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DESCRIPTION AND LIFE-HISTORY TRAITS OF A NEW SPECIES OF *PROCERAEA* WITH LARVAE INFECTING *ABIETINARIA TURGIDA*

(POLYCHAETA, SYLLIDAE & HYDROZOA, SERTULARIIDAE)

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ABSTRACT

A new species of the genus *Proceraea* (Polychaeta, Syllidae, Autolytinae), *P. rzhavskyi*, is described. Many specimens of this species at different stages of development were found within the hydrothecae and mucous tubes attached to colonies of the sertulariian hydrozoan *Abietinaria turgida* (Clark, 1867) at the coast of Mednyy Island, the Commander Islands, Northwest Pacific, 5-12 m depth, in August 1986. Larvae and juveniles are present within the hydrothecae from very early stages of development, which appears to be direct. This is the first report of a polychaete with symbiotic larval stages and free-living adults. The smallest specimens have a yolk, a single pair of eyes, and a tuft of short cilia at the apical part of prostomium, but lack setae. As larvae grow, the yolk and the tuft of cilia disappear. Setae and dorsal cirri appear on several anterior segments, the pharynx develops, and juveniles start feeding upon the host. Finally, they occupy the entire cavity of the hydrothecae. A conspicuous tubular addition to the hydrotheca is formed distally as a result of infestation. Upon reaching 10-11 setigers, the juveniles leave the hydrotheca, build mucous tubes attached to the stem or branches of the colony and continue their growth up to the adult stage. The proventriculus and the teeth of the trepan are formed when the worms leave the hydrothecae. Unlike *Autolytus* all the stages lack ciliary bands on the body. A female stolon (sacconereis) was examined. *Proceraea rzhavskyi* differs from closely related species, *P. okadai* and *P. mukaishimus*, in structure of the trepan and length of head appendages and nuchal epaulettes.

Keywords: Polychaeta, Syllidae, *Proceraea*, symbiotic larvae, life cycle, Hydrozoa, *Abietinaria*.

INTRODUCTION

Syllids are generally small or very small free-living worms, which crawl among the algae or live interstitially within coarse sediments. However, there are about 18 species of syllids reported as commensals and 10 species are considered to be parasites of sponges, cnidarians, decapods, echinoderms and ascidians (Martín & Britayev 1998).

Members of one of the four subfamilies of syllids, the Autolytinae, are specialised carnivores of colonial animals, like bryozoans and, especially, of hydrozoans (Fauchald & Jumars 1979). There is a specificity in feeding habits, so that an autolytine species usually feeds on only one or a few species of hydroids. When algae, boulders, or the surface of bivalves were observed as habitats of Autolytinae, these substrates were usually covered with hydrozoan colonies, suggesting a close association between the autolytines and hydrozoans (Gidholm 1967).

Reproduction in this family is particularly interesting and usually corresponds to the classical subfamilies (Franke 1999). Most species of Syllidae undergo marked morphological, behavioral and physiological modifications connected with sexual reproduction. In the case of Autolytinae epitocous modifications involve transformation of posterior end into a sexual stage (stolon). The adults produce a male "polybostrichus", or a female "sacconereis", stolon, or a chain of stolons; these are morphologically different from the adult "stock". Gametes fill each stolon. When mature, the stolons are successively budded off from the stock (Franke 1999). In many cases, each sacconereis produces a ventral sac containing the ova, which are fertilized by the polybostrichus. The pelagic life of the larvae after being released from the brooding sac is relatively short (Schiedges 1979; Quian & Chia 1989).

We have found a special type of reproduction in a new species of *Proceraea,* a member of the Autolytinae. The first report on the association of this *Proceraea* sp. with sertulariian hydroids was published recently (Britayev et al. 1998). The information presented here includes the description of the new species as well as the main phases of its larval and postlarval development, and some details of its reproductive biology.

RESULTS

Proceraea rzhavskyi sp. nov.

(Fig. 1 A-E)

Material examined. – Mednyy Island (Commander Islands), Gladkovskaya Bay, 54°44´N, 167°45´E, 6 m, on the hydroid *Abietinaria turgida,* holotype (ZMMSU 849, anterior fragment) and four paratypes (ZMMSU 850-853), coll. V.V. Oshurkov.

Description. – Length of holotype 10.2 mm (posterior end missing), width of setiger 10 without parapodia 0.35 mm, 50 setigers. Length of paratypes 3.0 – 4.8 mm, width without parapodia 0.25 – 0.55 mm, 32 – 49 setigers. Body elongate, slender, preserved material without colour markings, without ciliary bands. Prostomium (Fig. 1A) oval, slightly broader than long, with two pairs of reddish eyes in trapezoidal arrangement; eyes of anterior pair slightly larger than posterior ones; median antenna 1.5 times as long as lateral ones, extending to setiger 4 or 5, originating between posterior pair of eyes; lateral antennae arising from anterior margin of prostomium, between anterior eyes; antennae without articulation; palpi medially fused; dorsal tentacular cirri 1.5 times as long as ventral ones, nearly of the same length as lateral antennae, both without articulations. Two nuchal epaulettes starting from posterior edge of prostomium and extending postero-laterally to setiger 3 or 4. Dorsal cirri relatively long, often unequal in length.

Parapodia (Fig. 1D) uniramous, ventro-laterally directed, parapodia swollen in holotype and two paratypes (posterior ones more swollen than anterior ones), each with 2-15 compound setae and 2-3 aciculae; number of setae in parapodia progressively decreasing posteriorly. Compound setae (Figs. 1E, 2F, 5B) with distally bidentate blade and distally spinose shaft. Bayonet setae found in juveniles only (Figs. 2E, 5C). Pygidium (Fig. 1F) with two long anal cirri.

Pharynx (Fig. 1B) long, provided with trepan (Fig. 1C) of 9 large teeth, each alternating with 2-3 small ones; proventriculus short in setigers 14-17 (holotype). Number of muscular rings in proventriculus variable (35-43, 43 in holotype). Length of distal straight part of pharynx 0.95 mm, length of coiled basal part 4.63 mm, length of ovoid proventriculus 0.95 mm (holotype).

Remarks. – The shape of bayonet setae, elongate tapering dorsal cirri and absence of ciliary cover are characteristics of the genus *Proceraea.* The compound setae are similar in shape to those of *Autolytus okadai* Imajima, 1966 (probably a species of *Proceraea*), but Imajima's species differ because (1) its trepan has only 9 small teeth alternating with the 9 large ones; (2) its nuchal epaulettes extend through only one segment; and (3) two dorsal longitudinal black bands extend throughout the body. *Autolytus mukaishimus* Imajima, 1966 (probably also a *Proceraea*) has a trepan like that of *P. rzhavskyi,* but with even more small teeth between the large teeth. It also seems different in having (1) longer head appendages; (2) nuchal epaulettes confined to one segment; (3) some body pigmentation.

Etymology. – The new species is named in honour of the polychaetologist Alexander V. Rzhavsky, who drew our attention to it and provided the material.

Morphology of larvae and juveniles

Achaetous larvae (Figs. 2A-B, 3C). – Achaetous larvae were found in the hydrothecae at the base of the polyps (Fig. 3C). The spindle-shaped body widens at segments 2-3 (Fig. 2A), with flattened ventral surface and convex dorsum. The smallest specimen was 230 μm long. There are 10-11 segments, but they are difficult

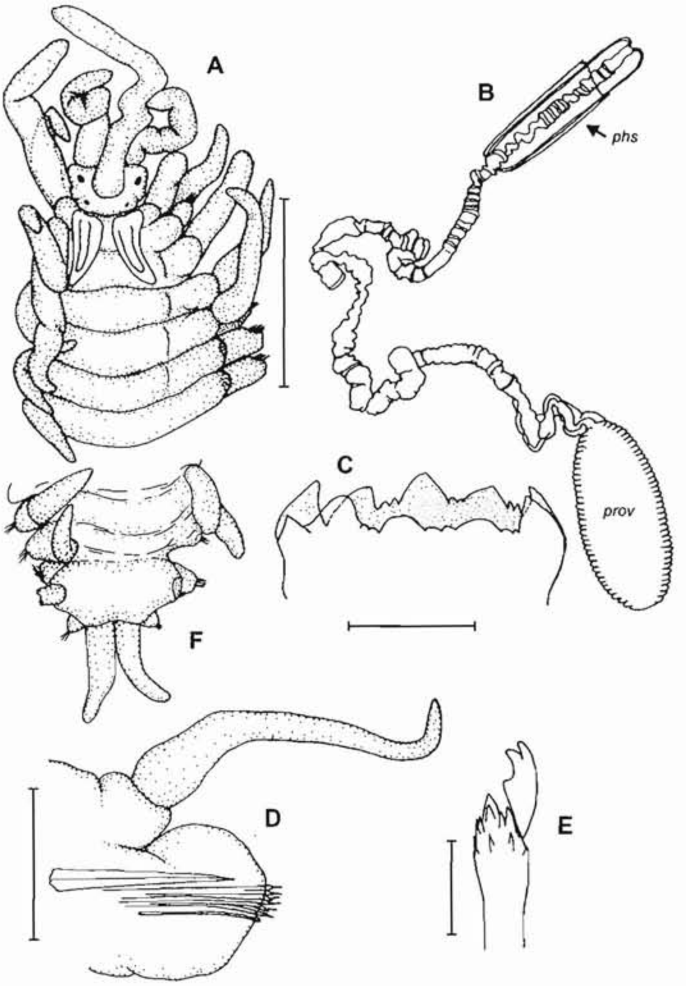

Fig. 1. *Proceraea rzhavskyi* sp. n. – A, anterior end in dorsal view. – B, details of proboscis; phs = pharyngeal sheath, prov = proventriculus. – C, trepan with nine large teeth alternating with 2-3 small teeth. – D, parapodium of setiger 11 – E, distal end of compound seta. – F, posterior end (dorsal view). Scale: A = 0.7 mm ; B, F = 0.5 mm ; C = 40 µm; D = 0.3 mm ; E = 5 µm .

to count since the borders of the posterior segments are indistinct. Prostomium is rounded with one pair of eyes, three rudimentary antennae and a small apical tuft of cilia. Pygidium bilobed with two oval anal cirri. An accumulation of yolk granules is still visible in anterior widened part of the body.

During larval development and growth the amount of yolk decreases, the apical tuft disappears, and the pharynx and anterior dorsal cirri are formed (Fig. 2B). Pharynx is not functioning, and nutrition is probably dependent on yolk at this stage; this is supported by the fact that these small worms coexist with undamaged host polyps (Fig. 3C).

Early juvenile (Fig. 2C). – Setae first appear in the anterior segments when the larvae reach a length of 450-500 µm. The tentacular segment has a single pair of tentacular cirri. Dorsal cirri are formed posteriorly. The number of segments does not increase. At this stage the worms probably start to feed on the polyps, since these tend to become fragmented and reduced in size (Fig. 3C). We call this an early juvenile stage.

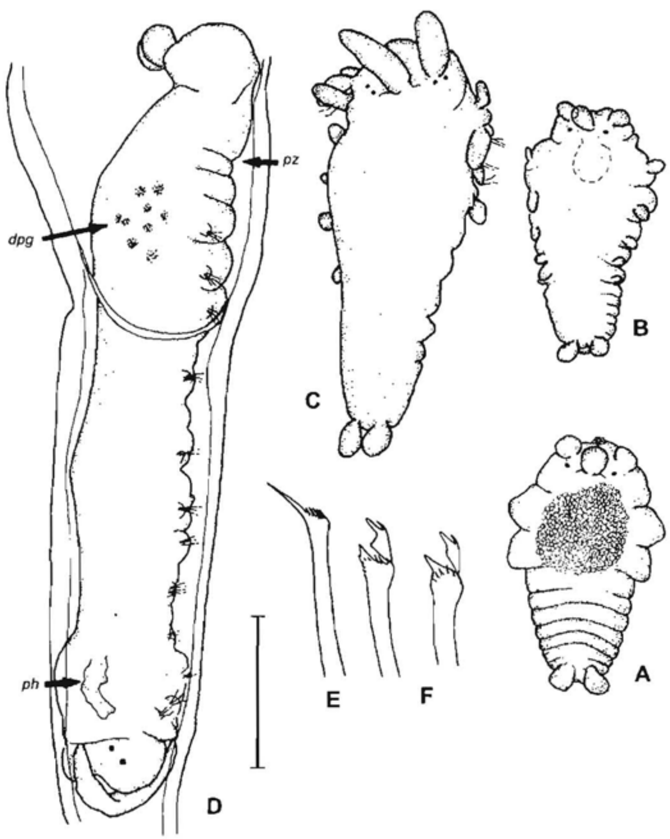

Fig.2. *Proceraea rzhavskyi* sp. n. – A, achaetous larva with yolk granules and apical tuft of cilia. – B, achaetous larva with dorsal cirri. – C, juvenile with two pairs of eyes and setae on anterior segments. – D, juvenile specimen in modified hydrotheca with head directed towards base of hydrotheca; arrows indicate dark pigment granules (dpg) characteristic for hydroids; ph = pharynx; pz = proliferation zone. – E, simple bayonet seta. – F, compound setae. Scale: A = 150 µm ; B-D = 180 µm ; E, F = 20 µm.

Juveniles in thecae (Fig. 2D) – The juveniles occupy either the base of the theca (jug) or the whole theca, including its distal part (Fig. 2D). The body becomes slender, vermiform, 0.9-1.0 mm long. The prostomium develops three antennae, all about the same length, and two pairs of eyes. The number of setigers is about 10-11. Granules of dark pigment are visible through the intestine walls. Their colour and size are similar to granules in the polyp's tissue. Two types of setae are present: 2 - 5 bayonet setae (Fig. 2E), with wide proximal part, and one compound seta (Fig. 2F) with the secondary tooth larger than the terminal one. At this stage, the host polyp has disappeared and the modified theca is completely occupied by the polychaete (Fig. 3B).

Juveniles in mucous tubes (Figs. 3D, 4A-C) – Juveniles 1 mm long leave the thecae and produce mucous tubes attached to the hydroid colony's stem or branches (3D). The smallest of these specimens has the same number of setigers (10-11) as the stage inside the thecae. New segments are produced in the narrow zone just preceding the pygidium. The boundaries between neighbouring segments are indistinct. The number of segments and length of head appendages and dorsal cirri increase in the growing juveniles.

One specimen 2.5 mm long has 28 setigers. The prostomium (Fig. 4A) is as long as wide, with two pairs of reddish eyes, arranged trapezoidally. The anterior pair of eyes is larger than the posterior pair; in the preserved specimen

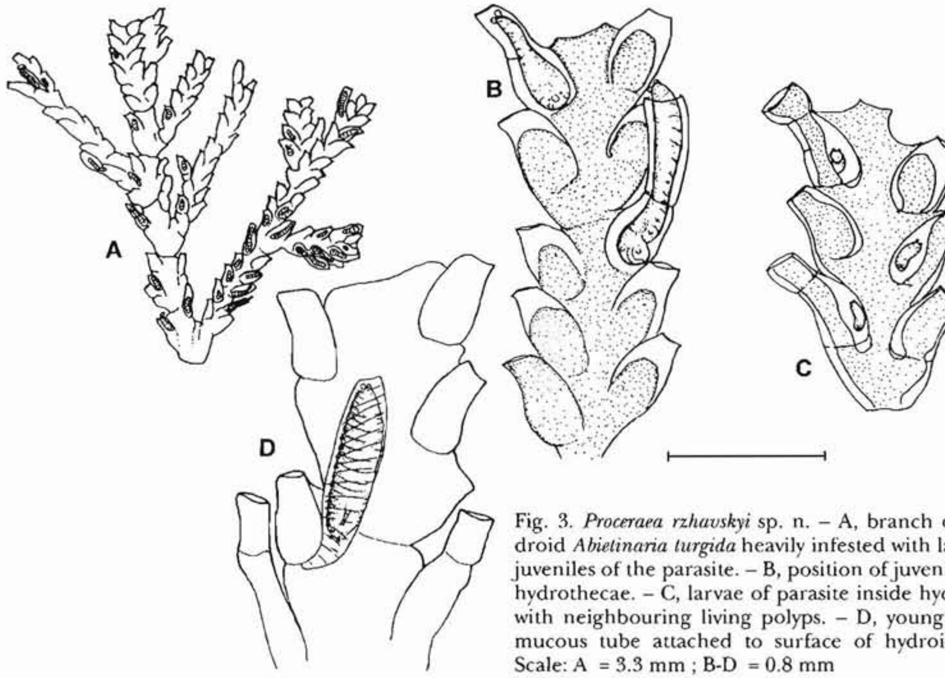

Fig. 3. *Proceraea rzhavskyi* sp. n. – A, branch of the hydroid *Abietinaria turgida* heavily infested with larvae and juveniles of the parasite. – B, position of juveniles in the hydrothecae. – C, larvae of parasite inside hydrothecae with neighbouring living polyps. – D, young worm in mucous tube attached to surface of hydroid colony. Scale: A = 3.3 mm ; B-D = 0.8 mm

only the median antenna is left, its base located in front of and between the anterior pair of eyes; extends back to setiger 3 and lacks annulation. The single tentacular cirrus extends back to setiger 2. Ventral cirri are absent. Dorsal cirri are short, oval, without articulation, nuchal epaulettes extend posteriorly from the hind border of the prostomium to middle of setiger 1. The proventriculus is small, ovoid, in setigers 4 and 5, not yet completely developed (4B). The trepan (Fig. 4C) has 16 teeth of equal size with pointed tips like saw teeth. Parapodia are ventro-lateral, each with 4-9 setae, fewer posteriorly. Each parapodium has one bayonet seta and several compound setae with distally bidentate blades. Pygidium with two long anal cirri.

Ecology

Location on host. – Larvae and young juveniles live inside modified hydrothecae (Fig. 3A-C), one specimen per hydrotheca. Larvae 230-450 µm long may share hydrothecae with living polyps (Fig. 3C), whereas juveniles longer than 450-500 µm occupy hydrothecae with little or no host tissue (Fig. 3B). Specimens at least 1.0 mm long leave the hydrothecae and produce transparent mucous tubes that are attached along the stem or a main branch of the colony (Fig. 3D). We found 7 inhabited tubes and one empty tube. All were situated in the basal or middle parts of the colonies. The bottom of the tube is usually closed. In most tubes the anterior end of the worm is directed towards the closed end. Tube length exceeds the worm length, the longest tube being 4.8 mm long and connecting neighbouring branches of the hydroid colony. Worms living in tubes occur more rarely than earlier stages living inside hydrothecae. No colony (or large branch) had more than one worm in a tube.

Hydrothecae modification. – Normal unmodified hydrothecae are short, jug-shaped and closely attached along the stem or branches (Fig. 3B-C, 5A). Hydrothecae inhabited by worms each consists of two parts: a basal jug-shaped part, similar to a normal hydrotheca, and a long, tubular distal part (Fig. 3B-C, 5A). In all, 222 specimens of *P. rzhavskyi* were found inside modified hydrothecae of *Abietinaria turgida*, one in an unmodified hydrotheca, and one in an unmodified gonotheca (a unique location). Larvae were usually found at the bases of the polyps (Fig. 3C). These observations suggest that a polyp respond to larval infestation by extending its body upwards and lengthening the

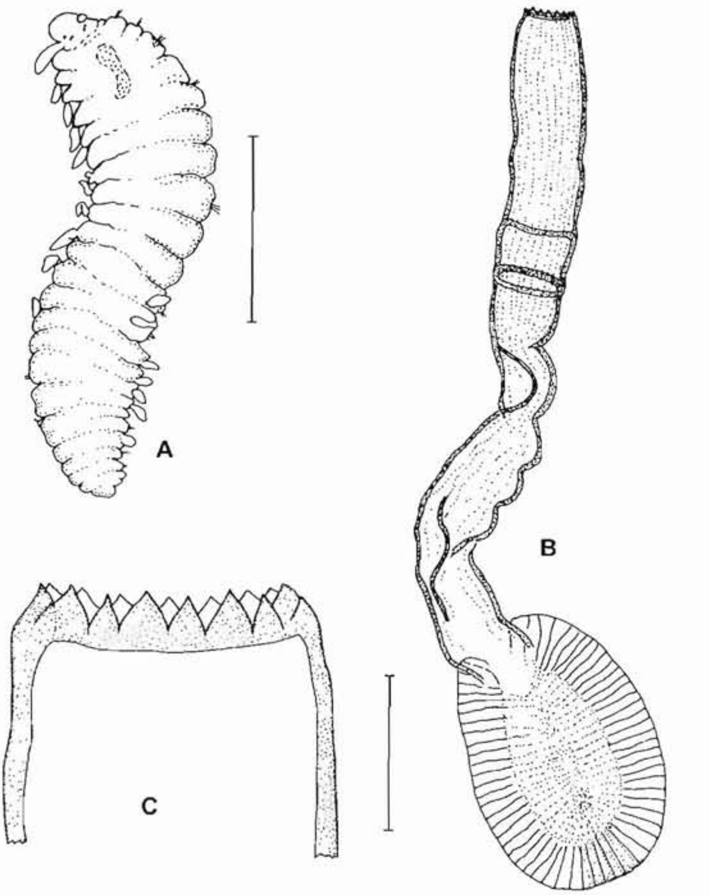

Fig. 4. *Proceraea rzhavskyi* sp. n. Young worm from mucous tube. – A, complete specimen, dorsal view. – B, proventriculus. – C, trepan with 16 saw-like teeth. Scale: A = 1.6 mm ; B = 0.1 mm , C = 10 µm .

distal cylindrical part of the theca. As a result, a good shelter is formed for the growing parasite, which eventually replaces the host polyp.

Percentage infested. – The evaluation is based on counting in 6 colonies or colony fragments of *Abietinaria* infested by *Proceraea*. The number of hydrothecae per colony varied from 67 to 1103, the number of symbionts per colony varied from 8 to 74. Infested hydrothecae varied from 3.8 to 33% of the total number.

Diet. – The following data support the hypothesis that the juveniles actively feed on the polyp tissue: (1) unlike larvae coexisting with host polyps, juveniles were always found with host fragmented, or reduced in size, or without host; (2) pigmented granules characteristic of the polyps were observed in the gut of the polychaetes (Fig. 2D); (3) some juveniles were seen to have their head inserted into the thecal opening of neighbouring polyps.

DISCUSSION

Fauchald (1977) considers absence of segmental ciliary bands as a diagnostic character for the genus *Proceraea,* and such "trochs" are indeed absent in larvae and juveniles of *P. rzhavskyi.* Only larvae in the earliest stage bear a rudimentary ciliation in form of an apical tuft. In contrast, the larvae of *Autolytus alexandri* Malmgren, 1867, have, at the stage of setal formation ("nectochaetae"), not only an apical tuft, but also an acrotroch, telotroch and metatroch, and a wide ventral ciliary band extending from mouth to pygidium (Qian & Chia 1989). *A. alexandri* has a pelagic larval phase of 1-2 weeks duration. For pelagic larvae, the cilia

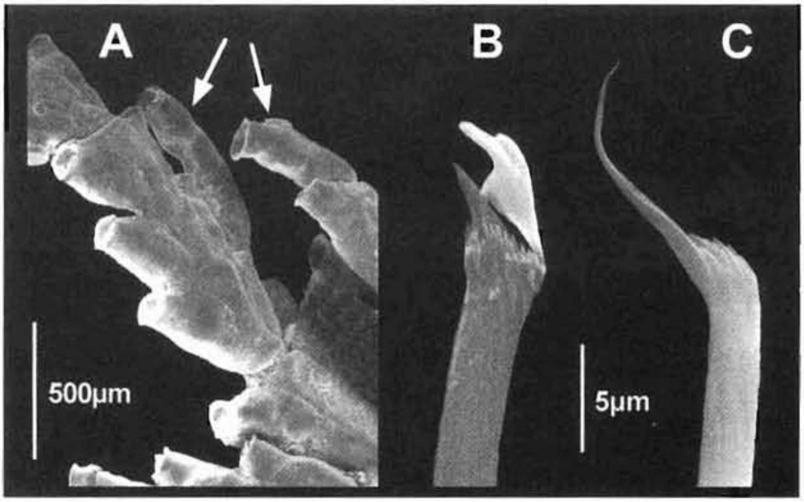

Fig. 5. *Proceraea rzhavskyi* sp. n. Scanning electron micrographs. – A, branch of the hydroid *Abietinaria turgida*, arrows indicate modified hydrothecae. – B, compound seta. – C, simple bayonet seta.

have two important functions – sensory and locomotory (Sveshnikov 1978; Nielsen 1987). Reduction of larval ciliation is connected with loss of active movement and substrate or host recognition, i.e., with the absence of pelagic and searching stages.

Two possible ways of *Abietinaria* infestation could be supposed: (1) settlement of planktonic larvae on the hydroids with subsequent invasion of hydrothecae, (2) oviposition directly into hydrothecae by gravid females. Settlement of planktonic larvae on a host is probably common among symbiotic polychaetes (Martín & Britayev 1998), but our data relating to *Proceraea* point to the second of the two possibilities, because absence of ciliation in *P. rzhavskyi* larvae indicates loss of the early searching stage, and the occurrence of only one larva or juvenile in each infested hydrotheca indicates oviposition. Settlement from plankton ic larvae would be expected to produce random or aggregated distribution of larvae. Finally, it seems unlikely that such delicate larvae could enter the hydrothecae through crowns of tentacles armed with nematocysts.

At this point the question arises, how is the species dispersed? Gidholm (1966) described epigamic reproduction in several species of *Autolytus* lacking polybostrichus and sacconereis stages, but we found a sacconereis of *P. rzhavskyi* inside a mucous tube attached to the branch of *Abietinaria*. Hence we suppose that the species produces sexual stolons as in other Autolytinae; after fertilization of eggs, the female stolon probably swims to find a colony of *Abietinaria turgida*, settles on a branch, and moves over the colony ovipositing in the hydrothecae .

To sum up, we hypothesize that the life cycle of *P. rzhavskyi* consists of five phases, with phases 1-3 and 5 symbiotic, and only phase 4 free-living, viz.: (1) larvae in hydrothecae consuming their yolk; (2) juveniles in hydrothecae feeding on the host polyps; (3) juvenile and adults living in mucous tubes attached to colony stems or branches and feeding on polyps; (4) swimming sacconereis and polybostrichus stages responsible for dispersion; (5) sacconereis stage that settles on a new colony and oviposits. If this is the case, the life cycle of *P. rzhavskyi* would be markedly different from those known for other Autolytinae (e.g., Malaquin 1893; Potts 1911; Allen 1921; Cognetti 1953; Schiedges 1979; Garwood 1991).

Life cycles with larvae parasitizing the hosts are not frequent among marine animals. Well known examples include copepods belonging to the family Monstrillidae, with larvae parasitizing sabellid polychaetes, to become pelagic adults (Gotto 1978), and pantopods with carnivorous adults and larvae parasitizing cnidarians (Dogiel 1948). Malaquin (1893) reported on the development of *Autolytus edwardsi*. This species has non-pelagic larvae, lives on bryozoans and hydroids, in which the eggs are placed on the branches, not inside the hydrothecae. *P. rzhavskyi* seems to be the first syllid found to have parasitic larval stages.

Some symbiotic polychaetes may produce scars, galls or blisters on their cnidarian hosts. Myzostomids live in galls or cysts on their echinoderm hosts (Grygier 1988). *Lumbrineris flabellicola* causes grooves in the skeletons of their scleractinian hosts (Zibrowius et al. 1975; Miura & Shirayama 1992). Scaleworms *Harmothoe melanicornis* and *Gorgoniapolynoe* spp. invade gorgonian and stylasterid corals, causing the hosts to grow around them, and thus to form tubular galls which shelter the worms (Britayev 1981; Pettibone 1991). There is at least one gall-forming species among syllids (Wright & Woodwick 1977): *Autolytus penetrans* induces the formation of small galls on the surface of its host, the stylasterid (hydrocoral) *Allopora californica.* However, prior to this description of *P. rzhavskyi* living on *Abietinaria turgida,* there seems not to be any account of a polychaete modifying hydrozoan hydrothecae.

MATERIALS AND METHODS

The host species, *Abietinaria turgida* (Clark, 1867), is recorded from the North Pacific, from the Bering Sea westwards to Sakhalin and the South Kurile Islands, and eastwards to San Francisco, and in the Arctic Ocean from the East Siberian Sea and the Canadian Arctic. The colonies are attached to hard substrates at depths ranging from the littoral zone to 140 m (Frazer 1937; Anculevich 1987), and between 5 and 130 m off the Commander Islands. According to Ricketts et al. (1985), *A. turgida* colonies may be up to 16-17 cm high. The jug-shaped hydrothecae are closely crowded along the stem and on the relatively short branches. The orifice of each theca is closed by a thin transparent cover (Ricketts et al. 1985).

About 27 samples of *A. turgida* from different localities near Bering and Mednyy Islands (Commander Islands) and some additional samples from Kamchatka and the North Kurile Islands were studied. Hydroids of *A. turgida* with modified thecae containing the syllids were found in two samples only. The material has been fixed in 4% formaldehyde in seawater and then preserved in 70% ethanol. More than 200 larvae and juveniles were found inside hydrothecae and 12 subadult and adult worms were inside mucous tubes attached to the colonies. In addition, several adult and subadult specimens were found on the bottom of jars containing infested hydroid colonies. The type series is deposited in the collections of the Zoological Museum of Moscow State University (ZMMSU). All the other specimens are in the collection of the A.N. Severtzov Institute of Ecology and Evolution (Moscow).

The drawings were prepared using a compound microscope provided with interference contrast optics (Nomarsky) and a camera lucida drawing tube. Scanning electron microscope (SEM) micrographs were made after critical point drying and gold coating (300Å) at SIDI (Servicio Interdepartamental de Investigación) of Universidad Autonoma de Madrid.

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