

**NEW DATA ON ENDOBIONTS OF POLYPLACOPHORA
(MOLLUSCA)**

© E. Schwabe,^{1*} J. A. Jardim,² K. Nagler,³ B. I. Sirenko⁴

¹ Bavarian State Collection of Zoology

Münchhausen Str. 21, 81247 München, Germany

² Museu de Zoologia da Universidade de São Paulo

Avenida Nazaré, 481, Ipiranga, Brazil

³ UIB — University of Bergen, Department of Biological Sciences

Thormøhlensgt, 53 A/B, 5020 Bergen, Norway

⁴ Zoological Institute, Russian Academy of Sciences

Universitetskaya nab., 1, 199034, St. Petersburg, Russia

* E-mail: enrico.schwabe@snsb.de

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The strictly marine benthic Polyplacophora serve as basibionts for a wide spectrum of endobiotic taxa. Here we present detailed observations of three yet unrecorded polyplacophoran — copepod endobioses, with highly modified females and males, which not fit into the current concept of the Chitonophilidae, to which we attribute them. Furthermore, presumed larvae of two of them show that even the ontogeny to the adult copepods is not strictly in line with the present understanding of this family. Range extension and additional morphological details are also presented for the chitonophilid copepod *Tesonasma reniformis* Avdeev and Sirenko, 1994. We also show the double infestation with chitonophilid copepods in a single basibiont, more specific the new record refers to a mesobiotic *Ischnochitonika* sp. and to one of the three endobiotic chitonophilids. Representatives of usually free-living nematodes are shown to occur also in two different basibionts. The last new record refers to a tentatively identified protist found in a North Pacific chiton. In an updated summary of yet known endobionts of Polyplacophora we not only refer to old literature records but indicate further records, which were out of focus of the present study. The compilation of 35 endobiotic records shows that only 3.1 % of the currently known extant polyplacophorans, which represent 16 genera within nine families serve as basibionts for a wide range of phyla. The majority of records refer to Protista, followed by Nematoda and Crustacea. Only a few endobionts utilize the polyplacophoran's valves as habitat, the overwhelming data refer to soft tissue infestations. Although the polyplacophoran anatomy of the involved taxa do not allow a prediction of endobiotic trends, the present data show a lack of basibionts from the more primitive polyplacophoran order Lepidopleurida. It is assumed that the scarcity of studied material of this primary deep-water group is more likely an explanation than the anatomical peculiarities of these polyplacophorans. The capability of polyplacophora as basibionts is definitively underrepresented and bears a wide source for future parasitological studies.

Key words: Nematoda, Crustacea, Copepoda, Chitonophilidae, chitons, endobionts, systematics, morphology.

НОВЫЕ ДАННЫЕ ПО ЭНДОБИОНТАМ ХИТОНОВ (MOLLUSCA)

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Ключевые слова: Nematoda, Crustacea, Copepoda, Chitonophilidae, хитоны, эндобionты, систематика, морфология.

Панцирные моллюски, исключительно морские бентосные организмы, служат хозяевами для широкого спектра представителей эндобiotических (паразитических) таксонов. В данной работе мы представляем детальные наблюдения над тремя еще не описанными эндобiotическими отношениями между хитонами и копеподами с модифицированными самками и самцами, слабо соответствующими современным представлениям о сем. Chitonophilidae, к которому их относят. Кроме того, строение вероятных личинок у двух из этих видов показывает, что их онтогенез также не соответствует напрямую онтогенезу, характерному для данного семейства. Показано расширение ареала и приведены дополнительные морфологические характеристики хитонофилидной копеподы *Tesones mareniformis* Avdeev et Sirenko, 1994. Мы также обнаружили двойное заражение одного и того же хозяина хитонофилидными копеподами, относящимися к мезобiotической *Ischnochitonica* sp. и к одной из трех эндобiotических хитонофилид. Показано также, что представители обычно свободноживущих нематод встречены в двух различных хозяевах. Приведены новые данные о протисте, определенном только ориентировочно, обнаруженном в северо-тихоокеанском хитоне. Литературный обзор хозяев-хитонов дополнен сведениями о новых находках, выходящих за рамки настоящей работы. Анализ находок 35 видов-эндобionтов показал, что только 3.1 % известных в настоящее время хитонов, представленных 16-ю родами из 9 семейств, служат хозяевами широкого круга таксонов. Большинство находок относятся к Protista, за ними следуют Nematoda и Crustacea. Только несколько эндобionтов используют щитки хитонов для обитания внутри них, большинство же обитает в мягких тканях. Хотя анатомия хитонов из изученных таксономических групп не дает основания для предсказания их склонности к заражению различными эндобionтами, имеющиеся данные показывают отсутствие хозяев эндобionтов среди представителей более примитивного отряда Lepidopleurida. По нашему мнению, однако, причиной этого факта являются не анатомические особенности первично глубоководных хитонов указанной группы, а, скорее, недостаточный объем имеющегося материала. Роль хитонов как хозяев различных эндобiotических организмов изучена совершенно недостаточно, что открывает широкие перспективы будущих паразитологических исследований.

During several years the first author collected available records (unpublished data) of polyplacophoran diseases in the broad sense (including associates whose effects on chitons are unclear). Despite a considerable amount on information it is obvious that one of the main categories is hardly studied in polyplacophorans: the endobiosis (here used in the sense of: one organism [endobiont] lives within another organism [basibiont]).

The study of polyplacophoran diseases should inevitably start with the summaries given by Hyman (1967), Cheng (1967), Lauckner (1983) and most recently Alvarez-Cerrillo et al. (2017). Especially Lauckner (1983) is a suitable tool for information on protistans, although some old records are missing.

Alvarez-Cerrillo et al. (2017) not only missed records of the main taxa of their study, but ignored also the endobiotic members of the copepod family Chitonophilidae, which were described by Avdeev and Sirenko (1994). Unfortunately one of the species, namely *Cookoides cordatus* Avdeev and Sirenko, 1994, was later comment-less interpreted as mesoparasite by Huys et al. (2002).

In addition to previous endobiotic records, Schwabe et al. (2006) mentioned the occurrence of a cyst building nematode in a SE Pacific chiton, which was figured in Reiff and Schwabe (2007).

Postmetamorphosed chitons, with their dorsal coverage of eight solid valves and a circumscribing hard structure-beset mantle, have a strict benthic semi-motile life-style. Unprotected tissue, like the foot, gills, mantle cavity and head lay ventrally and are those hard to access by symbionts. The flexible mantle is well pressed to the substratum and this condition is to varying degrees only inactive during moving, feeding, respiration, spawning and excretion. Currently unclear however is, how the majority of endobionts reach their final position in the chiton's body and how harmful they are. All yet recorded endobionts found in the valves display a burrowing behaviour and by protecting themselves they decrease the mechanical properties of the basibiont valves.

During anatomical studies on various chitons, a few new records of endobiotic copepods and further nematodes were discovered, which we aim to briefly introduce here. The present work attempts also to summarize the yet known endobiotic taxa with an up-dated classification to provide an overview of these associations in polyplacophoran molluscs.

MATERIAL AND METHODS

During years of studies on polyplacophoran anatomy the authors examined uncounted specimens of various species, covering almost all genera and families. If an individual polyplacophoran specimen showed evidence for an infection, we cross-checked available material of the same species from our institutes. The here treated endobionts were accidentally detected and consequently present absolute findings not useful to calculate prevalence, density and abundance.

We inspected the upper visceral cavity of the chitons by slightly lifting up either the sixth or the seventh valve. If we observed eggs, which obviously were different from chiton eggs (of damaged gonads), we carefully removed the single chiton valves (by cutting the underlying muscles) and uppermost tissue. If a biont was localized, we noted its position in the basibiont and tried to remove it careful from the chiton's innards. Unfortunately some of the here introduced species were detected as side effect during investigations of other colleagues and the partly damaged bionts were provided for study. In such cases detailed information on their exact position in their basibionts is often unclear.

Prior careful re-study of the biont-cleaned basibiont tissue, all basibiont remains were flushed again.

Size-depending or according to the amount of available material we had to choose the best promising method to illustrate the species. If applicable the bionts were photo documented with a light microscope prior to future handling. For this as well as for the scanning electron microscopy (SEM) study methods we refer to Schwabe et al. (2014).

Selected specimens were dyed either with congorod or lactophenol following the manufactory instructions.

Of these all specimens were mounted in Hydro Matrix® (Micro-Tech-Lab). Specimens were documented with composite autofluorescence imaging and bright field photography (combined with composite imaging). Fluorescence

microscopy was performed by an inverse fluorescence microscope BZ-9000 (BIOREVO, Keyence) with a DAPI filter ($\lambda = 358\text{--}461\text{ nm}$) and 4x, 10x and 20x lenses resulting in 40, 100 and 200 magnification. Stacks of images were processed with the freeware packages CombineZP (Alan Hadley) and ImageAnalyzer (Meesoft). Stereo images and final processing (Levels, sharpness, saturation) were done in Adobe Photoshop CS5.

Sizes, if not otherwise stated refer to length to width. Copepod terminology follows Huys and Boxshall (1991) and Boxshall and Halsey (2004), microhabitat terms are taken from Marchenkov (2001), thus of parasitology following Bush et al. (1997), and basibiont's anatomy is defined according to Hyman (1967) and Schwabe (2010). The systematic we used for the copepods is from Huys et al. (2002) for the polyplacophorans from Sirenko (2006), remaining taxa were classified in accordance with the WORMS database (<http://www.marinespecies.org/>).

Abbreviations

MZUSP — Museu de Zoologia da Universidade de Sao Paulo, Brazil

NSMT — National Museum of Nature and Science, Tsukuba (formerly National Science Museum, Tokyo), Japan

ZISP — Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia

ZSM — Bavarian State Collection of Zoology (Departments Mollusca and Arthropoda), Munich, Germany

RESULTS

Class **POLYPLACOPHORA** Gray, 1821

Order **CHITONIDA** Thiele, 1909

Suborder **Chitonina** Thiele, 1909

Family **ISCHNOCHITONIDAE** Dall, 1889

Stenosemus albus (Linnaeus, 1767) (fig. 1, 2).

Material examined: ZSM Mol 20131011 one specimen with 1 ovigerous female and 3 males of *Tesonema reniformis*, leg. B. Retzlaff, 28.10.2004, WH 268, FFS *Walther Herwig*, Greenland, Fiskenaes Bank, Stratum 2.1 (St. 1347), 63°07.12' N, 52°16.35' W, 152.3 m. ZSM Mol 20131012 one specimen with 1 ovigerous female and 2 males of *T. reniformis* (all still in situ) + a juvenile nematode supposedly belonging to the family Benthimermithidae, data as previous sample. ZSM Mol 20150311 one specimen with 1 ovigerous female, 5 males of *T. reniformis*, leg. M. Kolesnikov, 24.08.1988, cruise 35 of RV *Odyssey*, north-western part of the Sea of Japan (about 48° N) st. 63/88, grab, 101 m. ZSM Mol 20150312 one specimen with 1 ovigerous female and 1 male of *T. reniformis*, RV *Vitjaz*, the Bering Sea, st. 1516, 62°30.8' N, 179°35' W, 97 m, Petersen grab, 0.25 m², 14.06.1952.

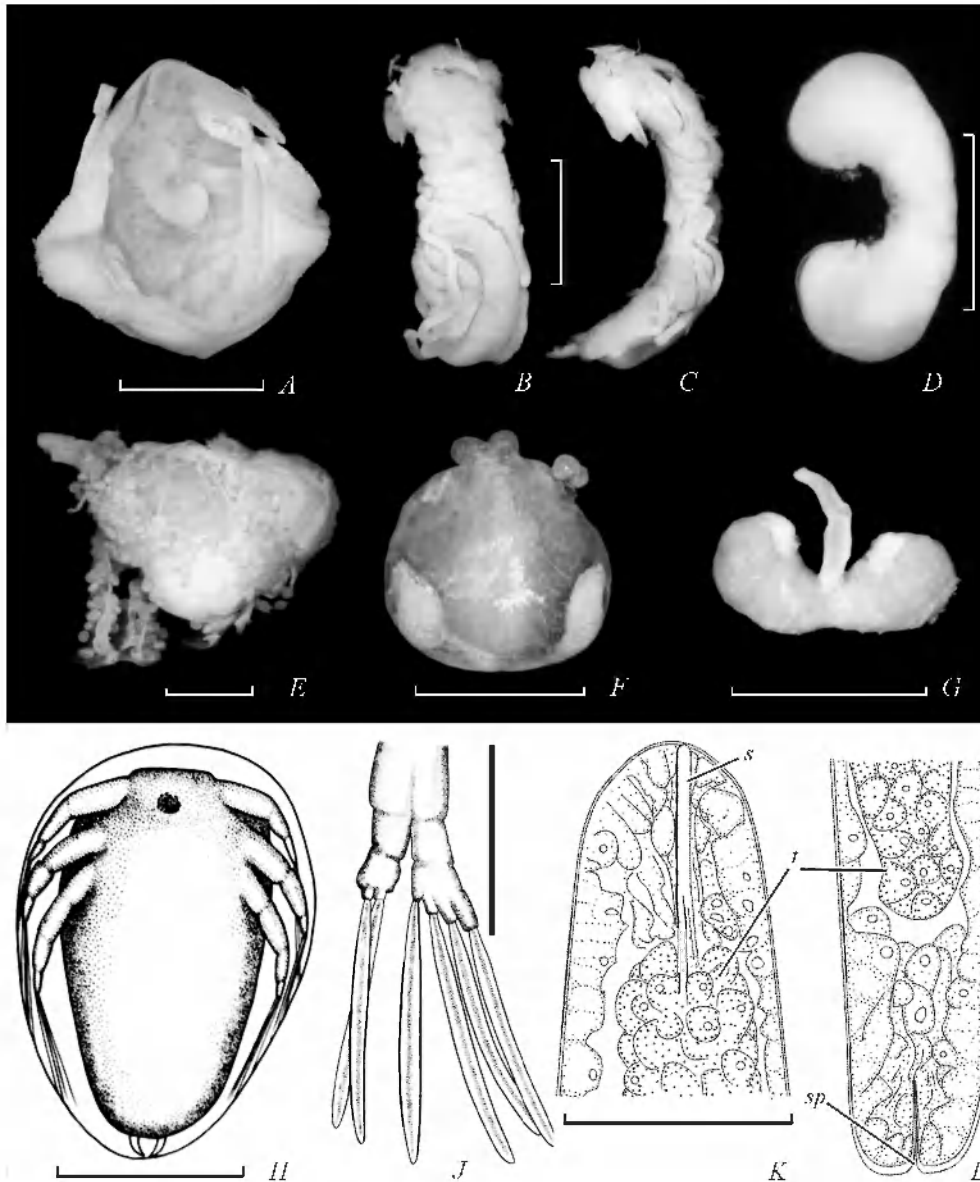


Fig. 1.

A — ventral view of *Stenosemus albus* with removed foot and innards to show the position of an adult female of *Tesonesma reniformis*; *B* — dorsal view of the innards of *S. albus* to show the arrangement of the female rootlet of *T. reniformis*; *C* — same as *B*, lateral view; *D* — isolated female of *T. reniformis* with removed rootlet, dorsal view; *E* — female (above) and male (below) of *T. reniformis* covered by egg bearing membrane, please note the preceding part of the rootlet at the left side; *F* — isolated male of *T. reniformis* dorsal view with attached eggs at the right side; *G* — isolated female of *T. reniformis* dorsal view with shortened rootlet; *H* — ventral view of a nauplius I stage of *T. reniformis* in egg from a specimen of *S. albus* from the Sea of Okhotsks 105 m (ZISP); *J* — same as fig. H showing a mandible; *K*, *L* — head and tail (respectively) of a juvenile Nematode of the family Benthimermithidae from the body cavity of *S. albus*. Abbreviations: *s* — stylet?, *sp* — spinneret, *t* — trophosome. Scale bars: *A–C*, *G* — 2 mm; *D–F* — 1 mm; *H* — 100 μ m; *J–L* — 50 μ m. Basibiont data: *A–D*, *K–L*: *S. albus* (ZSM Mol 20131012); *E–G*: *S. albus* (ZSM Mol 20150311).

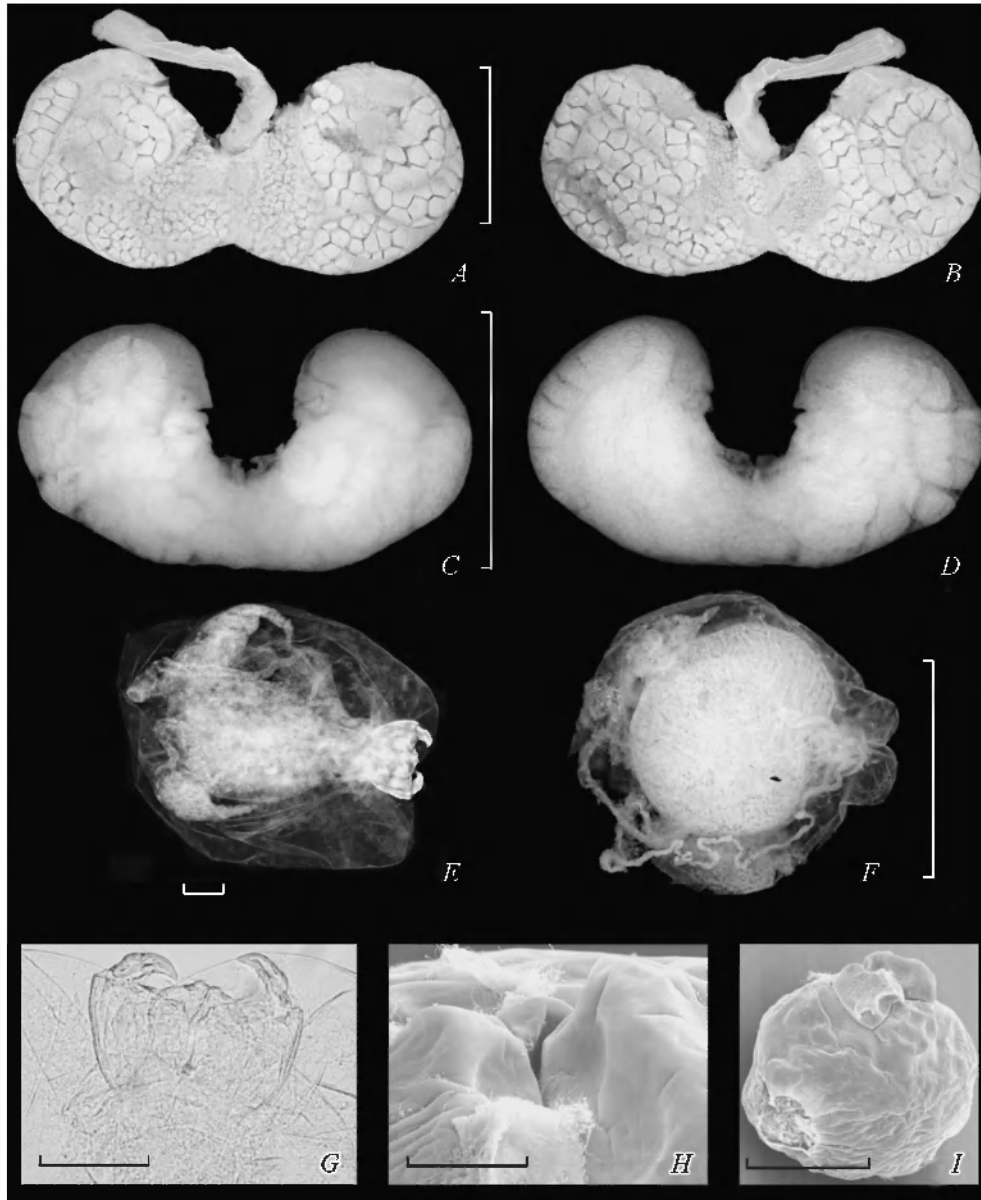


Fig. 2. *Tessonema reniformis*.

A, C — ventral view of adult female; *B, D* — dorsal view of adult female; *E* — ventral view of small male; *F* — dorsal view of adult male; *G* — mouth region of a small male; *H* — frontal view of the mouth region of an adult male; *I* — lateral view of an adult male. Scale bars: *A–D, F* — 1 mm; *E, G, H* — 100 µm; *I* — 500 µm. *A–F* — fluorescence microscope imaging; *G* — stereomicroscope illustrations; *H, I* — SEM imaging. Basibiont data: *A–B, H–I: Stenosemus albus* (ZSM Mol 20150311); *C–E, G–S. albus* (ZSM Mol 20131012); *F — S. albus* (ZSM Mol 20131011).

This chiton species is the basibiont for the well described chitonophilid copepod *Tesonema reniformis* Avdeev and Sirenko, 1994, which has a north-western Pacific distribution and was found in a bathymetric range between 37—194 m (see Schwabe et al., 2014). Here we document for the first time this particular copepod in north Atlantic populations of its basibiont. Examinations of *T. reniformis* from Greenland hardly show differences from populations we parallel studied from Bering Sea and the Sea of Japan. Generally the new material is smaller, but morphological we failed to detect specific characters which would allow a separation from the north-western Pacific populations. Huys et al. (2002) doubted earlier interpretations of Avdeev and Sirenko (1994), who considered the fleshy swellings next to the mouth of the males as highly transformed mandibles. Based on the present investigations we follow Huys et al. with slight alterations. We interpret the swellings as kind of antennary process and the mandible as shown in fig. 2, *E*, *G* obviously degenerate. In a male from ZSM Mol 20131011, only slightly larger than the figured (fig. 2, *E*, *G*), the distinct claws are crooked with their base and the mouthing is slightly sclerotized, while these conditions are no longer visible in larger specimens (fig. 2, *H*). Positionally all examined basibionts had the females in the cavity between the valves and the underlying innards, more or less at the level between valves vi and vii. The position of the associated males varied, some were even found between the loops of the basibiont's digestive tract. Only a single male was found to be in close contact to a female (fig. 1, *E*) and was completely covered by the egg-bearing membrane. The female's rootlet is not branching but as in mesobiotic chitonophilids (e. g. Schwabe et al., 2014) it was found to be adhered more or less to the basibiont's digestive tract (fig. 1, *B*, *C*), mainly restricted to the posterior part with the tip free ending either laterally or as in ZSM Mol 20150312 among the last loop of the digestive tract next to the anus. An exception was observed in the sample ZSM Mol 20150311 where the rootlet was also found directly under the valves (among the dorso-ventral muscles) and around the pericardium. It extended anteriorwards towards the half lengths of the radula, where also the tip was located. In this examined specimen of *Stenosemus albus* the digestive gland was unusual reduced compared to the other examined samples. Other damages were not observed and also external evidence for a parasitic infestation could not be detected in the preserved material.

Sample ZSM Mol 20131012 additionally provided a single specimen of an endobiotic nematode. Dr. Dmitry Miljutin (DZMB — German Centre for Marine Biodiversity Research, Senckenberg Research Institute, Wilhelmshaven, Germany) was so kind to examine the specimen on the first author's request and tentatively identified it as a juvenile representative of the family Benthimermithidae (fig. 1, *K*, *L*). Beside the illustrations he also provided some background information. According to him, juvenile stages of these worms are known as parasites infecting body cavities of marine invertebrates like free-living nematodes, priapulids, holothurians, polychaets and various crustaceans (Petter, 1980, 1983; Tchesunov, 1997; Tchesunov and Rosenberg, 2011; Miljutin, 2014), whereas the none-feeding adult nematodes are free-living. It is assumed that they reproduce in the sediment and their eggs are ingested by their deposit-feeding basibionts (Miljutin, 2014). If so, the finding of the present juvenile indicates a temporary damaging of the digestive tract, what we however failed in de-

tecting. Unusual, the present juvenile differs from other known juveniles of Benthimermithidae by the absence of a strongly sclerotized «stylet» in the terminal part of the pharyngeal internal lumen; this part looks rather like a tube with slightly sclerotized walls.

Family CALLISTOPLACIDAE Pilsbry, 1893

Ischnoplax pectinata (Sowerby, 1840) (fig. 3, 4).

Material examined: MZUSP one specimen Sao José da Coroa Grande (8°53' S, 35°08' W), Pernambuco, Brazil, 25.06.2013.

The specimen of *Ischnoplax pectinata* we show here is to our best knowledge the first case showing a double infection by chitonophilid copepods. After the partly dissection of an yet undescribed *Ischnochitonika* Franz and Bullock, 1990 by one of us (JAJ), the remains were sent to the first author to include the material in a study of mesobiotic chitonophilids in chitons (in progress). Once the opened chiton was closer examined, a distinct blackish swelling (arrowed in fig. 3, *A*) was observed in the afferent blood sinus at the level of the 6—7th ctenidia from posterior. Surprisingly at the same level a rootlet, without discernible connection to this structure started running backwards within the sinus (fig. 3, *C*). The opposite side penetrated the sinus wall and the foot tissue and following them the base of a branching rootlet system (fig. 3, *F*, *G*) was found above the digestive tract under valves vi-vii, free-lying in the coelom next to, what we here interpret as the fitting trunk (fig. 3, *H*, *J*), measuring about 7.3×3.3 mm. The unusually thin-walled trunk contained fluffy tissue, which is hard to interpret. Taken the general outline into account, preferable with this piece of branching rootlets, the structure resembles the gross morphology of a female *Ischnochitonika*, but differs: a) in the extremely thin cuticle which tends to be thread, b) in a very solid channel-like layer at the bottom of the branching roots (yellowish part in fig. 3, *G*), c) and in its endobiotic position. As in chitonophilid species the trunk practically 'solely' contains the reproduction system (e. g. Huys et al., 2002, Schwabe et al., 2014), the thin wall could be hypothetically transformed to the egg bearing membranes or tubes, which are characteristic for endoparasitic chitonophilids as shown for the above mentioned *Tesonema* (e. g. Huys et al., 2002). The solid channel-like layer could be hardened mesenchymatous tissue, which Schwabe et al. (2014) detected in a mesobiotic *Ischnochitonika*. This is quite likely, as the parallel running examination of further mesobiotic chitonophilids (in progress) shows a high degree of such hardening over various genera. Should be the observed structure (fig. 3, *F—J*) a female, the afferent blood sinus inhabiting structure might be a male (fig. 3, *B*; 4, *A*), although no evidence for a direct interaction was given. A second male (fig. 3, *D*, *E*; 4, *B*) was detected in the same vessel but more anterior. The males, measuring about 3.7—5.2 mm in length (size given of the whole structure, as figured) are medially swollen and blunt ending at one side, while the opposite end branches into testis containing tube-like lobes. The anterior end is here interpreted as fused antennary processes. The posterior lobes with the through shining testis show a remarkable stronger cuticle and resulting darker coloration. Anterior to the body centre a median swelling contains probably the mouth, with a pair of gonopores immediately behind (fig. 4).



Fig. 3. Light microscopic illustrations of Chitonophilidae gen. sp. 1 and its basibiont *Ischnoplax pectinata* (Sao José da Coroa Grande, 8°53' S. 35°08' W, Pernambuco, Brazil).

A — ventral view of dissected adult *I. pectinata* (arrow indicates dark part of the endobiont's male in the afferent blood sinus at the base of the posteriorly situated ctenidia); *B* — lateral view of a presumed copepod male with darker testis containing posterior lobes; *C* — part of the rootlets (arrowed) *in situ* at the base of the chiton's ctenidia; *D, E* — lateral views of a second male; *F, G* — outer (*F*) and inner (*G*) views of the base of the female's rootlet system (arrows indicate the base of the second branch), please note the yellowish thick tissue layer; *H, J* — different views of the presumed female trunk region, *H* — outer view, *J* — inner view. Scale bars: *A–G* — 1 mm; *H, J* — 2 mm.

Neither the feeding mode nor the association between the female and males can be interpreted from the damaged material at hand. Single eggs were found between the intestinal loops and among the digestive gland of the basibiont, but they were not considered here, as they also could originate from the earlier dissected mesobiotic ovigerous female. Future biotic studies of *Ischnoplax pecti-*

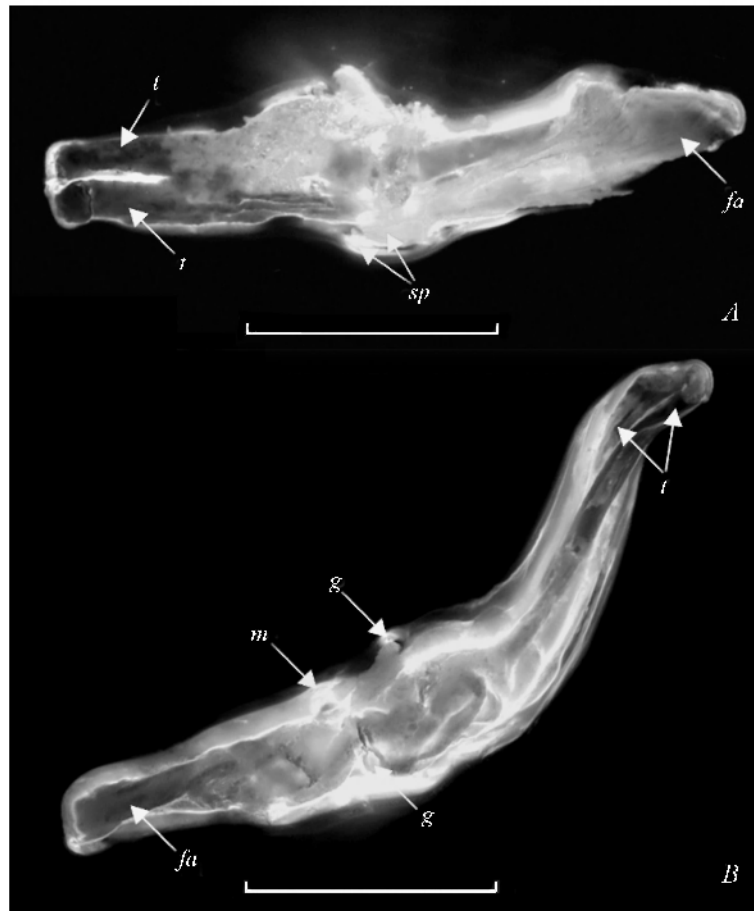


Fig. 4. Autofluorescence images of two males of Chitonophilidae gen. sp. 1 from the afferent blood sinus of *Ischnoplax pectinata*.

A — dorsal view (male from fig. 3, *B*), *B* — lateral view (male from fig. 3, *D*, *E*). Scale bars: 1 mm. *fa* — fused antennary process, *g* — gonopore, *m* — mouth, *sp* — spermatophore sac, *t* — testis.

nata might be more successful if prior to dissection the afferent blood sinus is carefully checked for either darker coloured males, or a slight thickening due to the copepod female's rootlets.

Snyder and Crozier (1922) shortly introduced a «bridge»-like malformation in *Chiton tuberculatus*, which was detected between the gills of this chiton. Unfortunately their notice is quite vague and this particular structure is not illustrated, so it remains unclear if it was affected by a parasite of similar behavior like the present.

Family CHITONIDAE Rafinesque, 1815

Rhysoplax olivaceus (Spengler, 1797).

Material examined: ZSM Mol 20041324 one specimen, Italy, Provincia di Livorno, Isola della Paolina (near Procchio), 42°47'19'' N, 10°13'47'' E, 2—4 m, bay with moderate surge, bolder field with heavy algal coverage and *Posi-*

Table 1

Morphometric data of examined specimens of *Bathylaimus* sp. endobiotic in *Rhyssoplax olivaceus* (Spengler, 1797)

Specimens: f — female, juv. — juveniles	f		juv.	
	f	juv.	f	juv.
Length (mm)	1.051	0.77	0.965	0.82
a	29.0	30.7	29.3	36.8
b	6.7	5.0	5.9	5.5
c	12.9	10.8	12.8	
c'	4.9	5.1	4.5	4.2
H dia.	14.0	11.2	14.0	
Labial setae			2.8	
Cephalic setae			5.5	
Subcephalic setae			4.5	
Bc: length — dia.	10.6—6.1	12.6—6.1	8.4—5.6	9.7
Oesophagus: length	156.2	154.0	163.2	149.3
Oesophagus: c. b. d.	27.9	22.3	26.5	20.9
Oesophagus: bulb length — dia.	19.5	16.7	16.7	15.9
Max. dia.	36.3	25.1	32.9	22.3
Vulva: from ant.	502.8		489.2	
Vulva: V (%)	47.8		50.7	
Vulva: c. b. d.	36.3		32.9	
Gonad f didelphic	181.4		148(?)	
Tail: length	81.5	71.1	75.3	64.2
a. b. d.	16.7	14.0	16.7	15.3

Note. Measurements in μm except for total length L [mm]; De Man's indices: a: relative thickness of the body: L divided by greatest body width (Max. dia.), b: relative length of oesophagus: L divided by the distance between the anterior end and the posterior margin of oesophagus, c: relative length of tail: L divided by tail length, c': relative length of tail: Tail length divided by anal body width (a. b. d.), V: Position of Vulva: Distance from the anterior body end to the vulva as a percentage of L. Abbreviations used H dia.: labial width: Distance between the farthest margins of the head or lip region, Bc: buccal cavity, length and width: Measured from anterior tip of body to posterior end of mouth cavity. Maximal width of stoma includes the thickness of the opposite walls, dia.: diameter, dist: distance, ant.: anterior, c. b. d.: corresponding body diameter, Max. dia.: Maximum diameter, body width: Greatest diameter of body measured at mid-body region, in female just prior to vulva, a. b. d.: anal body diameter/width: Diameter of the body measured on the posterior lip of the anus.

donia weed with coralligene stones, leg. Schwabe, Enrico and Bohn, Jens, 22.10.2004. (Prior to dissection specimen was kept for three days in aquarium).

Dr. Nicola Reiff (ZSM) was so kind investigating four specimens of nematods, the first author discerned in the coelom of the above mentioned specimen. She identified them as belonging to the genus *Bathylaimus* Cobb, 1894 (family: Tripyloididae Filipjev, 1918), a genus with free-living representatives. The specimens were re-examined by Dr. Jan Vanaverbeke (Ghent University, Belgium) and he confirmed this identification (17.09.2007): «the nematodes are *Bathylaimus*, especially because of the setae: it seems like they are „open” at the top end. In addition, the buccal cavity is large, and in one of the individuals there is a hint of a division of the buccal cavity. The amphid is difficult, but it fits the amphids I saw on my own specimens of *Bathylaimus*».

The following morphometric data (after Andr assy, 2005) were observed on two females and two juveniles (table 1).

Two our best knowledge this is the first association record of a species of the otherwise free-living *Bathylaimus*. Unfortunately the sample got lost during the return of the sample and could those not be illustrated.

Suborder **Acanthochitonina** Bergenhayn, 1930

Family LEPIDOCHITONIDAE Iredale, 1914

Cyanoplax dentiens (Gould, 1846) (fig. 5).

Material examined: ZSM Mol 20160010 one specimen, Canada, British Columbia, Strait of Georgia, Pender Island, leg. Julia Sigwart, 27.08.2003.

From the esophageal (or sugar) gland of the above mentioned sample we extracted a single drop-shaped structure, which has a reddish cuticulized «body» and kind of hardened branches. Intensive treatment with lactic acid failed in a cleaning of these branches and other structures are hardly visible (fig. 5). The «body» is about 139 µm long and 118 µm in high and is filled with granule-like tissue which at the opposite side of the branches tend to increase in size forming a darker pole. From the single minute object it is hard to evaluate a taxon attribution, but the general outline looks like a protist.

Family MOPALIIDAE Dall, 1889

Avdeev and Sirenko (2005: 541) mentioned an unidentified chitonophilid copepod from *Mopalia schrencki* Thiele, 1909. Although they do not indicated the exact position of the copepod, one of us (BS) confirms, that the species is a mesobiont as Schwabe et al. (2014) assumed. Unfortunately a final identificati-

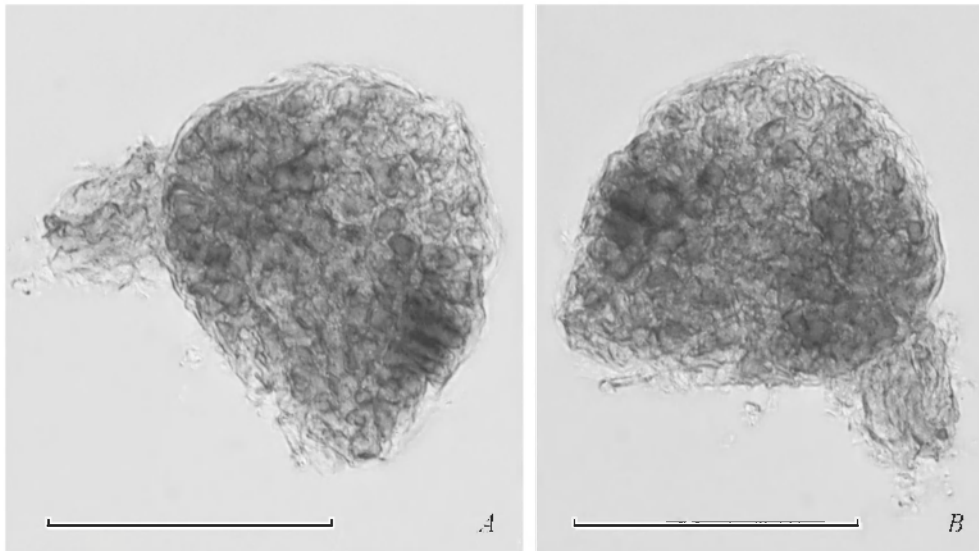


Fig. 5. Probably an isolated protist from the esophageal gland of *Cyanoplax dentiens*.
A — posterior-lateral view, B — lateral view. Scale bars: A—B — 100 µm.

on of this species is no longer possible, as we failed tracing the material. It is neither in ZISP (as declared) nor could we find it in the Institute of Biology and Soil, Vladivostok, where Avdeev was working. Avdeev (email: 15.05.2015) told us, he never had the material, so it must be considered lost.

Mopalia retifera Thiele, 1909 (fig. 6—11).

Material examined: NSMT (fig. 6—9) one specimen from Japan, Banda, Tateyama Bay (near south tip of Boso Peninsula, entrance of Tokyo Bay), from the underside of a stone at intertidal zone, leg. Hiroshi Saito, 26.04.1986. ZSM Mol 20150462 (fig. 10—11) one specimen, Japan, Pacific coast of Honshu, Suruga Bay, Osezaki, underside of rock, 3 m, leg. Hiroshi Saito, 27.06.2015.

Dr Hiroshi Saito (NSMT) informed us, that he observed years ago a parasitic copepod in *Mopalia retifera*, while studying the digestive system. The above mentioned basibiont specimen, from Banda (NSMT) showed irregularly arranged rootlets among the coiled intestine and originated from a drop-shaped body located next to the posterior end of the basibiont, above the anus. Hiroshi provided an illustration of what he observed, and it is obvious that the species resembles an endobiotic chitonophilid (fig. 6 — indicated by a question mark) different from all other yet described species in a) the drop-shape and b) in having a bifurcated long rootlet system.

Unfortunately this copepod is lost and not available for study. On our request Hiroshi provided the original sample and we were lucky detecting several structures (fig. 7—9), which are definitely not of polyplacophoran origin. Whether they belong to the copepod he saw is unclear, but some of the objects can be well interpreted as chitonophilids.

The sample was free of organs except for the whole digestive system. Seen the chiton from ventral, anterior at top, we found a considerable large structure (fig. 7, *F—H*; 8, *C—D*: here interpreted as chitonophilid female) in the right coelomic body wall behind the dorso-ventral muscle of plate iv. The paired roots were free-lying in the body cavity and entered anterior of the muscle. Immediately behind the fusion point of the roots there are two swellings visible (fig. 8, *D*), which we interpret as dorsally situated paired genital apertures with paired ovaries directly behind lying in postero-lateral lobes. A slight roundish thickening ventrally to the genital apertures is here interpreted as mouth region. The «body» from the lobes to the starting roots is about 2.2 mm in length. Opposite to the presumed female at the left coelom site at level between valves v-vi, also behind the chiton's dorso-ventral muscles we found a small sac-like structure, presumably the male (fig. 7, *A—C*) with a pair of broken (but at one site still connected) roots. The single, almost intact root pierced anterior of the dorso-ventral muscle of valve iv the coelomic wall and was free ending (but obviously cutted) in the body cavity. The remains of the second damaged root could not be found. The body shows posterior two distinct lobes, which are here interpreted as containing testis. A second male, found in close vicinity to the former, also behind the muscles, (fig. 7, *D—E*; 8, *A—B*) shows a more defined trunk and the posterior lobes more laterally folded. More interestingly, the trunk — root region is more pronounced, and although a clear bipartite of the root anlagen is given, they are not tube-like but more resembles a lappet. Gonopores are obviously at the anteriormost inner corner of the posterior lobes.

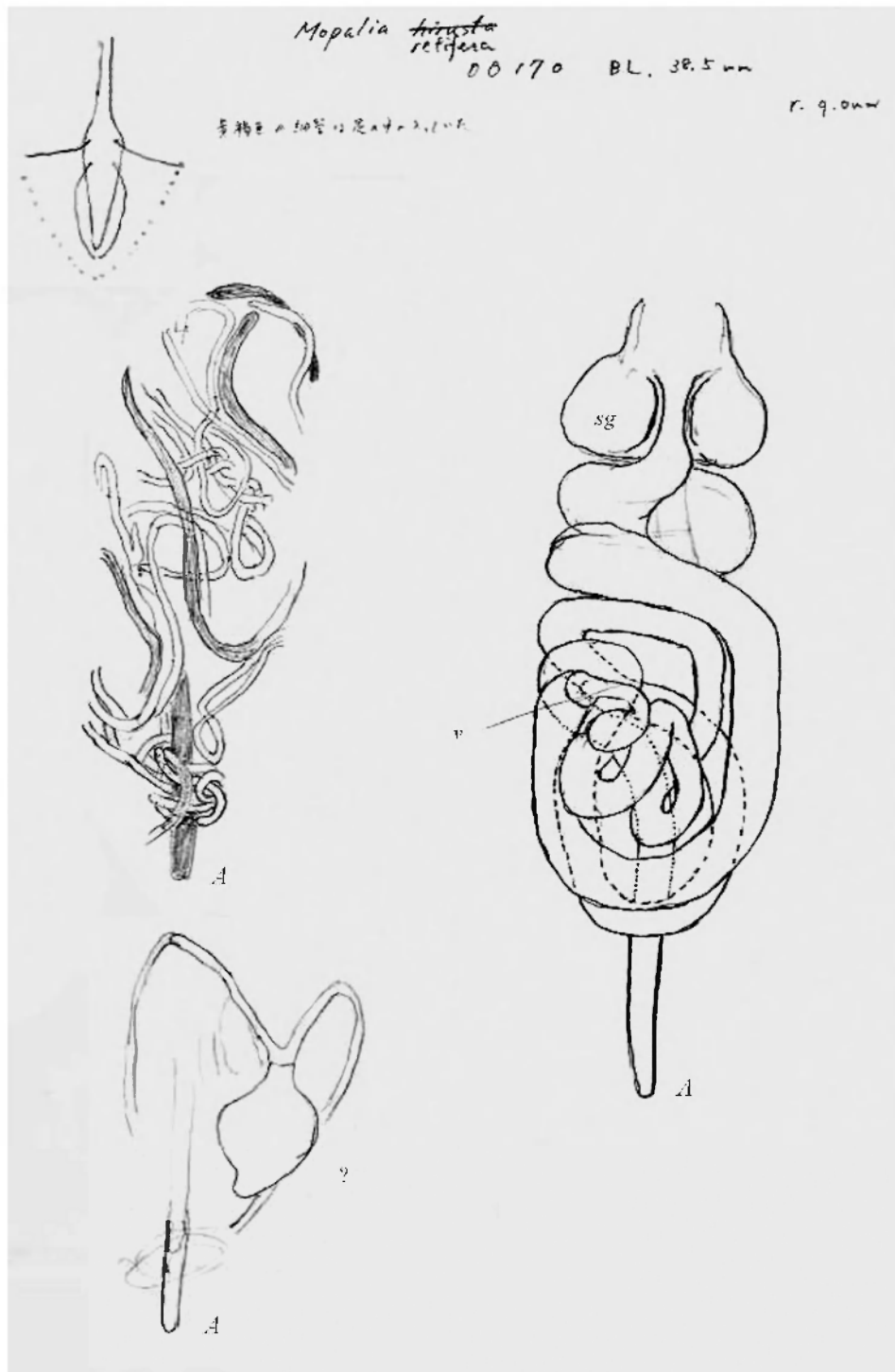


Fig. 6. Dr Hiroshi Saito's original sketch of a presumably male chitonophilid copepod (at bottom left question marked; «A» refers to basibiont's anus), prepared during the dissection of *Mopalia retifera* for digestive tract analyses. Not scaled.



Fig. 7. Chitonophilidae gen. sp. 2 from *Mopalia retifera* (NSMT).

A — dorsal view of presumed male with part of roots; *B* — ventral view of presumed male showing on root still connected; *C* — enlargement of fig. 7, *A* to show the male's trunk; *D*, *E* — dorsal (*D*) and ventral (*E*) views of a second presumed male; *F*–*H* — presumed female, *F* — ventral view, *G* — enlargement of fig. 7, *F*, *H*, lateral view; *J*–*N* — unknown structures, probably larval stages; *J*–*K* — presumable different development stages of males; *L*–*N* — presumed development stage of female. Scale bars: *A*–*B*, *D*–*H* — 1 mm; *C*, *L* — 500 μm; *J*–*K*, *M*–*N* — 200 μm.

We failed in seeing a mouth region in the males. The trunk sizes, measured without lobes and roots, of both males are about: $850 \times 800 \mu\text{m}$ (fig. 7, *A*–*C*) and $1000 \times 917 \mu\text{m}$ (fig. 7, *D*–*E*).

By careful removing of the basibiont's dorso-ventral muscles in the relevant regions we observed, further structures, which are definitively not of chiton origin, strongly cuticulized and of varying forms (fig. 7, *J*–*L*; 9). Despite the lack of clear organization of the inner structures, we hypothesize that the elongate structure in «fig. 7, *J*», $1200 \times 270 \mu\text{m}$, develops to «fig. 7, *K*» and the latter,

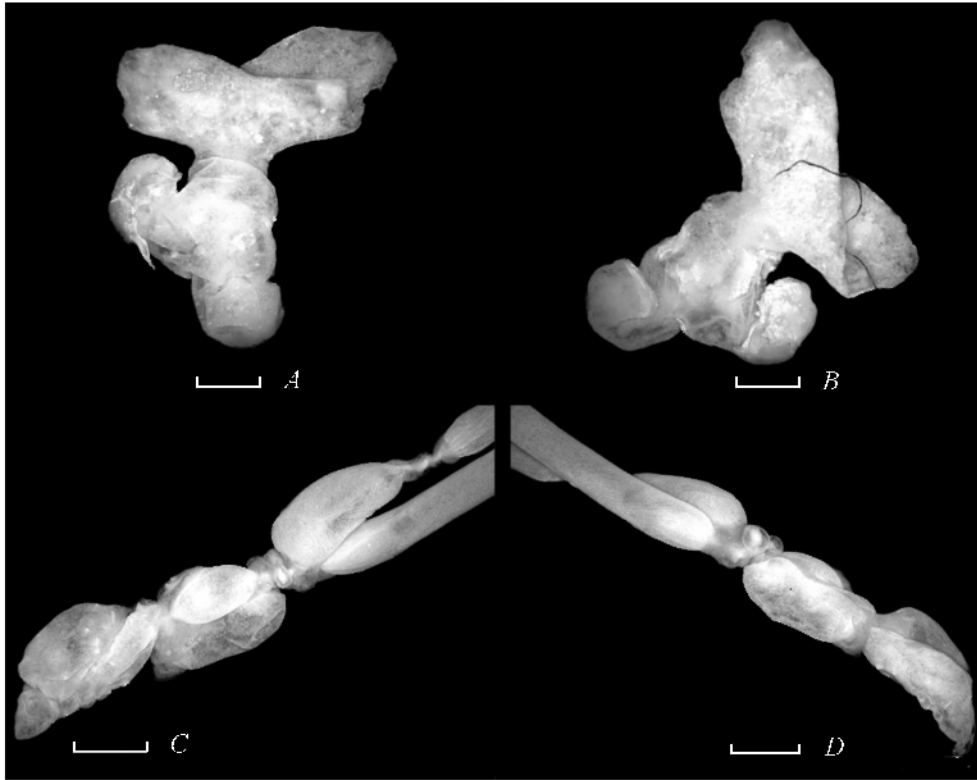


Fig. 8. Chitonophilidae gen. sp. 2 from *Mopalia retifera* (NSMT).

A — dorsal view of presumed male; *B* — ventral view of presumed male; *C, D* — lateral views of presumed female. All Scale bars — 500 μm .

already shows some similarity to the males. If this interpretation is true, we have to speak of two distinct larval developmental stages. The interpretation of the further structure (fig. 7, *L–N*; 9, *D–F*) is even more speculative. There is a tiny elongate «body» (265 \times 406 μm) with a bilobed structure attached to a single, slender, heavily cuticulized, smooth shaft (1125 \times 75 μm), which terminates to a thickened ring (fig. 9, *E*) that shows close similarity to a mouthring (e. g. in Huys et al., 2002: fig. 11, *A*). From here the shaft continues distinctly wider (fig. 7, *L*), of different coloration and with a striking spiral sculpture until it branches (775 \times 225 μm) into an undefined hardened root system (fig. 9, *D*). This distal part somewhat resembles the above mentioned hardened mesenchymatous tissue (see under *Ischnoplax pectinata*) and could also be traced in a small piece of root we found isolated under valve iv (fig. 9, *B*). Whether the shaft is kind of a modified mouth apparatus (stylet?) remains unclear, as well as its function and the way it has been build. Also unclear is, if the globular body develops to the above presumed female.

As all here listed structures originate from the same sample Dr. Saito investigated, his sketch has also taken into account. From the overall shape, we consider it closer to the males than to the female observed. Remarkable in this content however is that this structure was found entirely in the coelom and does not show the posterior-lateral lobes.

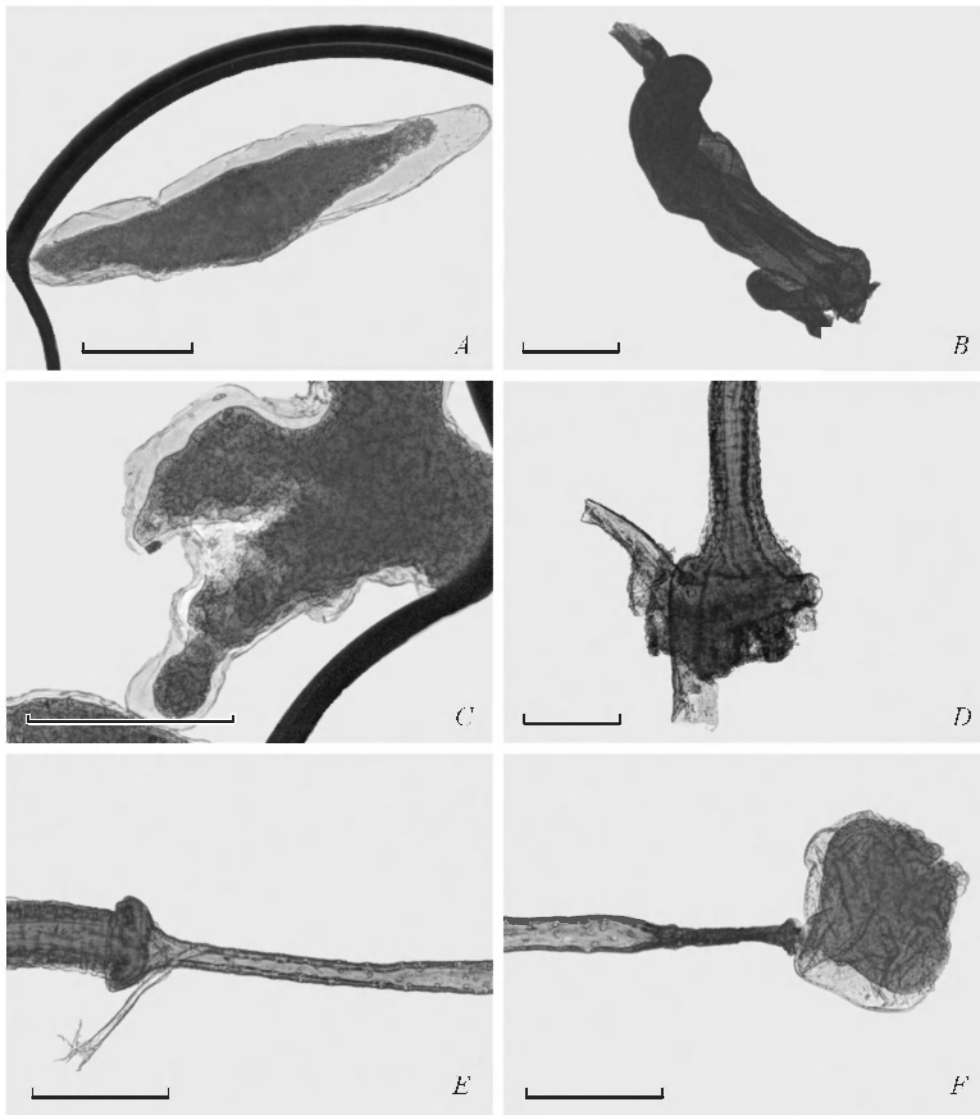


Fig. 9. Congored stained structures of Chitonophilidae gen. sp. 2 from *Mopalia retifera* (NSMT).

A — presumed early larval stage of males; *B* — piece of (females?) root with hardened tissue shining through; *C* — presumed later larval stage of males; *D–F* — presumable larval stage of female, *D* — distal part with undefined branches, *E* — transit region of shaft, showing the mouth ring like swelling, *F* — «trunk» with basal part of shaft. Scale bars: *B* — 1 mm, remaining — 250 μ m. *A*, *C* with blistering artefacts.

On our request Dr Saito attempted to re-collect the basibiont again for further studies. About 120 km eastward, separated by the Izu Peninsula, from the previous material he obtained a specimen of *Mopalia retifera*, which was obviously infected by a further endobiotic copepod that is morphologically distinct from the above mentioned. To check for bionts Dr Saito sliced the sole of the foot longitudinally along the side margins and recognized elongate, glossy eggs (fig. 10, *B*), measuring 123–223 \times 46–146 μ m (mean 146.9 [SD 24.4] \times

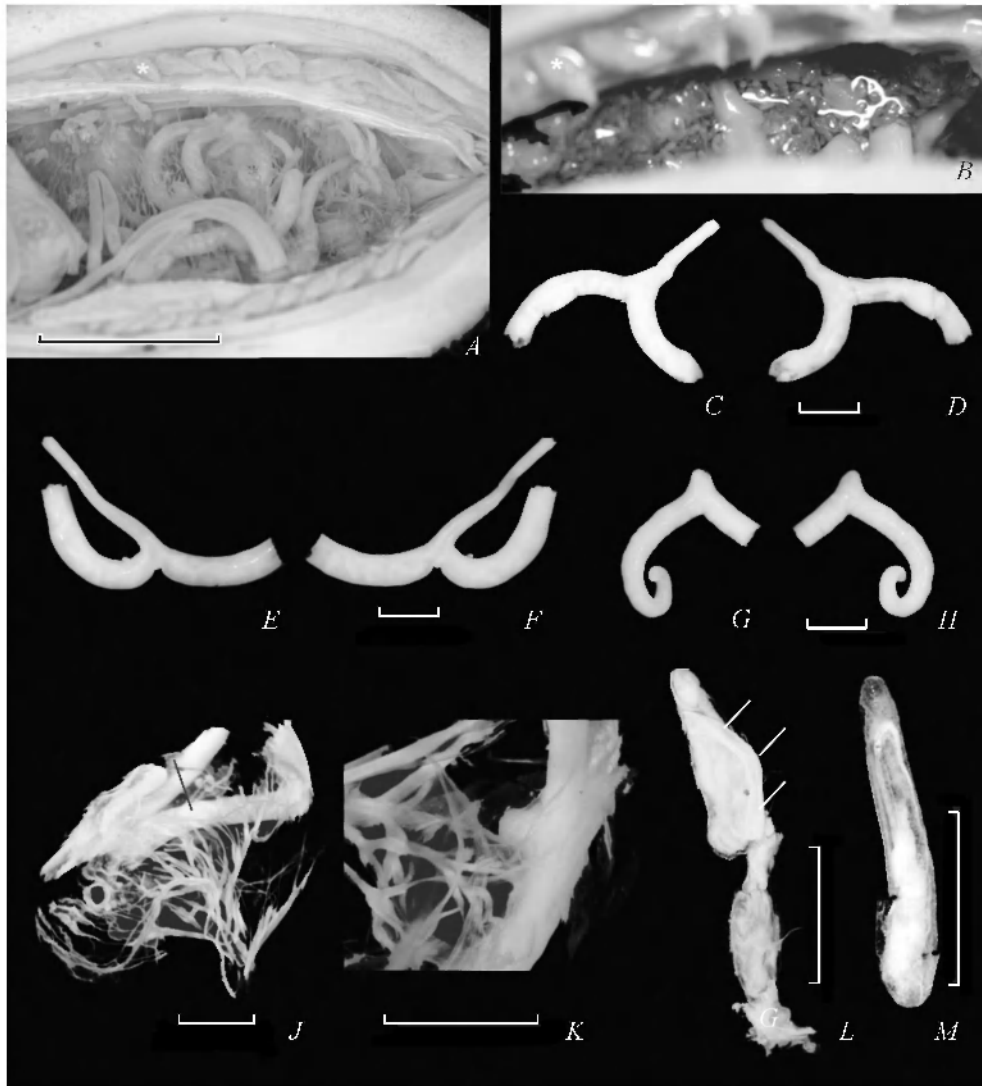


Fig. 10. Chitonophilidae gen. sp. 3 from *Mopalia retifera* (ZSM Mol 20150462).

A — ventral view of the opened basibiont, copepod eggs removed to show membranous tissue and males *in situ*; *B* — slightly opened fresh basibiont to show the densely arranged eggs of biont; *C–H* — in each case dorsal and ventral views of three males; *J* — membranous tissue, partly enwrapping male's rootlets, swelling of branching point indicated by arrow; *K* — lateral view of branching point of male's bipartite rootlet system; *L* — lateral view of adult female, posterior at top, arrows indicate part of the male's rootlet; *M* — lateral view of presumed larval stage of female, posterior at top. Scale bars: *A* — 5 mm, *B* — unscaled, *C–K* — 1 mm, *L–M* — 2 mm. Corresponding ctenidia in *A* and *B* marked by an asterisk. *B* image by Dr Hiroshi Saito, prior shipping of sample.

$\times 75.3$ [SD 25.6]) in 14 randomly selected eggs. In this condition we gained the sample for further studies.

The whole body cavity was carefully flushed with ethanol to remove the more or less loosely attached eggs from densely arranged membranous tissue strongly resembling a meshwork (fig. 10, *A*, *J*, *K*). The innards were additionally dorsally covered by several roots which were generally slightly wider than

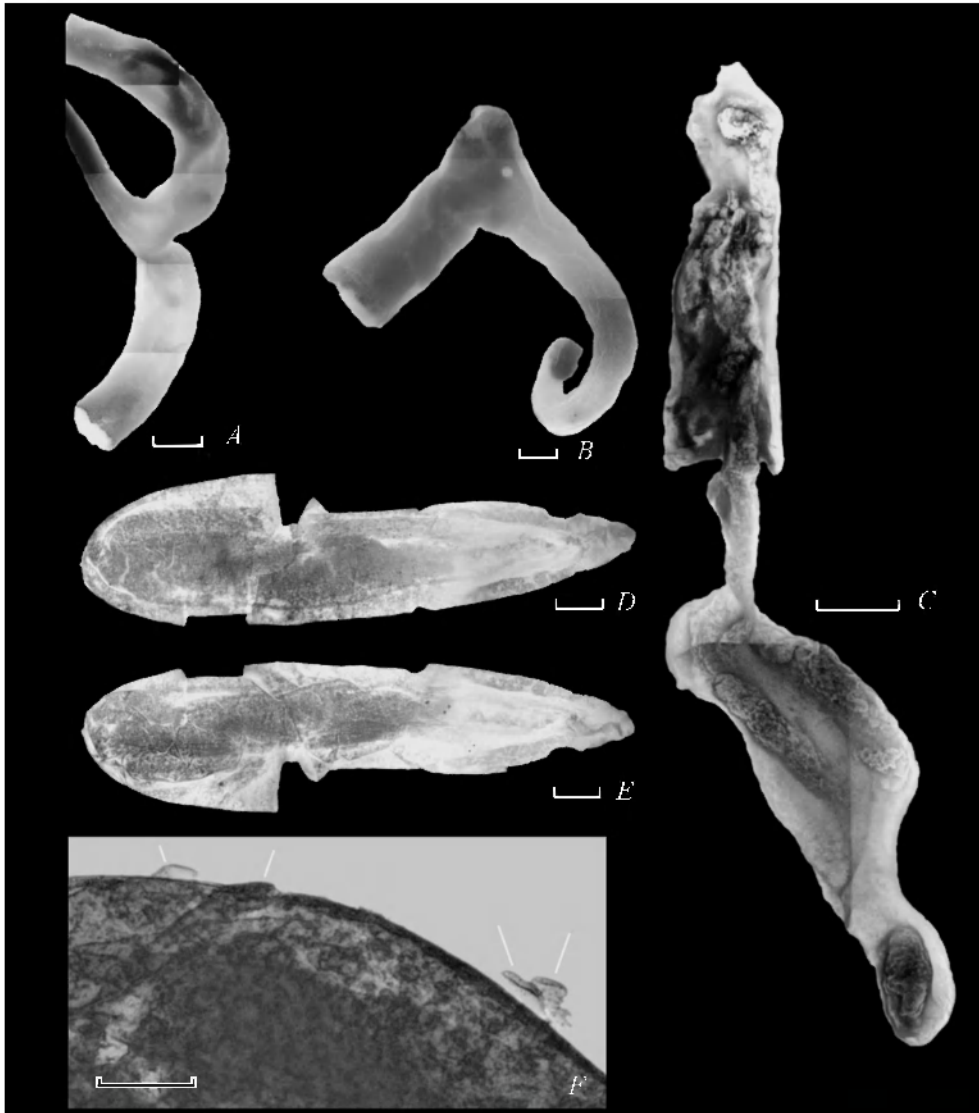


Fig. 11. Autofluorescence images of Chitonophilidae gen. sp. 3 from *Mopalia retifera* (ZSM Mol 20150462).

A, B — two different males; *C* — lateral view of female, anterior at top; *D, E* — both lateral views of presumed larval stage of female, posterior at right; *F* — detail of anterior portion of presumed female larval stage to show cephalic appendages. Scale bars: *A, C* — 500 μm ; *B* — 200 μm ; *D–E* — 250 μm ; *F* — 50 μm . *A–C* — mosaic images.

the basibiont's intestine. They originate from three randomly distributed males that show a tube like body with a pair of posterior enlarged and distally curved lobes, containing the testes (fig. 10, *C–H*; 11, *A, B*). Neither a transition between trunk and head/mouth region, nor gonopores could be identified. The splitting into a bipartite root system is assumed from the observations of pieces of isolated roots (fig. 10, *J*) where we found swellings of the same diameter as the extended trunk of the males has. At the posterior left coelom wall (seen from

ventral), dorsally above the nephridia a single structure was found, that we interpret as female. It is laterally flattened and centrally distinctly smaller. More interestingly, at this region the hinder part is (seen at longitudinal axis) clearly stepped. Anteriorly there are two distinct swellings which are heavier cuticulated than the remaining body, here interpret as remnants of cephalic appendages. A mouth region could have been not detected. The tapered part of the mid body shows ventrally additional a pair of small swellings, which could be the genital apertures. At least a considerable long ovary terminates there after passing kind of a posteriorly situated cement gland. Next to the female we found a larva that in its overall outline strongly resemble the adult, but for the lack of the central tapering and the stepped axis. Anlagen of the presumed cement gland are already visible as well as the developing ovary. The cephalic region of this larva bears additionally two pairs of minute appendages, which are smooth with their distal end flattened and laterally bent (fig. 11, *F*).

Remarks: None of the structures found in the present sample shows similarities to those of the preceding sample of the basibiont, which leads us to assume that *Mopalia retifera* serves as basibiont for two distinct endobiotic chitonophilid copepods.

DISCUSSION

Polyplacophorans are striking benthic marine organisms that are known to be inhabited by a variety of species, but in most cases the way these organisms interact with them is hardly explored. Parasitism is recorded for a few taxa only and mainly refers to protists, nematods and copepods. The latter group shows two main lineages, mesoparasitism and endoparasitism, all of them yet classified among the Chitonophilidae (e. g., Huys et al., 2002; Schwabe et al., 2014). Free-living harpacticoid copepod associates of polyplacophorans are also known (e. g. Huys, 2016), but such interaction is merely commensalism as basibiont damaging is not recorded. Unfortunately the information on the extend of impairment by chitonophilids on their basibionts is limited and refers principally to the enormous space requirements these copepods cause by their often extensively extended female rootlet system, which may completely fill the basibiont's body cavity. Tissue piercing points of mesobionts which could serve as entrance for additional invaders yet does not show any evidence for secondary skin irritations and double infections by different parasites was so far not observed. Besides the presence of the mentioned rootlet system, Huys et al. (2002) and Boxshall and Halsey (2004) characterized chitonophilids as copepods which highly modified bodies in both sexes, females without appendages and males with highly reduced number of appendages, lacking external segmentation, having paired genital system and with eggs either free laying in or clustered with membranous tissue. Additionally, development occurs via lecithotrophic naupliar and copepodid stages (in gastropod basibionts sometimes with additional metanaupliar stages) directly to transformed adults. Also typical is the considerably larger size of the females and the higher number of males associated to them.

The present paper deals with three potential endobiotic chitonophilid copepods. The species treated here share at least few characteristics with the above definition, but generally none of them fits yet known representatives of the fa-

mily neither from polyplacophoran nor from gastropod basibionts. Chitonophilidae gen. sp. 1 for example could lack the capability to form egg containing membranes or tubes, instead it shows some evidence for a strong modification of the trunk to such an egg-bearing structure. In Chitonophilidae gen. sp. 2 and 3 the presumed males show roots (while obviously lacking in the female of Chitonophilidae gen. sp. 3) and additionally intermediate forms that are here interpreted as additional larval stages. Male mouth regions were not observed in both forms and the question raises, whether feeding is completely absent in favor for a sperm transport via the roots as may suggested from the observations on the males of Chitonophilidae gen. sp. 3. Post-embryonic copepod developments are not necessarily restricted to the order given above, a further onychopodium stage is for example known from the ascidian biont *Gonophysema gullmarensis* Bresciani and Lützen, 1960 (revised in Huys, 2014). The latter however differs from the stage found in Chitonophilidae gen. sp. 3 not only in its dorso-ventral flattening but also for the presence of paired grasping antennae, which was not observed in such extend in the present form. Should be our interpretation of the chitonophilid taxa here presented manifested by further researches, the current contemporary concept of the family, which is largely based on the observed conditions of two gastropod infesting species (e. g. Huys et al., 2002), is in need of reconsideration. Schwabe et al. (2014) provided an updated list of known chitonophilids, their hosts and geographic and bathymetric occurrence. According to their data only two endobiotic copepods were previously recognized in polyplacophorans, namely *Cookoides cordatus* Avdeev and Sirenko, 1994 and the here treated *Tesonema reniformis* Avdeev and Sirenko, 1994, both known from different species of the ischnochitonid basibiont genus *Stenosemus*. While *C. cordatus* was recorded from the subantarctic South Atlantic, *T. reniformis* was prior this study only known from the Northwest Pacific. The new observations of the latter from the North Atlantic considerably extend the endobiont's distribution. The three additional chitonophilids of this study add further basibiont genera and families: the callistoplacid *Ischnoplax* and the mopaliid genus *Mopalia*. Both families are well documented for mesobiotic chitonophilids, whereby the genus *Ischnoplax* is for the first time recorded as basibiont for chitonophilids (Schwabe et al., 2014). Compared to the older endobiotic records, the three new chitonophilids inhabit exclusively shallow water, including the first record from the western tropical Atlantic.

The yet observed and recorded nematods found in polyplacophorans are obviously all, but for Ascarididae, from families that have free-living adults. That is also true for the present findings of the tripyloidid genus *Bathylaimus* in the Mediterranean *Rhyssoplax olivaceus* and the juvenile of the Benthimermithidae found in the North Atlantic *Stenosemus albus*. However, these records would suggest that polyplacophorans are intermediate basibionts only. The Ascarididae record by Plate (1897) was obviously never re-studied and confirmed, so it remains unclear whether a restricted polyplacophoran-nematod association may occur. The same is true for the unspecific «Nematoda» listed here (table 2). Our new observations add some remarkable endobionts to yet existing records, which have a long history, but were hardly analyzed in detail. To gain a better understanding of the role the polyplacophorans play within this form of interaction we attempt here to give a brief compilation of our present stage of knowledge on endobionts in Polyplacophora, mainly based on historical records

Table 2

Where applicable biont classification (Phylum, Class, Order, Family) follows *World Register of Marine Species* (<http://www.marinespecies.org/>), except for marked classifications (*) that follow their original description and are not necessarily ranked. Basibiont names in brackets refer to the original names used in literature

Biont	Biont classification	Locality	Basibiont	Biont position in basibiont	References
Bacteria					
«Spirochetes»	Spirochaetes	Mediterranean Sea	Chitons from Banuyls-sur-Mer	In the blood	Arvy and Gabe, 1949; Hyman, 1967
<i>Acanthopleuribacter pedis</i> Fukunaga, Kurahashi, Yanagi, Yokota and Harayama, 2008	*Acidobacteria, Holophagae, Acanthopleuribacteriales, Acanthopleuribacteraceae	NW Pacific	<i>Acanthopleura japonica</i>	Unspecified tissue	Fukunaga et al., 2008
Protista					
?Protist		NW Pacific	<i>Cyanoplax dentiens</i>	Esophageal gland	Herein
Ciliated Infusoria closely related to <i>Glaucoma</i> Ehrenberg, 1830		Mediterranean Sea	<i>Rhysoplax olivaceus</i>	In the blood	Arvy and Gabe, 1949; Hyman, 1967
<i>Chitonicium simplex</i> Plate, 1899		SE Pacific	<i>Acanthochitona fascicularis</i>		
			<i>Ischnochiton stramineus</i> [imitator]	In the mantle cavity, foot, ctenidia, mucous glands	Plate, 1899a, 1901; Fischer-Piette and Franc, 1960; Hyman, 1967; Kaas et al., 1998
			<i>Chaetopleura peruviana</i>		
			<i>Tonicia atrata</i> [fastigiata]		
			<i>Chiton cumingsii</i>		
«Coccidian»	Myzozoa, Conoidasida	NE Atlantic	<i>Acanthochitona fascicularis</i>	Salivary gland	Debaisieux, 1919; Lauckner, 1983
«Coccidian»	Myzozoa, Conoidasida	SE Pacific	<i>Callochiton puniceus</i>	Anterior digestive tract	Plate, 1899a
<i>Pseudoklossia chitonis</i> Debaisieux, 1919	Myzozoa, Conoidasida, Eucoccidiorida, Aggregatidae	NE Atlantic	<i>Acanthochitona fascicularis</i>	Digestive gland	Debaisieux, 1919, 1922

<i>Nematopsis legeri</i> de Beauchamp, 1910	Myzozoa, Conoidasida, Eugregarinorida, Porosporidae		<i>Lepidochitona caprea-</i> <i>rum</i>		Hatt, 1931 [not seen, following Lauckner, 1983]
<i>Haplosporidium chitonis</i> (Lankester, 1885)	Cercozoa, Ascetosporea, Haplosporida, Haplos- poridiidae	NE Atlantic	<i>Lepidochitona cinerea</i>	In the innards	The species was various- ly treated in lit. often as <i>Minchinia chitonis</i> , a detailed history of this species may be fo- und in Lauckner, 1983
<i>Haplosporidium chitonis</i> (Lankester, 1885)	Cercozoa, Ascetosporea, Haplosporida, Haplos- poridiidae	Sea of Okhotsk, Shelikhov Bay, 179 m NE Atlantic	<i>Stenosemus albus</i>	In the innards, in foot- tissue and mantle groove	Herein (BS)
«Sporozoa» different from « <i>Minchinia</i> <i>chitonis</i> (Lankester, 1885)»			<i>Acanthochitona crinita</i>		Fretter, 1937
<i>Creolimax fragrantissi-</i> <i>ma</i> Marshall, Celio, McLaughlin and Berbee, 2008	*Ichthyosporea, Mesomycetozoa, Opisthokonta	NE Pacific	<i>Katharina tunicata</i>	Digestive tract	Marshall et al., 2008
Undefined parasitic microorganisms		North Sea	<i>Lepidochitona cinerea</i> [<i>marginatus</i>]	Gill epithelium	Plate, 1897
Platyhelminthes					
Larval <i>Proctoeces ma-</i> <i>culatus</i> (Looss, 1901)	Platyhelminthes, Trema- toda, Plagiorchiida, Fellodistomidae	Mediterranean	<i>Acanthochitona fascicu-</i> <i>laris</i> [<i>discrepans</i>]	Connective tissue	Prévot, 1965
Nematoda					
Ascarididae [Ascaride]	Nematoda, Chroma- dorea, Rhabditida, Ascarididae	SE Pacific	<i>Tonicia chilensis</i>	Body cavity dorsally above the stomach	Plate, 1897

Table 2 (continuation)

Biont	Biont classification	Locality	Basibiont	Biont position in basibiont	References
Chromadoridae	Nematoda, Chromadorea, Chromadorida, Chromadoridae	SE Pacific	<i>Chiton magnificus</i>	Cyst in the mantle cavity	Schwabe et al., 2006; Reiff and Schwabe, 2007
<i>Euchromadora</i> cf. <i>permutabilis</i> Wieser, 1954	Nematoda, Chromadorea, Chromadorida, Chromadoridae	SE Pacific	<i>Chiton magnificus</i>	Cyst in the mantle cavity	Reiff and Schwabe, 2007
Benthimermithidae sp.	Nematoda, not classified, Benthimermithida, Benthimermithidae	N Atlantic	<i>Stenosemus albus</i>	Endoparasitic in the body cavity	Herein
«Nematoda»	Nematoda	Bering Sea, 136 m	<i>Stenosemus albus</i>	On apophyses of tail valve	Herein (BS)
«Nematoda (with eggs)»	Nematoda	Kerguelen Islands	<i>Hemiarthrum setulosum</i>	Digestive tract	Herein (BS)
«Nematoda» <i>Bathylaimus</i> sp.	Nematoda Nematoda, Enoplea, Enoplida, Tripyloididae	NE Atlantic Mediterranean Sea	<i>Chaetopleura angulata</i> <i>Rhysosoplax olivaceus</i>	Coelom In the body cavity	Herein (JAJ) Herein
			Annelida		
«Polychaeta»	Polychaeta	NE Atlantic	<i>Acanthochitona discrepans</i>	In scar tissue under a repaired valve defect	Herein (under study)
«Free-living polychaete»	Polychaeta	NE Pacific	<i>Chiton articulatus</i>	In the shell	Alvarez-Cerrillo et al., (2017)
			Mollusca		
<i>Leiosolenus aristatus</i> (Dillwyn, 1817)	Bivalvia, Pteriomorphia, Mytilida, Mytilidae	Gulf of Panama Caribbean NE Pacific	<i>Chiton stokesii</i> <i>Chiton tuberculatus</i> <i>Chiton articulatus</i>	In the shell	Bullock and Boss (1971) Alvarez-Cerrillo et al., 2017

<i>Leiosolenus spatiosus</i> (Carpenter, 1857)	Bivalvia, Pteriomorpha, Mytilida, Mytilidae	Gulf of Panama	<i>Acanthochitona hirudiniformis</i>	In the shell	Watters, 1981
<i>Pinctada mazatlanica</i> (Hanley, 1856)	Bivalvia, Pteriomorpha, Ostreida, Pteriidae	NE Pacific	<i>Chiton articulatus</i>	In the shell	Alvarez-Cerrillo et al., 2017

Crustacea

<i>Cookoides cordatus</i> Avdeev and Sirenko, 1994	Arthropoda, Hexanauplia, Cyclopoida, Chitonophilidae	S Atlantic	<i>Stenosemus exaratus</i>	In the body cavity	Avdeev and Sirenko, 1994
<i>Tesonesma reniformis</i> Avdeev and Sirenko, 1994	Arthropoda, Hexanauplia, Cyclopoida, Chitonophilidae	NW Pacific, N Atlantic	<i>Stenosemus albus</i>	Endoparasitic in the body cavity	Avdeev and Sirenko, 1994, 2005, herein
Chitonophilidae gen. sp. 1	Arthropoda, Hexanauplia, Cyclopoida, Chitonophilidae	SW Atlantic	<i>Ischnoplax pectinata</i>	In body cavity and afferent blood sinus	Herein
Chitonophilidae gen. sp. 2	Arthropoda, Hexanauplia, Cyclopoida, Chitonophilidae	NW Pacific	<i>Mopalia retifera</i>	Body cavity and behind dorso-ventral muscles	Herein
Chitonophilidae gen. sp. 3	Arthropoda, Hexanauplia, Cyclopoida, Chitonophilidae	NW Pacific	<i>Mopalia retifera</i>	Body cavity	Herein
<i>Cryptophtialus wainwrighti</i> Tomlinson, 1969	Arthropoda, Hexanauplia, Cirripedia, Cryptophtialida, Cryptophtialidae	NE Pacific	<i>Chiton articulatus</i>	In the shell	Alvarez-Cerrillo et al., 2017
<i>Cryptophtialus minutus</i> Darwin, 1854 [as <i>C. striatus</i> Berndt, 1903, <i>C. minutus</i> <i>striatus</i> Berndt, 1907]	Arthropoda, Hexanauplia, Cirripedia, Cryptophtialida, Cryptophtialidae	SE Pacific	<i>Chiton magnificus</i>	In the shell	Berndt, 1903, 1907 [revised in Tomlinson, 1969]
<i>Australophtialus melampygos</i> (Berndt, 1907)	Arthropoda, Hexanauplia, Cirripedia, Cryptophtialida, Cryptophtialidae	NZ waters	<i>Onithochiton neglectus</i> , <i>Chiton pelliserpentis</i> , <i>C. torri</i> , <i>C. glaucus</i> , <i>Plaxiphora obtecta</i>	In the shell	Batham and Tomlinson, 1965

and together with the herein treated material on own observations, as shown in table 2.

This compilation of 35 endobiotic records shows that polyplacophorans serve as basibionts for a broad range of taxa from Bacteria to Crustacea, whereby the most documented records refer to Protista (10), Nematoda (8) and Crustacea (8). While the three bivalve Mollusca exclusively were found in polyplacophoran valves, this microhabitat can be shared by Annelida and Crustacea, but representatives of the latter two may also found in soft tissues. Of the here listed endobionts, *Haplosporidium chitonis* (Lankester, 1885) is the only well studied species (e. g. Baxter and Jones, 1978). All other records were either reported as side effects of anatomical studies on polyplacophorans (e. g., Plate, 1899a, Fretter, 1937, Arvy and Gabe, 1949, the present work) or the basibionts were selectively chosen to test a known endobiont's distribution (e. g. *Australophialus melampygos* (Berndt, 1907)). Remarkably, of the approximately 990 known extant polyplacophoran species (first authors unpubl. data), only 31 (3.1 %) are yet recorded as basibionts for endobiotic taxa. These species cover 16 genera (21.9 %) and nine families (47.4 %) (according to Sirenko 2006: of 73 extant genera and 19 families), but none of these belongs to the more primitive order Lepidopleurida Thiele, 1909. This fact is interesting, as anatomical studies on lepidopleurids are known (e. g. Burne, 1895; Plate, 1899b) and members of this order show the highest infection by mesobiotic chitonophilids (Schwabe et al., 2014). As Lepidopleurida predominantly inhabits deeper water, and the basibionts in table 2 are mainly restricted to shallow water habitats, this discrepancy may be explained by a limited access to study material. Furthermore, mesobiotic infestation by chitonophilids for example is much easier to observe due to the parasite's egg sacs, while the present study demonstrated that no external evidence for endobionts of the same family was detectable.

The present data, however, demonstrate that polyplacophorans have a high potential for parasitologists and further studies may not only shed some more light into the biology of yet described taxa, but this basibiont class — hardly modified since their earliest occurrence in the Late Cambrian, with the conservative organization could also allow better insights into biont's evolution.

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