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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.

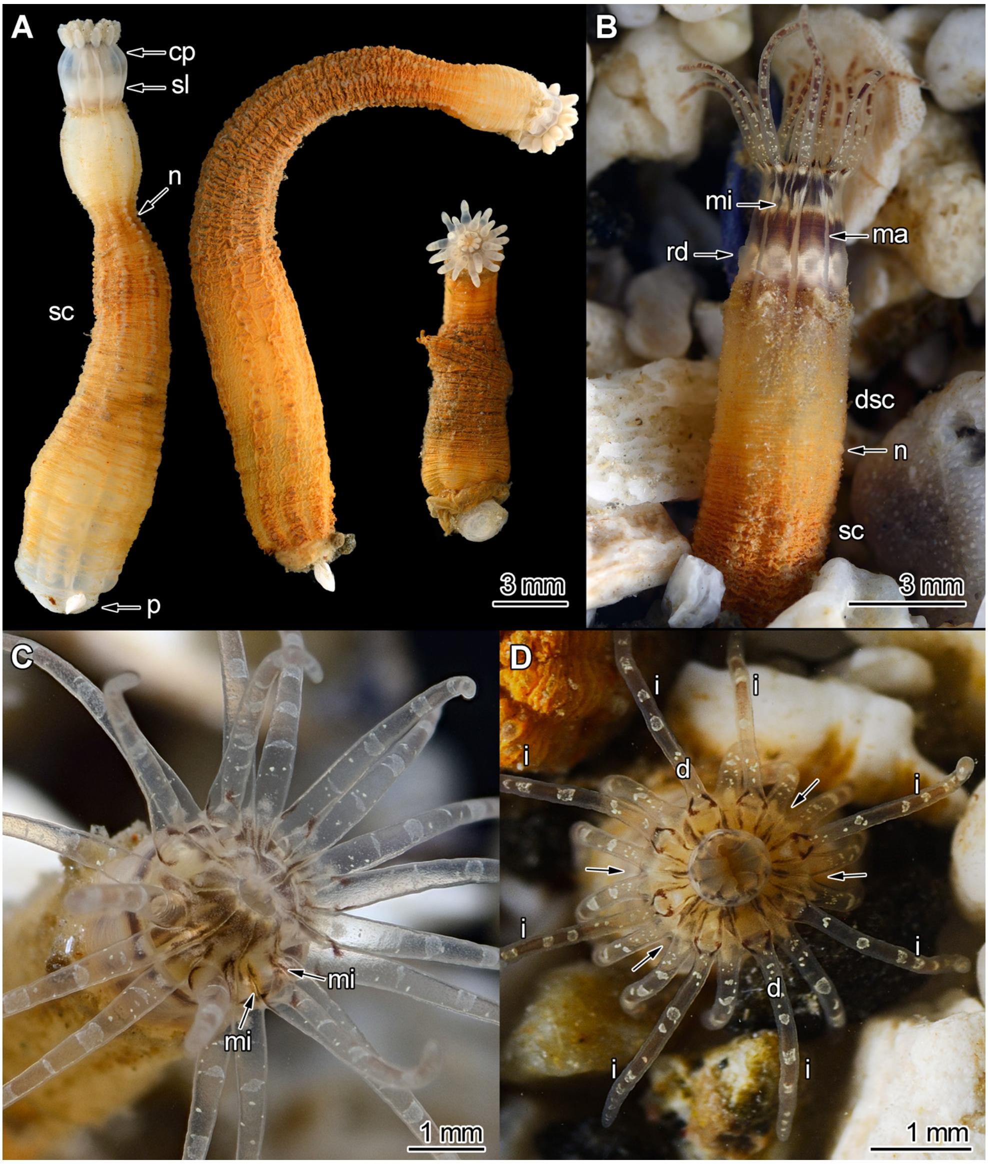

Fig. 1. *Edwardsianthus vostok* sp.n. A — fixed holotype (left) and two paratypes; B — lateral view of the upper part of a live specimen, showing scapus, scapulus, capitulum, and tentacles (the most distal ring of nemathybomes is indicated, which separates the main scapus from its distal portion, having 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

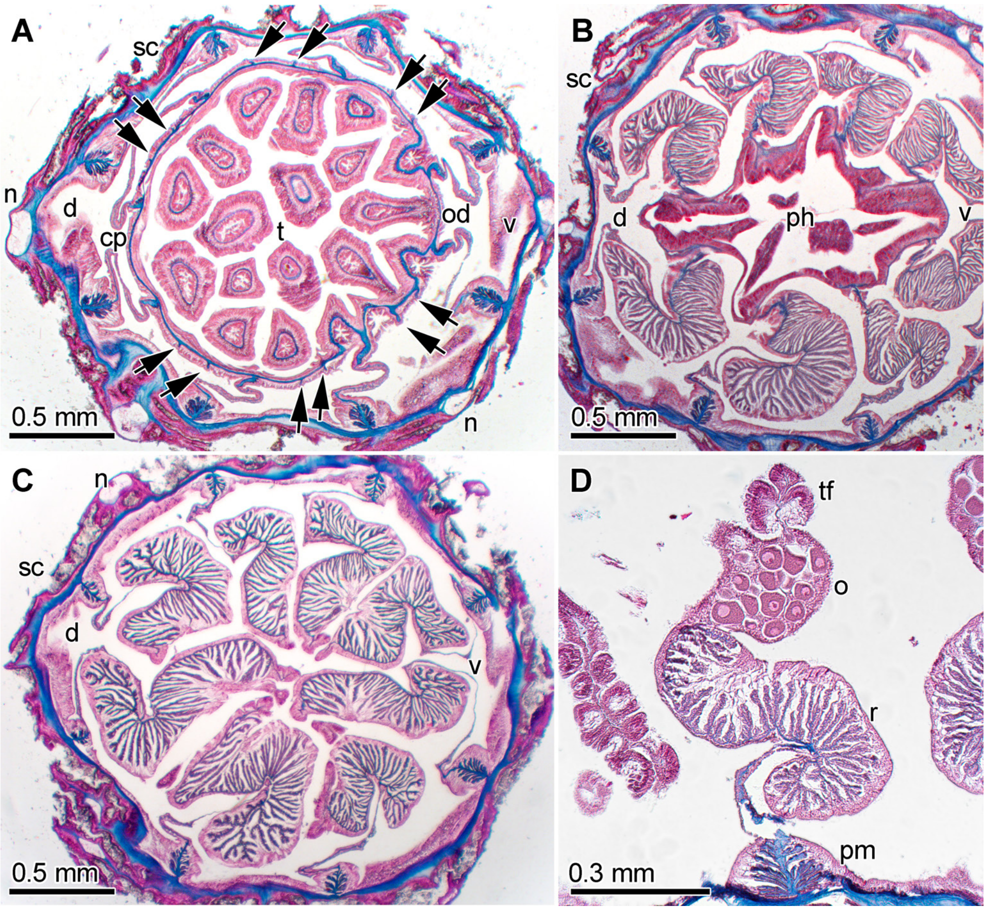

Fig. 2. *Edwardsianthus vostok* sp.n., transverse sections: A — through distal part of column at level of capitulum and oral disc (arrows indicate six pairs of microcnemes); B — through scapus at level of actinopharynx; C — through scapus below actinopharynx; D — through proximal part of scapus.
Abbreviations: 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).

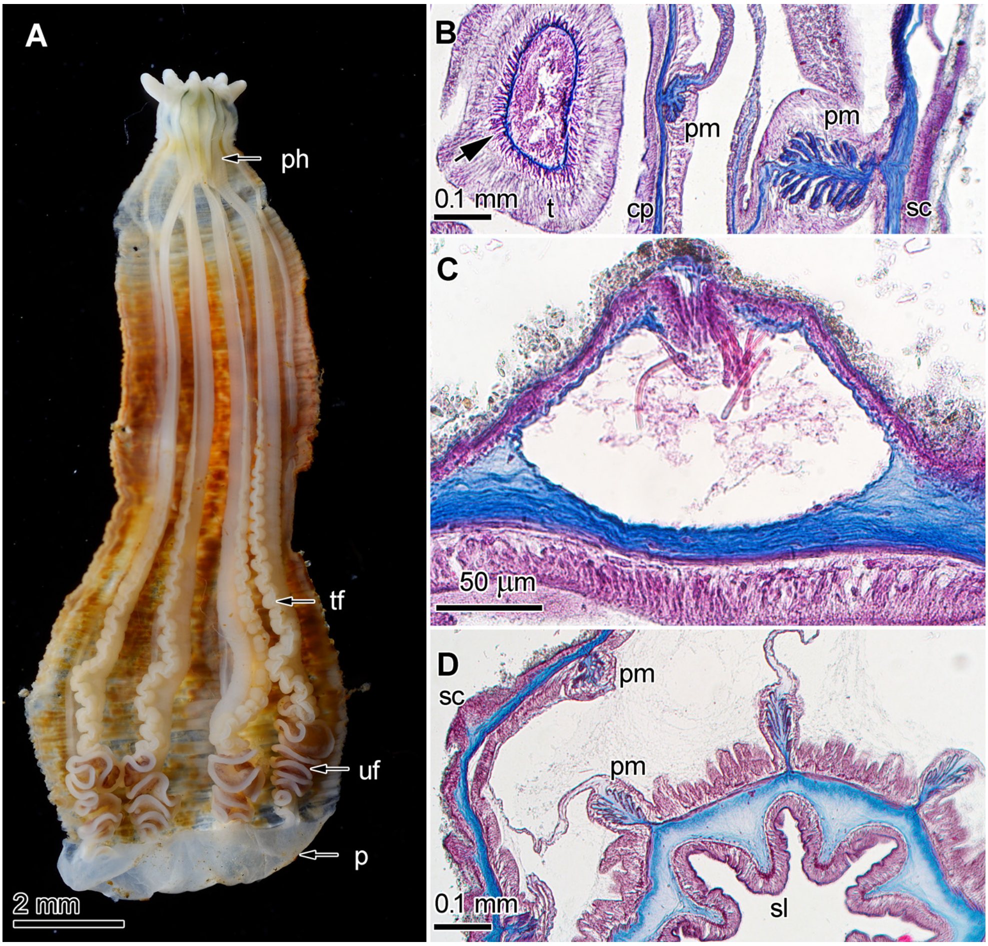

Fig. 3. *Edwardsianthus vostok* sp.n. A — longitudinal section through whole specimen; B — transverse section through the distal part of column, showing parietal musculature of macrocnemes in scapus and capitulum and longitudinal muscles of tentacle (arrow); C — nemathybome; D — transverse section through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

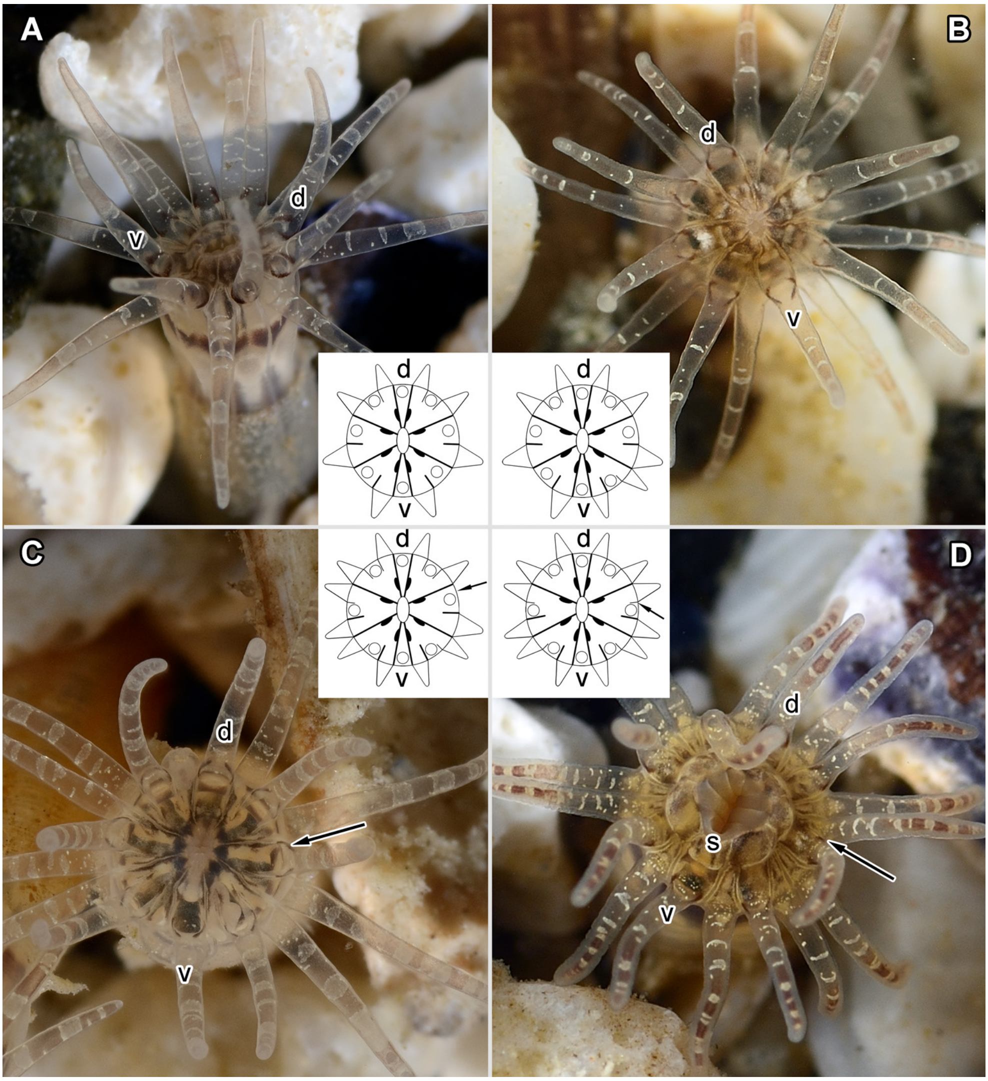

Fig. 4. *Edwardsianthus vostok* sp.n., arrangement of tentacles and mesenteries. A — 16 tentacles, 8+8; B — 17 tentacles, 8+9; C — 19 tentacles, 8+11 (arrow indicates the position where the last microcneme is missing); D — 20 tentacles, 8+12 (arrow indicates the last microcneme, which is smaller than 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-

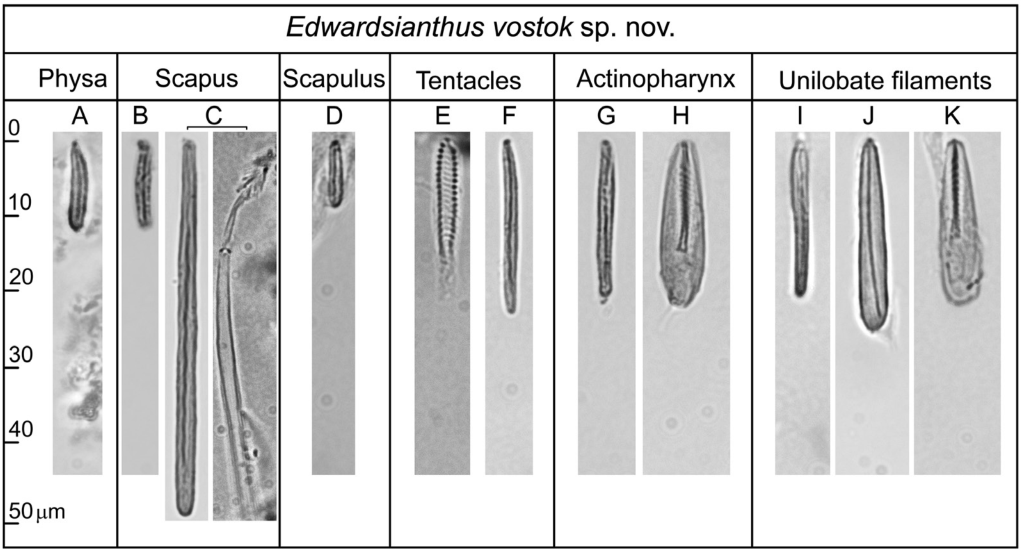

Fig. 5. *Edwardsianthus vostok* sp.n., cnidom.

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.

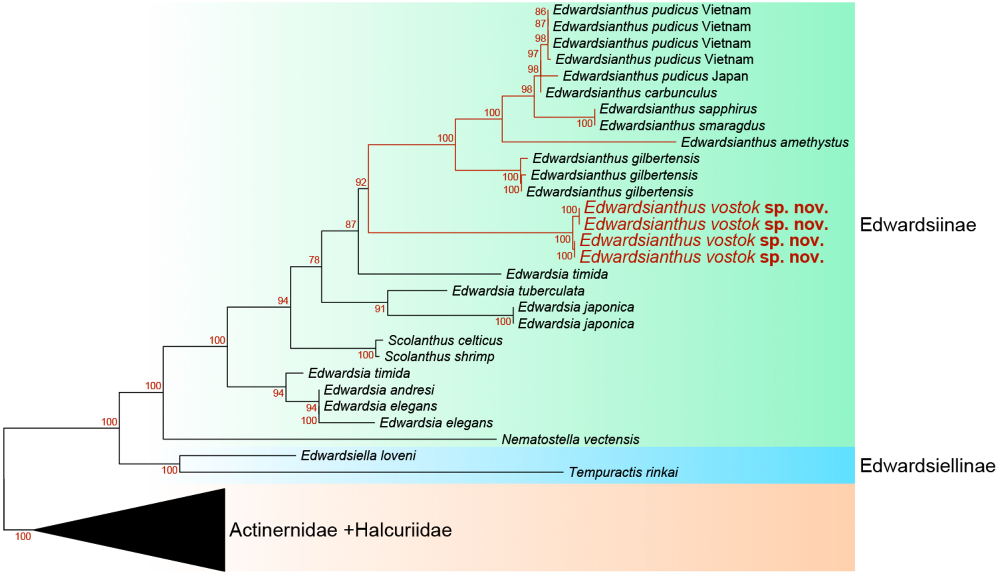

Fig. 6. Maximum Likelihood tree inferred from 12S + 16S + 18S + 28S + COIII concatenated dataset sequences; numerals are bootstrap values. Only a sub-tree containing edwardsiid taxa is shown. For full phylogenetic tree generated during the present study, see Supplement Fig. 1.

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

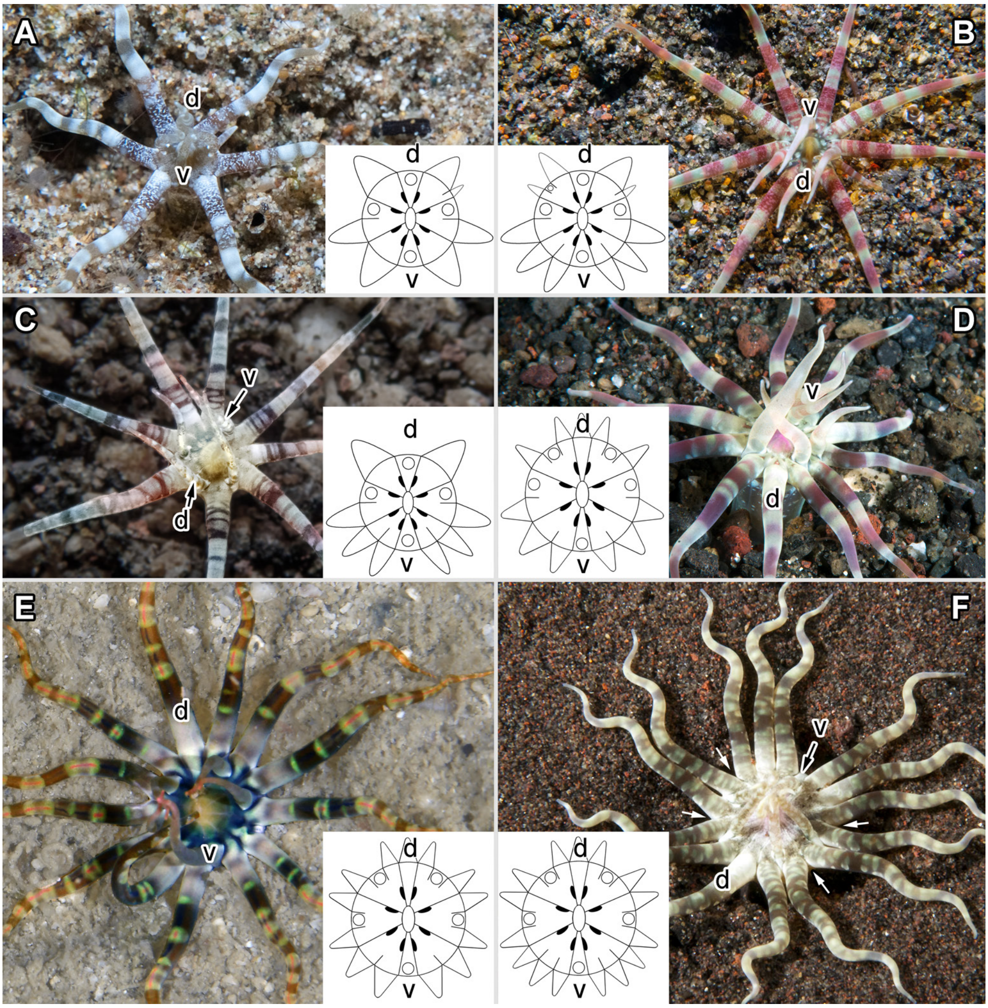

Fig. 8. A — *Edwardsianthus* sp. with 11 tentacles, 4+7 (Batangas, Philippines; photo by Georgina Jones / CC BY-SA 4.0, iNaturalist, 2025, observation 21935549); B — *Edwardsianthus* sp. with 15 tentacles, 5+10 (Indonesia, Bali Island; photo by Scott and Jeanette Johnson / CC BY-NC 4.0, iNaturalist, 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

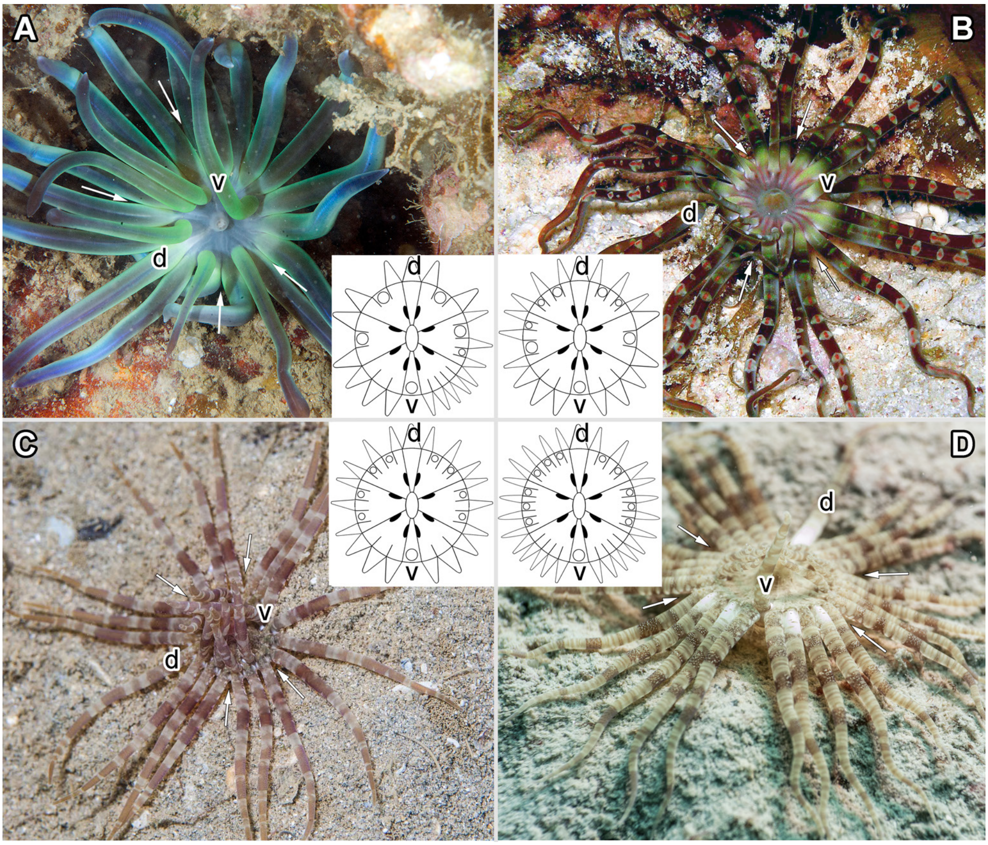

Fig. 9. A — *Edwardsianthus sapphirus* with 24 tentacles, 6+18 (Indonesia; photo by Andrey Ryanskiy); B — *Edwardsianthus pudicus* with 26 tentacles, 8+18 (Red Sea; photo by Sven Kahlbrock); C — *Edwardsianthus* sp. with 28 tentacles, 9+19 (New Caledonia; photo by juju98/ CC BY-NC 4.0, iNaturalist, 2025, 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).

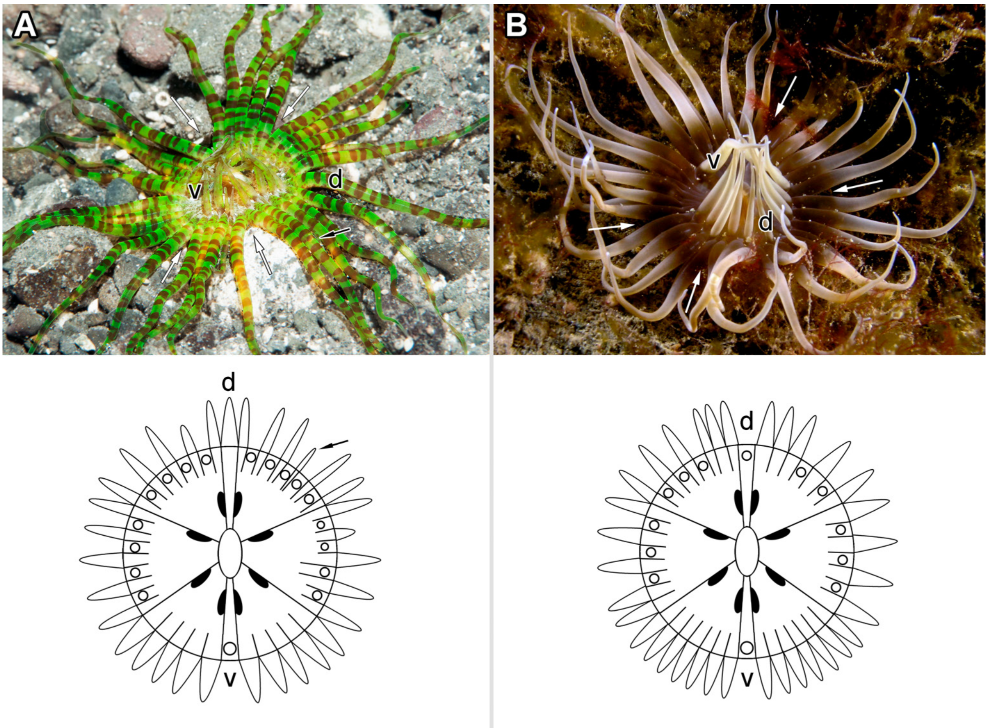

Fig. 10. Edwardsiidae sp. (reconstruction of mesenterial arrangement). A — specimen with 50 tentacles, 18+32 (Papua New Guinea, Milne Bay; photo by Andrey Ryanskiy; black arrow indicates the most slender tentacle of the outer cycle); B — specimen with 47 tentacles, 13+34 (East Timor; photo by Nick Hobgood / 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.

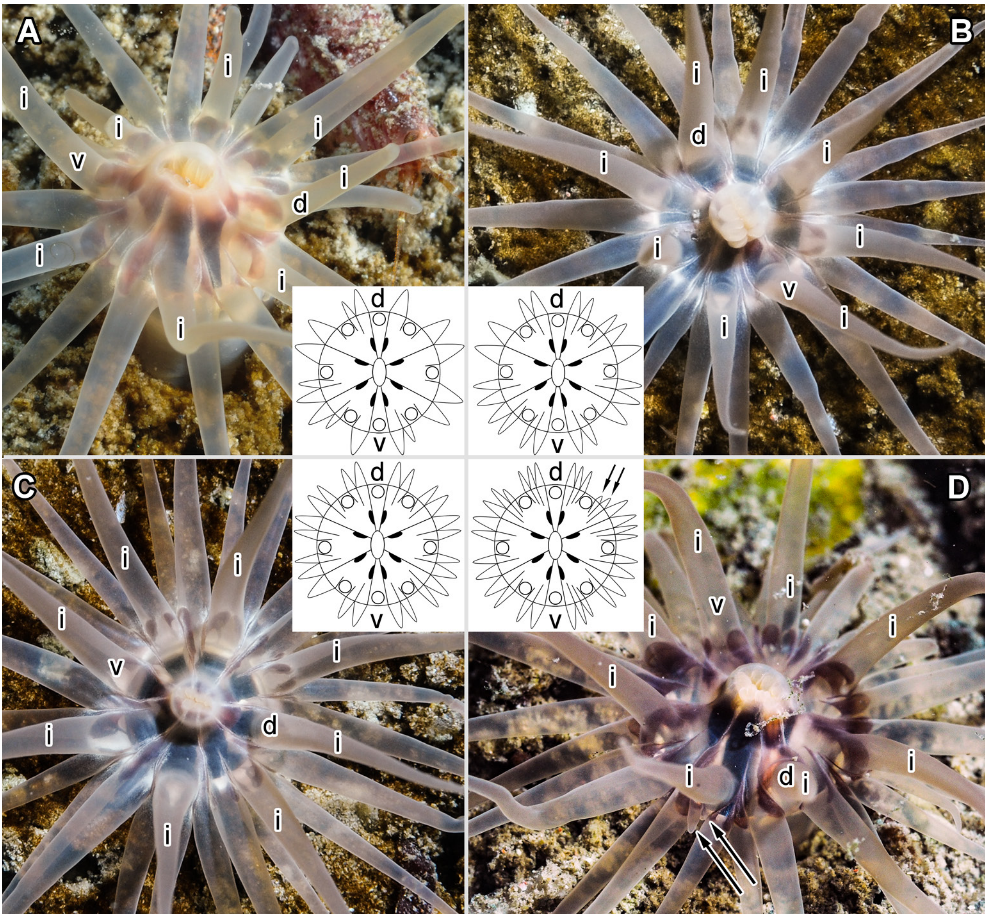

Fig. 11. *Edwardsia inachi*, arrangement of tentacles and mesenteries (photos by Dirk Schories). A — 24 tentacles, 8+12+4; B — 28 tentacles, 8+12+8; C — 31 tentacles, 8+12+11; D — 38 tentacles, 8+12+12+6 (arrows indicate the two smallest tentacles).
Abbreviations: d — dorsal directive tentacle; i — tentacle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

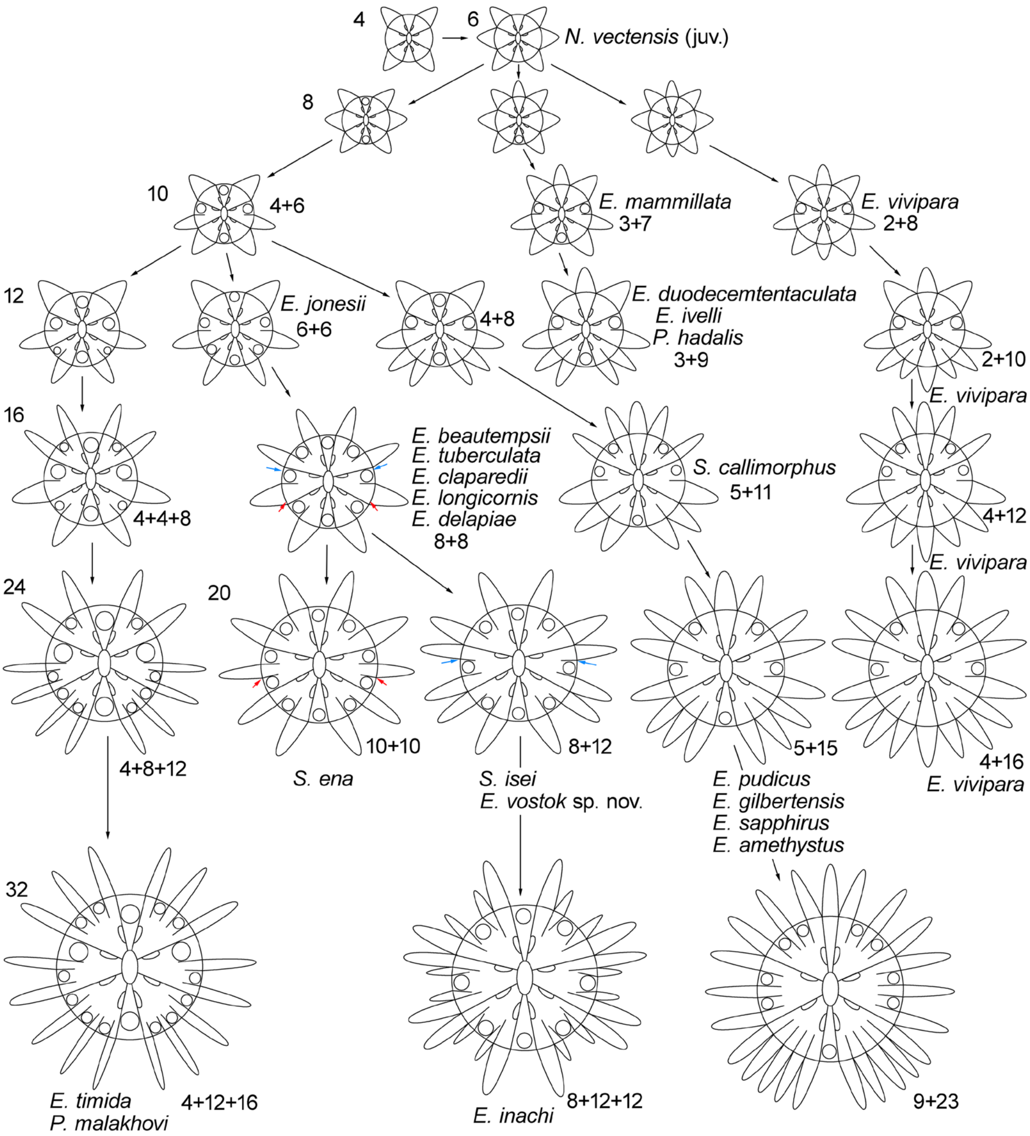

Fig. 12. Development of mesenteries and tentacles in Edwardsiinae. Numerals on the left indicate tentacle counts in the horizontal series of diagrams; tentacle numbers per cycle and representative species exhibiting each arrangement are shown on the right or under the diagrams. Colored arrows indicate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

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