



Tetracoelactis ioran, a new genus and species of deep-sea anemones of the family Exocoelactinidae (Cnidaria: Anthozoa: Actiniaria) from the Northwestern Pacific Ocean

Tetracoelactis ioran, новый род и вид глубоководных актиний семейства Exocoelactinidae (Cnidaria: Anthozoa: Actiniaria) из северо-западной части Тихого океана

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Abstract. *Tetracoelactis ioran* **gen. et sp. nov.** is described from abyssal depths of the NW Pacific and assigned to the family Exocoelactinidae. The genus is unique in having of only four meristematic zones, the lowest number among all species of Actiniaria.

Резюме. *Tetracoelactis ioran* **gen. et sp. nov.** описан с абиссальных глубин северо-западной части Тихого океана и отнесен к семейству Exocoelactinidae. Уникальным признаком нового рода является наличие всего четырех зон закладки мезентериев – наименьшее число среди всех видов отряда Actiniaria.

Key words: sea anemones, mesenterial arrangement, abyssal, NW Pacific, Anthozoa, Actiniaria, Exocoelactinidae, *Tetracoelactis*, new genus, new species

Ключевые слова: морские анемоны, организация мезентериев, абиссаль, Северо-Западная Пацифика, Anthozoa, Actiniaria, Exocoelactinidae, *Tetracoelactis*, новый род, новый вид

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Introduction

The arrangement of the mesenteries is one of the most important morphological features in the systematics of Actiniaria. In most species of Actiniaria, the pairs of the mesenteries are arranged in cycles with the first cycle usually composed of six pairs of the mesenteries (Stephenson, 1928). The subsequent pairs of the mesenteries appear in the exocoels between the mesenteries of preceding cycles: the mesenteries of the second cycle in the exocoels between the pairs of the first cycle; the

mesenteries of the third cycle in the exocoels between the pairs of the first and the second cycle; and so on (Stephenson, 1928). Therefore, starting from the third cycle, the number of the mesenterial pairs of each subsequent cycle is doubled. In other words, in the species with such arrangement of the mesenteries, the number of so called “meristematic zones” (the definite places where new mesenteries appear; see Grebelny, 1982) is not fixed and doubled with each added cycle of the mesenteries. However, a few groups of Actiniaria have a strongly deviating pattern of insertion of

the mesenteries. One of such groups is the family Exocoelactinidae which until now has contained one genus *Exocoelactis* Carlgren, 1925 comprising two species, *E. tuberosa* (Hertwig, 1882) and *E. actinostoloides* (Wassilieff, 1908) (Arellano & Fautin, 2001; Yanagi et al., 2015). In this genus, the mesenteries, starting from the third cycle, are added bilaterally and the number of the meristematic zones is fixed; both species of this genus have 12 such zones. In the present paper, we describe an extremely interesting new species which in many features resembles two known members of *Exocoelactis* but has only four meristematic zones.

Material and methods

The specimens were collected in the NW Pacific during the cruise 22 (1990) of RV *Akademik M. Keldysh* (P.P. Shirshov Institute of Oceanology) by a Sigsbee trawl and stored in formalin. For the preparation of histological sections, the isopropanol-mineral oil method was used (outlined in Sanamyan et al., 2019). For the general histology, 7 µm sections were stained in the following sequence: Ponceau S (5 minutes), Phosphomolybdic acid (5 minutes) and Aniline blue (5 minutes). Cnidae terminology is the same as in our previous papers (see Sanamyan et al., 2012 for details). Cnidae were measured according the method of Hand (1954) for reasons explained by Sanamyan & Sanamyan (2013). Size ranges of cnidae in each body region are given, but statistical data (mean and standard deviation) are not calculated (see Sanamyan et al., 2019).

The type specimens of the new species are deposited in the Zoological Institute of the Russian Academy of Sciences, St Petersburg (ZIN).

Results

Order **Actiniaria** Hertwig, 1882

Family **Exocoelactinidae** Carlgren, 1925

Diagnosis (modified from Carlgren, 1949; significant changes are given in italics). *Actiniaria with the definite base and the mesogloea sphincter. Acontia not present.* The tentacles arranged peculiarly in connection with the bilateral development of younger mesenteries. After the stage with *six or 12* pairs of mesenteries, the later mesenteries

arise bilaterally *in certain or* in each sector of the animal, so that the youngest mesenteries appear in the middle of *the primary or* the secondary exocoels. In each pair of the younger mesenteries, one mesentery is larger than its partner and its longitudinal muscles are on the side turned to the mesentery of preceding cycle.

Included genera. *Exocoelactis* Carlgren, 1925 and *Tetracoelactis* **gen. nov.**

***Tetracoelactis* gen. nov.**

Diagnosis. Exocoelactinidae with weak sphincter, the upper part of the column cannot completely cover the tentacles. Longitudinal muscles of the tentacles and radial muscles of the oral disc are mesogloea. Two broad siphonoglyphs and two pairs of the directives. Mesenteries of the first cycle (six pairs) are perfect. In lateral and “ventral” primary exocoels, each later pair consists of a larger and smaller mesentery arranged bilaterally with the youngest pairs in the middle of primary exocoels. The stronger member in each of these pairs is usually perfect, the smaller is imperfect. In “dorsal” primary exocoels, mesenteries are normally arranged and equally developed within each pair. All mesenteries of the first cycle and most other perfect mesenteries are sterile and have filaments; imperfect mesenteries without filaments and nearly all of them are fertile. Cnidom consists of spirocysts, basitrichs, p-mastigophores A, and p-mastigophores B1.

Type species *Tetracoelactis ioran* **sp. nov.**

Etymology. The generic name refers to the most distinctive feature of this genus, the presence of only four meristematic zones, and derives from Ancient Greek τέτταρες (four), κοίλος (hollow) and ακτίς (ray). The gender is feminine.

Remarks. *Tetracoelactis* **gen. nov.** resembles *Exocoelactis* but differs in the arrangement of the mesenteries. In *Tetracoelactis* **gen. nov.**, the mesenteries of the first cycle (six pairs) are arranged normally and the mesenteries of the subsequent cycles arranged bilaterally in lateral and “ventral” exocoels, while the first two cycles (12 pairs) in *Exocoelactis* are arranged normally and the bilateral arrangement occurs starting from the third mesenterial cycle. *Tetracoelactis* **gen. nov.** has only four meristematic zones (one zone in each of two lateral and two “ventral” primary

exocoels) and therefore its body has bilateral symmetry, while *Exocoelactis* has 12 such zones (in all secondary exocoels; see Carlgren, 1918; Grebelny, 1982) and has radial symmetry.

***Tetracoelactis ioran* sp. nov.**

(Figs 1–5)

Holotype. NW Pacific, 53°05.4'N, 161°55.2'E – 53°07.0'N, 161°56.12'E, 4890–4984 m, Research Vessel Akademik M. Keldysh, cruise 22, station 2323, 10 Aug. 1990 (ZIN 11882).

Paratype, same data, one specimen (ZIN 11883).

Description. Two available specimens are similar and have a distinctive appearance (Fig. 1A, B). They are large, the holotype is 10 cm in height and 6 cm in diameter, the paratype is about 7 cm in height and 5 cm in diameter. The body is barrel-shaped. In both specimens, the edge of the pedal disc is bent in and the base is deeply invaginated into the column forming a cavity as in some species of the genus *Actinauge* Verrill, 1883 (Fig. 1C–E). In the holotype, the opening of this cavity is about 2 cm in diameter and the cavity contains no mud or other foreign matter (Fig. 1D). In the paratype, the edges of the pedal disc (the limbus) hide the pedal disc completely; the cavity is closed and contains some loose mass of sediment (Fig. 1C, E). The distal part of the column cannot cover the tentacles completely.

The wall of the column is not especially thick; the thickness of the mesogloea varies from 2 to 5 mm. Deep narrow furrows divide the surface of the column into numerous flat-topped tubercle-like structures. In the holotype, these tubercles are crowded and rather regularly distributed, all of more or less similar size and shape: low, flat and round in outline (Fig. 1A). In the paratype, the tubercles are less regular and do not form such a distinct pattern (Fig. 1B). The surface of the column is almost clear from attached sand or other foreign matter; few sediment particles may be present in furrows. Most of the ectoderm of the column is abraded; the ectoderm is retained only in furrows between the tubercles.

Both specimens have about 70 tentacles. The tentacles are finger-like, thick-walled, without a noticeable mesogloea thickening on the aboral side, with deep longitudinal furrows and folds, up to 2 cm in length (Fig. 2A, B). They are on the

outer third of the oral disc, peculiarly arranged according to the bilateral arrangement of the mesenteries in four primary exocoels (Fig. 4). The inner tentacles are longer than the outer ones.

The oral disc in the preserved specimens is deeply invaginated (Fig. 2A); in live ones, its diameter probably significantly exceeds the diameter of the column. Its mesogloea forms thick radial ridges along each exo- and endocoels; the ridges over the endocoels are wider than those over the exocoels (Fig. 2C).

The marginal mesogloea sphincter muscle is weak and short (about 1 cm in length), wider in the distal and middle parts and gradually narrowing proximally (Fig. 2E). It adjoins to the endodermal side of the wall of column and occupies half or less of the thickness of the mesogloea. The sphincter is distinctly reticular, with crowded muscle meshes and thin strands of the mesogloea forming a characteristic network (Fig. 2F, G). The sphincter is not separated from the endodermal circular muscles of the column. The longitudinal muscles of the tentacles are mesogloea, well developed, placed either closer to the endodermal side of the mesogloea (on the oral side) or in its middle layer (Fig. 2B). They are more or less evenly developed on the oral and aboral sides and along the length of the tentacle. The radial muscles of the oral disc are very strong, mesogloea and occupy the most width of the mesogloea. They are arranged into thick separate bundles running over each exo- and endocoel, interrupted along the insertions of the mesenteries (Fig. 2C). Circular muscles of the column are meso-endodermal.

The actinopharynx is long, voluminous and thick-walled; the thickness of its mesogloea is almost the same or more than that of the mesogloea of column. The inner surface of the actinopharynx is longitudinally ridged; the number of the ridges corresponds to the number of the perfect mesenteries (Fig. 1F, 2D). There are two very large thick-walled aborally prolonged siphonoglyphs (Fig. 1E, F).

Equal number of the mesenteries is present distally and proximally, 72 mesentery are in the holotype and 74 in the paratype. They are arranged in a following way:

– The first cycle of the mesenteries consists of six pairs, two of them are directives attached to

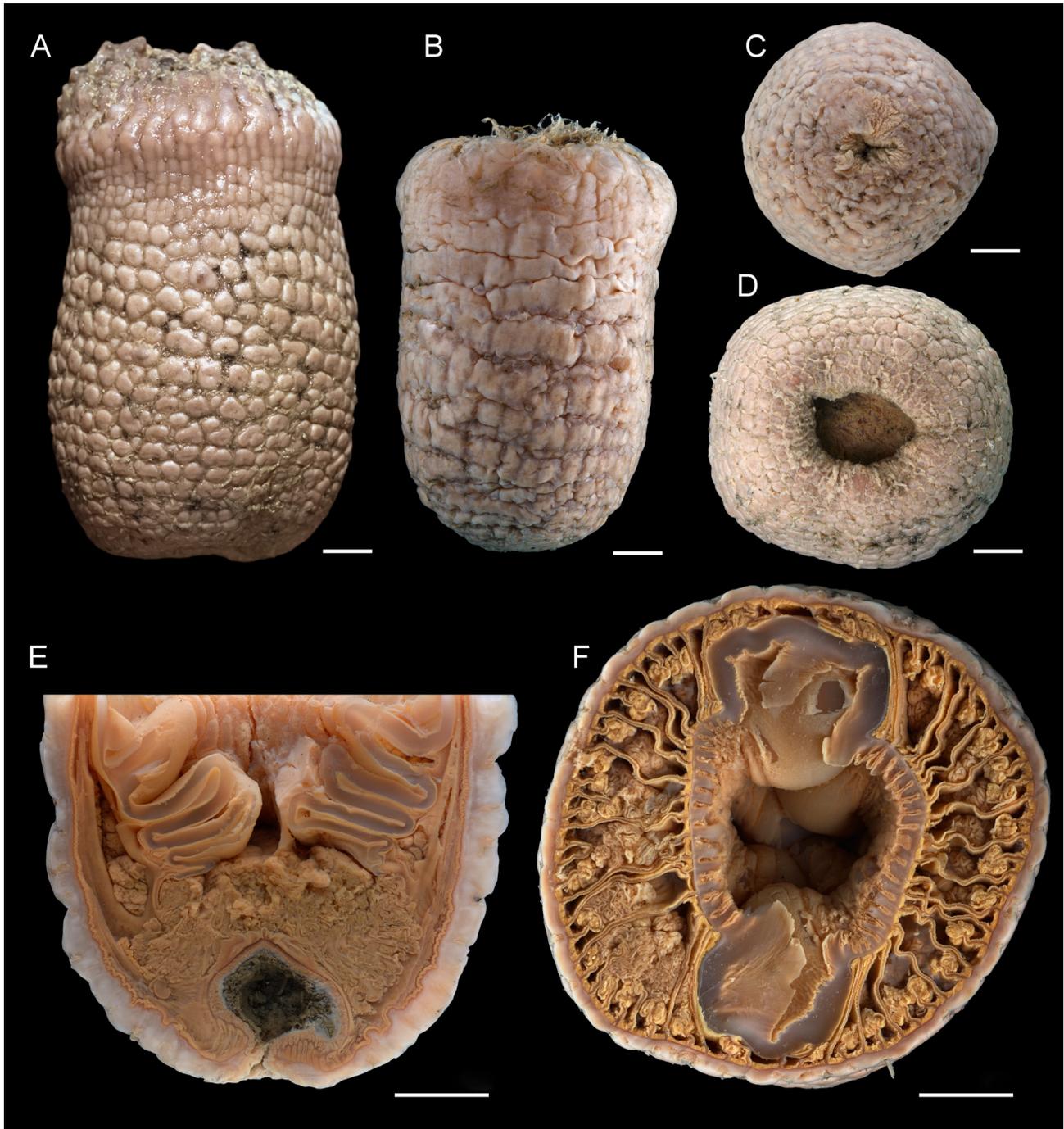


Fig. 1. *Tetracoelactis ioran* gen. et sp. nov. **A, B**, habitus in lateral view; **C, D**, habitus in aboral view; **E**, longitudinal section of proximal column showing invaginated base; **F**, transverse section on level of actinopharynx. Holotype (A, D, F) and paratype (B, C, E). Scale bars: 1 cm.

the siphonoglyphs. They are perfect and sterile (Fig. 2D, 3).

– In the two primary exocoels situated on the sides of a directive pair conditionally called “dorsal” (“dorsal” directives “*dd*” and “dorsal” exocoels “*de*” in Fig. 3), the mesenteries are normally po-

sitioned. Only three pairs of the mesenteries are present in each primary “dorsal” exocoel: a pair of the perfect and sterile mesenteries of the second order, and two pairs of the imperfect fertile and equally developed mesenteries of the third cycle on two sides of it.

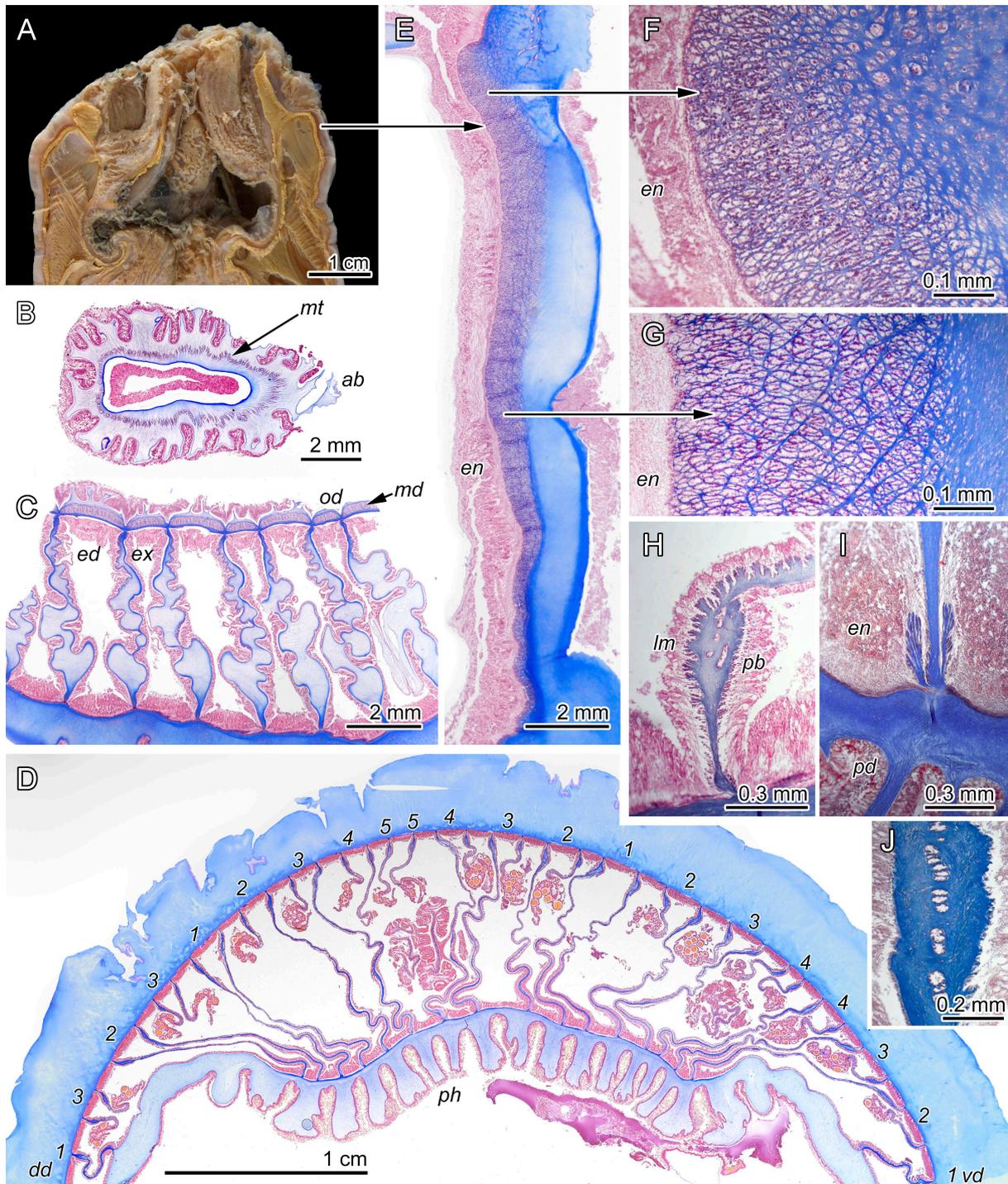


Fig. 2. *Tetracoelactis ioran* gen. et sp. nov. **A**, longitudinal section of distal column showing position of sphincter muscle; **B**, transverse section of tentacle; **C**, transverse section through distal part of column and oral disc; **D**, transverse section through column on level of actinopharynx; **E**, sphincter muscle; **F**, **G**, details of sphincter muscle, enlarged; **H**, transverse section through parietal part of mesentery; **I**, longitudinal section through pedal disc showing basilar muscles; **J**, mesogloea muscle meshes in region of parietobasilar muscles. Holotype (**A**, **B**, **C**, **E**, **F**, **G**) and paratype (**D**, **H**, **I**, **J**). *ab* – aboral side, *dd* – “dorsal” directives, *ed* – endocoel, *en* – endoderm, *ex* – exocoel, *lm* – longitudinal muscles of mesentery, *md* – radial mesogloea muscles of oral disc, *mt* – longitudinal mesogloea muscles of tentacle, *od* – oral disc, *pb* – parieto-basilar muscles, *pd* – pedal disc, *ph* – actinopharynx, *vd* – “ventral” directives, numbers (1, 2, 3, 4) indicate cycle number of mesenteries or mesenterial pairs. Scale bars: 1 cm (**A**, **D**); 2 mm (**B**, **C**, **E**); 0.1 mm (**F**, **G**); 0.3 mm (**H**, **I**); and 0.2 mm (**J**).

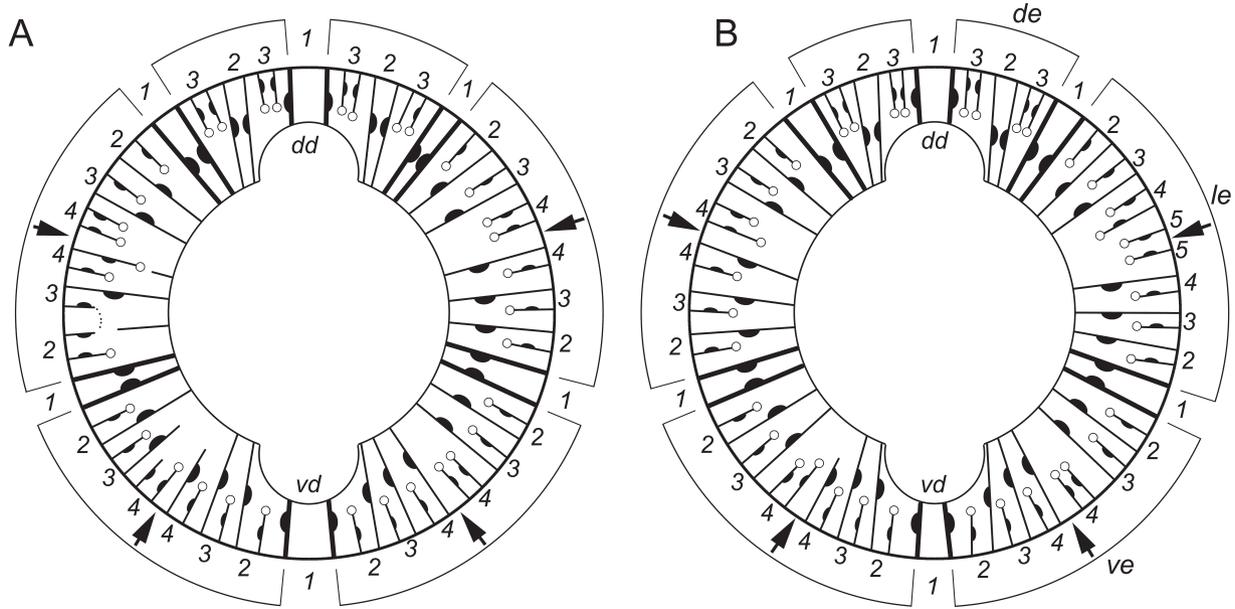


Fig. 3. *Tetracoelactis ioran* gen. et sp. nov., arrangement of the mesenteries. **A**, holotype; **B**, paratype. *dd* – “dorsal” directives, *de* – “dorsal” exocoel, *le* – lateral exocoel, *vd* – “ventral” directives, *ve* – “ventral” exocoel, numbers (1, 2, 3, 4, 5) indicate cycle number of mesenterial pairs or individual mesenteries, arrows point to proliferation zones, gonads are marked by small circles.

– In the other four primary exocoels (two lateral and two “ventral”), the mesenteries are arranged bilaterally as in *Exocoelactis*: the younger mesenteries arise on two sides of a meristematic zone situated at the middle of each primary lateral and “ventral” exocoel. In most of these primary exocoels, six mesenterial pairs are present: two pairs of the second, two of the third and two of the fourth cycle (the paratype has in addition two mesenteries of the fifth cycle in one primary lateral exocoel; Fig. 3). In these primary exocoels, each mesenterial pair consist of a smaller imperfect fertile mesentery and a larger, usually perfect and usually sterile mesentery. Their arrangement is bilateral and regular; the smaller mesentery in each pair is always closer to the nearest mesentery of the preceding cycle. This creates similarity with the *Actinostola* rule. Thus, the presence of a smaller number of the mesenteries in the “dorsal” primary exocoels and the development of a larger number of them in the lateral and “ventral” ones, and their different arrangement, determines the bilateral symmetry of the entire polyp body.

The mesenteries are of the ordinary thickness (not thin); the width of the mesogloea is similar

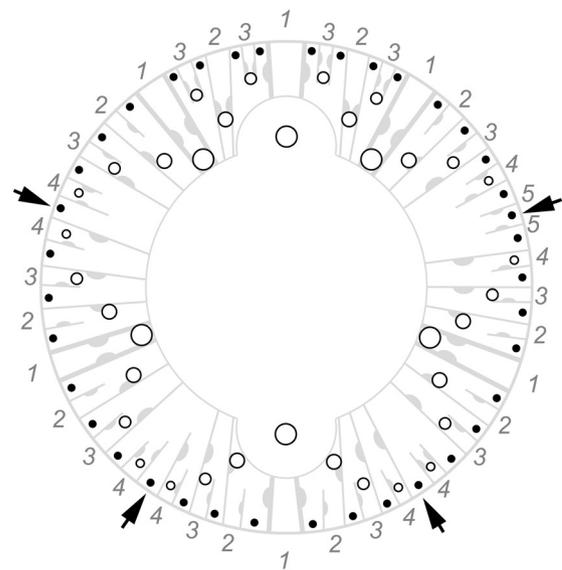


Fig. 4. *Tetracoelactis ioran* gen. et sp. nov., diagram of arrangement of tentacles in paratype. Numbers (1, 2, 3, 4, 5) indicate cycle number of mesenterial pairs or individual mesenteries, arrows point to proliferation zones, exocoelic tentacles are marked by black dots, endocoelic tentacles by circles.

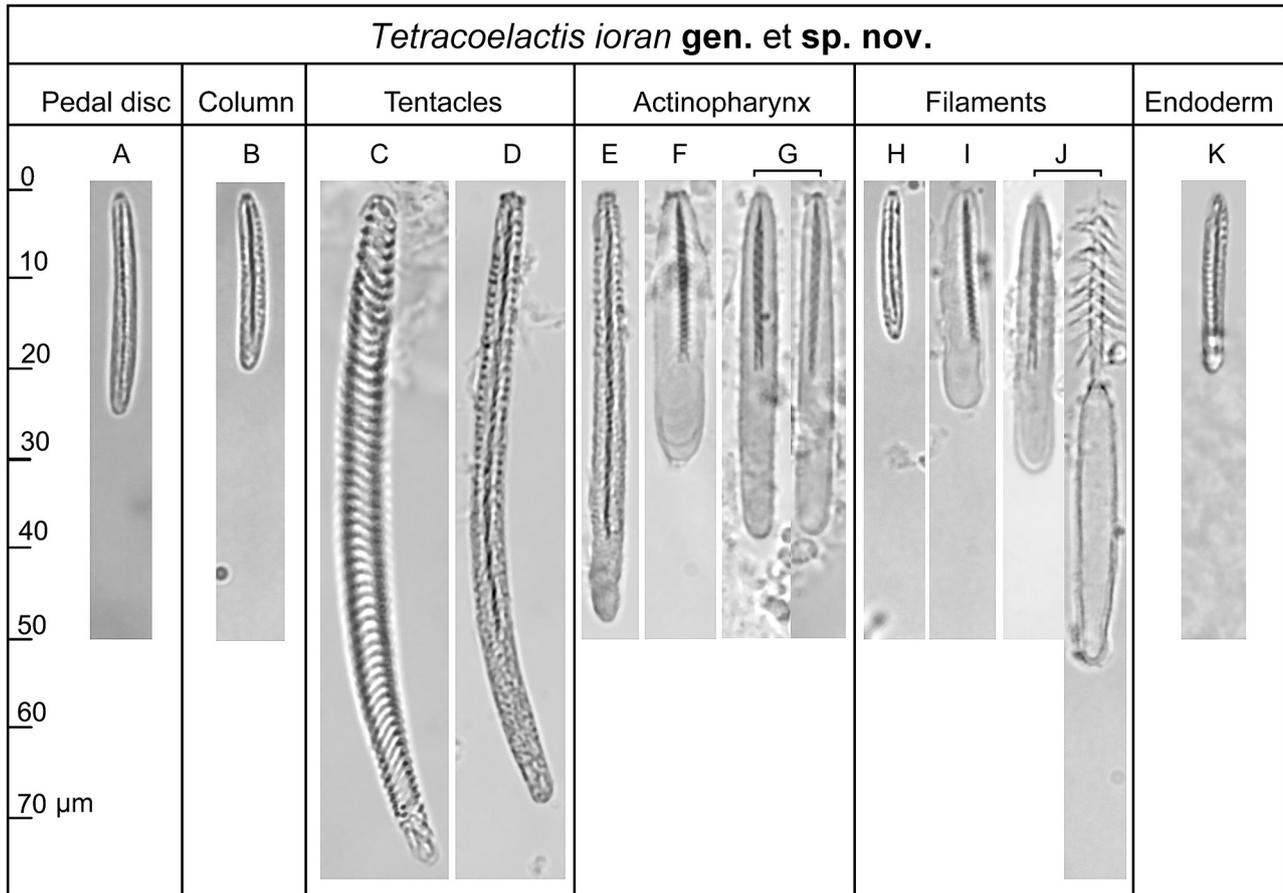


Fig. 5. *Tetracoelactis ioran* gen. et sp. nov., cnidom.

in smaller and larger mesenteries (Fig. 1F, 2D). In the upper part of the body (between the distal part of column and the oral disc), the mesogloea of all mesenteries is very thick and peculiarly ridged (Fig. 2C). Mesenterial retractor muscles are diffuse and weak, similarly developed in all mesenteries. Parietobasilar muscles are weak, sometimes with a small flap (Fig. 2H). The mesogloea of the outer (parietal) part of all mesenteries is thickened in the region of the parietobasilar muscles and contains meshes with muscle fibers which probably derived from the parietobasilar musculature (Fig. 2H, J). Basilar muscles are well developed (Fig. 2 I). Filaments are abundantly developed on the large sterile mesenteries but all fertile mesenteries lack them.

Both specimens are females with ova up to 350 μ m in diameter.

The cnidom (Fig. 5, Table 1) includes gracile spirocysts, basitrichs, p-mastigophores A, and p-mastigophores B1. Cnidoglandular tracts of the

filaments (which have ectodermal origin) contain only p-mastigophores A and B1 (Fig. 5I, J), while small and rare basitrichs (Fig. 5H) are present in the endodermal part of the filaments. The same basitrichs (Fig. 5K) are present in the endoderm of column and mesenteries, including the distal parts of fertile mesenteries which lack the cnidoglandular tracts. The V-shaped funnel on the shaft of some p-mastigophores B1 in the actinopharynx and filaments may be poorly developed, and such cnidae resemble b-mastigophore (capsule on the right side in Fig. 5G). P-mastigophores B1 are stained by basic stains (safranin or toluidine blue) in the same way as all basitrichs and as p-mastigophores B1 of some actiniids (e.g. in *Cribrinopsis* Carlgren, 1921; see Sanamyan et al., 2019) and as drop-shaped p-mastigophores B1 in filaments of *Artemidactis victrix* Stephenson, 1918 (see Sanamyan et al., 2015b). P-mastigophores A and spirocysts are not stained by basic stains.

Table 1. Size ranges (length × width, in microns) and distribution of cnidae of *Tetracoelactis ioran* gen. et sp. nov. Letters in brackets correspond to letters in Fig. 5.

Body region	Cnidae	Holotype	Paratype
Pedal disc	(A) basitrichs (common)	21–30 × 2–3	17–24 × 2–3
Column	(B) basitrichs (common)	18–27 × 2–3	15–21 × 2–3
Tentacles	(C) spirocysts (numerous)	35–87 × 3–6	29–72 × 3–6
	(D) basitrichs (common)	54–74 × 3.5–5	52–67 × 3.5–4.5
Actinopharynx	(E) basitrichs (common)	41–65 × 3–4.5	41–56 × 3–4
	(F) p-mastigophores A (common)	27–37 × 4–6.5	27–37 × 4.5–6
	(G) p-mastigophores B1 (numerous)	32–46 × 3–5	29–46 × 3–4.5
Filaments	(H) basitrichs (few)	15–21 × 2–2.5	14–24 × 2–2.5
	(I) p-mastigophores A (common)	25–34 × 4.5–6.5	24–30 × 4.5–6
	(J) p-mastigophores B1 (common)	30–37 × 3.5–4.5	26–34 × 3–4.5
Endoderm	(K) basitrichs (few)	16–19 × 2–2.5	17–20 × 2–3

Etymology. The name is a noun in apposition, derived from the Russian abbreviation of the P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences (IORAN).

Remarks. The most distinctive feature of *Tetracoelactis ioran* sp. nov. is the bilateral arrangement of the mesenteries in four primary exocoels. Similarly arranged mesenteries occur only in the secondary exocoels of *Exocoelactis*, the only previously known genus of the family Exocoelactinidae. There is no doubt that the two known species of *Exocoelactis*, *E. tuberosa* and *E. actinostoloides*, and *T. ioran* sp. nov., are related. However, they have significant differences in the arrangement of the mesenteries. In *Exocoelactis*, the bilateral arrangement of the mesenteries starts from the third cycle and occurs, therefore, in 12 secondary exocoels, while the bilateral arrangement of mesenteries in the species described here occurs earlier starting from the second cycle, in the four primary exocoels. The mesenteries in the two “dorsal” primary exocoels in *T. ioran* sp. nov. are arranged normally (in the same way as in most species of Actiniaria), but these exocoels contain only the mesenteries of the second and third cycles

in both available specimens, while the mesenteries of fourth and occasionally fifth cycles are developed in all other primary exocoels. Therefore, we conclude that after developing of the third cycle of the mesenteries, the further addition of the mesenteries in primary “dorsal” exocoels is prohibited and, starting from this stage, this species has only four meristematic zones: one zone in the middle of each lateral and “ventral” primary exocoel. *Exocoelactis* has 12 meristematic zones (see Carlgren, 1918; Grebelny, 1982); *Tetracoelactis* has only four zones. This feature is important and sufficient to warrant establishing the new genus within the family Exocoelactinidae.

The type species of *Exocoelactis*, *E. tuberosa*, is known from several specimens from Japanese waters (34°7′N, 138°0′E, 1028 m), originally described by Hertwig (1882a) and redescribed by Carlgren (1918, 1928) who also referred to a specimen collected in the Indian Ocean off the coast of Java (0.4°3.2′S, 98°33.8′E, 371 m; see Carlgren, 1928). The surface of the column of *E. tuberosa*, which is “beset with roundish knobs” according to Hertwig (1882b: 63), resembles that of *T. ioran* sp. nov., but the column is vase shaped and expanded

distally; the tentacles are very numerous (about 200 according to Hertwig, 1882b, and 184 in the specimen examined by Carlgren, 1928), short and provided with very large mesogloea swelling at the base.

The second species of *Exocoelactis*, *E. actinostoloides*, differs from *T. ioran* **sp. nov.** by numerous external (e.g. smooth column, more numerous tentacles) and internal features (e.g. the arrangement of the mesenteries and the presence of the filaments on fertile mesenteries) and by the cnidom. This species was revised by Arellano & Fautin (2001). These authors discovered that the two species described from Japan, *Cymbactis actinostoloides* Wassilieff, 1908 and *C. maxima* Wassilieff, 1908, are conspecific and belong to *Exocoelactis*. They synonymised these two species and *E. valdiviae* Carlgren, 1928, a species discovered off the coast of Somali, under the name *Exocoelactis actinostoloides* and assigned to this species the material they examined from New Caledonia, Palau and Philippines. The description of *E. actinostoloides*, provided by these authors, is based on features observed on specimens from distant geographic locations, and the reported range of variations is large, e.g. the diameter of the oral disc ranges from 30 to 200 mm, the number of the tentacles is from 85 to about 200, large basitrichs in column are present only in large specimens, etc. They noted that small rare basitrichs were recorded in the tentacles of the type specimen of *E. actinostoloides* but they are not present in the specimens from New Caledonia, Palau and Philippines, examined by them. All these differences were treated as not significant. However, small basitrichs, similar to those of the type specimen, were recorded in the tentacles of a specimen of *E. actinostoloides* collected subsequently in its type locality (Yanagi et al., 2015), and their presence may be taxonomically significant. The specimen described in details by Yanagi et al. (2015) is large, but large basitrichs in its column are significantly smaller than those reported by Arellano & Fautin (2001) for large specimens in their material. These and other differences mentioned by Yanagi et al. (2015) cast a doubt on whether the discussed above specimens from distant geographic locations are conspecific.

The cnidom of *T. ioran* **sp. nov.** is characterised by the presence of two types of p-mastigophores,

p-mastigophores A and B1. Unfortunately, previous authors failed to distinguish among the types of p-mastigophores in *E. actinostoloides* (a crucial feature for inferring a taxonomic position of a taxon). However, from the photographs published by Arellano & Fautin (2001) and Yanagi et al. (2015), we suppose that *E. actinostoloides* also has two types of p-mastigophores, A and B1. The picture in Arellano & Fautin (2001, Fig. 6E) clearly shows p-mastigophore A from the filaments or the actinopharynx (these authors used the same photographs to illustrate nematocysts from different body regions), and Fig. 7M in Yanagi et al. (2015) shows p-mastigophore B1 while Fig. 7K in the same work is more similar to p-mastigophore A. Arellano & Fautin (2001) reported robust spirocysts in *E. actinostoloides*, but the photograph illustrating this spirocysts (Fig. 6B in Arellano & Fautin, 2001) shows a large spirocyst of a gracile type with regularly packed tubule, very different from the true robust spirocysts found e.g. in Hormathiidae which have tubule wound in an untidy fashion and are wider than the gracile spirocysts of a similar length (Daly et al., 2004; Fautin & Barber, 1999; Riemann-Zürneck, 1978, 1991; Sanamyan & Sanamyan, 2007; Sanamyan et al., 2009, 2015a). In *T. ioran* **sp. nov.**, all spirocysts are of gracile type. Thus, in general, the cnidom of *T. ioran* **sp. nov.** is similar to the cnidom of *E. actinostoloides* but differs in details (no columnar spirocysts, size ranges, etc.).

In phylogenetic analysis based on 16S and 12S rDNA performed by Yanagi et al. (2015), *Exocoelactis* nestled between actinostolid genera *Actinostola* Verrill, 1883 and *Stomphia* Gosse, 1859. Despite this fact these authors chose not to move *Exocoelactis* to Actinostolidae and retained the genus in the family Exocoelactinidae. We agree with them and support this approach: the arrangement of the mesenteries in *Exocoelactis* differs significantly from that in Actinostolidae, and despite of found similarity in two molecular markers, the family Exocoelactinidae should be retained. We also agree with Grebelny (2014, 2017) and Grebelny et al. (2018) who pointed that various mechanisms (including the so far poorly understood or unknown recombination processes) can strongly influence the similarity and difference of molecular markers, and in the cases of contradic-

tion between morphological and molecular data, the priority should not be given automatically to molecular data.

Tetracoelactis ioran sp. nov. has the lowest number of meristematic zones (four) among all species of Actiniaria. Previously the lowest number of meristematic zones in Actiniaria was known in *Actinernus* Verrill, 1879 which has eight stable meristematic zones. In other Anthozoa, only one meristematic zone is present in Ceriantharia, and two zones in Zoantharia (see Grebelny, 1982), that makes their bodies bilaterally symmetric. Four meristematic zones in Anthozoa were known previously only in fossil corals Rugosa (Tetracorallia). Many Rugosa also have bilaterally symmetric polyps, and their four meristematic zones are in the same four primary exocoels as in skeletonless *Tetracoelactis* gen. nov. However, new septa are added in Rugosa in a different way. In *Tetracoelactis* gen. nov., two pairs of each newly appearing cycle of mesenteries are laid in the middle of primary exocoels and diverge from meristematic zone (bilaterally). In Rugosa, new septa arise near one side of primary exocoels and are added serially in one direction: from cardinal septum to alar septum in “ventral” exocoels and from alar septum to counter-lateral septum in lateral exocoels (see Duerden, 1905, 1906; Yakowlew, 1915).

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