Morphogenesis of *Tedania gurjanovae* Koltun (Porifera)

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DURING THE COURSE of a study of the marine sponges of the San Juan Archipelago, Washington, the discovery of several specimens of *Tedania gurjanovae* Koltun (Koltun, 1958:65, fig. 20) was of special interest because of the opportunity provided to observe its larval metamorphosis. This species had been known previously only from the eastern part of the Tatar Strait, off Sakhalin, USSR, at depths of 60 to 100 m (Koltun, 1958, 1959). The present specimens (No. 30, 58, 90, 112, lot 163) were dredged in depths of 73 to 198 m in President Channel and San Juan Channel, San Juan Archipelago, Washington, and now reside in this writer's personal collection. An account of the morphology, larval metamorphosis, ecology, and taxonomy of the Washington population is given here.

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ADULT MORPHOLOGY

Tedania gurjanovae is an amorphous encrusting sponge that shows a tendency to macerate after being dissected or upon being collected in broken pieces and preserved. It commonly measures up to 12 mm thick but broken pieces of No. 163 attained a size of up to 4 cm by 3 cm by 2 cm. These fragments probably represented portions of a larger specimen. Specimen No. 90 is an encrusting form that intermittently covers plates of *Balanus* and measures up to 1 mm thick.

The color in life ranges from very light cinnamon to Lido (Maerz and Paul, 1950: pl. 12, D-4, F-5; pl. 13, C-3). In alcohol it is beige to nearly white. The species is odorless so far as is known.

The sponge surface may be smooth but often is gently to roughly undulated (Fig. 1). It is feltlike to the touch. The consistency is moderately soft and spongy. The surface may be slippery because of detritus and production of mucus. The dermal anatomy is considerably obscured in some preserved specimens and observations on living material are useful. Oscules may be absent but, if present, are usually numerous, irregularly distributed, open at the body surface, and measure up to 1 mm in diameter. Some oscules have an accumulation of hastate tornotes around their periphery. Pores are abundant and range from 21 to 68 μ in greatest diameter. In No. 163 they were no longer observed after about one hour in the preservative, indicating that they had closed.

The dermal membrane measures from 20 to 25 μ thick. Hastate tornotes (Fig. 2*b*), arranged more or less perpendicular to the body surface, occur immediately below the dermal membrane. They are loosely distributed and often simulate short wisps of commercial glass wool. Groups of about 10 perpendicular tornotes occasionally occur. In a few regions tornotes are almost parallel to the sponge surface. Hastate tornotes and styles (Fig. 2*a*) sometimes penetrate up to 50 μ beyond the dermal membrane.

The endosomal mesenchyme ranges from being loose and fluffy to cotton-like. Style tracts extend toward and sometimes penetrate the body surface. The tracts measure from 34 to 55 μ in diameter and the styles are united by small amounts of spongin. Numerous hastate tornotes and some styles are found irregularly distributed

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FIG. 1. *Tedania gurjanovae* Koltun (× ⅔). Small sample, Specimen No. 58. Large sample, Specimen No. 112, encrusting on *Modiolus*.

throughout the endosome. Onychaetes (Fig. 2*c–e*) occur both scattered and in trichodragmata. Excurrent canals measure up to 500 μ in diameter, whereas smaller canals range down to 83 μ in diameter. Canals are moderately numerous.

The spicules and their dimensions are listed in Table 1. The mean dimensions of each spicule category of specimen No. 30 and 112 are based on 10 measurements, and each size range is represented by 1 minimum and 1 maximum measurement.

The styles are often curved. Occasional juvenile styles were observed. Hastate tornotes sometimes have very slightly inflated ends. Onychaetes are straight or slightly curved and occur in two size ranges. The smaller forms (I) tend to be prominently roughened, whereas the larger sizes (II) are only slightly rugose (Fig. 2*c–e*). Juvenile onychaetes also occur. One measurement is 81 × 1 μ. Onchaetes are often found in trichodragmata measuring from 60 to 100 μ thick.

ECOLOGICAL NOTES

Tedania gurjanovae is collected chiefly from a biotic community of lamellibranchs (mussels) and barnacles. In some specimens the endosome is contaminated by a few sand grains.

Biological associates include: No. 30, *T. gurjanovae* partly encrusting on barnacles (*Balanus*) with another sponge (*Halichondria*), all of which are encrusting on the carapace of a crab; No. 58, *T. gurjanovae* encrusting around a barnacle (*Balanus*) with attached polychaete tubes (Fig. 1); No. 90, *T. gurjanovae* encrusting on barnacles (*Balanus*); No. 112, a few foraminifera on the sponge surface, *T. gurjanovae* encrusting on a mussel (*Modiolus modiolus* Linnaeus) and surrounding a barnacle (*Balanus*) and several large polychaete tubes (Fig. 1); No. 163, one large endosomal polychaete tube. Koltun (1959:156) reported that *Tedania gurjanovae* is frequently found encrusting on the valves of scallops (*Chlamis*).

TABLE 1

SPICULE MEASUREMENT (in μ) OF *Tedania gurjanovae* KOLTUN

Author	Bakus	Bakus	Koltun, 1958
Specimen No.	30	112	2974
Depth and Habitat	192 m rock-shell bottom	110–128 m rock-shell bottom	shell bottom
Style:			
Length	296–324–335	318–340–373	260–343
Width	9–11–12	10–12–13	8–14
Hastate Tornote:			
Length	204–226–248	222–236–252	202–280
Width	5–6–7	4–6–7	4–8
Onychaete I:			
Length	40–75–91	58–69–89	77–157
Width	2.2–2.7–3.5	2.2–2.6–3.0	3–4
Onychaete II:			
Length	142–168–265	150–174–265	197–312
Width	1.5–1.7–1.8	1.2–1.4–1.6	2

LARVAL METAMORPHOSIS

The dissection of a specimen of a sponge (lot No. 163) on 26 July 1959 revealed living embryos attached by the posterior end to the parental mesenchyme (Fig. 3*a*). Motile cilia were distributed over the entire surface except for the posterior pole. A minute region at the anterior end was very slightly pigmented. Both embryos and subsequently released larvae were cream colored. The larvae were typical parenchymulae, roughly oblong in shape, and measured from 500 μ long by 332 μ in mid-length diameter to 576 μ by 433 μ. In released larvae the anterior pole had very short cilia; cilia were lacking on the posterior end (Fig. 3*b*). Elsewhere the cilia were longer and of approximately equal dimensions. Several larvae contained one or two visible parental (?) spicules passing through their mesenchyme. This had no apparent effect on their swimming behavior. The presence of spicules in larvae of Demospongiae is common. Ali (1956:558–559), in a study on the development of *Lissodendoryx similis* Thiele, found that the larvae contained both microscleres and megascleres and in greater density than found in the adult.

Larval spiculation was studied in preserved embryos. A mature embryo, ready to leave the parent sponge, contains several hundred onychaetes of both adult size groups, but the majority are of the smaller category (I). Moreover, there are about 25 to 35 conspicuously tapering and mildly echinated acanthostyles that measure about 120 μ in length by 10 μ in basal shaft diameter or 5 μ in mid-shaft diameter. Both onychaetes and acanthostyles are concentrated into a dense packet near one pole, though many onychaetes occur elsewhere throughout the larva. Since the larval acanthostyles apparently do not occur in the adult they may undergo further change to the stylote configuration. The late embryonic spicule distribution of *Tedania gurjanovae* looks something like that of the *T. charcoti* embryo as figured by Burton (1932:362, fig. 47L). Burton (1932:361) reported that acanthostyles are the first spicules to appear in embryos of *T. charcoti* Topsent and that they become converted into smooth styles as development progresses. Further growth is indicated by a segregation of styles in a neat bundle at the "aboral pole of the embryo" and a rapid increase in numbers of rhaphides. Burton believes that rhaphides are probably the prototypes of adult onychaetes.

The larvae swam with the anterior end directed forward and completed spiral gyrations.

One larva was observed swimming with the posterior pole directed forward. It was not unusual for natatory parenchymulae to pause for several minutes on the bottom of the glass finger bowl.

There appeared to be no obvious negative or positive phototaxis. Lévi (1956:119) noted that the larvae of *Haliclona indistincta* (Bowerbank) showed no particular taxis. Larvae of *Lissodendoryx similis* (Ali, 1956:557) and *Mycale syrinx* (O. Schmidt) (Wilson, 1935: 287) have shown negative phototaxis. Whether or not sensory cells are associated with this behavior is unknown at the present time (Jones, 1962:13–14). Further observations on larval behavior are discussed by Jones (1962:13–14, 49–50). Ali (loc. cit.) and Wilson (loc. cit.) both reported that some sponge larvae swim upwards then adhere to the water surface film and eventually die or disperse into scattered fragments and disintegrate.

Four larvae were removed from their attachment to the parent and placed in a finger bowl of sea water to observe settling behavior. Two of the larvae were fixed to the bottom of the finger bowl 6 hr later; of the remaining larvae one appeared to be caught in the water surface film, the other attached to the bottom of the finger bowl after about the 7th hr. A few larvae appeared to have a slightly invaginated posterior pole just prior to fixation on the glass substratum (Fig. 3*c*).

Larvae of *Lissodendoryx similis* (Ali, 1956: 575) commence attachment to a substratum after about 40 hr; almost 24 hr of this period is spent swimming near the water surface. Sexual larvae of *Esperella sordida* (Bowerbank) (Delage, 1892:370) swim for about 20 hr, whereas those of *Mycale syrinx* remain motile for 1 to 3 days (Wilson, 1935:295). Some larvae of *Mycale syrinx* rotate on a substratum for as long as 10 days before fixation. The duration of the larval period of *Halisarca metschnikovi* Lévi is 2 days, and that of *Halisarca dujardini* Johnston, less than 1 day (Lévi, 1956:79). Asexual larvae of *Esperella fibrexilis* Wilson (Wilson, 1894:298) swim freely for 1 to 2 days, whereas, those of *Callyspongia diffusa* (Ridley) (Sivaramakrishnan, 1951:287) show natatory activities for only 6 to 8 hr. It is known that within a single species of marine animal the planktonic period varies considerably with temperature, the availability of food, and the proper substratum (Thorson, 1957:482; Moore, 1958:314). *Tedania gurjanovae* apparently has a brief swimming period, at least under laboratory conditions.

In the present study, as a parenchymula larva attached to the glass substratum by the anterior end, the ciliary beat slackened in frequency and within 10 to 15 min all cilia appeared to be motionless. Approximately 30 min after fixation the typical larval habitus became completely disorganized. The mesenchymal cells collapsed from their original position and spread into a flat light-yellow circular plate measuring about 600 μ in diameter (Fig. 3*d*). Segregation and spreading of cells continued. At 3 hr of age the

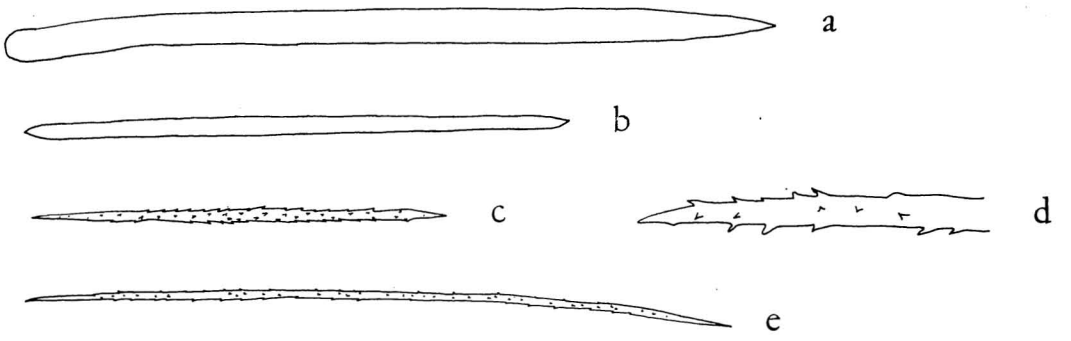

FIG. 2. Spiculation of *Tedania gurjanovae* Koltun. *a*, Style, × 375; *b*, tornote, × 375; *c*, onychaete I, × 560; *d*, end of onychaete I, × 1260, note the echinations; *e*, onychaete II, × 375, note the comparatively finer echinations.

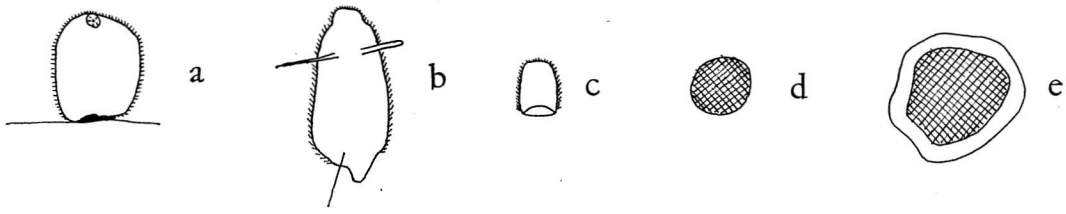

FIG. 3. Larvae and metamorphosis of *Tedania gurjanovae* Koltun. *a,* Sketch of a living embryo obliquely joined to parental mesenchyme, × 32. It is nearly ready to detach as a parenchymula larva. *b,* Sketch of a natatory parenchymula, lateral view, × 46. Note the parental (?) style and onychaete piercing the larva. *c,* Sketch of a parenchymula showing a slightly invaginated posterior pole, lateral view, × 16. *d,* Sketch showing from above a spherical mass of mesenchymal cells (pattern) resulting from fixation of a larva to a glass substratum for about 30 min, × 14. *e,* Sketch made from above the same larva after a fixation period of 3 hr, × 18. Mesenchymal cells occupy the cortical region (pattern) and are encompassed by a transparent band of syncytium-like protoplasm.

disc measured 1065 μ in diameter and consisted of an internal subspherical light-yellow mass 800 μ in diameter surrounded by a transparent band of protoplasm containing no observable cell boundaries (Fig. 3*e*). The rate of development in *Tedania gurjanovae* during the early stages of metamorphosis seems to be considerably more rapid than that described for *Lissodendoryx similis* (Ali, 1956). The length of time necessary for *Tedania gurjanovae* to reach histological maturity was not determined in the present study. Wilson (1935:295) reported that the formation of choanocyte chambers and canals in some cultures of *Mycale syrinx* occurred within 3 to 4 days after discharge of the larvae from the parent, and Lévi (1956:81) noted that the histogenesis of *Halisarca dujardini* into a functional rhagon took about 2 days after larval fixation.

At 1 day of age the juvenile encrustation revealed several small styles that were irregularly scattered in the mesenchyme. These may still have been the embryonic acanthostyles, but with the 112.5 × magnification of a dissecting microscope echinations were not apparent. At 7 days of age the styles were showing some evidence of orientation perpendicular to the substratum. After 13 days most of the styles, especially in the center of the disc, were oriented perpendicular to the substratum. Hastate tornotes were observed for the first time. A very thin dermal membrane with scattered mesenchymal cells constituted the sponge surface. The endosome was translucent and archeocytes were concentrated at the sponge base and around perpendicular megascleres. The sponge had almost doubled in thickness since the seventh day of attachment. No oscules were observed. At 19 days of age the colonies were almost unchanged except for increased thickness. One specimen had formed a fistule about 1.5 mm high.

The colonies were last observed on 28 August 1959 (at an age of 33 days). They had remained relatively minute. The largest two sponges measured roughly 1.5 mm by 0.75 mm and 2.0 mm by 0.75 mm in diameter. Their thickness did not exceed 2 mm. None of the specimens showed evidence of oscule formation. Perhaps in culture these sponges remained in a diminutive condition because their environmental conditions present in the laboratory differed from their natural deeper water habitat.

TAXONOMIC DISCUSSION

The holotype of *Tedania gurjanovae* Koltun is specimen No. 2974, Zoological Institut, Akademia Nauk, Leningrad, USSR. The habitat, habitus, and natural color of this species as reported by Koltun (1958:65) closely resemble that of local San Juan representatives. The spicule morphology and size are also very similar to local forms except that the onychaetes are longer and more rugose in the Russian specimen. The endosomal anatomy is too briefly described to make a useful comparison. Koltun (1959: 156) states: "The main skeleton is in appearance like an irregular net of organized bundles of spines."

Burton (1932:345) recognized the Vancouver Island specimen of *Tedania fragilis* Lambe (see Lambe, 1895:136) as 1 of the 24 valid species of its genus. De Laubenfels (1961:197) collected *Tedania fragilis* from a depth of 50 to 60 m, northeast of Blakeley Island (San Juan Archipelago). I examined the holotype (USNM No. 7401) of *Tedania fragilis* Lambe and found that it differs from specimens discussed in this paper in the following features: the spiculation is larger and onychaetes are often erratically curved. The short-size category of onychaetes is lacking. The hastate tornotes often have slightly inflated ends that may be microspined. Some tornotes have one end hastate and the other rounded or subtylote. Style tracts are more abundant and interstitial styles are irregularly distributed, although some meshes do occur. The holotype is dry and exceptionally fragile. The specimens from the San Juan Archipelago described in this paper are placed tentatively in *Tedania gurjanovae* Koltun.

SUMMARY

The adult morphology, larval metamorphosis, biological associates, taxonomic status, and distribution of *Tedania gurjanovae* Koltun are described. This species has been dredged from a rock-shell substratum on the continental shelf and apparently ranges from the San Juan Archipelago in the northeast Pacific to Tatar Strait in the northwest Pacific. The larval natatory period is 6 to 7 hr. Metamorphosis involves a complete collapse of the larva into an amorphous mass somewhat platelike in over-all shape, within which many cells can be seen. Segregation occurs; this results in a core of inner cells (archeocytes) and an outer transparent layer of protoplasm not shown definitely to be cellular. Development continues to a miniature adult-like habitus which is reached after about 2 to 3 weeks.

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