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Golfingicola abyssalis gen. et sp. nov., a new endoparasitic copepod (Crustacea) in a sipunculan from abyssal depths of the Northwest Pacific Ocean

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Abstract

Marine copepods, which inhabit the entire water column down to the seafloor, are key contributors to the food web, mainly providing a food source for many organisms in the form of zooplankton. Furthermore, they also play an important ecological role as associates or even parasites with various degrees of harm to their hosts. Copepods are found in almost all habitats and can be associated with virtually every metazoan group. A female and four males of a new endoparasitic copepod genus and species (*Golfingicola abyssalis)* are described from the trunk coelom of the sipunculan *Golfingia muricaudata* (Southern, 1913), collected from the abyssal depths of the Northwest Pacific Ocean near the Kuril-Kamchatka Trench. This sipunculan species is a typical deep sea representative of the northwestern Pacific region, occurring in the Bering Sea and the abyssal regions east of the Kuril Island chain. Despite numerous records of this species, a copepod association has not been reported prior to this paper. The new parasitic copepod species is tentatively placed in the *Akessonia* group given its endoparasitic behaviour in Sipuncula, the elongated shape, the enlarged egg strings, and the presence of subchelate antenna, as well as lateral processes in males. *Golfingicola abyssalis,* however, shows some peculiarities that clearly differentiate it from the remaining endoparasites in Sipuncula. As the first abyssal endoparasite in Sipuncula, the species is characterized by the complete lack of any processes in females, the presence of a mandible in

females, a weakly defined prosome-urosome boundary in females, the presence of a mouth in males, the free living behaviour of males, a distinctly reduced number of trunk processes in males, as well as a more modified male antenna, displaying an endopodite and a highly modified setal element. A detailed review on the morphological characters of the four species currently grouped in the *Akessonia* group, and systematic and biogeographic information of their relevant host taxa is provided. On the basis of morphological and ecological similarities, the new species seems to be more closely related to the northern Atlantic *Akessonia occulta* Bresciani and Lützen, 1962 than to *Siphonobius gephyreicola* Augener, 1903 and *Coelotrophus nudus* Ho, Katsumi and Honma, 1981.

1. Introduction

Among crustaceans, the aquatic copepods are a highly speciose group, comprising more than 12,000 validated species (Bron et al., 2011) and undoubtedly at least an equal number of unrecognized species (Huys and Boxshall, 1991). What makes them remarkable is not only their worldwide distribution, but also their adaptation to nearly all habitats and environmental conditions. Such adaptations are displayed by wide eurybathic and eurythermic tolerances, various feeding strategies, and a heterogenic morphology. Planktonic copepods play an important role in the food web as primary consumers of phytoplankton, on the other hand, their parasitic counterparts may cause considerable damage to their hosts. About 50% of all known copepods live an associated lifestyle and virtually all other metazoan phyla are utilized as hosts by copepods. The most highly modified copepods are endoparasites. Boxshall and Halsey (2004) gave an impressive overview of the diversification of copepods, and the number of exclusively endoparasitic species is considerable high.

Sirenko (2013) summarized the diversity of free-living copepods (excluding parasitic forms) from Russian waters and he mentioned a total of 178 species from the Sea of Japan (SJ), 120 from the Sea of Okhotsk (SO) and 298 from the open waters east of and including the Kuril Islands (KI). Remarkably, 91 SJ species were not mentioned from the SO and KI, while 10 SO species are missing in the SJ and KI. The KI region has 170 species which are not recorded from the two other regions. This is surely influenced by the deep Japan and Kuril-Kamchatka Trenches, which show a remarkable fauna partly limited in their vertical distribution (e.g., Brodsky, 1955; Itoh et al., 2011; Markhaseva, 1981, 1986). The copepod diversity recorded by Sirenko (2013) is an underestimation as the parasitic forms with free-

living larval stages are not included. In addition, some families of benthic taxa are completely missing (e.g., Kitahashi et al., 2011, 2013; Schmidt, 2013).

Parasitic copepods are frequently recorded from the northwestern Pacific region and cover a broad range of host taxa from vertebrates (e.g., Avdeev, 2001; Ho, 1987; Nagasawa, 1984; Nagasawa and Maruyama, 1987; Poltev, 2010; Poltev and Faizulin, 2013; Uchida et al., 1998) to invertebrates, including molluscs (e.g., Avdeev, 1977a; Avdeev and Kurochkin, 1977; Avdeev and Sirenko, 1991, 1994, 2005; Avdeev et al., 1986; Ho, 1981; Kim, 1995; Nagasawa et al., 1991; Schwabe, 2013), echinoderms (e.g., Avdeev, 1977b; Ho, 1982) as well as other host taxa (e.g., Ho, 1984; Ho et al., 1981; Kim, 1998).

Among the phyla parasitized by copepods is Sipuncula. They are quite diverse in the northwestern Pacific region, with 31 species from the SJ, 11 from the SO and 15 species from the KI region (e.g., Cutler, 1977; Maiorova and Adrianov, 2013a, b; Murina, 1957, 1958). Recent investigations in the SJ and KI regions yielded additional taxa and enhanced the understanding of vertical and geographical distribution enormously (see Maiorova and Adrianov, 2013a, b, and references therein).

Copepoda-Sipuncula associations are known, but while ectoparasites or "surface symbionts" (Illg, 1975) are not uncommon (e.g., genera *Catinia*, *Myzomolgus*, *Heliogabalus*, *Ventriculina*), endoparasitism is recorded for only three species (Cutler, 1994; Boxshall and Halsey, 2004; Lauckner, 1980). Augener (1903) found a single female of 1 mm body length and the nauplii of *Siphonobius gephyreicola* Augener, 1903, within a tubular membrane overlaying the retractor muscle of the tropical shallow water sipunculan *Aspidosiphon brocki* Augener, 1903 [= *Aspidosiphon elegans* (Chamisso and Eysenhardt, 1821), according to Cutler and Cutler, 1989; Cutler, 1994]. The second sipuncle endoparasite, *Akessonia occulta* Bresciani and Lützen, 1962, is so far known exclusively from shallow waters of the northeastern Atlantic along Sweden's west coast. The species was found in the coelomic cavity of *Nephasoma minutum* (Keferstein, 1862) and does not exceed 1.6 mm (Bresciani and Lützen, 1962). The most recently discovered endoparasitic copepod in sipunculans is *Coelotrophus nudus* Ho, Katsumi and Honma, 1981, which was found in the coelomic cavity of *Phascolosoma scolops* (Selenka and de Man, 1883). The sipunculan was collected at diving depth off Sado Island in the Sea of Japan. With a body length of nearly 11 mm it is so far the largest known endoparasite in Sipuncula.

In the course of an expedition to the Kuril-Kamchatka Abyssal Plain area, diverse megafauna was collected by means of an Agassiz Trawl (AGT) but macrofauna also occurred in the

catches. Typical components of the benthic community were Sipuncula, including a single infested specimen of *Golfingia muricaudata* (Southern, 1913). This deep water species (Maiorova and Adrianov, 2013b) is widely distributed (Table 1) but was not yet encountered in the adjacent Seas of Japan and Okhotsk. The examination of the host revealed a hitherto unreported endoparasitic copepod, which is described herein.

2. Material and methods

During the joint German/Russian deep sea expedition KuramBio (Kurile Kamchatka Biodiversity Study, 2012) along the Kuril Kamchatka Trench and adjacent abyssal plain onboard the R/V *Sonne* (SO 223), we conducted 19 successful AGT deployments. The AGT had a total net length of 7.5 m, with a rectangular anterior net opening of 3.5 x 0.4 m. While the overall mesh size was 10 mm², the last 1.2 m possessed an additional liner with a mesh size of 6 mm². This net tail usually retains a high amount of sediment and contributes to the macro- and even meiofaunal elements in an otherwise megafauna dominated catch. Once the samples arrived on deck, larger animals were handpicked and immediately transferred to the laboratories to be measured, photographed and finally fixed in pre-cooled 96% ethanol. Sediment (and inhabiting smaller animals) was carefully flushed with running sea water through meshes of 1000, 500 and 300 μm prior to lab handling. Only sieve remains above 1000 μm were additionally sorted in the lab, while those of the 500 and 300 µm meshes were immediately fixed in pre-cooled 96% ethanol. Sorting of these samples was conducted both during the cruise and afterward in the Bavarian State Collection of Zoology (ZSM), Munich, Germany. Trawling distance was calculated in accordance with the epibenthic sledge equation "2" in Brenke (2005). Concomitantly, CTD (Conductivity, temperature and density data logger) deployments were conducted at each station.

The infection of a single sipunculid with copepods was discernible through its transparent body wall. The sipunculid was at this stage already fixed in borax buffered formaldehyde. For species identification of the sipunculid the body wall was longitudinally opened. During this procedure, the copepod males as well as the ovigerous female were removed from the coelom and stored separately. It cannot be excluded that during this process, potential larval stages were lost.

Light microscopic photographs were taken with a Jenoptic ProgRes C12P^{plusP} digital camera mounted on an Olympus SZX12 stereo microscope. Image acquisition was controlled by ProgRes Capture Pro 1.0.0-control software, and afterwards z-stacks were processed with Helicon Focus Pro, Version 5.3.

Prior to micro-computed tomography (microCT) scanning, the anterior and posterior portions of the female and a single male the preparations were contrasted with Phosphotungstic acid following Metscher (2009) for two days. Subsequently, the samples were placed centrally in a vial filled with agarose gel. The agarose gel was first heated to 80°C, dripped partially into the vial and cooled down to room temperature before objects were placed in the gel. Once oriented, they were slowly covered with additional heated gel, ensuring a bubble-free coverage of the object. The vial was distally fixed on a glass stick which was mounted in a microCT scanner. Scanning was performed with a Nanotom m (GE Sensing and Inspection Technologies GmbH, Wunstorf, Germany) at 50 kV and 440 mA for 2 h (1,440 projections at 360°, 1.03 μm voxel size).

The microCT dataset was visualized by volume rendering with DRISHTI 2.3. software (Limaye, 2012). In DRISHTI transfer functions in the 2D histogram were applied. Individual color and transparency settings for multiple transfer functions permitted tissues with different density attributes to be discerned (following Handschuh et al., 2013).

In preparation for scanning electron microscopy (SEM), the examined male and parts of the female were placed in a dish with hexamethyldisilazane (Sigma-Aldrich) and permitted to evaporate for at least 24 h. The chemically dried objects were sputter coated with gold for 120 s (POLARON Equipment Ltd., Watford, United Kingdom) and afterwards examined with a LEO 1430VP SEM (Electron Microscopy Ltd., Cambridge, United Kingdom).

As the female's body outline prevents a clear positional orientation, we refer here to an anterior-ventrally location of the mouth and ventrally lying genital openings.

Systematics of the copepod follow Boxshall and Halsey (2004), systematics of the Sipuncula refer to Cutler (1994).

2.1. Abbreviation

SNSB-ZSM – Bavarian State Collection of Zoology, Munich, Germany (Departments: Arthropoda varia and Evertebrate varia)

3. Systematics

Subphylum **Crustacea** Brünnich, 1772

Class **Maxillopoda** Dahl, 1956

Subclass **Copepoda** Milne-Edwards, 1840

Order **Cyclopoida** Burmeister, 1834

Family **unknown**

? *Akessonia* – group

3.1. *Golfingicola* gen. nov.

Diagnosis

Female highly transformed, body cylindrical without processes. Head discoid-roundish with anterior-ventrally lying, transverse mouth opening. Bipartite mandible as only visible appendage. Probably with degenerated vestiges of antennules. Genito-abdominal region small, caudal rami present. Midgut straight, without anal opening. Bipartite oviduct lying ventrally, running parallel with branched ovary. Cement gland, spherical, situated posteriorly next to genital openings. Paired multiseriate egg strings several times longer than body.

Male distinctly smaller than female, highly transformed. Body elongate with 2 pairs of lateral processes. Subchelate 2-segmented antenna, comprising of voluminous basal segment with modified setal element and crescentic distal corner and terminal hook like segment with basal hook-shaped endopodit, as only appendage. Mouth opening, anterio-dorsally situated knob-like process, elongate midgut, and paired genital openings present. Males not attached to females.

Type species

Golfingicola abyssalis gen. et sp. nov., by original designation.

Etymology

The generic name is derived from the generic name of the sipunculan host, *Golfingia*, and the Latin *colere*, meaning inhabiting. Gender: masculine.

3.2. *Golfingicola abyssalis* sp. nov.

(Figs 1–7)

Material. Holotype SNSB-ZSM A20140101 (ovigerous female, now disarticulated, partly SEM-mounted) (Fig. 1B). Paratypes: 3 males SNSB-ZSM A20140103 (Figs 1E-J, M), 1 male SNSB-ZSM A20140102 (SEM-mounted) (Figs 1K-L).

Host: *Golfingia muricaudata* (Southern, 1913) (Golfingiidae) (SNSB-ZSM E20140122) (Figs 1A, 3A).

Microhabitat within the host: Female free lying within the most posterior part of the trunk coelom of the host (Fig. 1A). Distal end of egg strings loosely attached to the brain region of the host and extending, looped, along the host's digestive tract (Fig. 3A). Males not attached to female, found freely in coelomic fluid (Fig. 1M).

Type locality: Northwest Pacific Ocean, Kuril-Kamchatka Abyssal Plain, KuramBio Station So223/10-11, 41°12.04'N 150°05.87'E to 41°10.78'N 150°06.34'E; 5257-5236 m, coll. 27 Aug 2012.

Habitat: The sampled area consists of muddy sediment. Abiotic factors of the nearest CTD Station (10-02) refer to: pressure 5358.921 db; temperature 1.55°C; salinity 34.67 and an oxygen saturation of 7.71.

Etymology: The species name refers to the bathymetric occurrence of the species.

Description

Female. Body (Fig. 1B) highly transformed and elongate-cylindrical, length about 29 mm (curled). Cephalic region rounded (Figs 1B, 4A), with anterio-ventral transverse mouth opening (Fig. 2A). Externally no evidence of cephalic limbs, except for bipartite oligomerised mandible, comprising cuticular process with rectangular tip carrying two pairs of small denticles distally (Figs 2A-C). Possibly a pair of degenerated vestiges of antennule underlying the cuticle (see below). Trunk transparent without expressed segmentation, appendages or processes. Prosome-urosome boundary weakly indicated (Fig. 1N). Genital somite slightly swollen (Fig. 1N) with ventrally lying truncate lobe and paired genital openings (Figs 5B, D, F). Lobe fused with caudal rami, each armed with single apical seta (Fig. 2D). Posterior extremity of abdomen not divided, knob like (Figs 5C, E). No anus traceable.

Paired multiseriate egg strings (Figs 1C, 3A-B) longer than body, loosely attached to host's brain area and partly looped around retractor muscles and intestines of host (Fig. 3A). Individual egg string up to 13 cm and approximately 300 µm in diameter; individual eggs about 130 µm in length and 95 µm in diameter (Fig. 3C).

Brief description of female's anatomy. Mouth immediately leading into wide oesophagus (Figs 4B, D), narrowing distinctly within encompassing germinal part of ovary (Figs 4B, D). Posterior to cephalic disk knob-like structure functioning as router (Figs 4A, C). Posteriorly opening into straight, sac-like midgut (Fig 4) with smooth walls. Midgut ending blind and completely encompassing globular cement gland (Figs 1N, 5B, D, H). Router with two lateral knobs (Fig. 4D) opening into bipartite, parallel, ventro-laterally situated oviducts. Each oviduct with strongly branching ovary (Fig. 1D). Oviducts passing ventro-laterally both sides of cement gland and uniting with very short cement gland duct (Figs 5B, D, F) shortly before terminating at genital pores. Cement gland (Figs 5B, D, F, H) with thick outer layer and inner structure comprising laminated layer, concentrically arranged towards periphery, while central arrangement rather loose. Antennal glands (Fig. 4D) situated anterior to germinal portion of ovary (Figs 4B, D), underneath boundary of externally visible part of cephalic disk and cuticle. Glands with two ducts (Fig. 4B), anterior duct corresponding to boundary area, second duct terminating at internal part of cephalic region (covered by cuticle) and displaying paired structures (Fig. 4C), possibly degenerate vestiges of antennules.

Male. Distinctly smaller than female. General appearance puppet-like, resulting from two pairs of elongated thoracic processes. Body elongate, slightly bent posteriorly, measuring 1.8–3.2 mm in length (Figs 1E-L). Head with anterio-dorsally situated knob-like process, more distinct in smaller specimens (Figs 1I-L, 7C, E). One traceable limb: well developed, 2-segmented subchelate antenna (Figs 7C, E). Basal segment voluminous with thickened crescentic distal corners (Figs 6B, D) and blunt, highly modified setal element (Figs 6B, C). Terminal segment with single blunt-ended (Fig. 6E), inward-bent hook with pair of minute denticles distally (Fig. 6B); hook-shaped endopodit at base (Figs 6B, E). Mouth opening round (Fig. 6A). Trunk unsegmented, with two pairs of elongate processes. First pair immediately behind head, with extremely thickened base in larger specimens (Figs 1E-F), reflecting state of developmental of underlying testis. Second pair of processes usually slightly longer than first. Prosome-urosome boundary not indicated. Abdominal segment knob-like, with paired lateral folds each terminating in slit-like genital opening (Fig. 6F). No anus traceable.

Brief description of male's anatomy. Mouth opening into very short, straight oesophagus (Fig. 7G) terminating in sac-like, blind-ending midgut at level of posterior processes (Figs 7D, F).

Antennal glands reduced (Fig. 7D), situated anterior to midgut. Apparently glandular structure underlying dorsal knob-like process (Figs 7D, G).

Paired testis located anteriorly at base of first thoracic process (Figs 1E-F, 7D), leading into long, coiled genital duct nearly completely filling thoracic processes. Spermatophore sacs (Figs 7B, D, F, G) posterior to midgut, underlying genital pores. Complex system of muscles (Figs 7B, D, F, G) running through body.

3.2.1. *Biology*

Despite the extreme length of the egg strings no obvious differences in the development stages of the eggs along its length were observed. We therefore assume that either the eggs are released within a very short time frame or morphogenesis is extremely slow. Free naupliar or copepodid stages were not observed, but as mentioned earlier, it cannot be excluded that they were lost during the initial opening of the host. The host specimen did not contain any sipunculid eggs but the gonads (Fig. 3A) were intact and mature. Co-occurring specimens of the same size class of *Golfingia muricaudata* yielded eggs. None of the copepod males were attached to the female, thus they probably live freely within the host's coelomic fluid (Fig. 1M). A microscopic examination of the fluid indicated fully intact erythrocytes. Sperm or spermatophores could not be detected either from host or the parasites respectively. We observed damaged cell types, which might be due to the feeding activities of the copepods. This, as well as the relatively large size of the female within the host's body cavity would be in line with a generalized interpretation of what is called castrator (Lafferty and Kuris, 2009). However, from the present observation, castration in the sense of fecundity reduction cannot be ascertained.

3.2.2. *Systematic remarks*

Golfingicola does not resemble any previously known copepod genus. It also differs from the three already known monotypic genera of copepod endoparasites known to infest sipunculans, i.e. the *Akessonia* group as defined by Boxshall and Halsey (2004): *Akessonia* Bresciani and Lützen, 1962, *Coelotrophus* Ho, Katsumi and Honma, 1981 and *Siphonobius* Augener, 1903. These differences are a) in the adult female: the complete absence of thoracic processes, the lack of lateral lobes in the cephalic region, a weak indication of a prosome-urosome boundary, and the presence of caudal rami; b) in adult males: the reduced number of much more extended thoracic processes, the presence of a more complex antenna (modified setal element at basal segment plus endopodite), the presence of a mouth, and the free position

within the host coelomic fluid. We summarize the main characteristics of copepod species endoparasitic on sipunculans in Table 2. The systematic placement of *Golfingicola abyssalis* gen. et sp. nov. requires not only information on larval stages of the species but also a clear concept of the potentially related taxa of the *Akessonia* group, as already indicated by Boxshall and Halsey (2004). We thus establish a new genus *Golfingia*, with uncertain familiar affiliation, tentatively placed into the *Akessonia* group.

Table 1 about here
Table 2 about here

3.3. Discussion

Infestation of the phylum Sipuncula by copepods is – compared to other marine invertebrates – rarely recorded (e.g. Cutler, 1994; Boxshall and Halsey, 2004; Ilg, 1975; Lauckner, 1980). The phylum comprises two classes, the Sipunculidea and the Phascolosomatidea, mainly defined by the absence of perioral tentacles in the former. If hooks are present in the distal part of the introvert, they are generally simple and less uniformly ordered in Sipunculidea, while they are usually sharplycurved and closely packed in a ringformation in Phascolosomatidea. According to Boxshall and Halsey (2004) the Phascolosomatidea serve as host for the externally associated copepod genera *Heliogabalus* Leigh-Sharpe, 1934 and *Ventriculina* Bassett-Smith, 1903 (both Ventriculinidae), while Sipunculidea has been found to be associated with *Heliogabalus*, *Catinia* Bocquet and Stock, 1957 and *Myzomolgus* Bocquet and Stock, 1957 (both Catiniidae). For the endoparasitic forms it is shown (herein, Table 1) that Phascolosomatidea are infested by *Siphonobius gephyreicola* and *Coelotrophus nudus* and the class Sipunculidea by *Akessonia occulta* and *Golfingicola abyssalis*. Have endoparasitic copepod co-evolved with their sipunculan host clades, as indicated for various other parasites (Campbell, 1983)? Available data suggest that taxa parasitizing Phascolosomatidea inhabit tropical to subtropical shallow waters. Additionally the adult females a) show a single process situated anterio-dorsally, b) lack cephalic limbs (but see Tab. 2), c) have no mouth, and d) have at least some eggs lying freely within the host. On the other hand female endoparasitic copepods in the Sipunculidea have a) obviously no cephalic processes, b) at least a mandible (and potentially reduced antennules), c) a mouth, d) reduced or lacking trunk ventral processes. In addition, the males have a reduced number of lateral trunk processes. The representatives of the latter group occur either in colder North Atlantic

waters or inhabit the deep sea. Contradictory to this are the reproductive peculiarities which would link *C. nudus* and *G. abyssalis* closer together by the shared paired spermatophore sacs and the multiseriate egg strings. Genetic analyses may offer more conclusive answers to phylogenetic and evolutionary questions, once suitably fixed material is available. *Golfingicola abyssalis* is the largest of the known endoparasites in Sipuncula and has the deepest bathymetric occurrence. What makes the species especially interesting was the presence of four males, none of which were attached to the female. Each male shows a body size depending more or less on a well pronounced anterior dorsal knob-like process, which is missing in males of other genera. The function of this process is so far unknown, but the underlying potential gland resembles positional the anterior gland that Nishida (1989) described for male calanoid copepods underlying the cephalosome dorsal hump. Neither Ho et al. (1981) nor Bresciani and Lützen (1962) reported more than two males in *C. nudus* or *A. occulta*, and the males were always attached to the posterior ventral side of the female. The males of both species lack a mouth opening, contrary to *G. abyssalis*. Morphogenesis in *G. abyssalis* likely is very slow, as the extremely long egg strings do not show traceable differences in the developmental stages of individual eggs. Longevity and decelerated growth is not a generality but is well substantiated for several deep sea invertebrates (Gage and Tyler, 1991). Active feeding may thus be essential in a nutrient poor environment like the deep sea to survive the long period between larval infestation and maturity; hence we hypothesize that the retention of the mouth in both sexes is an adaptation to the extreme depth at which the species was found.

At the type locality we trawled with a ship speed of 1 kn a distance of 3272 m, over what corresponds to an area of 11452 m². Although catching by means of an Agassiz trawl may not allow a quantitative analysis of the catch due to the open net and the rather large mesh size, the low number of Sipuncula and thus potential hosts suggests a low infection rate and also a rigid host selection. At this station we found a total of 14 Sipuncula individuals, belonging to three species (*Golfingia muricaudata*, *Nephasoma diaphanes* (Gerould, 1913) and *Phascolion sp.* juvenile), within two different families. The typical host *G. muricaudata* was represented by eight individuals (57% of the total). The present parasitic material is from a single specimen only and was not observed in the other examined specimens. Moreover, *G. muricaudata* was collected in ten further stations (out of 11 stations with 40 towed gear deployments) with an overall total of 53 adults and juveniles. The area covered depth ranges

from 4580–6130 m and is located between 47°15'N 154°43'E at the northernmost point, 39°43'N 147°10'E at the southernmost point and 43°58'N 157°20'E at the easternmost point. The reason for such a low infection rate is unclear and can only be the subject of speculation. Host availability cannot be considered a limiting factor, as Sipuncula occurs worldwide, in all depth zones and among a variety of habitats. Gage and Tyler (1991) classified them as a typical component of deep sea benthos. We assume that epidermal structures like papillae, hooks and shields can also be rejected as factors limiting parasitism, since other marine invertebrates possess similar structures and are infested at higher rates. Sediment inhabiting taxa like *Golfingia* and *Sipunculus* serve as hosts for both endo- and ectoparasites (Boxshall and Halsey, 2004), so their burrowing behavior does also not protect them from infestation. Cutler (1994) gives a comprehensive overview of various defense mechanisms sipunculans may have. Besides a primitive immune system, the coelomic fluid of some Sipuncula show highly modified cell-types – the so called urn cell complex as well as additional hemocytes and granulocytes. These exhibit certain antibacterial activities, whose main function are entrapping, engulfing, encapsulating and/or inactivating foreign substances (e.g., Bang and Bang, 1980; Ying et al., 2010). We speculate that some of them, or combinations of them, might be the reason for a limited sipunculan-copepod association.

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3.6. **Figure explanation**

Fig. 1 *Golfingicola abyssalis* gen. et sp. nov. (B-N) and its host species *Golfingia muricaudata* (Southern, 1913). **(A)** *Golfingia muricaudata* (Southern, 1913), intact, showing the posteriorly located parasite, **(B)** Female of *Golfingicola abyssalis* gen. et sp. nov., complete, with shorten egg strings, **(C)** portion of egg string, **(D)** close-up of female body, showing the arrangement of oviduct and ovary, **(E-M)** different views of the males, **(E), (G), (I), (K), (M)** ventral view, **(F), (H), (J), (L)** dorsal view, **(M)** male (corresponds to G, H) embedded in host coelomic fluid, **(N)** ventro-lateral view of posterior portion of female, showing arrangement of reproductive systems, arrow indicates prosome-urosome boundary. Scale bars A, B 5 mm, C-N 1 mm.

aa – antenna, **ad** – abdomen, **cf** – coelomic fluid, **cg** – cement gland, **dk** – dorsal knob like process, **es** – egg strings, **i** – intestine, **in** – introvert, **mg** – midgut, **nc** – nerve cord, **od** – oviduct, **ov** – ovary, **pr** – lateral process, **rm** – retractor muscles, **ss** – spermatophore sac, **t** – testis, **ta** – tail.

Fig. 2 SEM images of female of *Golfingicola abyssalis* gen. et sp. nov. **(A)** mouth opening and position of mandibles, **(B)** close-up of mandible, **(C)** close-up of figure B, showing the second part with distal denticles, **(D)** ventral view of genito-abdominal region, showing caudal rami with setae and one genital opening. Scale bars A 50 μm, B 10 μm, C 2 μm, D 100 μm.

cr – caudal rami, **d** – denticle, **geo** – genital opening, **md** – mandible, **mo** – mouth opening, **s** – seta.

Fig. 3 *Golfingicola abyssalis* gen. et sp. nov. and its host species *Golfingia muricaudata* (Southern, 1913). SEM images of a portion of egg string of *Golfingicola abyssalis* gen. et sp. nov. (B-C). **(A)** *Golfingia muricaudata* opened, showing the relative position of parasites egg strings to the hosts anatomy, free at left refers to former position of female parasite, **(B)** portion of egg string of *Golfingicola abyssalis* gen. et sp. nov., lower half intact, upper half longitudinally sectioned , showing the arrangement of eggs, **(C)** close-up of figure B, showing an isolated egg. Scale bars A 5 mm, B 100 μm, C 10 μm.

a – anus, **cf** – coelomic fluid, **es** – egg strings, **gon** – gonad, **i** – intestine, **in** – introvert, **nc** – nerve cord, **ne** – nephridium, **rm** – retractor muscles, **ta** – tail.

Fig. 4 MicroCT data (volume rendering) and DRISHTI 2.3. software visualization. Different views of the cephalic region of female of *Golfingicola abyssalis* gen. et sp. nov. using clipping functions to highlight internal organs. **(A)** right lateral view, **(B)** cross section, right lateral view, **(C)** posterior view, **(D)** horizontal section at level of mid-rooter, dorsal view. Scale bar for all figures 100 µm.

ag – antennal gland, **an** – antennule (?), **go** – germinal portion of ovary, **mg** – midgut, **mo** – mouth opening, **od** – oviduct, **oe** – oesophagus, **r** – rooter.

Fig. 5 MicroCT data (volume rendering) and DRISHTI 2.3. software visualization. Different views of the posterior region of female of *Golfingicola abyssalis* gen. et sp. nov. using clipping functions to highlight internal organs. **(A)** left lateral view, **(B)** cross section, left lateral view, **(C)** abdominal view, **(D)** horizontal section at level of genital openings, abdominal view, **(E)** posterior-dorsal view, **(F)** vertical section at level of genital openings, seen from posterior-dorsal, **(G)** frontal view, **(H)** vertical section at level of central cement gland, seen from frontal. Scale bare for all figures 500 µm.

ad – abdomen, **cd** – cement gland duct, **cg** – cement gland, **cr** – caudal rami, **geo** – genital opening, **mg** – midgut, **od** – oviduct, **ov** – ovary.

Fig. 6 SEM images of a male of *Golfingicola abyssalis* gen. et sp. nov. **(A)** ventral view of mouth region, **(B)** postero-lateral view of antenna, **(C)** ventro-lateral view of basal segment of antenna, showing highly modified setal element, **(D)** ventro-lateral view of basal segment antenna, showing thickened crescentic distal corner, **(E)** distal view of antenna, showing elements of second segment, **(F)** ventral view of genito-abdominal region. Scale bars A-E 10 µm, F 20 µm.

aa – antenna, **ad** – abdomen, **cdc** – crescentic distal corner, **d** – denticle, **e** – endopodit, **geo** – genital opening, **h** – hook, **mo** – mouth opening, **ms** – modified setal element.

Fig. 7 MicroCT data (volume rendering) and DRISHTI 2.3. software visualization. Different views of a male of *Golfingicola abyssalis* gen. et sp. nov. using clipping functions to highlight internal organs. **(A)** abdominal view, **(B)** vertical section at level of genital region, seen from posterior, **(C)** dorsal view, **(D)** horizontal section at level of genital openings, dorsal view, **(E)** right lateral view, **(F)** cross section, right lateral view, at level of mouth opening, **(G)** cross section, right lateral view, at level of central left antenna. Scale bar for all figures 500 µm. **aa** – antenna, **ad** – abdomen, **ag** – antennal gland, **ang** – anterior gland (?),**dk** – dorsal knob like process, **gd** – genital duct, **geo** – genital opening, **m** – muscle, **mg** – midgut, **mo** – mouth opening, **oe** – oesophagus, **pr** – lateral process, **ss** – spermatophore sac, **t** – testis.

Table 1 The known Sipuncula host species of endoparasitic copepods, their classification and ecological aspects, based on AM's database and Saiz (2013).

Species	*Aspidosiphon elegans* (Chamisso and Eysenhardt, 1821) (= *Aspidosiphon brocki* Augener, 1903)	*Phascolosoma scolops* (Selenka and de Man, 1883)	*Nephasoma minutum* (Keferstein, 1862)	*Golfingia muricaudata* (Southern, 1913)
Family	Aspidosiphonidae	Phascolosomatidae	Golfingiidae	
Order	Aspidosiphonida	Phascolosomatida	Golfingiida	
Class	Phascolosomatidea		Sipunculidea	
Bathymetry	shallow water	intertidal and shallow depths (< 30 m)	intertidal to 50 m	60 – 6860 m
Distribution	Widespread and common in the Indian and western Pacific oceans, from south-central Japan to northern Australia to Hawaii, the Red Sea, and Israel. In the Caribbean from northern Brazil to the Florida Keys and Bermuda. Not known from the eastern Pacific or eastern Atlantic	Red Sea, Indo-West Pacific (from N- Japan to N-Australia, eastwards to Hawaii), W-Africa?	North Atlantic Ocean	Common at bathyal and abyssal depths in the North Atlantic from Cape Hatteras up to 58º N, across to Europe. At bathyal depths near coast around Africa. Unknown from the rest of the Indian Ocean. In the North Pacific from British Columbia, around the Bering Sea, to Japan. A single record from the far southern Pacific by Murina (1978).
Associated endoparasitic copepod	*Siphonobius gephyreicola* Augener, 1903	*Coelotrophus nudus* Ho, Katsumi and Honma, 1981	*Akessonia occulta* Bresciani and Lützen, 1962	*Golfingicola abyssalis* gen. et sp. nov.
Female's position in host	in a tubular membrane overlying the retractor muscle	coelomic cavity	coelomic cavity	coelomic cavity

Table 2 Endoparasitic copepods of the *Akessonia*-group and their main characteristics. Data on the mature copepods are from the respective original descriptions and the summary in Boxshall and Halsey (2004), n.a. – not available

	Siphonobius gephyreicola Augener, 1903	*Coelotrophus nudus* Ho, Katsumi and Honma, 1981	*Akessonia occulta* Bresciani and Lützen, 1962	*Golfingicola abyssalis* gen. et sp. nov.
FEMALE				
Shape	cylindrical	cylindrical	cylindrical	cylindrical
Size	ca. 1mm	ca. 11 mm	max. 1.6 mm	ca. 29 mm
Cephalic processes	- single anterior dorsal - pair dorsally, at tip bifurcated (may refer to a limb)	- a pair bilobate lateral - a pair trilobate dorsal - single anterior dorsal	unclear, see limbs	absent
Cephalic limbs	Unclear, while Augener (1903) interpreted the paired structure as distally divided "Fühler" (antenna), Boxshall and Halsey (2004) refer to cephalic processes	absent	- Bresciani and Lützen (1962) do not find strong evidences for antennules or antennae, but stated: "2 pairs of rounded bulges of the very anteriormost portion of the body may be interpreted as such". These bulges carry small circular papillae on their surface. - labrum chitinized, with medially incised posterior margin - mandible conical, with single blade - labium chitinized, anteriorly slightly concave, laterally covered by the next limb - probably maxilliped? (Bresciani and Lützen, 1962), according to	- possible degenerated vestiges of antennule underneath the cuticle - bipartite mandible with two pairs of small denticles distally

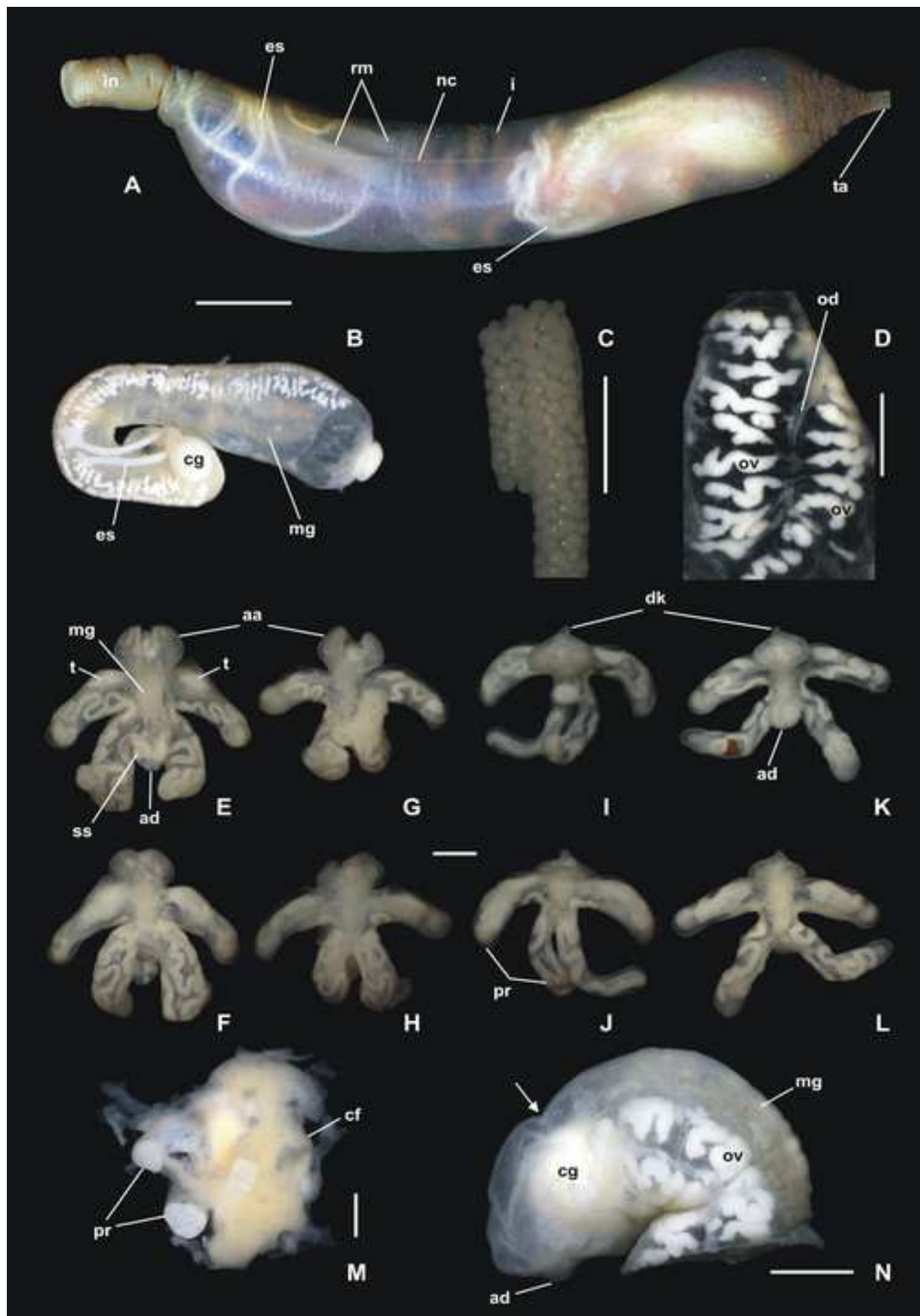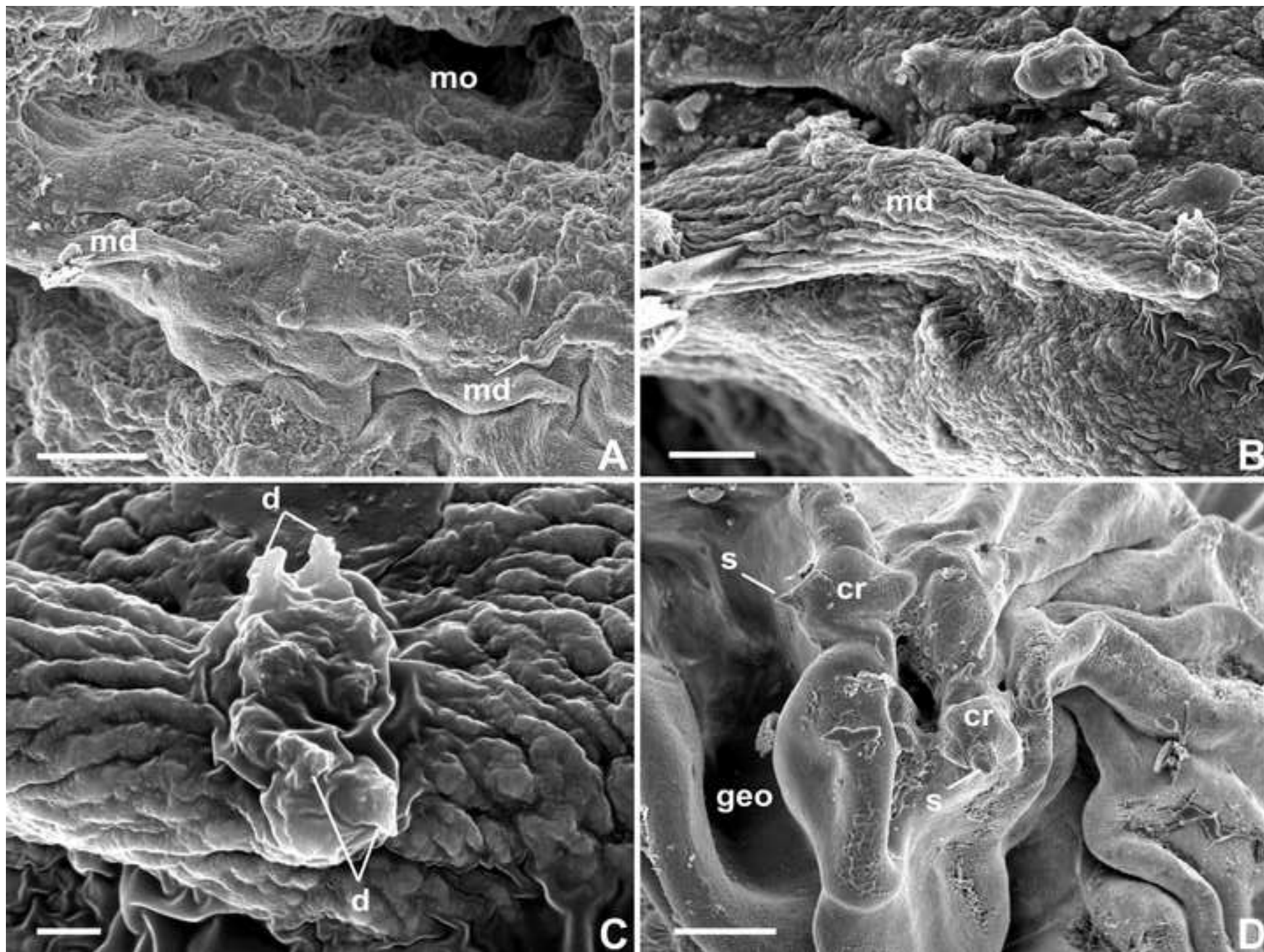|			Boxshall and Halsey (2004) possible maxilla	
Mouth	not found	absent	present	transversal
Trunk processes	- pair dorsolateral - 5 pairs ventrally (first pair probable an appendage)	- 5 pairs lateral, large - 3 pairs lateral, small - 3 pairs dorsally - 7 single ventrally	- 4 pairs dorsolaterally - 2 pairs lateral, posterior - 3 pairs ventrally - 5 single dorsally	absent
Prosome-urosome boundary	not defined	not defined	not defined	weakly indicated
Posterior extremity of abdomen	bifurcated	small lobe	small lobe	knob like
Egg strings	no eggs, but nauplii were found	paired, multiseriate, several times longer than female, often free in host	paired, uniseriate, several times longer than female	up to 130 mm, multiseriate, paired
MALE				
Position in host	n.a.	attached to female's ventral surface, posterior	attached to female's ventral surface, posterior (usually 2 per female)	free in coelomic fluid
Size	n.a.	max. 4.4 mm	400-500 µm	max. 3.2 mm
Shape	n.a.	elongate	elongate	elongate
Cephalic processes	n.a.	- pair of horns - 2 pairs small	- pair lateral	single anterior-dorsally, knob like
Cephalic limbs	n.a.	2-segmented subchelate antenna	2-segmented subchelate antenna (?) ("probably 1st pair of antennae")	2-segmented subchelate antenna
Mouth	n.a.	absent	absent	round
Trunk processes	n.a.	5 pairs, laterally	4 pairs, laterally	2 pairs, laterally
Prosome-urosome boundary	n.a.	not defined, but posteriorly bent	not defined	not defined
Posterior extremity of abdomen	n.a.	knob like	small and slender furca	knob like
Spermatophore sac	n.a.	paired	single	paired

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7