of non-directive macrocnemes.

Edwardsianthus specimens with more than 20 tentacles

In *Edwardsianthus* specimens with more than 20 tentacles, which are occasionally found, additional tentacles (and the corresponding pairs of microcnemes) may arise in any non-directive macrocoels (dorso-lateral, lateral, and ventro-lateral). In such specimens, if a pair of microcnemes arises in the dorso-lateral and lateral macrocoels, the corresponding endocoelic tentacle is added to the inner cycle and is directed upward, while the new exocoelic tentacle is positioned horizontally and is added to the outer cycle (Fig. 9). If a pair of microcnemes arises in the ventro-lateral macrocoels, then both new tentacles (endocoelic and exocoelic) are added to the outer cycle and positioned horizontally, similarly to all other tentacles in the ventro-lateral macrocoels (Fig. 9A, D). The additional tentacles of the inner cycle (often having a smaller diameter and length compared to those of the primary endocoelic tentacle within the same macrocoel, Fig. 9B) and their corresponding pairs of microcnemes (marked by visible insertions on the oral disc) in lateral macrocoels can develop on either side of existing microcneme pairs (Fig. 9A, B). Consequently, any non-directive macrocoels in different species of *Edwardsianthus* may contain two pairs of microcnemes (Fig. 9A–C), while dorso-lateral and lateral macrocoels may contain three or four pairs of microcnemes (Fig. 9D). Such a number of microcneme pairs is also observed in a *E. sapphirus* specimen with 35 tentacles (12 in the inner cycle, 23 in the outer) from the Philippines where nearly all the additional microcneme pairs show asymmetric distribution relative to the directive axis, with four microcneme pairs present in the dorso-lateral and lateral macrocoels (iNaturalist, 2025, observation 197206844).

***Edwardsianthus*-like arrangement of tentacles in unidentified Edwardsiidae with numerous tentacles**

Rowlett (2020: 252) published photographs of two species referred to as "Edwardsiidae sp." that resemble tropical species of *Edwardsianthus* but have numerous (up to 50) tentacles arranged into a pattern similar to that in *Edwardsianthus*: in the ventro-lateral macrocoels, all the tentacles are horizontal; in other macrocoels, all or almost all endocoelic tentacles are vertical, and the exocoelic tentacles are horizontal.

In the specimen from Milne Bay (New Guinea), the tentacles are arranged into two cycles: 18+32=50 (Fig. 10A). The outer tentacles are arranged into six (corresponding to the number of the non-directive macrocoels) groups of five tentacles + one dorsal tentacle. One dorso-lateral macrocoel contains a thin sixth horizontal tentacle (Fig. 10A, black arrow) and an additional vertical tentacle. This macrocoel, thus, bears five vertical tentacles, whereas the other non-directive macrocoels (except the ventro-lateral ones) possess only four vertical tentacles each in the inner cycle. The putative arrangement of the mesenteries in this species, reconstructed from the photograph, is shown in the diagram (Fig. 10A). According to our reconstruction, it should have two pairs of microcnemes in the ventro-lateral macrocoels and four or five pairs in the remaining non-directive macrocoels.

The specimen from East Timor (Fig. 10B) has 47 tentacles: 13 vertical in the inner cycle and 34 horizontal tentacles in the outer cycle (seven tentacles in the ventro-lateral macrocoels and four to six in the remaining non-directive macrocoels). The dorsal tentacle here, as it seems, is vertical and belongs to the inner cycle, while the two adjacent endocoelic tentacles are horizontal and belong to the outer cycle. According to our reconstruction, the macrocoels of this species contain three or four pairs of microcnemes (as shown in the diagram in Fig. 10B).

Thus, these two unidentified specimens resemble "overgrown" individuals of *Edwardsianthus* species with multiple pairs of microcnemes in six macrocoels. These specimens may either be conspecific with typical 20-tentacled *Edwardsianthus* species exhibiting similar color pattern (such specimens are documented at iNaturalist, 2025, e.g. observations 214308769 and 42266438) or represent distinct species characterized by a fairly regular arrangement of multiple pairs of microcnemes in all non-directive macrocoels (Figs 9C, D; 10). This regular pattern differs markedly from the aberrant pattern observed in *E. sapphirus* (see iNaturalist, 2025, observation 197206844).

Edwardsianthus*-like arrangement of tentacles and mesenteries in *Scolanthus

The arrangement of the tentacles characteristic of *Edwardsianthus* is reported for some species of *Scolanthus* Gosse, 1853. In the type species of *Scolanthus*, *S. callimorphus* Gosse, 1853, 16 tentacles "are arranged into two cycles, 5+11, those of the inner cycle being distinctly the shorter" and the outer ones arranged as *3+1+3+1+3* (Manuel, 1988: 204, fig. 75B). This arrangement is similar to that of young specimens of tropical *Edwardsianthus* species having 16 tentacles (Fig. 8D). On the other hand, Izumi, Fujita (2018: 17, fig. 6A) reported for *S. armatus* (Carlgren, 1931) and *S. kopepe* Izumi et Fujita, 2018 an arrangement of 16 tentacles into two cycles (8+8), similar to that observed in young 16-tentacled specimens of *E. vostok* sp.n.

Moreover, Izumi, Fujita (2018) described two species of *Scolanthus* which had a pattern of microcnemes arrangement as in *Edwardsianthus*: 12 microcnemes, one pair in each non-directive macrocoel. Both species had 20 tentacles in two cycles. In one species, *S. isei* Izumi et Fujita, 2018, they were arranged as in *E. vostok* sp.n. (8+12), while in the other, *S. ena* Izumi et Fujita, 2018, the tentacles were arranged in a different way, as 10+10. The latter arrangement is a result of a different placement of the tentacles in the lateral macrocoels, with the endocoelic tentacle belonging to the outer cycle and two exocoelic tentacles belonging to the inner cycle (Izumi, Fujita, 2018: 17, fig. 6B). This difference is probably due to the exocoelic development of secondary microcnemes in the lateral macrocoels of *S. ena*, which growing ventrally in relation to the outer-cycle tentacle, rather than dorsally in relation to the inner-cycle tentacle, as observed in *S. isei* and *E. vostok* sp.n. (colored arrows in Fig. 12). Only one specimen of *S. ena* was collected, and it is still impossible to determine the stability of such an unusual arrangement of the tentacles in this species.

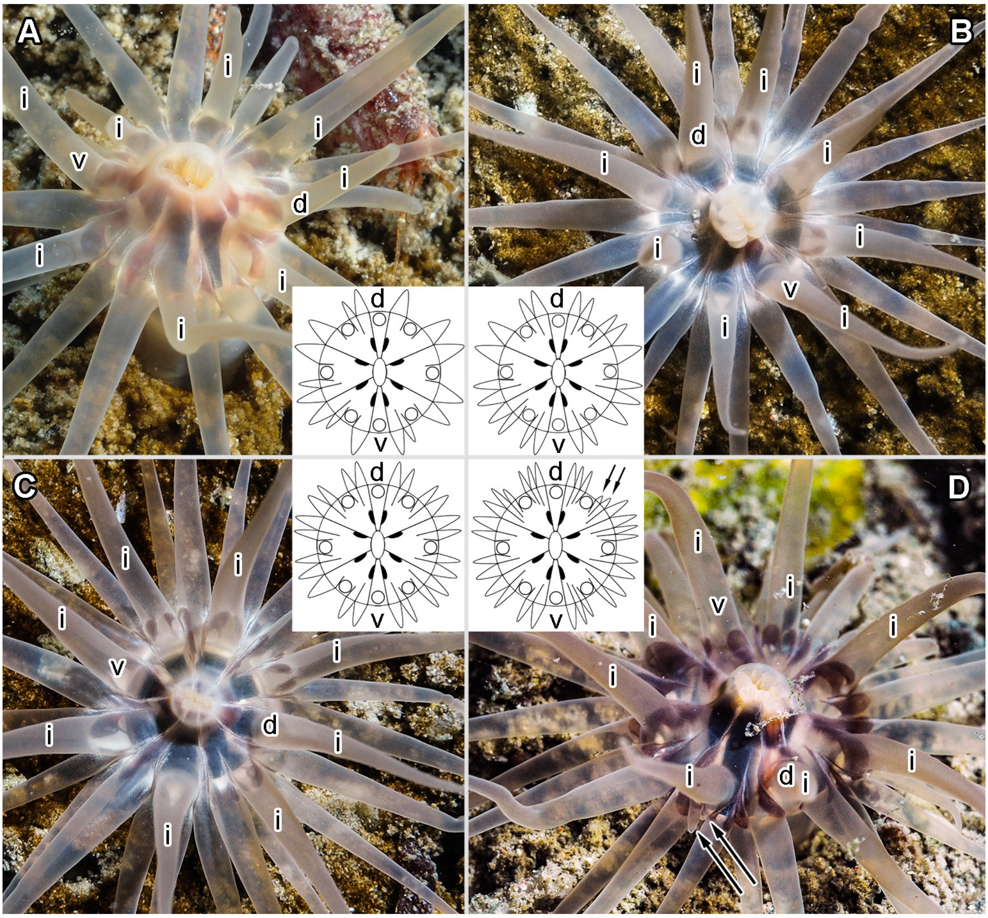

Fig. 11. *Edwardsia inachi*, arrangement of tentacles and mesenteries (photos by Dirk Schories). A — 24 tentacles, 8+12+4; B — 28 tentacles, 8+12+8; C — 31 tentacles, 8+12+11; D — 38 tentacles, 8+12+12+6 (arrows indicate the two smallest tentacles).
Abbreviations: d — dorsal directive tentacle; i — tentacle of the first cycle; v — ventral directive tentacle. Tentacles of the first cycle in diagrams are indicated by circles.

All four species described by Izumi, Fujita (2018) were assigned to *Scolanthus* because they had no physa. It is noteworthy that the two 20-tentacled species described by these authors differ from the 16-tentacled species not only in their microcneme arrangement but also in possessing p-mastigophores, a feature not typical of *Scolanthus* (see Manuel, 1981, who considered their lack in *Scolanthus* a genus-level diagnostic character). It is also relevant to note the similarity between *E. vostok* sp.n., *S. callimorphus* (see Manuel, 1981), and *S. isei* (see Izumi, Fujita, 2018: 13, fig. 4B) in color pattern: tentacles profusely spotted with opaque white or cream speckles, with each outer tentacle bearing a whitish spot at the base on the aboral side, and the inner tentacles often ringed with dark brown pigment at the base; eight white spots on the scapulus between macroneme insertions are also characteristic.

The molecular data for these *Scolanthus* species are not available, but their described morphology suggests a possible relationship between *Edwardsianthus* and *Scolanthus*. It is possible that the presence or absence of the physa is a phylogenetically less significant character than the arrangement of the mesenteries, and, in this case, at least *S. isei* may be transferred to the genus *Edwardsianthus*. Another assumption is that the *Edwardsianthus*-like mode of mesente-

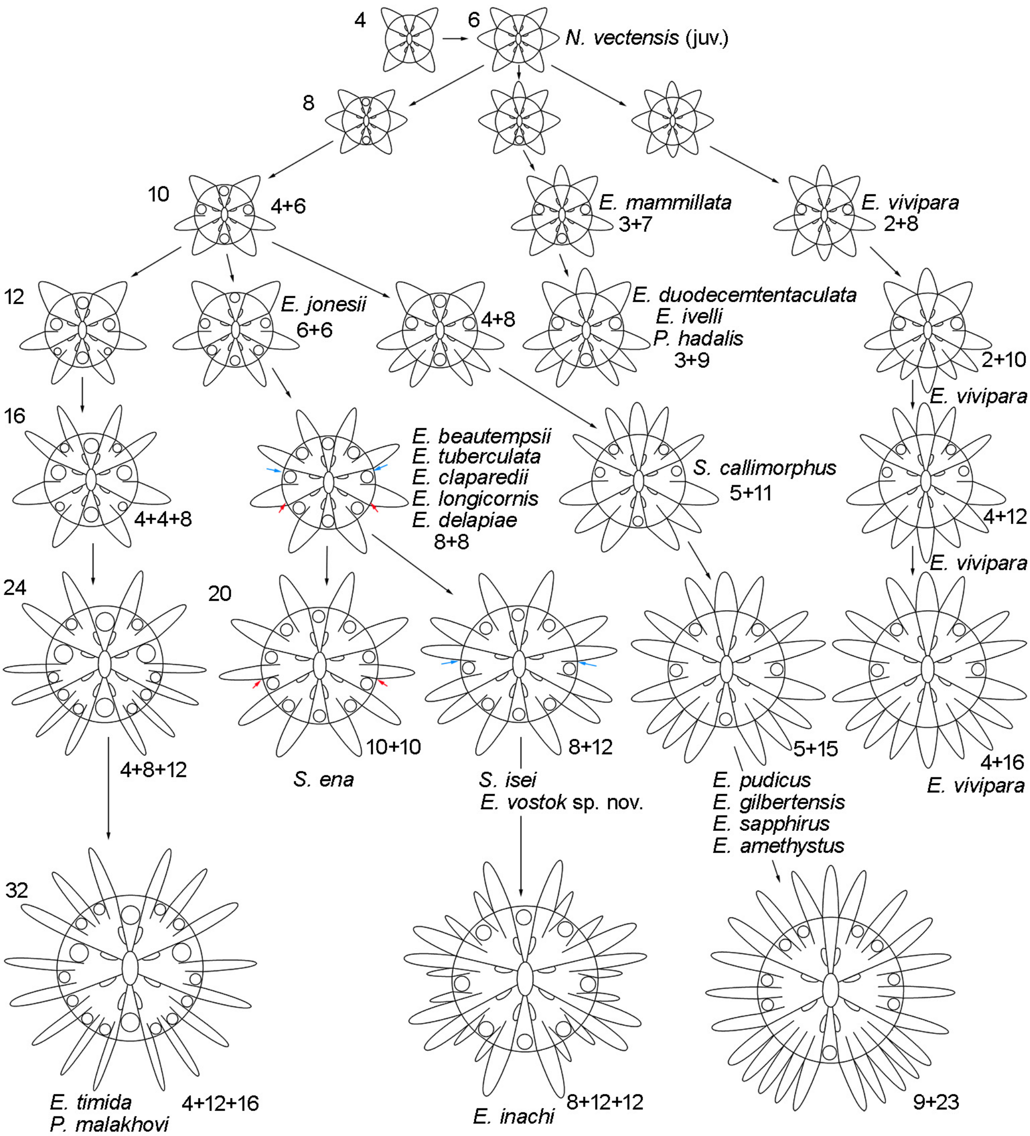

Fig. 12. Development of mesenteries and tentacles in Edwardsiinae. Numerals on the left indicate tentacle counts in the horizontal series of diagrams; tentacle numbers per cycle and representative species exhibiting each arrangement are shown on the right or under the diagrams. Colored arrows indicate insertion points of secondary microcnemes in lateral macrocoels.

rial arrangement is more common in edwardsiid genera than previously thought.

Arrangement of tentacles in some of *Edwardsia* and *Paraedwardsia* species

Some species of *Edwardsia* and *Paraedwardsia*, for which arrangement of the tentacles is described, also have an inner ring of vertical tentacles: three tentacles in *E. mammillata* Bourne, 1916, *E. duodecemtentaculata* Carlgren, 1931, *E. ivelli* Manuel, 1975, and *P. hadalis* Sanamyan et Sanamyan, 2018; four in *E. timida* Quatrefages, 1842 (see Manuel, 1977: 490, 1988: 202) and *P. malakhovi* Sanamyan et Sanamyan, 2021; and eight in *E. beautempsii*

Quatrefages, 1842 (see Manuel, 1977: 485), *E. tuberculata* Dueben et Koren, 1847, *E. claparedii* (Panceri, 1869) (see Manuel, 1988: 198), *E. longicornis* Carlgren, 1921, and *E. delapiae* Carlgren et Stephenson, 1928.

Edwardsia mammillata has only 10 tentacles and only two microcnemes (one microcneme in two lateral macrocoels). Two photographs of this species were published by Rowlett (2020: 251, the top image and the left image in the second row, excluding other photographs on this page). In these specimens, three shorter tentacles are in the inner cycle, and seven tentacles of the outer cycle are distributed between them as *2+3+2*. The three inner tentacles correspond to the ventral and two dorso-lateral primary endocoels, while all other tentacles, including the dorsal endocoelic one, belong to the outer cycle (Fig. 12).

A similar arrangement is found in the 12-tentacular *E. duodecemtentaculata*, *E. ivelli*, and *P. hadalis*. They have all four primary microcnemes (one in each of the lateral and ventro-lateral macrocoels), with two endocoelic tentacles in the ventro-lateral macrocoels added to the outer cycle, and, correspondingly, nine tentacles in the outer cycle distributed as *3+3+3*, alternating with three inner cycle tentacles. These two patterns resemble the 10- and 12-tentaculed stages of development in tropical *Edwardsianthus*, except for the position of the dorsal tentacle, which in young *Edwardsianthus* species typically stands vertically upright in the inner cycle (Figs 8A–C, 12). The arrangement of tentacles at such early stages in *Edwardsianthus gilbertensis* remains unknown — it differs significantly from other *Edwardsianthus* species and may be closer to small, short-tentacled edwardsiids such as *Edwardsia mammillata* and *E. duodecemtentaculata*, in which the dorsal endocoelic tentacle at the 10- and 12-tentacled stages belongs to the outer cycle.

In the species with four tentacles in the inner cycle, *E. timida* and *P. malakhovi*, these four inner tentacles correspond to the two directive and two dorso-lateral primary endocoels, while the remaining endocoelic tentacles belong to the second cycle, and all the exocoelic tentacles are in the third cycle. Hence, these species may have up to 36 (or more) tentacles.

Most 16-tentaculed species of *Edwardsia* have eight tentacles in the inner cycle and eight in the outer cycle (Fig. 12). *Edwardsia jonesii* Seshaiya et Cuttress, 1969 possesses 12 tentacles arranged in two cycles (6+6) (Seshaiya, Cutress, 1969: 74), resembling juvenile stages of edwardsiids with undeveloped pairs of micronemes in the dorsolateral macrocnemes (Fig. 12).

Arrangement of the tentacles and mesenteries in *Edwardsia vivipara*

The South Australian species *Edwardsia vivipara* Carlgren, 1950, as stated in the original description, has about 12 tentacles, but their arrangement has not been described since Carlgren examined the fixed material (four specimens) in the "introverted stage" (Carlgren, 1950: 121–122). At iNaturalist (2025), there are over 40 photographs of one Edwardsiidae species from the Adelaide area (type locality of *E. vivipara*), Melbourne, and northern Tasmania (the subtropical zone between 33.56–40.74°S and 115–145°E) (Fig. 7C, D). The tentacles and the oral disc of this anemone, spread over sandy bottom, are brown in color and densely covered with white spots: the brown coloration (which appears to be localized in the endoderm, as can be seen in the tentacles when viewed against the light in some photographs) agrees with Carlgren's note about "numerous zooxanthellae" in the endoderm of *E. vivipara*. The tentacle arrangement of this sea anemone is unusual but resembles tropical *Edwardsianthus*: the tentacles are arranged into two cycles, but in most specimens, only two short tentacles point upward, while the rest are lying horizontally on the substrate (Fig. 7C). This pattern closely resembles the tentacle arrangement in *Antennapeachia* Izumi et Yanagi, 2016. However, unlike *Antennapeachia*, this species lacks a conchula, and its mesenterial arrangement, marked by oral disc insertions, mirrors that of edwardsiids, with only eight complete mesenteries. Half of the photographs of this species presented at iNaturalist (2025) have 12 tentacles (2+10), as described by Carlgren (1950); six specimens have 10 tentacles (2+8); the rest have from 14 to 20 tentacles, with two to four vertical tentacles in the inner cycle (Fig. 7D). Two specimens have 20 tentacles arranged as 4+16.

Specimens with 10 tentacles have only two microcnemes, with one located in each lateral macrocoel, forming pairs with the dorso-lateral macronemes. The tentacles developing from these endocoels constitute an inner cycle of two tentacles. The outer cycle includes two directive tentacles and is divided by the two tentacles of the inner cycle into two groups: one group contains three dorsal tentacles, and the other contains five ventral ones (Fig. 12).

Specimens with 12 tentacles have all four primary microcnemes characteristic of edwardsiids, but in the ventro-lateral macrocoels, the additional tentacles are positioned horizontally in the outer cycle, as in all tropical *Edwardsianthus* species. In this case, the two inner cycle tentacles divide the outer cycle of tentacles into three dorsal and seven ventral ones (Fig. 12).

The next tentacles first appear in the dorsolateral macrocoels: the inner-cycle tentacles develop between two pairs of secondary microcnemes, and two tentacles are added to the outer cycle. Thus, in 16-tentacled specimens, two cycles of tentacles are present: 4+12 (Fig. 12).

When the number of tentacles increases to 20, secondary microcnemes appear in the lateral and ventro-lateral macrocoels, following the same pattern as in *Edwardsianthus*, resulting in one pair of microcnemes per non-directive macrocoel. The arrangement of the tentacles in this case differs from that in tropical *Edwardsianthus* only by the horizontal orientation of the ventral tentacle in the outer cycle (Figs. 7D; 12). Externally, *E. vivipara* also closely resembles spotted tropical *Edwardsianthus* species.

Arrangement of the tentacles and mesenteries in *Edwardsia inachi*

Edwardsia inachi Sanamyan, Sanamyan et Schories, 2015 has a noteworthy arrangement of the tentacles and mesenteries, resembling that of *E. vostok* sp.n. It was not described in detail in the original description (Sanamyan *et al.*, 2015), and we have reexamined this material. The specimens have 23–38 tentacles, arranged into three or four cycles. The inner cycle is composed of eight endocoelic tentacles located in two directive macrocoels and between a pair of microcnemes in the middle of six non-directive macrocoels, as in *E. vostok* sp.n. The similarity with *E. vostok* sp.n. is especially evident for the specimens having 23 and 24 tentacles (Fig. 11A), in which one pair of microcnemes is present in two or three non-directive macrocoels. In all six non-directive macrocoels, new microcnemes and tentacles are developed in the endocoel formed by this first pair of microcnemes (Fig. 11D). As a result, the tentacle of the inner cycle remains in the middle of the macrocoel, and one, two, or three smaller microcnemes appear on both sides of it, between which the tentacles of the outer cycles are located (Fig. 11).

Thus, the pattern of arrangement of the tentacles and mesenteries in *E. inachi* may be derived from that of *E. vostok* sp.n. by the bilateral development of younger microcnemes in the endocoels of the first six pairs of microcnemes (Figs. 11, 12), suggesting a possible relationship between these species. In contrast, in the tropical species of *Edwardsianthus*, new microcnemes develop in pairs in the exocoels, on the sides of the first pair of microcnemes (Fig. 12).

Conclusion

Edwardsianthus vostok sp.n. differs substantially from all other (tropical) species of this genus in the position of the endocoelic tentacles in the dorsal and ventro-lateral macrocoels. To date, only few species of Edwardsiidae have been sequenced, and it is still unclear how phylogenetically significant this feature can be. The appearance of new mesenteries (microcnemes) in the endocoels, described here, was previously known, among Actiniaria, only for Actinernoidea, a group of sea anemones that have no evident morphological similarities with Edwardsiidae but always appear in the same clade with Edwardsiidae in molecular analyses (Supplementary Fig. 1). The existence of different modes of mesentery addition in Edwardsiidae (in exocoels and endocoels, either in pairs or bilaterally) suggests this group of sea anemones may represent a relict lineage that has retained the ancestral capabilities of different developmental pathways.

Electronic supplements.

The following materials are available online.

Supplementary Table 1. List of taxa and sequences used for phylogenetic analysis. Sequences generated in this study are highlighted in bold.

Supplementary Fig. 1. ML phylogenetic tree based on concatenated datasheet, see text for details. Numbers indicate bootstrap values for Maximum Likelihood. The tree was prepared for publication using EasyTreeEditor software.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare no conflicts of interest.

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Supplementary Table 1. List of taxa and sequences used for phylogenetic analysis. Sequences generated in this study are highlighted in bold.

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 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
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	KR051002	-	-	KR051002
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	-	-	-
Anthopleura sp. Green	-	KY789337	-	KY789370	KY789273
Anthopleura sp. aff. *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
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
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
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 akv	PP902549	PP902554	PP902559	PP902564	PP915637
Cribrinopsis fernaldi BC1	MH385364	MH385369	MH376917	MH380009	MK304508
Cribrinopsis fernaldi BC2	MH385364	MH385369	MH376918	MH380010	MK304508
Cribrinopsis fernaldi BC3	MH385364	MH385369	MH376918	MH380011	MK304508
Cribrinopsis olegi	MH385361	MH385366	MH376911	MH380004	MK304505
Cribrinopsis rubens 1	MH385363	MH385368	MH376914	MH380007	MK304507
Cribrinopsis rubens 2	MH385363	MH385368	MH376915	MH380008	MK304507
Cribrinopsis rubens 3	MH385363	MH385368	MH376916	MH380008	MK304507
Cribrinopsis similis BS1	MH385365	MH385370	MH376919	MH380012	MK304509
Cribrinopsis similis NF1	MK287981	MK307748	MK307728	MK307740	MK304514
Cribrinopsis similis NF2	MK287981	MK307748	MK307729	MK307741	MK304514
Cribrinopsis sp. red_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
Diadumene lineata Japan	JF832965	JF832973	JF832987	KJ483107	JF833007
Diadumene lineata USA	EU190730	EU190774	EU190860	KJ483108	FJ489506
Diadumene sp.	JF832960	JF832976	JF832980	KJ483130	JF833005
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 42_1	**PX056171**	**PX056175**	**PX056183**	**PX056191**	-

Edwardsianthus pudicus 42_2	-	**PX056176**	**PX056184**	**PX056192**	-
Edwardsianthus pudicus 42_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	KT851988	KT852050	KT852118	KT852245	KT852269
Epiactis handi	KT852009	KT852072	KT852140	KT852255	KT852292
Epiactis handi 1	KT852002	KT852064	KT852132	KT852251	KT852284
Epiactis japonica 1	KT851991	KT852053	KT852121	-	KT852272
Epiactis japonica 2	KT852025	KT852090	KT852155	-	KT852310
Epiactis japonica 3	KY789317	KY789352	-	KY789382	KY789285
Epiactis japonica 4	KT852048	KT852116	KT852178	-	KT852333
Epiactis japonica Pacific 1	KT310193	KT310203	-	-	KT310215
Epiactis japonica Pacific 2	KT310194	KT310204	-	-	KT310215
Epiactis japonica Pacific 3	KT310195	KT310205	-	-	KT310215
Epiactis japonica Pacific 4	KT310196	KT310206	-	-	KT310215
Epiactis lisbethae 1	KT852006	KT852069	KT852137	KT852253	KT852289
Epiactis lisbethae 2	EU190727	EU190771	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	-	-	-
Galatheanthemum profundale	KJ482919	KJ482954	KJ483011	KJ483119	KJ482978
Galatheanthemum sp.	KJ482918	KJ482955	KJ483012	KJ483065	KJ482977
Glyphoperidium bursa	KJ482923	KJ482961	KJ483033	KJ483136	KJ482982
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	-	-
Halcampoides purpureus	EU190735	EU190780	AF254380	EU190824	-
Halcampoides purpureus full	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	-
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
Isotealia antarctica	JQ810720	JQ810722	-	-	JQ810727
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 senile fimbriatum (Japan)	-	JF832974	JF832988	JF832996	JF833009
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	MZ569953	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	MT676784	MT676788	MT790708
Sicyonis denisovi MIMB 41366	MZ569948	MZ567258	MZ569920	MZ569973	MZ576880
Sicyonis denisovi MIMB 41367	MZ569949	MZ567259	MZ569921	MZ569974	MZ576881
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	MZ569952	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	-	-
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
Verrillactis paguri	FJ489414	FJ489433	-	KJ483046	FJ489503

Supplementary Fig. 1. ML phylogenetic tree based on concatenated datasheet, see text for details. Numbers indicate bootstrap values for Maximum Likelihood. The tree was prepared for publication using EasyTreeEditor[1] software (see brief description under the tree).

[1] **EasyTreeEditor** is available from https://sanamyan.com/easytreeeditor

- It supports standard tree file formats (Newick or Nexus) and displays them as rectangular cladograms.
- All labels (taxa, clades) can be edited directly on the tree as plain text (including italic and bold formatting).
- Line colors, thickness, collapsing/expanding clades, and color highlighting - all these can be easily modified without navigating through menus.
- The topology comparison between two trees is particularly convenient.
- ML support values and Bayesian probabilities from two trees can be automatically combined ("95/0.99") into a single tree - the program will automatically match corresponding branches and copy values where needed.
- Tree export for publication in PDF. You can specify the page width in millimeters to match journal requirements - extremely useful in some cases.