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Scanning electron microscopical description and biology of three new endoparasitic *Ceratosomicola* species from tropical Indo-Pacific nudibranch hosts

(Crustacea, Copepoda, Poecilostomatoida, Splanchnotrophidae)

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The Splanchnotrophidae are bizarre copepod endoparasites of shell-less opisthobranch gastropods which were rarely found in the Indo-Pacific. The genus *Ceratosomicola* Huys, 2001 included only the type species, *C. sacculata* (O'Donoghue, 1924), from tropical Western Australia. The present study points towards a much higher diversity: three new species, *C. coia* spec. nov., *C. delicata* spec. nov. and *C. mammillata* spec. nov., are described from chromodoridid nudibranch hosts from Sulawesi, Indonesia. The parasite morphology was examined in detail using SEM. All female *Ceratosomicola* possess 3 pairs of elongate body processes, 4 pairs of cephalic appendages (two pairs of antennae, one pair of mandibles and one pair of maxillae) and highly reduced thoracopods. Major specific differences refer to the body shape, presence and number of dorsal and ventral bulges, and the structure of labrum, labium and thoracopods. The new species are sexually dimorphic, dwarf males of *Ceratosomicola* are herein described for the first time. Morphological structures are discussed comparatively; both intraspecific and intersexual variability is addressed. The genus *Ceratosomicola* is regarded as monophyletic, radiation may have occurred in and south of the Indonesian Archipelago, by host switching. All four *Ceratosomicola* species appear to be host specific, with females showing positional preferences inside their hosts. Biological adaptations of splanchnotrophids to special hosts and aspects of co-evolution are discussed.

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Introduction

The Splanchnotrophidae is a small family of bizarre and poorly known endoparasitic poecilostomatoid copepod crustaceans. All splanchnotrophids are specialized parasites of shell-less opisthobranch gastropods (Jensen, 1987), and some species may cause fatal damage to their hosts (e.g. Schrödl, 1997;

Marshall & Hayward, 2006). Recently, Huys (2001) gave a detailed approach on resolving the “taxonomic myopia” related to the family Splanchnotrophidae. Members of the family were characterized by having a strong and 3-segmented antenna, a 2-segmented maxilla, a biramous second and third thoracopod, and a pair of caudal rami. The sexes are strongly dimorphic concerning the body shape and

size. Females have a swollen body, which possesses 3-6 pairs of long appendages at the thorax, whereas males are dwarfs and not showing any thoracic appendages besides the more or less reduced legs. Of the five genera regarded as valid by Huys (2001), the species-rich *Ismaila* Bergh, 1867 already was revised by Haumayr & Schrödl (2003); and Schrödl (2003) discussed biological aspects of these host-parasite relationships. Emphasizing the high prevalence of *Ismaila* especially within central Chilean sea slugs, Schrödl (2002) also pointed to the geographic separation of the Caribbean and eastern Pacific *Ismaila* from the boreo-Mediterranean *Splanchnotrophus* Hancock & Norman, 1863 and *Lomanoticola* Scott & Scott, 1895. These latter genera are, however, in a state of taxonomic confusion; a number of nominal species were created within old descriptions which do not present adequate information for proper re-identification (see Marshall & Hayward, 2006). The two Indo-Pacific, thus far monotypic genera *Arthurius* Huys, 2001 and *Ceratosomicola* Huys, 2001 have been subject to our recent investigations.

Currently, the genus *Ceratosomicola* includes a single species, *C. sacculatus* (O'Donoghue, 1924). After his re-examination of one of the two female syntypes, Huys (2001: 43) stated a set of unique characters which are not present in other splanchnotrophids, like the "... presence of dorsal bulges on the prosome, the further reduced swimming legs, the greater length of the ventro-lateral appendages, and additional discrepancies noted in the mouthparts". Males were, however, not available for study.

In the present study three new *Ceratosomicola* species are described, based on detailed morphological investigation using the scanning electron microscope. SEM examinations were shown to be very suitable providing objective detail information on tiny crustaceans like early decapod larvae (Meyer et al., 2006) or splanchnotrophids (Haumayr & Schrödl, 2003); i.e., most taxonomically relevant splanchnotrophid structures such as body shape, mouthparts and (often atrophied) legs were detected by SEM without any need to dissect and destroy rare specimens. Our ultrastructural results on *Ceratosomicola* spp. are compared critically with light microscopical data on *C. sacculata* O'Donoghue, 1924 acquired by Huys (2001). Male specimens of the genus are found and described for the first time herein. Additionally, new data on the geographical distribution and biology of *Ceratosomicola* are provided.

Material and Methods

During the past ten years, nudibranch and sacoglossan Opisthobranchia have been collected from all over the world in search of endoparasitic copepods by our workgroups and associated researchers (e.g. Schrödl, 2002; Burghardt et al., 2006). The three nudibranch species *Chromodoris coi* Risbec, 1956, *Chromodoris geometrica* Risbec, 1928 and *Risbecia tryoni* Garrett, 1873 (Fig. 1), found in the Banda Sea, Sulawesi, Indonesia (Fig. 2), were infested with splanchnotrophid endoparasites of the genus *Ceratosomicola*. Photographs of living host specimens were taken by NW. The parasites were dissected out of the preserved hosts and examined with an Olympus SZX 12 binocular equipped with a "Jenoptic ProgRes C12" camera. For SEM-examination the copepods were dehydrated in an acetone series. The parasites were critical-point dried in a BAL-TEC CPD 030 device. They were mounted on SEM stubs and coated with gold in a POLARON SEM COATING SYSTEM for 120 seconds. A LEO1430 VP scanning electron microscope was used for ultrastructural analysis and digital documentation.

Descriptive Terminology

Terms used herein are adopted from Gruner et al. (1993), Huys (2001) and Haumayr & Schrödl (2003). The body is described as comprising cephalothorax (five head segments fused with a variable number of thorax segments), thorax and abdomen. The segmental designation is based on 1) externally recognizable segment borders, 2) presence of (paired) extremities on segments or body parts, respectively, 3) literature knowledge on homology regarding Copepoda and Splanchnotrophidae; e. g. on the assumption that first thoracopods (maxillipeds) are always absent in splanchnotrophids (Ho, 1987), and that genital apertures are located on the first abdominal segment (Gruner et al., 1993).

Taxonomy

Class Copepoda H. M. Edwards, 1840
 Order Poecilostomatoida Thorell, 1859
 Family Splanchnotrophidae Norman & Scott, 1906

Genus *Ceratosomicola* Huys, 2001

Ceratosomicola coia, spec. nov.
 (Figs 3-6)

Material. Holotype (SEM mounted ♀, Zoologische Staatssammlung München-ZSM 20060211), 4 paratypes (SEM mounted: 1♀, ZSM 20060212, 1♂, ZSM 20060213, 1♂, ZSM 20060214; wet preserved: 1♀, ZSM 20060215;

all partly damaged), collected by Nerida Wilson, buoy 3 and buoy 5, Home reef, Palau Hoga, Tukangbesi archipelago, southeast Sulawesi, Indonesia 05°28'29"S, 123°45'40"E, 29 August and 02 September 2002. Host: *Chromodoris coi* (Risbec, 1956) (ZSM Mol 20060062, 20060063). 2♀, 2♂ examined by SEM.

Etymology. The species name refers to the host *Chromodoris coi*.

Description

Female. Elongate body measuring up to 5.1 mm in length. Cephalothorax (five head segments and first thorax segment) distinctly set off from long and only partly segmented thorax (second and third segment detectable); 3-segmented abdomen very short.

Coloration yellowish; head and anterior part of thorax reddish, abdomen and processes slightly translucent. Rows of eggs shining through cuticle, forming a network in parts of thorax and processes. Two ducts (probably oviducts) running parallel along abdomen (Fig. 3A,B).

Cephalothorax with three lobes, middle lobe represents head with mouthparts, one pair of lateral lobes (Fig. 3C,D). Antennule (Fig. 3E) indistinctly 4-segmented and unbranched, bearing four large and strong spines on first segment; second segment with three setae situated in distal part; third segment with three setae; fourth segment with eight setae at apex. Antenna (Fig. 3F) 3-segmented and unbranched; first segment enlarged and unarmed; second segment with one short seta proximally; third segment hook-shaped bearing six small spines, three surrounding a hole (Fig. 3F, arrow). Labrum large (about two thirds of antenna length), bilobate; small inverted "U"-shaped process at posterior edge (Figs 3D, 4A). Mandible (Fig. 4A) with thick and broad base, blade more slender, hook-shaped with several small processes at both margins. Maxillule not detectable. Maxilla (Fig. 4B) unarmed and slender, tapering into pointed tip; base of maxilla not fully visible, but probably referring to lateral round swelling as seen in males (Fig. 5F). Labium (Fig. 4A) bears one pair of pinnate paragnaths at base; zig-zag-shaped slit running from posterior edge over one third of whole length; two setular patches laterally of slit.

First thoracopod (maxilliped) absent. Second thoracopod consisting of three separated elements, exopod, endopod and outer pinnate seta (Fig. 4C). Exopod biramous, longer ramus rather flat, shorter ramus round and pinnate, both rami with pointed tip; one small spine at base of exopod and one below base of shorter ramus. Endopod a spinous element. Third thoracopod (Fig. 4D) as second one; exopod with at least one basal spine. Fourth thoracopod a

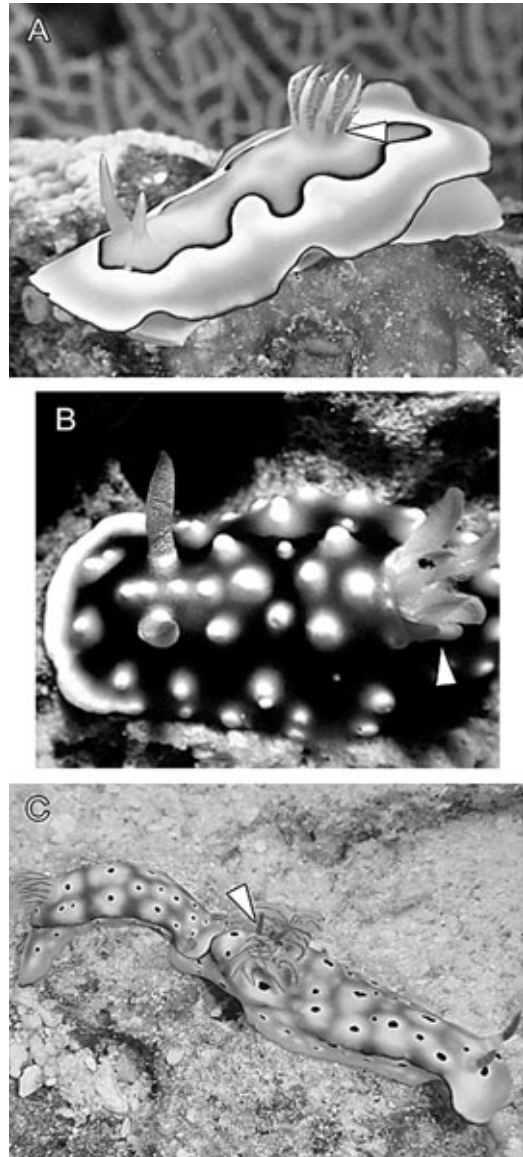


Fig. 1. Hosts of *Ceratosomicola*. **A.** *Chromodoris coi*. **B.** *Chromodoris geometrica*. **C.** *Risbecia tryoni*. Female parasite egg-sacs protruding inside gill circle (arrows).

minute and pinnate, seta-like process (Fig. 4E). Thoracopods five and six absent.

First thoracic segment fused to head (cephalothorax). Following two segments enlarged, not distinctly demarcated. Enlarged segments with three pairs of lateral appendages, each as long as or longer than whole animal. All appendages tapering abruptly after 1/3 of length, into pointed tip. First pair



Fig. 2. Collecting area of the nudibranch hosts infested with *Ceratosomicola*.

of appendages situated at level of second thoracopod. Second and third pair fused at base (Fig. 3C) at level of third thoracopod. Thorax dorsally with two transversal bulges (Fig. 3B), one between first and second appendage, one at level of third appendage. Posterior part of thorax more slender, bent dorsally (due to position inside host).

Abdomen indistinctly 3-segmented (Fig. 4F). First segment bearing genital openings. Egg sacs banana- or stick-shaped, elongate, containing numerous eggs. In living specimens egg sacs orange coloured (see Fig. 1A). Lateral constrictions on second abdominal segment. Caudal rami (Fig. 4F) short, with one accessory element; posterior most abdomen position attached to SEM stub, no further examination possible.

Male. Body size up to 3 mm. Cephalothorax (head plus thoracic segments one to three) enlarged, no external segmentation detectable; dorsally with large hemisphere-shaped swelling and lateral outgrowths on third segment. Thorax slender with two or three indistinctly demarcated segments (Fig. 5C). Abdomen short, no external segmentation detectable.

Specimens yellowish, translucent. Inside cepha-

lothorax, two round structures, slightly pink. Ducts run from round structures in cephalothorax over lateral outgrowths into abdomen. Whitish network of ramified ducts shining through integument on ventral side of cephalothorax (Fig. 5A,B).

Cephalic appendages as in female (see Fig. 5D,E). Maxilla with broad base, extending to slender sickle-shaped ramus (Fig. 5F).

First thoracopod absent. Second (Fig. 6A) thoracopod with biramous exopod, one slender and shorter ramus with pointed tip; second ramus long, stronger and blunt, near base one pinnate seta. Endopod spinous, situated closer to body midline. Third thoracopod (Fig. 6B) arising from a small fold. Exopod biramous; one broad and blunt ramus and one slender, longer ramus with two pointed elements at apex; long seta with pointed tip at base. Endopod with apical spine. Fourth thoracopod represented by single minute seta (Fig. 6C). No further thoracopods detected.

First abdominal segment bearing slit-shaped genital openings (Fig. 6D). Genital lobes, each armed with two spinous setae (Fig. 6E). No further segmentation externally detectable. Caudal rami globular, small; each ramus with at least three short and pointed setae at apex (Fig. 6F).

Biology. In one host specimen two females and one male were found; in the second host specimen one female and one male. The female abdomens were penetrating the host's integument inside the gill circle. The female parasites were situated inside the host's body cavity with their head towards the host's head and with their dorsal side towards the dorsal side of the host. The mouthparts were in touch with the gonad, but were easy to remove during dissection. After removal, a small fold remained in the gonad, but no tissue damage was detected. The lateral processes of female parasites were wrapped around the inner organs of the slugs. Males were located freely in the body cavity, always close to a female.

Remarks. The two female parasites examined show a high resemblance concerning the body size and shape and the length and position of the lateral processes. One specimen possesses a heavy deformation of the first process on the right side (Fig. 3A). In both females, the morphology of mouthparts and thoracopods is very similar. The homology of the thoracopod herein described as the fourth is questionable because of the unclear segmentation of the thorax. The reddish colouration of parts of the thorax and the head probably results from the host's gonad, which was lilac coloured (in preserved condition). Male parasites are similar concerning the

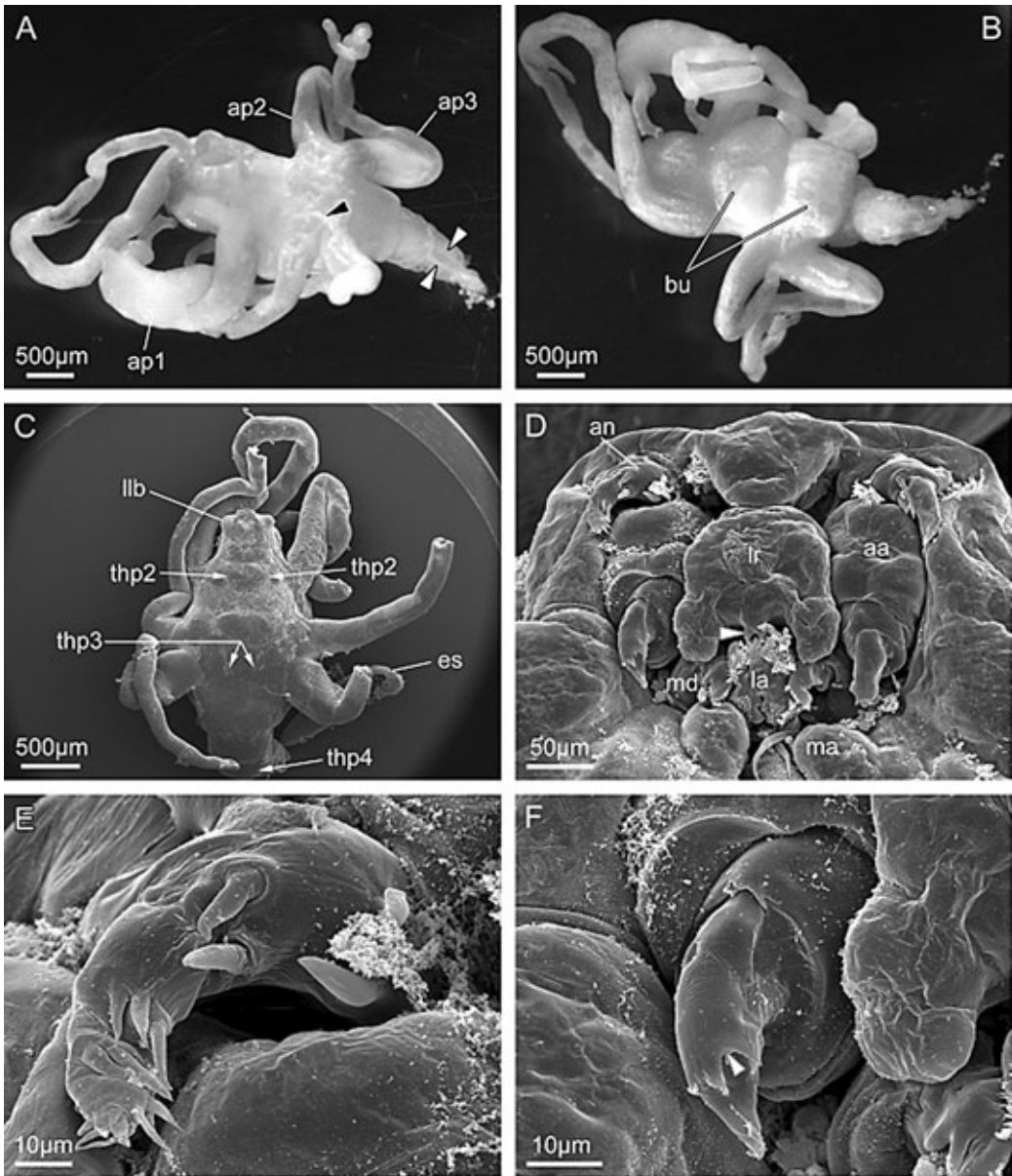


Fig. 3. *Ceratosomicola coia* spec. nov., ♀. **A,B.** light microscope pictures. **A.** Habitus, ventral view (female I). Rows of eggs shining through tissue (white arrows). Oviducts (black arrow). Deformation of ap1. **B.** Habitus, dorsal view (female I). Dorsal bulges. **C-F.** SEM-micrographs. **C.** Habitus, ventral view (female II) with position of thoracopods. **D.** Cephalic appendages. **E.** Antennule (right). **F.** Antenna (right). Hole on third segment (arrow). – aa, antenna; an, antennule; ap1-3, appendage 1-3; bu, bulges; es, egg sac; la, labium; llb, lateral lobe; lr, labrum; md, mandible; ma, maxilla; thp2-4, thoracopods 2-4.

mouthparts and the body shape, but the exact number of thorax segments could not be established. Marked sexual dimorphism exists regarding the body size and shape. There is little morphological

variation in cephalic appendages among the sexes, though slight differences exist in the number and position of hairs and processes of mandible and labium. Specimens of both sexes had a very delicate

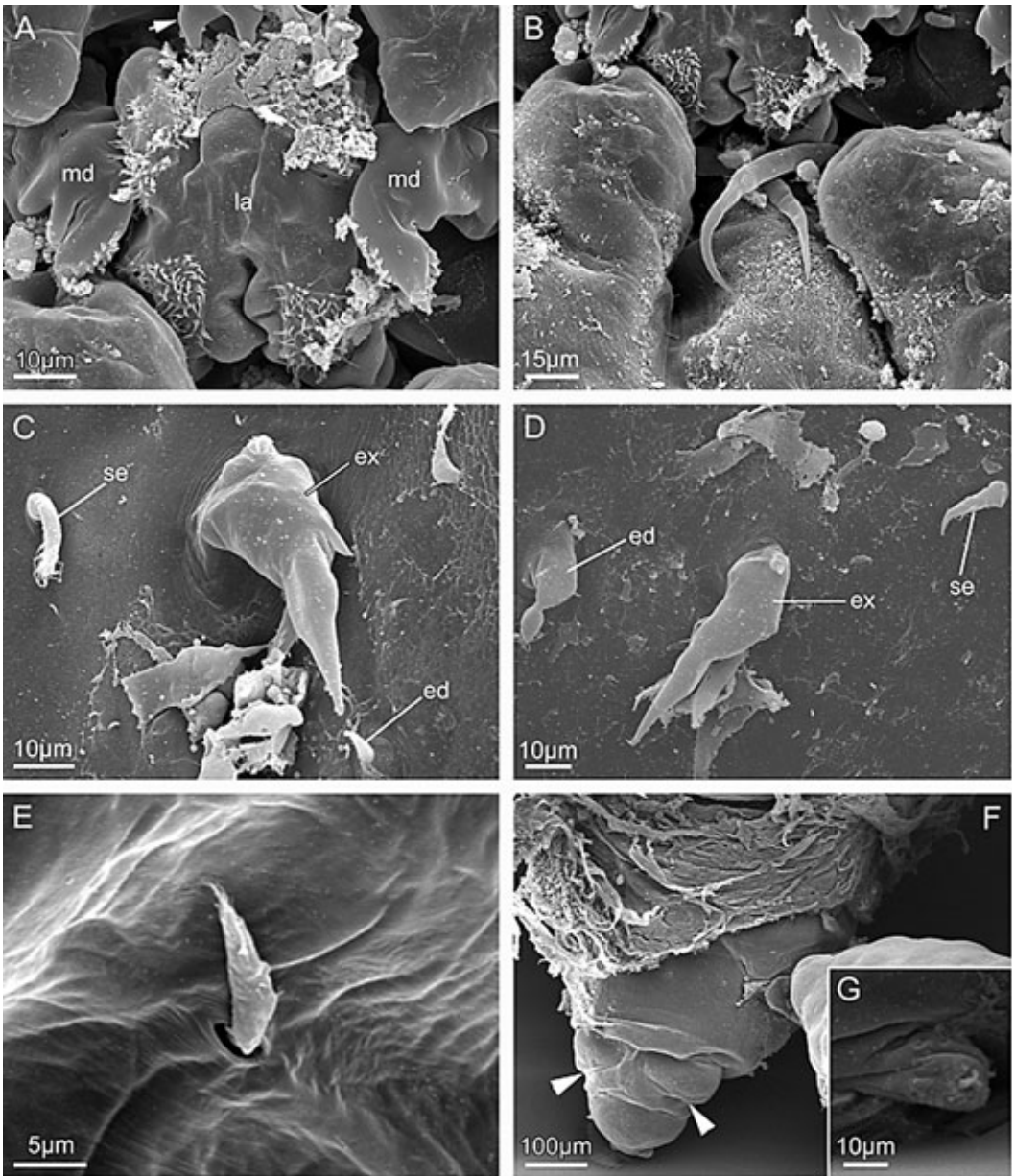


Fig. 4. *Ceratosomicola coia* spec. nov., ♀. SEM-micrographs. **A.** Mandible blades, labium, “U-shaped” process of labrum (arrow). **B.** Maxillae. **C.** Second thoracopod (right). **D.** Third thoracopod (left). **E.** Fourth thoracopod (left). **F.** Abdomen. Second segment with lateral constrictions (arrows). **G.** Caudal ramus (left). – **ed**, endopod; **ex**, exopod; **la**, labium; **ma**, maxilla; **md**, mandible; **se**, seta.

cuticle, which was sensitive to contact.

The specimens examined belong to the genus *Ceratosomicola*, due to their special thoracopod morphology, the position and shape of the lateral processes, the dorsal bulges, the absence of the maxillule

and the shape of the mouthparts (see Huys, 2001).

The only species known so far is *Ceratosomicola sacculata* (O’Donoghue, 1924), which was redescribed by Huys (2001; female, male unknown). Both species, *Ceratosomicola coia* spec. nov. and *C. sacculata*, are

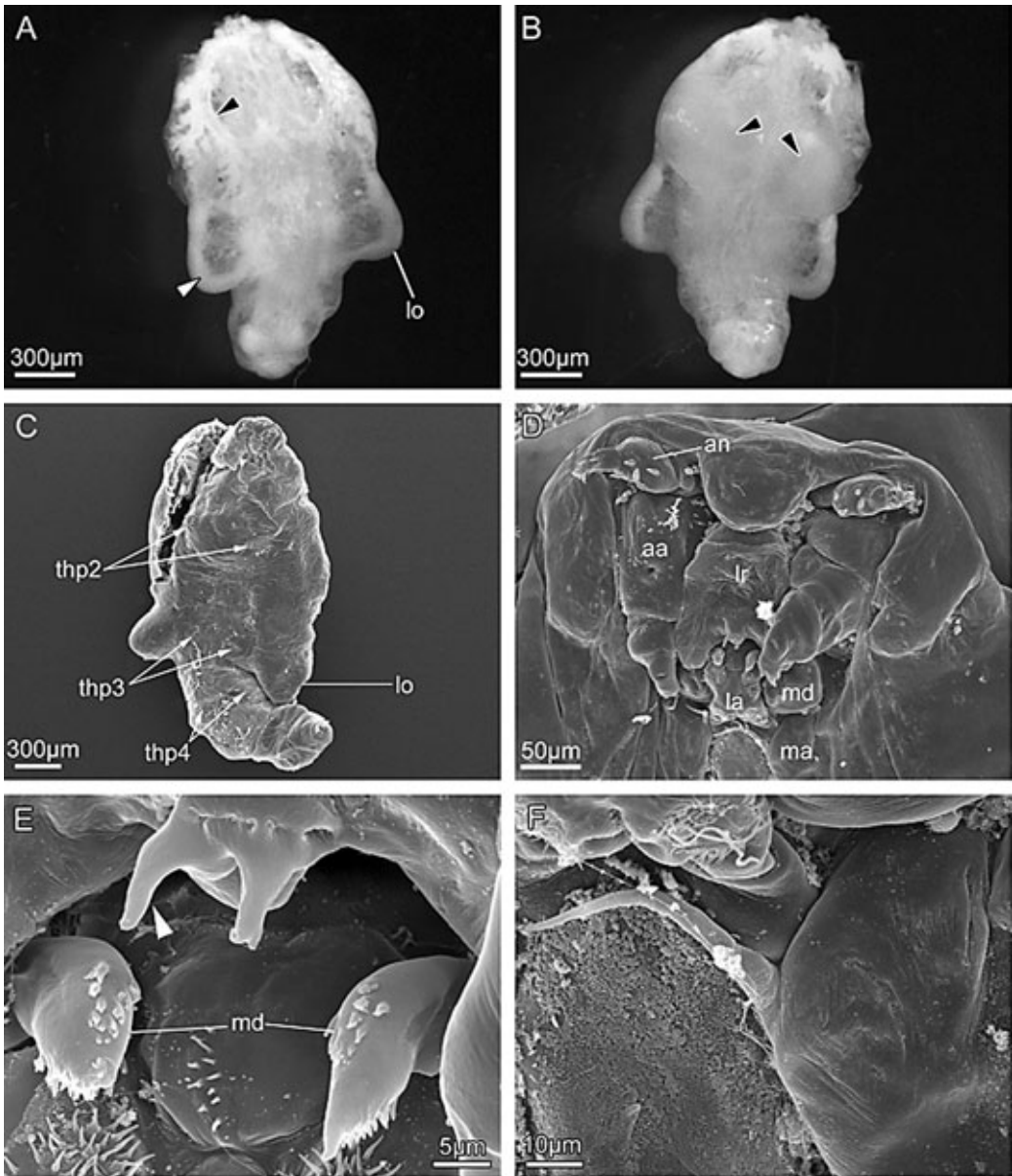


Fig. 5. *Ceratosomicola coia* spec. nov., ♂. **A,B.** light microscope pictures. **A.** Habitus (male I), ventral view. Networks (white arrow), and ducts shining through cuticle (black arrow) in lateral outgrowth. **B.** Habitus (male I), dorsal view. Round structures (black arrows) shining through cuticle. **C-F.** SEM-micrographs. **C.** Habitus, ventral view (male II). Position of thoracopods. **D.** Cephalic appendages. **E.** Oral area. Labium, mandible blades, inverted “U-shaped” process (arrow). **F.** Maxilla (left). – aa, antenna; an, antennule; la, labium; lo, lateral outgrowth; lr, labrum; ma, maxilla; md, mandible; thp2-4, thoracopods 2-4.

similar concerning the shape of the thorax, the shape and position of the lateral processes and the shape of the abdomen and egg sacs. The new species can be distinguished from *C. sacculata* due to differ-

ences in the morphology of cephalic appendages and thoracopods (see Tab. 1). *Ceratosomicola coia* spec. nov. has a hole on the third segment of the antenna, which was not mentioned from *C. sacculata* (see

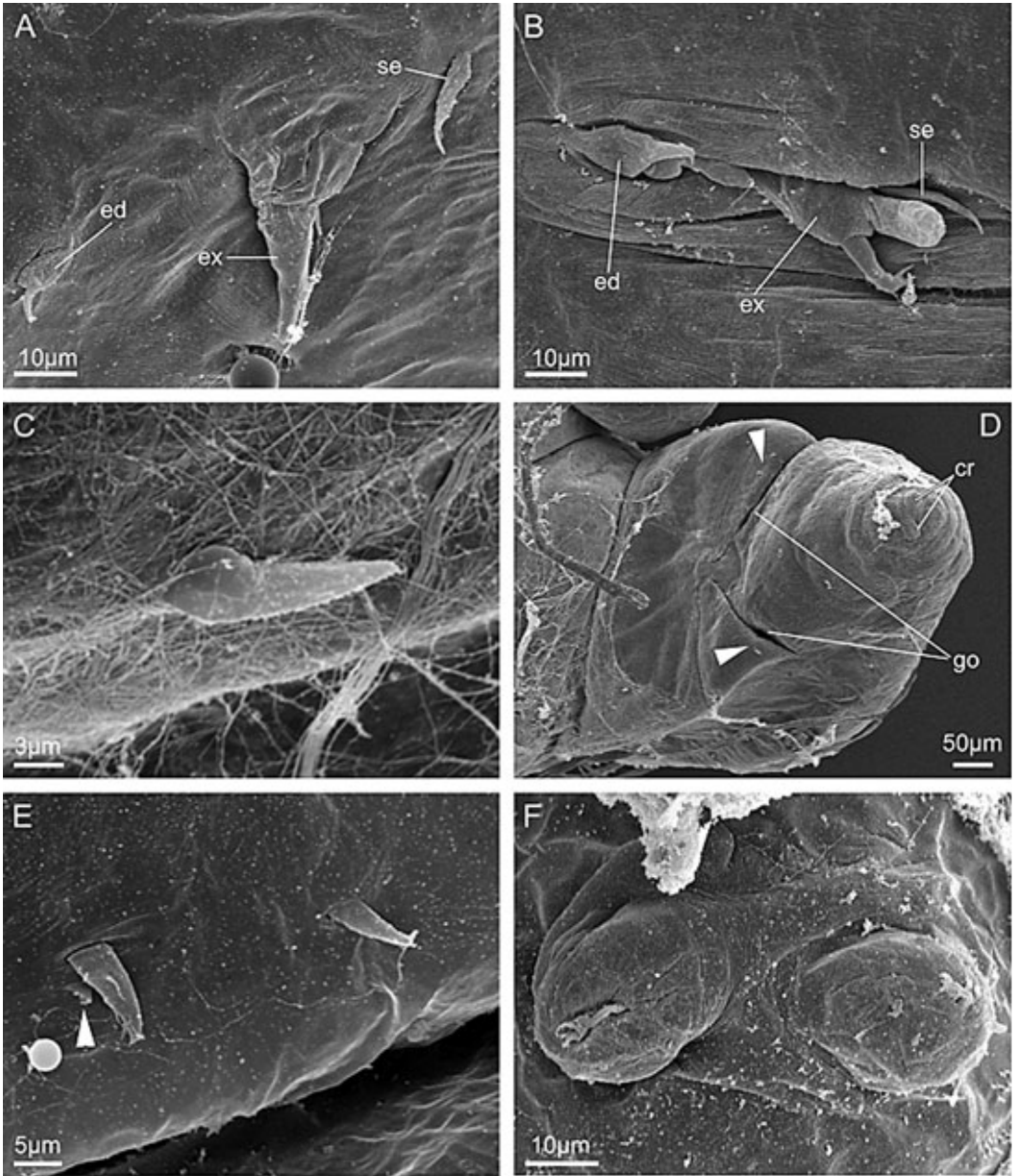


Fig. 6. *Ceratosomicola coia* spec. nov., ♂. SEM-micrographs. **A.** 2nd thoracopod (left). **B.** 3rd thoracopod (left). **C.** 4th thoracopod (left). **D.** Abdomen. Arrows indicating position of setae. **E.** Setae on genital lobes (left), note minute 3rd one (arrow). **F.** Caudal rami. – cr, caudal rami; ed, endopod; ex, exopod; go, genital opening; se, seta.

Huys, 2001). Further, more significant differences refer to the labrum bearing a small inverted “U”-shaped process at the posterior edge, and the labium having a vertical situated, zig-zag-shaped slit (Fig. 4A). Both features, process and slit, were not described for *C. sacculata* by Huys (2001).

In females of both species, the endopod and exopod of the second and third thoracopod (“leg 1 and 2” according to Huys, 2001) arise from separate bases. In *C. coia* spec. nov. the exopod is biramous, while in *C. sacculata* it is uniramous. Exo- and endopod of the fourth thoracopod of *C. sacculata* are

separated (Huys, 2001), whereas in *C. coia* spec. nov. this thoracopod is represented by a single pinnate, seta-like process. Furthermore, *C. sacculata* has an additional pair of thoracopods ("leg 4" according to Huys, 2001), that is absent in *C. coia* spec. nov..

The slender part of the females thorax tapers constantly from the enlarged segments to the abdomen in *C. coia* spec. nov. (see Figs 3A-C), while in *C. sacculata* Huys (2001, p: 131) describes this part as "... inverted pear-shaped, swollen anteriorly ...". The enlarged part of the thorax bears three transversal bulges in *C. sacculata* (Huys, 2001), but only two in *C. coia* spec. nov. Living specimens of *C. sacculata* and *C. coia* spec. nov. differ also by the colouration of their egg sacs, which are "golden yellow" coloured in *C. sacculata* (O'Donoghue, 1924), while those of *C. coia* spec. nov. are orange (Fig. 1A).

Ceratosomicola sacculata was found in the host *Ceratosoma brevicaudatum* Abraham, 1876 (O'Donoghue, 1924), and *Ceratosomicola coia* spec. nov. in *Chromodoris coi* Risbec, 1956. Both host species belong to the same nudibranch family, the Chromodorididae.

Due to the reasons mentioned above, morphological differences, egg sac colour and different host species, *C. coia* spec. nov. is regarded as a new species of the genus *Ceratosomicola*. A comparison of *C. coia* spec. nov., *C. sacculata* and two further species described herein is given in Tabs 1 and 2.

***Ceratosomicola delicata* spec. nov.**
(Figs 7-10)

Material. Holotype (SEM mounted ♀, ZSM 20060216), 1 paratype (SEM mounted ♂, ZSM 20060216), both partly damaged, collected by Nerida Wilson, Kaledupa double spur, Palau Kaledupa, Tukangbesi archipelago, southeast Sulawesi, Indonesia 05°28'26"S, 123°43'46" E, 27 June 2002. Host: *Chromodoris geometrica* Risbec, 1928 (ZSM Mol 20060066). 1♀, 1♂ examined by SEM.

Etymology. The specific name refers to the sensitive cuticle of these parasites, which was easily damaged during dissection.

Description

Female. Body length 2.1 mm. Body elongate. Cephalothorax (head plus first thoracic segment) indistinctly set off from partly segmented thorax. Enlarged, unsegmented part of thorax with three pairs of lateral processes (partly damaged). Abdomen short.

Parasites whitish, slightly pink; lateral processes translucent. Strings of eggs shining through integument, forming a network in anterior part of thorax and distal part of processes. Eggs lilac-coloured on

left side of thorax ventrally (see Fig. 7A,B,C).

Cephalic appendages situated on a fold of cephalothorax ventrally (Fig. 7C). Antennule (Fig. 7D,E) 3-segmented, short and unbranched; first segment inflated with four strong spines, second segment with two small setae, third segment with at least four short setae at apex. Antenna (Fig. 7D) 3-segmented, unbranched; first segment enlarged and unarmed, second segment with one small spine proximally, third segment with five short spines, distal part drawn out into claw. Labrum (Fig. 7D) well developed, bilobate. Mandible (Fig. 7D,F) with thick and broad base tapering into recurved blade with long, pointed tip; blade bearing several short dentiform processes on both sides. Maxillule not detected. Maxilla (Fig. 7D,F) 2-segmented; first basal segment swollen, unarmed; second segment slender, with pointed tip; connection between first and second segment not visible. Labium (Fig. 7D,F) asymmetrical, right side large with hairy patch, left side thin without hairs; deep vertical slit at posterior edge.

First thoracopod (maxilliped) absent. Second thoracopod consisting of three separated elements, exopod, endopod and outer pinnate seta, situated at level of fist process, above an integumental pore (Fig. 8A,B). Exopod biramous, with swollen base; both rami of same length and with pointed tip, one ramus more slender. Endopod spinous element. Third thoracopod comprises three elements, situated at level of posterior edge of third process (Fig. 8A). Exopod uniramous, with two apical, claw-shaped elements; near base one outer seta. Endopod rudimentary, seta-like (Fig. 8C). No further thoracopods detected.

Enlarged second and third segment of thorax with three pairs of lateral processes (Fig. 7C). Processes are at least as long as body (probably longer, but damaged). Bases of second and third processes fused. Dorsal side of thorax with two transversal bulges. Slender part of thorax consists of two, externally visible segments.

Abdomen 3-segmented, first segment bearing genital openings (Fig. 8D), third segment damaged. Egg sacs pink coloured and club-shaped in living animal (see Fig. 1B).

Male. Body pear-shaped (Fig. 9C), measuring 0.74 mm in length (probably longer, abdomen bent). Cephalothorax consists of head and thoracic segments one to three; second and third thoracic segments enlarged; third segment with lateral outgrowths. Following thorax- and abdomen-segments not detectable (thorax bent).

Parasite slightly pink, translucent (Figs 9A,B). Two white patches situated at posterior edge of cephalothorax shining through integument. Enlarged

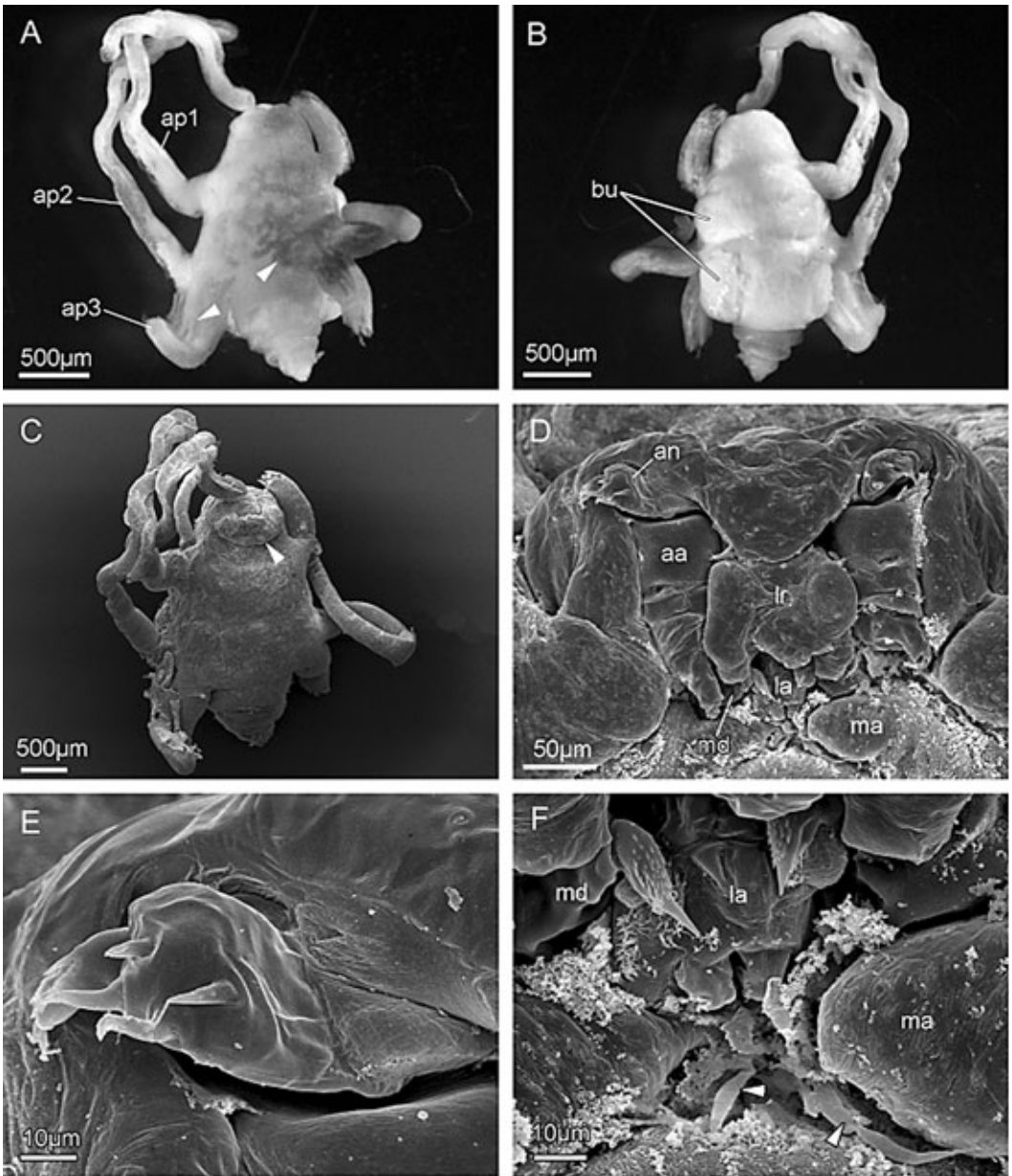


Fig. 7. *Ceratosomicola delicata* spec. nov., ♀. **A,B.** light microscope pictures. **A.** Habitus, ventral view. Rows of eggs shining through tissue (arrows). **B.** Habitus, dorsal view. Dorsal bulges. **C-F.** SEM-micrographs. **C.** Habitus, ventral view. Fold of cephalothorax (arrow). **D.** Cephalic appendages. **E.** Antennule (right). **F.** Oral area, with mandibles, labium, maxillae (second segments marked by arrows). – aa, antenna; an, antennule; ap1-3, appendage 1-3; bu, bulges; la, labium; lr, labrum; md, mandible; mx, maxillule.

segments dorsally with two swellings, tissue shining through right one (Fig. 9B). Whitish ducts running through lateral outgrowth into abdomen.

Cephalic appendages as in female (Fig. 9D).

Labium symmetrically, hairs not distinctly visible (covered by dirt) (Fig. 9E). Maxillule (Fig. 9E) 2-segmented, first segment swollen, second segment slender, tapering into pointed tip.

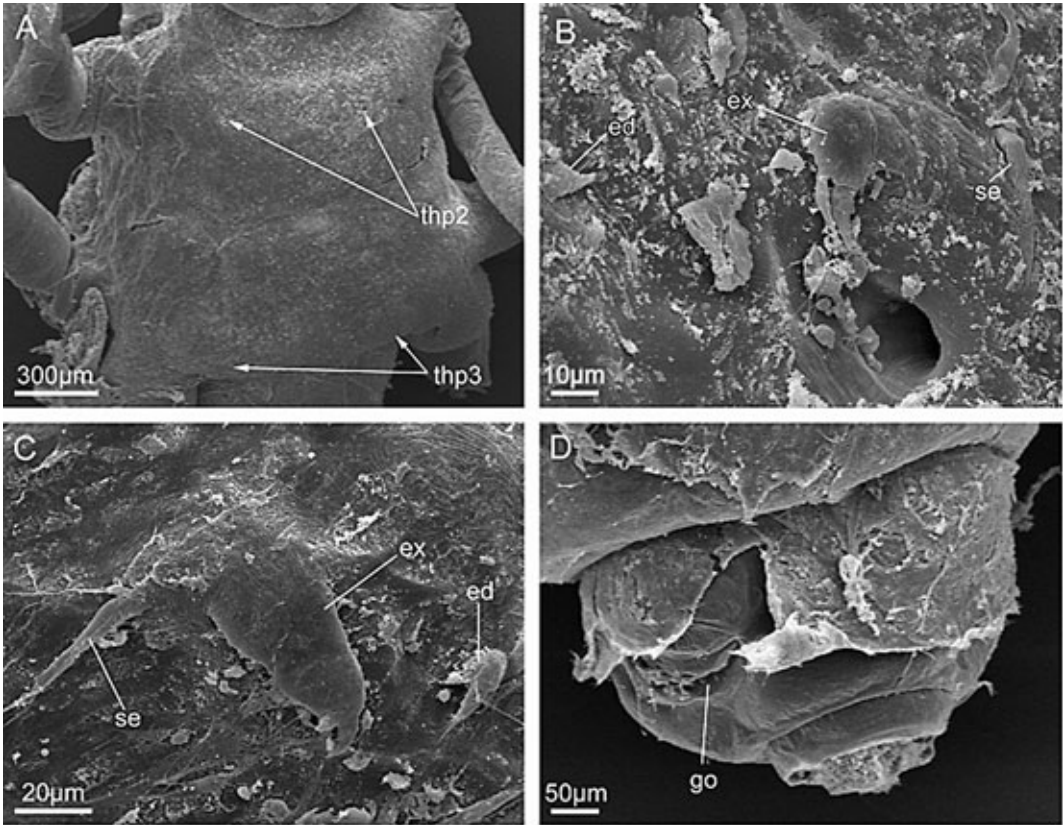


Fig. 8. *Ceratosomicola delicata* spec. nov., ♀. SEM-micrographs. **A.** Habitus, ventral view. Position of thoracopods 2-3. **B.** 2nd thoracopod (left). **C.** 3rd thoracopod (right). **D.** Abdomen. – ed, endopod; ex, exopod; go, genital opening; se, seta; thp2-3, thoracopods 2-3.

First thoracopod absent. Second thoracopod minute (Fig. 9F); exopod biramous, both rami with pointed tip, shorter ramus more slender. Endopod a pinnate basal seta. Third thoracopod minute (Fig. 10A); exopod uniramous with one subapical spinous element, basal seta as long as exopod. Endopod a minute, blunt process. Fourth thoracopod not detected. Fifth thoracopod rudimentary spine with basal thorn (Fig. 10B).

Exact number of abdominal segments not detectable (abdomen bent). Three spinous setae, one of them minute (Fig. 10C,D), situated near slit (probably genital opening). Caudal rami globular, small; each ramus with four setae at apex (Fig. 10E).

Biology. The host specimen was infected with one female and one male parasite. The abdomen of the female was protruding through the host's integument inside the gill circle. The head was orientated towards the host's head and the lateral processes

were wrapped around the host's inner organs. The cephalic appendages were in touch with the gonad, but easily to remove. Mouthparts caused no detectable damage on the gonad. The male was lying freely in the body cavity, close to the female's abdomen but not in contact with it. Both sexes had a very delicate cuticle, which was sensitive to contact.

Remarks. The specimens show a marked sexual dimorphism concerning the body size and shape. Regarding the cephalic appendages, morphological variation is marginal. The female's labium is asymmetrical (right side larger and with hairs), whereas the male's labium is symmetrical. Thus, it is likely that the deformation of the female's labium is an individual abnormality. The true nature of the pore close to the second thoracopod of the female is unknown. The position of the male's first abdominal segment is indicated by the three spinous setae (Fig. 10D). The slit nearby probably is a genital opening (compare *Ceratosomicola coia* spec. nov., Fig. 6D).

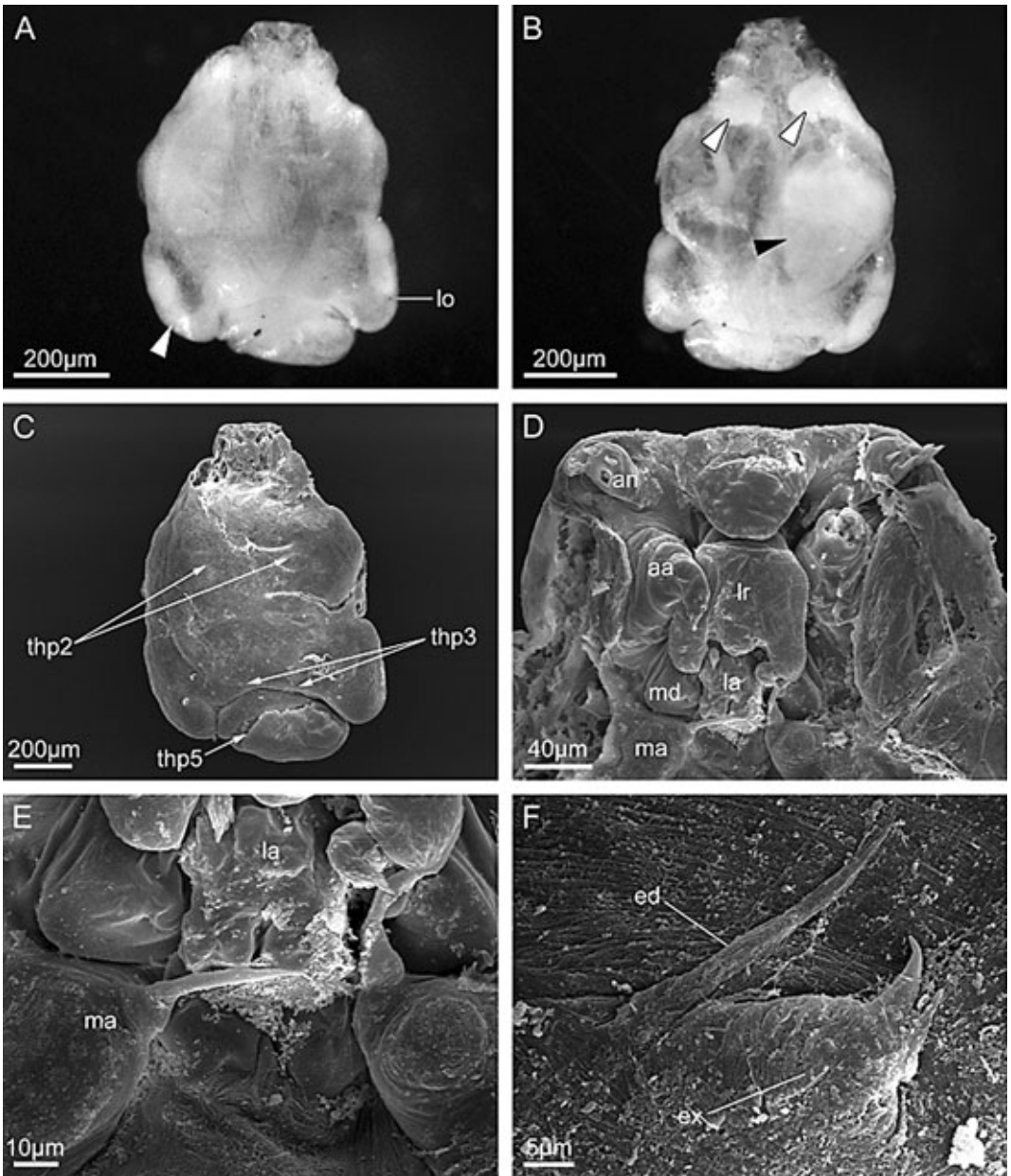


Fig. 9. *Ceratosomicola delicata* spec. nov., ♂. **A,B.** light microscope pictures. **A.** Habitus, ventral view. Ducts shining through cuticle (arrow) in lateral outgrowth. **B.** Habitus, dorsal view. White patches (white arrows) and tissue (black arrow) shining through cuticle. **C-F.** SEM-micrographs. **C.** Habitus, ventral view. Position of thoracopods. **D.** Cephalic appendages. **E.** Oral area. Labium, maxillules. **F.** 2nd thoracopod (right). – aa, antenna; an, antennule; la, labium; lr, labrum; lo, lateral outgrowth; ma, maxilla; md, mandible; ed, endopod; ex, exopod; thp2-3,5, thoracopods 2-3, 5.

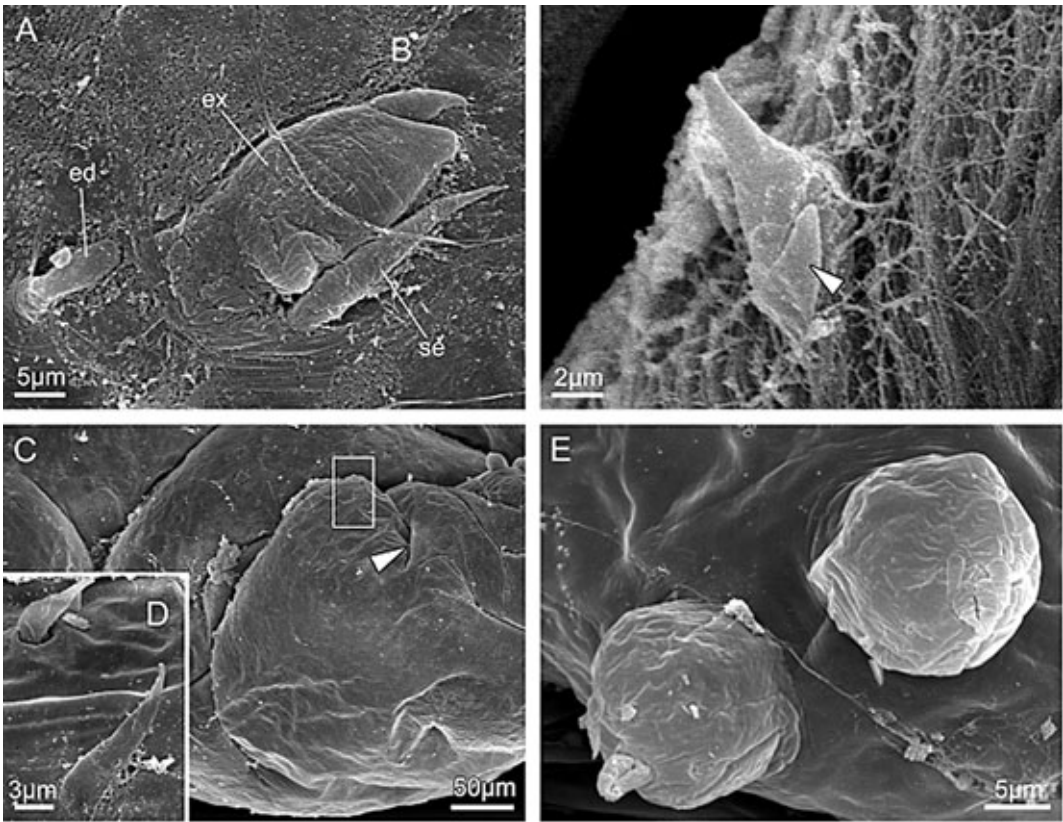


Fig. 10. *Ceratosomicola delicata* spec. nov., ♂. SEM-micrographs. A. 3rd thoracopod (right). B. 5th thoracopod (right). C. Abdomen. Arrow marks constriction or (genital) opening, respectively. D. Two setae, probably on genital lobe. E. Caudal rami. – ed, endopod; ex, exopod; se, seta.

Due to the fact that only one specimen of each sex was found and examined by SEM, nothing can be said about intraspecific variation until more specimens are studied.

The specimens examined belong to the genus *Ceratosomicola*, due to their special thoracopod morphology, the position and shape of the lateral processes, the dorsal bulges, the absence of the maxillule and the shape of the mouthparts (see Huys, 2001). The female of *Ceratosomicola delicata* spec. nov. resembles the females of *C. sacculata* and *C. coia* spec. nov. concerning the body shape, the shape and position of the lateral processes and the shape of the egg sacs. The male of *C. delicata* spec. nov. is similar to males of *C. coia* spec. nov. regarding the body shape, the ducts inside the lateral outgrowth and the shape of the cephalic appendages.

In contrast to the other species, the female of *C. delicata* spec. nov. has two transversal bulges on the dorsal side of the thorax and none on the ventral

side (Tab. 1). The cephalothorax has no lateral lobes and the cephalic appendages are situated on its ventral side. *Ceratosomicola delicata* spec. nov. has pink coloured egg sacs, while those of congeners are lilac, yellow or orange (Tab. 1). *Ceratosomicola delicata* spec. nov. has a 3-segmented antennule, instead of a 4-segmented one as the other two species. Another difference is the morphology of the second and third thoracopods of both sexes (Tabs. 1,2). Female *C. delicata* spec. nov. may be special in lacking the fourth thoracopod (see Tab. 1), but dirt and tissue covered the area where it could be expected. The male has an additional thoracopod, but due to the unclear thorax segmentation, it is questionable whether this is the fourth or fifth thoracopod.

Ceratosomicola delicata spec. nov. was found in the host species *Chromodoris geometrica*, Risbec, 1928. This species was not known as a host of splanchnotrophids before (see Huys, 2001).

Ceratosomicola mammillata spec. nov.

(Figs 11-14)

Material. Holotype (SEM mounted ♀, ZSM 20060217), 5 paratypes (SEM mounted: 1♀, ZSM 20060218; 1♂, ZSM 20060219; 1♂, ZSM 20060220; wet preserved: 1♀ and 1♂, ZSM 20060221), coral gardens, Palau Hoga, Tukangbesi archipelago, southeast Sulawesi, Indonesia 05°28'29"S, 123°45'40"E, 09.08.2002, host: *Risbecia tryoni* (Garrett, 1873) (ZSM Mol 20060064); 2 paratypes (wet preserved 1♀ and 1♂, ZSM 20060222), buoy 4, Home reef, Palau Hoga, Tukangbesi archipelago, southeast Sulawesi, Indonesia 05°28'29"S, 123°45'40"E, 09.08.2002, host: *Risbecia tryoni* (Garrett, 1873) (ZSM Mol 20060065). All collected by Nerida Wilson. 2♀, 2♂ examined by SEM.

Etymology. The specific name refers to the mammillae-like small bulges on the females ventral side.

Description

Female. Elongate body measuring about 8.5 mm in length (probably longer, body bent). Long cephalothorax (head plus first thoracic segment) with lobate outgrowths distinctly set off from trunk; thorax with enlarged second and third segment and slender posterior part; 3-segmented abdomen short. Most parts of body translucent; ventrally between processes whitish to yellowish and brown coloration. Rows of eggs lying close under cuticle, mainly in thorax and processes. Strong white duct (probably oviduct) inside posterior part of thorax and abdomen (Fig. 11A-C).

Cephalothorax with two pairs of dorsolateral lobate outgrowths in proximal part. Cephalic appendages (Fig. 11D) small compared to body size. Antennule (Fig. 11E) indistinctly 4-segmented; first segment with four short blunt spines; second segment with three small spines and one seta; third segment with two setae; fourth segment with several setae at apex. Antenna (Fig. 11F) 3-segmented, unbranched; first segment enlarged, second segment with one spine; third segment drawn out into strong apical claw, with four spines, one near a hole situated in middle part. Labrum well developed, bilobate. Mandible (Fig. 11G) with broad and thick base, tapering into curved apex demarcated by constriction; apex with several dentiform processes. Maxillule not detectable. Maxilla (Fig. 12A) 2-segmented; segment one enlarged; segment two slender, long and unarmed with pointed tip. Labium trapezeshaped, with hairy patch in each corner and vertical slit between posterior patches.

First thoracopod (maxilliped) absent. Second thoracopod (Figs 12B,C) minute, consisting of three elements with separate bases, exopod, endopod and outer seta. Exopod uniramous, with two strong apical elements and one subapical small spine. Endopod

a spinous and pinnate process. Third thoracopod (Figs 12C) represented by uniramous exopod with minute basal spine, apex with two strong elements; endopod long and pointed, arising from separate base; outer seta with sickle-shaped apex and hairs on middle part. Fourth thoracopod represented by minute seta-like process (Fig. 12D). Thoracopods five and six absent.

Thorax with three pairs of lateral appendages; base of second and third appendage fused. Third pair lying parallel to thorax (Fig. 11C). Appendages about twice as long as whole specimen; short proximal part thicker, longer distal part slender with pointed tip. Several bulges on dorsal and ventral side of thorax. Ventral (see Figs 11A,C): three bulges between first pair of processes, middle one larger than others. One central bulge situated at level of anterior edge of second pair of processes and a second central bulge a bit more posterior. Two small bulges at level of anterior edge of third pair of processes. Dorsal (see Fig. 11B): two bulges posterior of first processes, each with white tissue shining through cuticle and four bulges with common base, situated at level of third process.

Abdomen consisting of three externally detectable segments; first one bearing club-shaped, short egg sacs (Figs 12E), lilac coloured in living animal (Fig. 1C). Third abdominal segment with two globular caudal rami; each bearing several small spines at apex (Fig. 12F).

Male. Body inverted pear-shaped, measuring 1.25-1.7 mm in length. Cephalothorax comprises head and thoracic segments one to three: second and third segment enlarged, latter with lobate lateral outgrowths (Fig. 13A,C). No distinct segmentation visible. Thorax without lateral processes. Integument translucent; two heart-shaped structures shining through on dorsal side of cephalothorax (Fig. 13B) and a whitish duct running from top of each "heart", over lateral outgrowths, into abdomen, ending in two oval, transparent orange sacs (Fig. 13A,B).

Cephalic appendages as in female. Antenna and maxilla covered, no examination possible (Fig. 13D).

First thoracopod absent. Second thoracopod (Fig. 13C,E) small; exopod with pointed tip and one small spine; minute endopod separated with pointed tip; more laterally, a single outer seta. Third thoracopod (Fig. 13C,F) with separated exopod and endopod and long, pinnate outer seta. Exopod uniramous, with one subapical spine; endopod nearly as long as exopod, with pointed tip. Fourth thoracopod rudimentary, seta-like (Figs 13C, 14A). Fifth thoracopod not detected.

Abdominal segmentation not externally detectable. Genital openings with genital lobes, each with

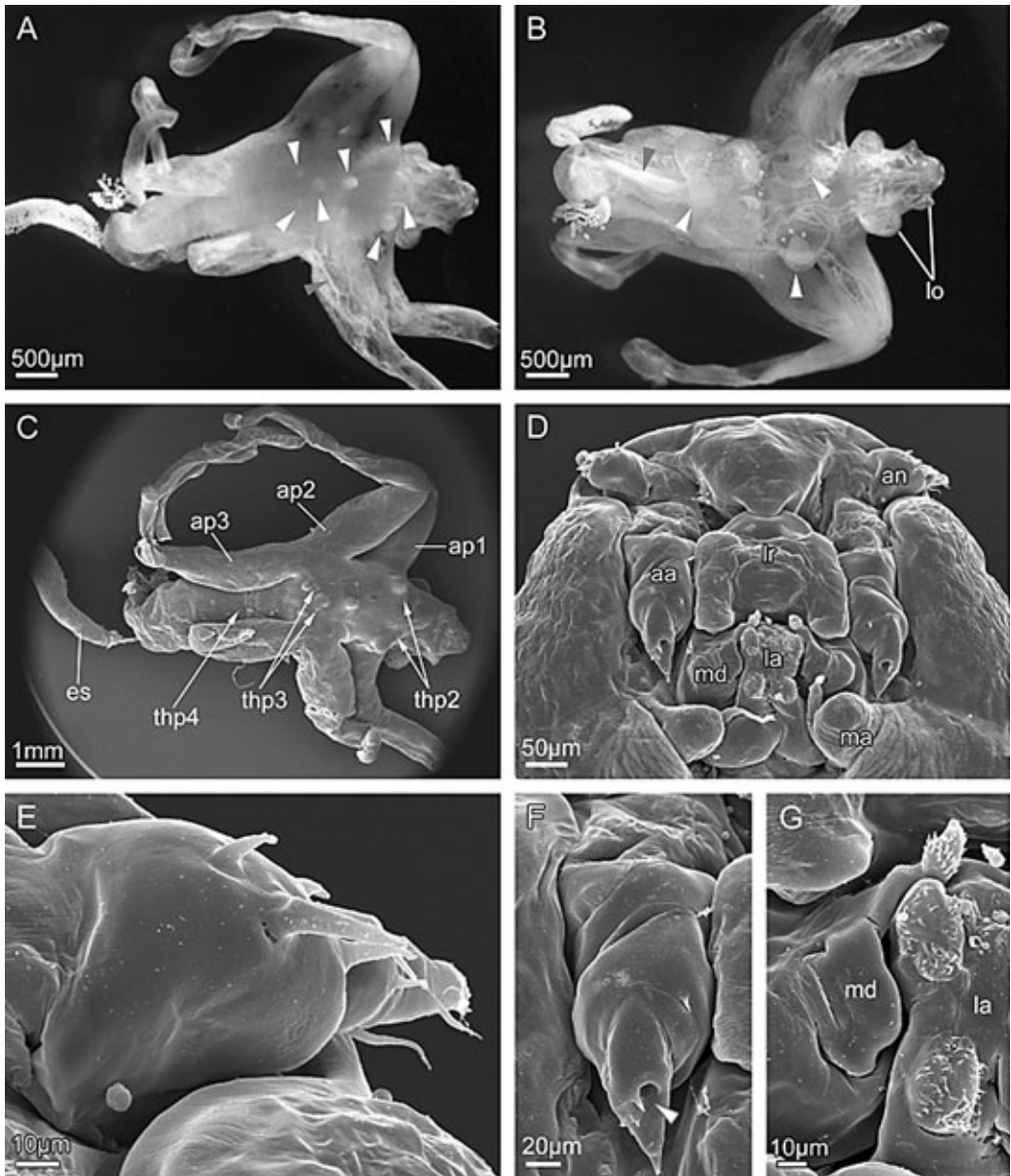


Fig. 11. *Ceratosomicola mammillata* spec. nov., ♀. **A,B.** light microscope pictures. **A.** Habitus, ventral view. White arrows mark ventral bulges. Rows of eggs shining through tissue (dark arrow). **B.** Habitus, dorsal view. White arrows mark dorsal bulges. Oviduct (dark arrow). **C-G.** SEM-micrographs. **C.** Habitus, ventral view. Position of thoracopods 2-4. **D.** Cephalic appendages. **E.** Antennule (left). **F.** Antenna (right). Hole on third segment (arrow). **G.** Mandible (right), right side of labium. – aa, antenna; an, antennule; ap1-3, appendage 1-3; es, egg sac; la, labium; lo, lateral outgrowth; lr, labrum; md, mandible; mx, maxillule; thp2-4, thoracopods 2-4.

three setae, one of them minute (Fig. 14B,C). Caudal rami globular, with four short spines at apex (Fig. 14D).

Biology. Two female and two male parasites were found in one of the hosts. The other two host specimens were each infested by one female and one male parasite. The females were situated inside the hosts

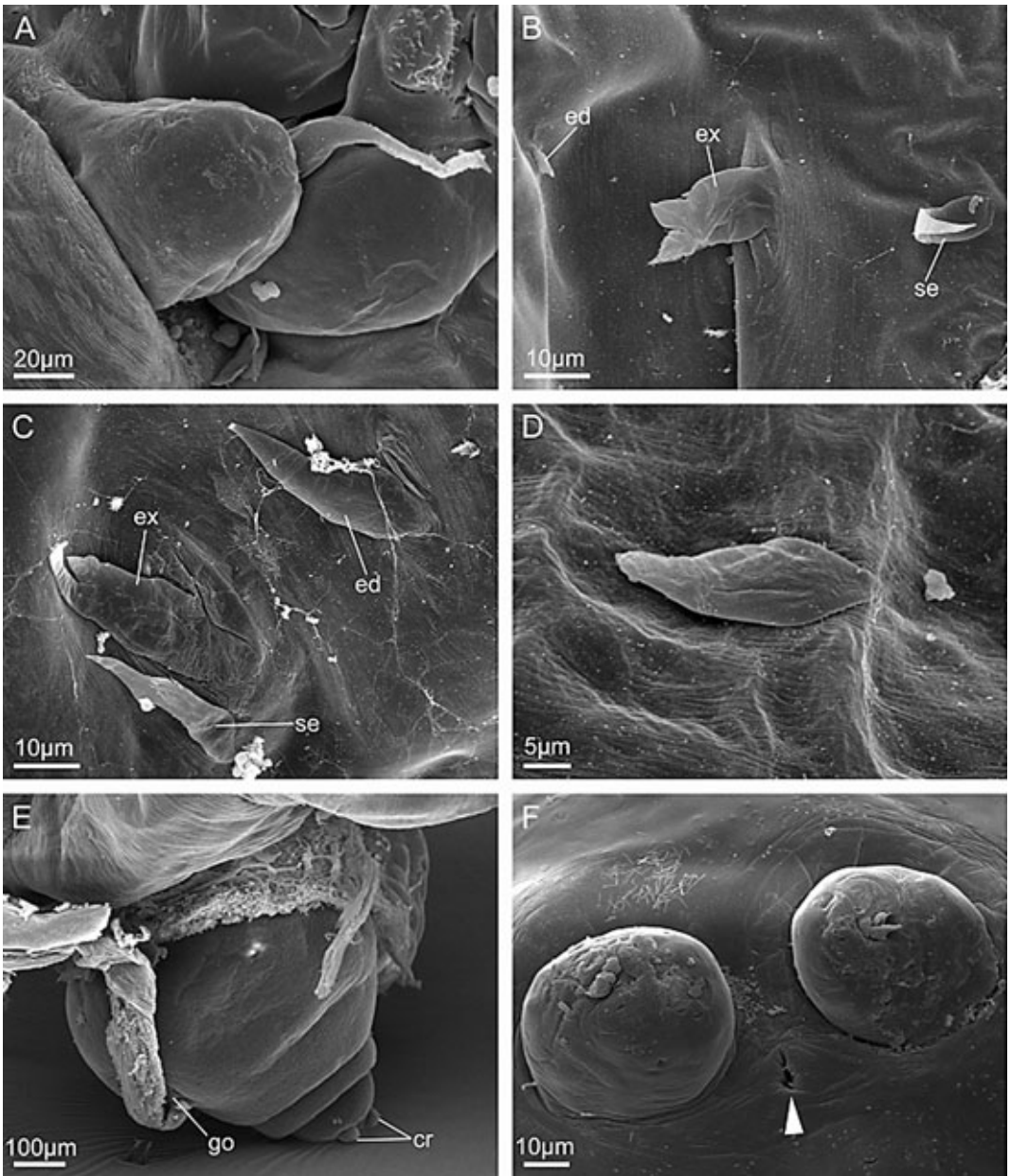


Fig. 12. *Ceratosomicola mammillata* spec. nov., ♀. SEM-micrographs. A. Maxilla (right). B. 2nd thoracopod (left). C. 3rd thoracopod (left). D. 4th thoracopod (left). E. Abdomen. Egg sac envelope attaching genital opening. F. Caudal rami, anal opening (arrow). – cr, caudal rami; ed, endopod; ex, exopod; go, genital opening; se, seta.

with their heads pointing towards the host's head, their abdomens were penetrating the host's integument inside the gill circle. Their mouthparts were in contact with the gonad (which may be the reason for brown and yellowish coloration on the parasites'

ventral side), but were easy to remove. A small fold remained in the gonad, but no damage was detected. The lateral processes were wrapped around the inner organs and embedded within strong connective tissue. Males were lying freely in the body cavity,

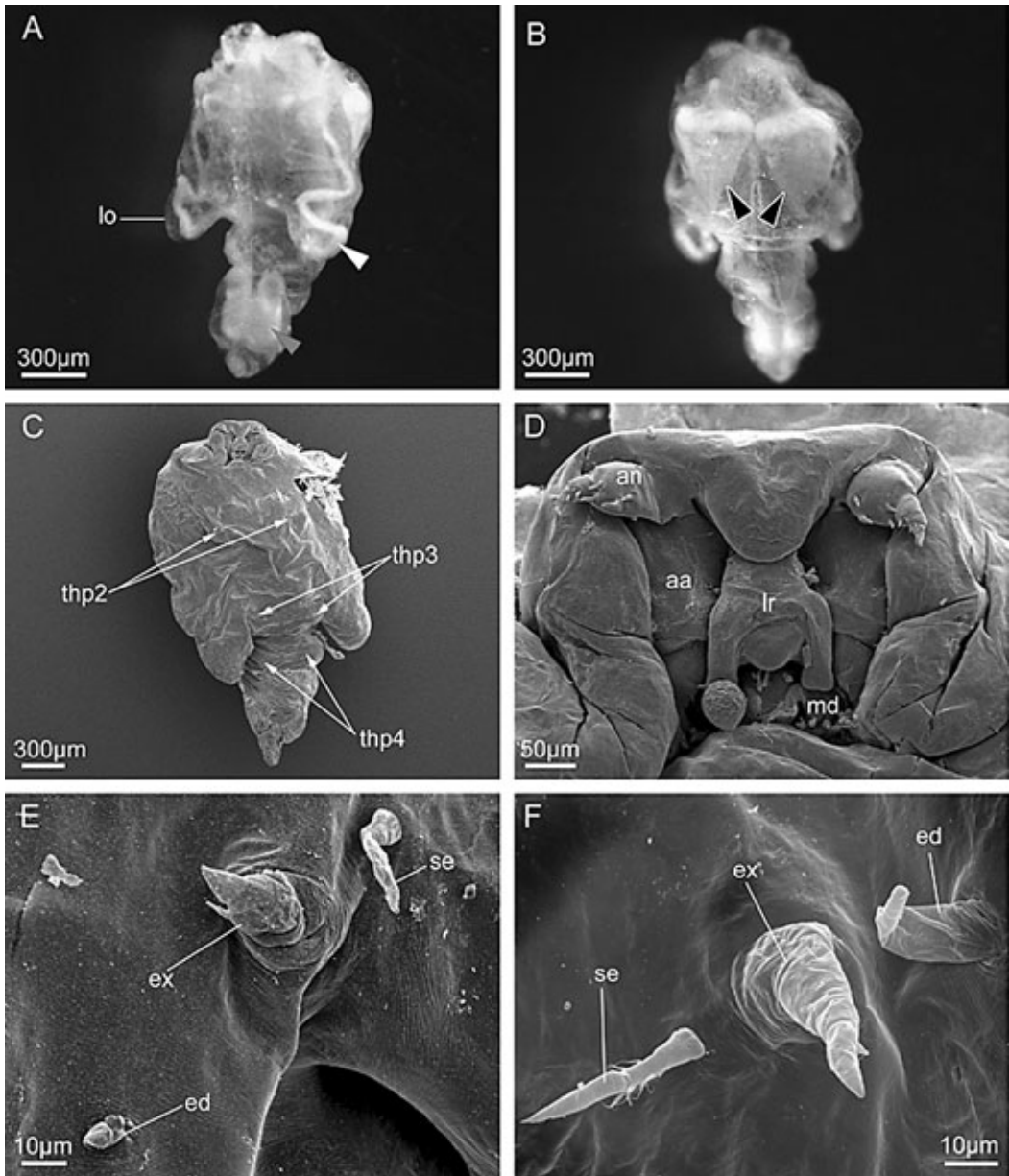


Fig. 13. *Ceratosomicola mammillata* spec. nov., ♂. **A,B.** light microscope pictures. **A.** Habitus, ventral view. White duct running inside lateral outgrowth (white arrow), ending in oval orange structure (dark arrow). **B.** Habitus, dorsal view. Heart-shaped structures shining through cuticle (arrows). **C-F.** SEM-micrographs. **C.** Habitus, ventral view. Position of thoracopods 2-4. **D.** Cephalic appendages. **E.** 2nd thoracopod (left). **F.** 3rd thoracopod (right). – aa, antenna; an, antennule; ed, endopod; ex, exopod; lo, lateral outgrowth; lr, labrum; md, mandible; se, seta; thp2-4, thoracopods 2-4.

two near the females but never in touch. The parasites had a delicate cuticle and so were very sensitive to contact.

Remarks. Within the sexes, the specimens examined resemble each other regarding the morphology of the mouthparts and size and shape of the body. The

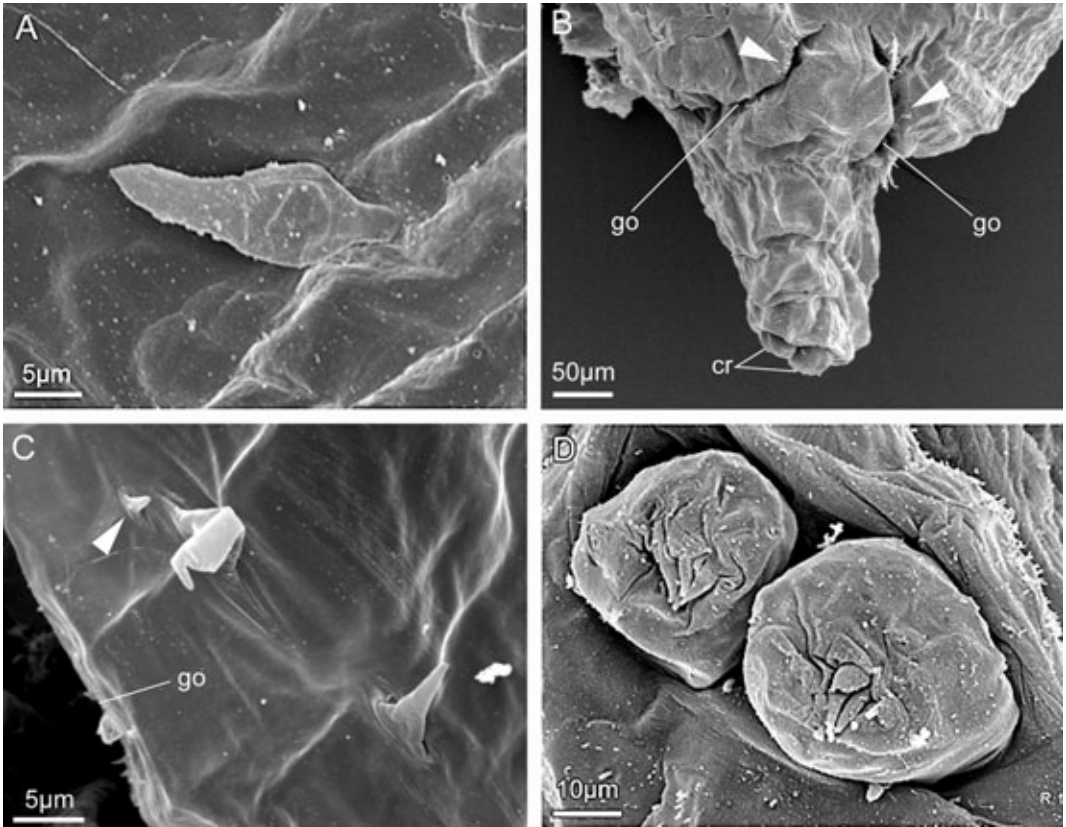


Fig. 14. *Ceratosomicola mammillata* spec. nov., ♂. SEM-micrographs. **A.** 4th thoracopod (right). **B.** Abdomen with genital opening. Setae on genital lobes indicated by arrow. **C.** Setae near genital opening. Note minute spine (arrow). **D.** Caudal rami. – cr, caudal rami; go, genital opening.

females are nearly identical in size and number of the dorsal and ventral bulges. In contrast, the morphology of the thoracopods is very variable in both sexes. Cephalic appendages in both males and females are very similar. *Ceratosomicola mammillata* spec. nov. shows a marked sexual dimorphism, concerning the body size and shape and, apparently, the morphology of thoracopods. The latter could be considered as intraspecific variation until more individuals are examined by SEM.

The present species is undoubtedly congeneric with other *Ceratosomicola* species (Tab. 1). In all four species the females show the same body shape, dorsal bulges on the thorax, very long lateral processes, a 3-segmented abdomen and rudimentary thoracopods. Males correspond concerning the body shape, the ducts running inside the lateral outgrowths and the three setae on the genital lobes.

Females of *C. mammillata* spec. nov. have seven

small bulges on the ventral side, which are not known in such an amount for *Ceratosomicola sacculata* (see Huys, 2001; O'Donoghue, 1924). In the original description of *C. sacculata* (O'Donoghue, 1924) only two pairs of ventrally situated, "rounded papilliform processes" are described. *C. coia* spec. nov. and *C. delicata* spec. nov. completely lack ventral bulges (see Tab. 1). Furthermore, *Ceratosomicola mammillata* spec. nov. differs from its congeners by two anteriorly and four posteriorly situated bulges on the dorsal side of the thorax (see Tab. 1). The cephalothorax has two pairs of lateral outgrowths (Tab. 1). In male, as well as female *C. mammillata* spec. nov. the second and third thoracopod have a uniramous exopod without an outer seta. Furthermore, egg sacs in the living specimens are lilac-coloured (Tab. 1). *Ceratosomicola mammillata* spec. nov. is the only splanchnotrophid species (see Tabs. 1, 2) to occur in the chromodorid host *Risbecia tryoni* Garrett, 1873.

Discussion

External comparison of aberrant and highly modified copepod parasites such as splanchnotrophids essentially depends on a suitable hypothesis on organ homology, i.e. knowledge of body segmentation. Therefore, cephalic and thoracic extremities are herein described and comparatively discussed for splanchnotrophids before comparing gross body shapes and body processes that are not homologous with extremities.

Cephalic appendages. All splanchnotrophids, except species of the genera *Arthurius* and *Ceratosomicola*, possess five pairs of cephalic appendages: antennules, antennae, mandibles, maxillules and maxillae (Huys, 2001; Haumayr & Schrödl, 2003; present study). In the genus *Ceratosomicola* maxillules are lacking. All specimens examined herein show cephalic appendages that correspond in number and shape to the generic diagnoses given by Huys (2001). Within each of the three new species, antennules, antennae and mouthparts of females and males are equal.

The splanchnotrophid antennule is generally 2- or 4-segmented (Huys, 2001; present study). Only *Ceratosomicola delicata* spec. nov. has a unique 3-segmented antennule. Under the SEM, *Ceratosomicola* specimens show a hole on the third segment of the strong and 3-segmented antennae, this was also reported for *Ismaila* and interpreted as opening of an antennal gland (Haumayr & Schrödl, 2003).

In all four *Ceratosomicola* species the labrum is well-developed and bilobate (Huys, 2001; present study). Specimens of *C. coia* spec. nov. have a unique, inverted “U-shaped” process, situated at the posterior margin of the labrum.

Maxillules could not be detected in any female or male *Ceratosomicola* examined herein; it is likely that they are absent in all *Ceratosomicola* species as indicated for *C. sacculata* by Huys (2001).

Thoracopods. First thoracopods (i.e. maxillipeds) were detected in copepodid stages of *Ismaila occulta* Ho, 1981 by Ho (1987), but are always absent in adult *Ceratosomicola* as well as in all other adult splanchnotrophids (e.g. Huys, 2001; Haumayr & Schrödl, 2003). Female *Ceratosomicola* have second and third thoracic segments bearing a pair of (second and third) thoracopods. These thoracopods are rudimentary, consisting of three elements (endopod, exopod and seta) arising from separate bases. The fourth thoracopods of the three new species examined herein are uniramous and rudimentary (present study), while those of *C. sacculata*, according to Huys (2001) are separated in endo- and exopod. Amongst splanchnotrophids, female *Ceratosomicola* are unique in having highly reduced thoracopods consisting of



Fig. 15. Geographical distribution of the genus *Ceratosomicola* (● data from Huys, 2001; ◆ new records from this study)..

three separated elements (at most), and thus are suitable distinguishing characters between the genera. On the other hand, this obvious reduction leads to a high morphological variation of second and third thoracopods within the females of *Ceratosomicola* species (see Tab. 1). The taxonomic significance of thoracopod characters amongst *Ceratosomicola* species needs to be confirmed.

All male *Ceratosomicola* bear one pair of thoracopods on the second and third thoracic segment; these are rudimentary and consist of three elements (as in females). Male *Ceratosomicola* possess two or three setae close to the genital openings (Huys, 2001; present study), but it seems that they are situated on the first abdominal segment, and thus they are not homologous to thoracic legs.

Body shape and processes. The three new *Ceratosomicola* species show a strong sexual dimorphism regarding the size and shape of the body. Therefore, sexes are discussed separately.

Female. Female *Ceratosomicola* have five head segments, each characterised by bearing one pair of extremities (Huys, 2001; present study). The first thoracic segment is supposed to be fused to the head, together building the cephalothorax; maxillipeds have never been detected.

The second and third thoracic segments are enlarged and bear three pairs of processes located laterally, which may be about twice as long as the whole body. In females only three distinct thoracic segments could be detected (Figs 3C, 7C, 11C). The abdomen of *Ceratosomicola* is 3-segmented, the caudal rami on the third abdominal segment are globular with several small setae at the apex.

The egg sacs of the three new species consist of one straight lobe per sac and are of lilac, orange or pink colour in living specimens.

Male. The body of male *Ceratosomicola* is pear-shaped. Males have five head segments, each characterised by one pair of extremities; two or three thoracic segments are fused to the head building the cephalothorax (Huys, 2001). The cephalothorax of adult males is strongly enlarged on the dorsal side. Additionally, specimens have lateral outgrowths at the posterior edge of the cephalothorax (third segment). The exact number of thoracic and abdominal segments could not be determined. The globular caudal rami of *Ceratosomicola* stand in contrast to the elongate rami present in all other splanchnotrophid genera (Huys, 2001, Haumayr & Schrödl, 2003).

Taxonomy. Females of the three new *Ceratosomicola* species described herein can be clearly distinguished from the type species *C. sacculata* due to the different number of dorsal bulges, the shape of the posterior thorax, different labrum and labium structures, and by the morphology of their fourth thoracopods (see Tab. 1). However, they all resemble *C. sacculata* regarding features which Huys (2001) considered diagnostic for establishing the genus *Ceratosomicola*, i.e. in having four cephalic appendages (maxillule absent), highly reduced second and third thoracopods consisting of three elements, and globular caudal rami. These features are unique at least within Splanchnotrophidae and most probably are autapomorphies which support the monophyly and, thus, the validity of the formerly monotypic genus *Ceratosomicola*. Our findings show a radiation of quite similar *Ceratosomicola* species has taken place.

Occurrence. Until now, the genus *Ceratosomicola* was represented only by the type species *Ceratosomicola sacculata* (O'Donoghue, 1924). Its only known host species *Ceratosoma brevicaudatum* occurs from southern Western Australia along the southern Australian coast north to northern New South Wales, but the parasite was only found at the western Australian coast (Huys 2001). Herein, three new species from further tropical Indo-Pacific localities could be added. The geographical distribution of *Ceratosomicola* thus covers a wider range (Fig. 15). Additionally, one new host species could be established for each of the newly described *Ceratosomicola* species; *Chromodoris coi* for *C. coia* spec. nov., *Chromodoris geometrica* for *C. delicata* spec. nov., and *Risbecia tryoni* for *C. mammillata* spec. nov. With present knowledge, *Ceratosomicola* species appear strictly host specific. The radiation of *Ceratosomicola* species thus apparently was related to different hosts of the nudibranch family Chromodorididae, and probably has occurred in the area within and south of the Indonesian archipelagos. Since both nudibranch hosts and parasites usually have pelagic larval stages with high dispersal capacity, we can

Tab. 1. Comparison of *Ceratosomicola* species (females).

Species	<i>Ceratosomicola sacculata</i> O'Donoghue (1924)
Data source	Huys (2001)/O'Donoghue (1924)
Host	<i>Ceratosoma brevicaudatum</i> Abraham, 1876
Locality	Houtman Abrolhos Islands, Western Australia
Colour of egg sacs	golden yellow
Shape of posterior thorax	swollen posteriorly
Cephalothorax	trilobate (2 pairs of lateral lobes)
Dorsal bulges	3, transversally
Vental bulges	4
3rd segment of antenna	without hole
Shape of labrum	bilobate
Shape of labium	paired spinulose lobes anteriorly and posteriorly, no slit
2nd thoracopods	with 1 outer basal seta
Exopod	uniramous, 2 apical elements
Endopod	spinous
3rd thoracopods	with basal seta
Exopod	uniramous, 1 subapical element
Endopod	curved apical element
4th thoracopods	exo- and endopod separated
Exopod	unisetose lobe
Endopod	single seta
5th thoracopods	single basally swollen seta

assume speciation by host switching rather than by divergence through long-lasting geographic separation.

Prevalence. In the tropical Indo-Pacific, the region with the by far highest opisthobranch diversity, only a couple of nudibranch and sacoglossan species were known to host splanchnotrophids, and an infection of only one or very few specimens appeared to be the rule (Huys, 2001; Schrödl, 2002). Obviously, more records of parasites and probably some further undescribed species can be expected from intensified and more focused collectings. In general terms, however, a comparatively low prevalence of infection in the tropical Indo-Pacific is confirmed by this work, where three new species are described, each from one or just a few specimens of three different hosts species which all are relatively abundant in the survey areas as well as throughout the tropical Indo-Pacific. Such scarcity of splanchnotrophid parasites stands in contrast to high splanchnotrophid prevalence in other, usually temperate regions such as central Chile and Europe (Schrödl, 2002).

<i>Ceratosomicola coia</i> spec. nov.	<i>Ceratosomicola delicata</i> spec. nov.	<i>Ceratosomicola mammillata</i> spec. nov.
present study	present study	present study
<i>Chromodoris coi</i> Risbec, 1956	<i>Chromodoris geometrica</i> Risbec, 1928	<i>Risbecia tryoni</i> Garrett, 1873
Tukangbesi archipelago, southeast Sulawesi, Indonesia	Tukangbesi archipelago, southeast Sulawesi, Indonesia	Tukangbesi archipelago, southeast Sulawesi, Indonesia
orange	pink	lilac
slender	slender	slender
1 pair of lateral lobes	no lateral lobes	2 pairs of lateral lobes
2, transversally	2, transversally	2, anteriorly; 4, posteriorly
–	–	7
with hole	?	with hole
bilobate, additional inverted »u«-shaped process	bilobate	bilobate
hairy paragnaths; vertical, zig-zag-shaped slit	hairy paragnaths, vertical slit	trapeze-shaped, hairs in each corner; vertical slit
with 1 outer pinnate seta	without outer seta	with outer seta
biramous, 2 proximal spines spinous	biramous pinnate seta	uniramous, 2 apical elements spinous, minute seta
with 1 pinnate outer seta	with 1 outer seta	outer seta, apex sickle-shaped
biramous, 1 proximal spine spinous	uniramous, 2 apical elements small seta	uniramous, 2 apical elements strong seta
single pinnate seta	not detected	single minute seta
absent	not detected	absent

Tab. 2. Comparison of *Ceratosomicola* species (males; male of *C. sacculata* unknown).

Species	<i>Ceratosomicola coia</i> spec. nov.	<i>Ceratosomicola delicata</i> spec. nov.	<i>Ceratosomicola mammillata</i> spec. nov.
Data source	present study	present study	present study
Host	<i>Chromodoris coi</i> Risbec, 1956	<i>Chromodoris geometrica</i> Risbec, 1928	<i>Risbecia tryoni</i> Garrett, 1873
Locality	Tukangbesi archipelago, southeast Sulawesi, Indonesia	Tukangbesi archipelago, southeast Sulawesi, Indonesia	Tukangbesi archipelago, southeast Sulawesi, Indonesia
Shape of labrum	bilobate, additional inverted "u"-shaped process	bilobate	bilobate
Shape of labium	vertical, zig-zag-shaped slit	vertical slit	vertical slit not detected
2nd thoracopods	with 1 outer pinnate seta	–	with 1 outer seta
Exopod	biramous	biramous	uniramous
Endopod	spinous	pinnate seta	spinous, minute
3rd thoracopods	–	–	outer, pinnate seta
Exopod	biramous, 1 basal seta	uniramous, 1supapical element, long basal seta	uniramous, subapical spine
Endopod	spinous	blunt seta	strong seta
4th thoracopods	not detected	not detected	single seta
5th thoracopods	not detected	rudimentary spine with basal thorn	absent

However, some of the Chilean *Ismaila* species appear to be equally rare, e.g. *I. obtusa* Haumayr & Schrödl, 2003 was found in its large and very common nudibranch host *Archidoris fontaini* (D'Orbigny, 1837) only once, and only 3 out of 243 *Phidiana lottini* (Lesson, 1831) were infected with *I. robusta* Haumayr & Schrödl, 2003. Strikingly, *Ismaila aliena* Haumayr & Schrödl, 2003 shows up to 100 % prevalence of infection in central Chilean *Thecacera darwini*, while no infection was detectable in northern Chilean populations (Schrödl, 2002). This is surprising, since *T. darwini* is an annual rather than an ephemeral host species which was encountered in abundant and stable populations all along the Chilean coast.

Low prevalence of splanchnotrophids in the presence of stable host populations, in the tropics and elsewhere, does not conform either to the present knowledge about splanchnotrophid reproduction. In addition to numerous eggs within the egg sacs, the thorax and major parts of the lateral processes of mature females are completely filled with further, obviously well-developed eggs (e.g. Huys, 2001; Haumayr & Schrödl, 2003; this study). Experiments by Schrödl (1997; unpublished information) showed, that egg sacs of *Ismaila* species are renewed over night after hatching of larvae or after removing egg sacs artificially. *Ismaila* larvae have a free swimming, probably pelagic nauplius stage (Ho, 1987; Schrödl, unpublished information), suggesting a considerable dispersal ability. Therefore, there must be other, still unknown factors in addition to dispersal capacity limiting the prevalence of parasites in certain hosts or regions.

Biology. Biological data on splanchnotrophid copepods are limited to occasional observations, to ontogenetic studies on *Ismaila occulta* by Ho (1987), to Chilean *Ismaila* species, where sex ratios and the parasites' position inside the host were investigated (Schrödl, 2002; Haumayr & Schrödl, 2003), and to recent observations on *Splanchnotrophus willemi* Canu, 1891 by Marshall & Hayward (2006). Interestingly, most male *Splanchnotrophus willemi* and all male *Ceratosomicola* moved freely in the hosts' body cavities, i.e. none of the male *Ceratosomicola* was closely attached to the females. While immature *Ismaila* stages also migrate freely within the hosts, in every host of *Ismaila* at least one mature male is intimately aggregated to the female; abdomens of both, males and females penetrate the body integument of the hosts (Haumayr & Schrödl, 2003). Marshall & Hayward (2006) assumed that males of *S. willemi* have the freedom to move around since there was never more than a single male per female and host, and, thus, no competition for paternity.

Sex ratios seem to be usually 1 also in the new *Ceratosomicola* species, but with up to two females and males per host in *C. mammillae* spec. nov.

Female *Ceratosomicola* are highly specific concerning their position in the host. Their heads were orientated towards the host's heads, and their abdomens always were protruding through the hosts' integument inside the gill circle. In Chilean *Ismaila* species (Schrödl & Haumayr, 1999; Haumayr & Schrödl, 2003), special positions of females show little intraspecific variability but differ between the various parasite and host species involved. Such special positions thus certainly do not occur by chance but are evolutionary adaptations and are likely to be products of co-evolution with their referring hosts. One major point for the parasites is optimizing the space requirements within the anatomically quite different host groups. Maximizing own growth while causing minimum damage to the host would contribute to a longer own lifespan and higher reproductive success. Developing long body appendages that wrap around the still intact and functional host organs, female *Ceratosomicola* reach a large body volume which is obviously needed as space for egg production and storage (as observed by light microscopy). However, the extremely incompact, "papillate" body construction of female *Ceratosomicola* (and most other female splanchnotrophids) also guarantees for a large body surface. Otherwise, obtaining enough oxygen from their hosts' hemolymph might be a problem for larger endoparasites, especially in tropical waters. The very thin body cuticle of female *Ceratosomicola*, in comparison with *Ismaila* and *Splanchnotrophus* species, is herein regarded to be an adaptation to enhance diffusion. If there is a low splanchnotrophid diversity and prevalence in the tropics, this may be at least partly due to problems related with limited oxygen supply.

Splanchnotrophid egg sacs always have direct contact with sea water, but their actual position is almost invariably associated to certain body outgrowths of their respective hosts (Schrödl, 1997, 2002; Haumayr & Schrödl, 2003); e.g. egg sacs may be buried among aeolid cerata, hidden under mantle rim papillae or closely attached to doridoidean gills. Abdomens and egg sacs of female *Ismaila aliena* Haumayr & Schrödl, 2003 usually protrude between the non-retractable gills and the extrabranchial processes of their hosts, the phanerobranch dorid *Thecacera darwini* Provot-Fol, 1950. Like other shell-less opisthobranchs, *T. darwini* most probably possesses deterrent chemical substances; in the field *T. darwini* was observed to be avoided by any kind of potential predators including crustaceans, sea stars and fishes (Schrödl, unpublished information).

Therefore, a protective function of and evolutionary adaptation to special egg sac (and female copepod) positions can be suspected. *Ceratosomicola* egg sacs protrude from inside the gill pocket of their chromodorid cryptobranch hosts which can be fully closed in case of danger. A protective function of that special egg sac and females' position is obvious.

Whether or not the special position of female *Ceratosomicola* is (also?) related to feeding is unclear: heads of all females examined herein were always attached to the gonads of the hosts, however, without any tissue damage detectable during dissection. For similar reasons, *Ismaila* specimens were generally considered to be hemolymph suckers by Haumayr & Schrödl (2003); gonad destruction (or atrophy) that was observed in the small aeolidoidean host *Flabellina* sp. 1 whenever it was infected with *I. damnosa* Haumayr & Schrödl, 2003 (as *Ismaila* sp., see Schrödl, 1997) was interpreted as space competition rather than active tissue feeding. The absence of anal openings in *Ismaila* and *Ceratosomicola*, and the even more reduced mouthparts of *Ceratosomicola* species may indicate they may be likewise peaceable hemolymph suckers as well.

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Buchbesprechung

10. Klaas, P.: Vogelspinnen: Herkunft – Pflege – Arten.
– 3., völlig neu bearbeitete Auflage, Ulmer Verlag,
Stuttgart, 2007, 142 pp., ISBN 978-3-8001-4660-4.

Maria Sibylla Merian (1647–1717) ist durch ihre Darstellungen von Gliedertieren und ihrer Verwandlung (Metamorphose) berühmt geworden. Unter den Kupferstichen, die nach ihrer Reise nach Surinam entstanden, findet sich auch die Darstellung einer großen, haarigen Spinne mit einem von ihr erbeuteten Kolibri. Linné gab der Spinne aufgrund dieser Abbildung den Namen *Aranea avicularia*, d.h. "einem kleinen Vogel ähnlich". Heute nennen wir die ganze Gruppe, zu der die von Merian abgebildete Spinne gehört, Vogelspinnen, und man findet hier auch die Gattung *Avicularia*. Peter Klaas, der mit dem hier besprochenen Werk eine völlig neubearbeitete Auflage seines schon länger sehr erfolgreichen Buches über Vogelspinnen vorlegt, ist der Meinung, dass es sich hier nicht nur um "Zooloogenlatein" handelt, sondern dass Vogelspinnen tatsächlich im Schwirflflug dahinschwebende Kolibris erbeuten könnten.

Wie dem auch sei – Vogelspinnen mit ihrer Größe, ihrer skurrilen Schönheit und Farbigkeit, wie auch ihrem scheinbar gefährlichen Erscheinungsbild, gaben sei jeher Anlass zu Mythen und begeistern seit langem Tierliebhaber auf der ganzen Welt. Mit seinem sachkundigen, paraxisorientierten und mit wunderschönen Fotos dieser

einzigartigen Spinnen garnierten Buch wendet sich der Autor insbesondere an Spinnenfans, die mehr über die Tiere erfahren und sie im Terrarium halten möchten. Der Leser findet kompetente Auskunft über Morphologie, Systematik und Verwandtschaft der Vogelspinnen, ebenso über Ihre Verbreitung und Lebensweise. Dazu kommen ausführliche Kapitel über die Haltung und Zucht in Terrarien. Außerdem findet man Angaben über den Erwerb von Vogelspinnen sowie behördliche Regelungen über den Import, der offenbar nach wie vor in nicht geringem Maße stattfindet. Das Kernstück dieses sehr gelungenen Buches bildet m.E. aber das Kapitel "Ausgesuchte Vogelspinnenarten". Hier werden die wichtigsten Arten aus 40 Gattungen in Form von meist etwa 1-seitigen Steckbriefen vorgestellt. Unter anderem findet man Daten zur Biologie und zur Haltung, sowie sehr gelungene Erläuterungen zur Namensgebung. Das Buch wird durch eine kurze, aber sorgfältig zusammengestellte Bibliographie, eine Artenliste und ein Glossar abgerundet.

Das Buch von Peter Klaas ist jedem Vogelspinnen-Begeisterten, der über die passive Freude des Betrachtens hinaus etwas über seine Spinnen wissen und sie möglichst kompetent und artgerecht halten möchte, unbedingt zu empfehlen.

Roland Melzer