

Coralliotantulus coomansi* gen. et sp.n.: First record of a tantulocaridan (Crustacea: Maxillopoda) from shallow subtidal sands in tropical waters

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Summary

A new genus of Tantulocarida, *Coralliotantulus*, is described based on material from shallow subtidal coralline sand collected in the Great Barrier Reef, Australia. Several stages of development were found attached to the thoracopods and urosome of a female *Longipedia scotti* G.O. Sars (Copepoda, Harpacticoida). The new genus is placed in the Deoterthridae Boxshall & Lincoln on the basis of its larval characters, being the absence of a rostrum, the cephalic pore pattern, the setation on the exopod of thoracopod 1, and the two-segmented abdomen. The trunk sac containing the adult male is formed posterior to the sixth tergite as in *Deoterthron lincolni* (Boxshall) and this position corroborates the earlier removal (Huys, in press a) of the isopod-infesting species from the genus *Deoterthron* Bradford & Hewitt and the subsequent establishment of the family Doryphallophoridae Huys. The morphology of the male abdomen and penis is unique and might be typical for the Deoterthridae. Significant differences between *C. coomansi* and other known males are also found in the number of aesthetascs on the cephalothorax, and the morphology and ornamentation of the thoracopods. *C. coomansi* is the fifth tantulocaridan to be reported from the Australian zoogeographical province.

Résumé

Coralliotantulus, un nouveau genre de Tantulocarida, est décrit à partir de matériel provenant de sable sublittoral peu profond de la Grande Barrière, Australie. Plusieurs stades de développement ont été trouvés attachés aux thoracopodes et à l'urosome d'une femelle de *Longipedia scotti* G.O. Sars (Copepoda, Harpacticoida). Les caractéristiques des larves: absence d'un rostre, patron des pores céphaliques, soies sur l'exopodite du thoraco-

pode 1 et abdomen bisegmenté, classent ce nouveau genre dans la famille des Deoterthridae. Le sac thoracal contenant le mâle adulte est formé postérieurement au tergite 6, comme chez *Deoterthron lincolni* (Boxshall). Cette position confirme le transfert des espèces du genre *Deoterthron* Bradford & Hewitt, infestant les Isopodes, dans une nouvelle famille, les Doryphallophoridae Huys. La morphologie de l'abdomen mâle et du pénis sont uniques et pourraient être typiques pour les Deoterthridae. Le mâle de l'espèce-type *C. coomansi* diffère des mâles connus, par le nombre des aesthetasques sur le céphalothorax, et par la morphologie et l'ornementation des thoracopodes. *C. coomansi* est le cinquième Tantulocaride décrit de la région zoogéographique australienne.

Introduction

Copepods infest a variety of invertebrates, as well as fishes. Using Humes (1985) as a yardstick it was found that about 180 species are known as symbionts (i.e. commensalism, parasitism, mutualism) of crustacean hosts. Conversely, this number is in strong disproportion with the number of crustacean symbionts reported from copepods. The only documented case of crustaceans inhabiting the body surface of calanoids is shown by the epicaridean isopods whose life cycle involves two hosts. The free-swimming epicaridium larva is released from the female's marsupium in synchrony with her molt and that of the host. Once liberated, it attaches itself to the surface of the copepod host, undergoing six successive molts and changing progressively into

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two distinct larval stages known as the microniscus and cryptoniscus. Upon reaching the latter stage of development the parasite leaves the calanoid host and descends to locate the benthic decapod final host by chemoreception (Overstreet 1983). Dale & Anderson (1982) found that all three examined species of *Probopyrus* readily infested *Acartia tonsa* Dana, but Bopyridae are known to parasitize other calanoids as well (Sars 1899; Marshall & Orr 1955).

Although relatively few hyperparasites are known in the marine environment (Rohde 1982), the phenomenon of hyperparasitism is well documented for parasitic copepods. The pedunculate barnacle *Conchoderma virgatum* (Spengler) has been found attached to pennellid (Siphonostomatoidea) and lernaeid (Cyclopoida) copepods which parasitized nine species of teleosts and two species of whales (Hastings 1972). Williams (1978) reported the same barnacle on the pandarid *Dinemoura latifolia* (Steenstrup & Lütken) which does not permanently attach to its elasmobranch host. Benz (1984) found *C. virgatum* also on other Pandaridae, *Pandarus satyrus* Dana and *Perrisopus dentatus* Steenstrup Lütken.

Apart from these two specialized cases it appears that crustacean ectosymbionts are not common in the copepod realm though many other symbionts have been reported [see e.g. Ho & Perkins (1985) for an overview]. The only striking exception is found in the Harpacticoda whose integument seems to provide a suitable attachment site for the small-sized Tantulocarida, a recently established, small class of maxillopodan crustaceans (Boxshall & Lincoln 1983). Since Becker's (1975) description of *Basipodella harpacticola* five more species of harpacticoid-infesting tantulocaridans have been described (Boxshall & Lincoln 1983; Boxshall 1988; Huys & Boxshall 1988; Boxshall & Huys 1989; Huys in press a). They were found attached to representatives of Canuellidae, Tisbidae, Diosaccidae, Cylindropsyllidae and Huntmanniidae and some species belonging to the Basipodellidae, displayed a relatively low level of host specificity (*B. harpacticola* Becker, *Stygotantulus stocki* Boxshall & Huys). The locality data of the species described prior to the discovery of *S. stocki* suggested that the Tantulocarida constituted a primarily

cold water-inhabiting taxon found either at high latitudes in both the northern and southern hemispheres or in the deep sea ranging from the continental slope down to the abyssal plain. A first indication that tantulocaridans might be widespread in (sub)tropical waters as well was given by the find of the anchialine cave-dwelling basipodellid *S. stocki*, since the water temperature in its type locality, a lava pool on Lanzarote, measured 18.4°C at the time of sampling. During a survey of the harpacticoids collected in 1967 during the Belgian Expedition to the Great Barrier Reef of Australia, a female *Longipedia scotti* G.O. Sars (Harpacticoida, Longipediidae) was found to be heavily infested by a new genus and species of tantulocaridan to be described below. The host harpacticoid was caught in shallow subtidal sand and bore various stages of development attached on the thoracopods and the urosome. The new tantulocaridan is the fifth species to be reported from the Australian zoogeographical province (Bradford & Hewitt 1980; Boxshall & Lincoln 1983; Lincoln & Boxshall 1983; Boxshall 1988).

Materials and methods

The tantuli and the adult male were examined as temporary preparations in glycerine. All drawings were made under oil immersion using a Leitz Dialux 20 microscope with interference contrast. Judicious manipulation of the coverslip allowed careful examination of the detailed morphology of the thoracopods and the cephalon. After completing the description, specimens were transferred to lactic acid mounting medium and the preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). One of the endopods of leg 2 and the urosome of the host harpacticoid were prepared for scanning electron microscopy. The respective parts were dehydrated through graded ethanol, critical point dried, mounted on stubs, sputter coated with gold, and examined on a JEOL JSM-840 electron microscope. The descriptive terminology of the protopodal parts of the thoracopods follows that of Huys & Boxshall (1988) and Boxshall et al. (1989).

Systematics

Class Tantulocarida Boxshall & Lincoln 1983
 Family Deoterthridae Boxshall & Lincoln 1987

Genus **Coralliotantulus** gen. n.

Diagnosis. – Family Deoterthridae. Tantulus larva comprising cephalon, 6 pedigerous somites, and a 2-segmented abdomen. First thoracic tergite largely concealed beneath posterior margin of dorsal cephalic shield. Cephalic shield rounded anteriorly; ornamentation consisting of 4 anterior plus 7 posterior pairs of pores and distinct longitudinal surface lamellae connected by small transverse ones. Cephalic stylet slightly curved. Thoracopods 1 to 5 each with well developed medial endite borne on separate praecoxa (leg 1) or undivided protopod (legs 2–5). Exopod of thoracopods 1 to 5 apparently 2-segmented with 2 (leg 1) or 4 setae (legs 2–5) on distal segment. Endopod 1-segmented with 1 seta (leg 1) or 1 slender plus 1 strong seta (legs 2–5). Thoracopod 6 without distinct rami, with coupling spines on medial margin of protopod and 2 setae apically. Abdominal somites with numerous, short, transverse and longitudinal lamellae. Caudal rami distinct, armed with 1 short and 2 long, simple setae. Trunk sac containing adult male formed posterior to sixth tergite. Male cephalothorax incorporating first and second thoracic somites; ornamented with 3 pairs of aesthetascs and 7 pairs of bifid sensillae. Thoracopods 1–5 biramous with 1-segmented rami; exopod with 5 geniculate plus 2 minute setae (leg 1) or 5 articulate, distally serrate plus 1 simple setae (legs 2–5); endopod with 4 (legs 1–3) or 5 setae (legs 4–5). Thoracopod 6 uniramous, 3-segmented, with 6 setae on exopod but without syncoxal brush setae. Abdomen 2-segmented, first somite short, with midventral process bearing long, curved penis at its dorsal face; second somite enclosing penis and with converging caudal rami carrying 3 short, dorsolateral setae. Ectoparasitic on harpacticoid copepods.

Etymology. – The generic name is derived from the Greek *korallion*, meaning coral and *tantulus*, which forms part of the name Tantulocarida, and refers to

the type locality where the species was found, i.e. the Great Barrier Reef. Gender: masculine.

Type and unique species. – *Coralliotantulus coomansi* gen. et sp. n.

Coralliotantulus coomansi sp. n.

Type locality. – Belgian Expedition to the Great Barrier Reef, Australia, 1967; at about 1 km from Yonge Reef, coralline sand taken with grab at 35 m depth (leg. Prof. Dr. A. Coomans; 28 September 1967).

Material (Fig. 1). – An adult female *Longipedia scotti* G.O. Sars was found to be infested with the following stages (sac-like tantuli belonging to the male sequence are called here “male precursors”): right P2 with 2 tantuli and 1 head shield on exopod, with 1 tantulus on basis, with 1 female and 1 empty male precursor; left P2 with 2 empty male precursors and 1 tantulus on endopod; intercoxal sclerite of P3 with male precursor containing full-grown male (not included in fig. 1); right P5 with 1 tantulus on exopod; genital double-somite with 1 tantulus ventrally and 1 tantulus laterodorsally; right caudal ramus with 1 empty male precursor near anterior margin and with another empty one attached to inner terminal seta (V). Holotype tantulus containing male deposited in the British Museum (Natural History), London; male dissected and mounted on 3 slides. Urosome of *L. scotti* carrying paratypes and right P2 with male precursor and early female stage mounted on stubs for SEM and retained in personal collection of author.

Etymology. – I have pleasure in dedicating this species to Prof. Dr. August Coomans, director of the Zoology Institute, State University of Gent, who collected it more than twenty years ago during the Belgian Expedition to the Great Barrier Reef.

Description. –

Tantulus (Figs. 2A–D; 3A–C; 7A–B; 8B)

Body comprising a cephalon covered by a dorsal



Fig. 1. A, host harpacticoid *Longipedia scotti* G.O. Sars 1903 infested with various stages of tantulocaridan *Coralliotantulus coomansi* gen. et sp. n.; B, middle and distal endopod segments of left P2 with one tantulus and two male precursors; C, middle and distal endopod segments of right P2 with one male precursor and one early female stage.

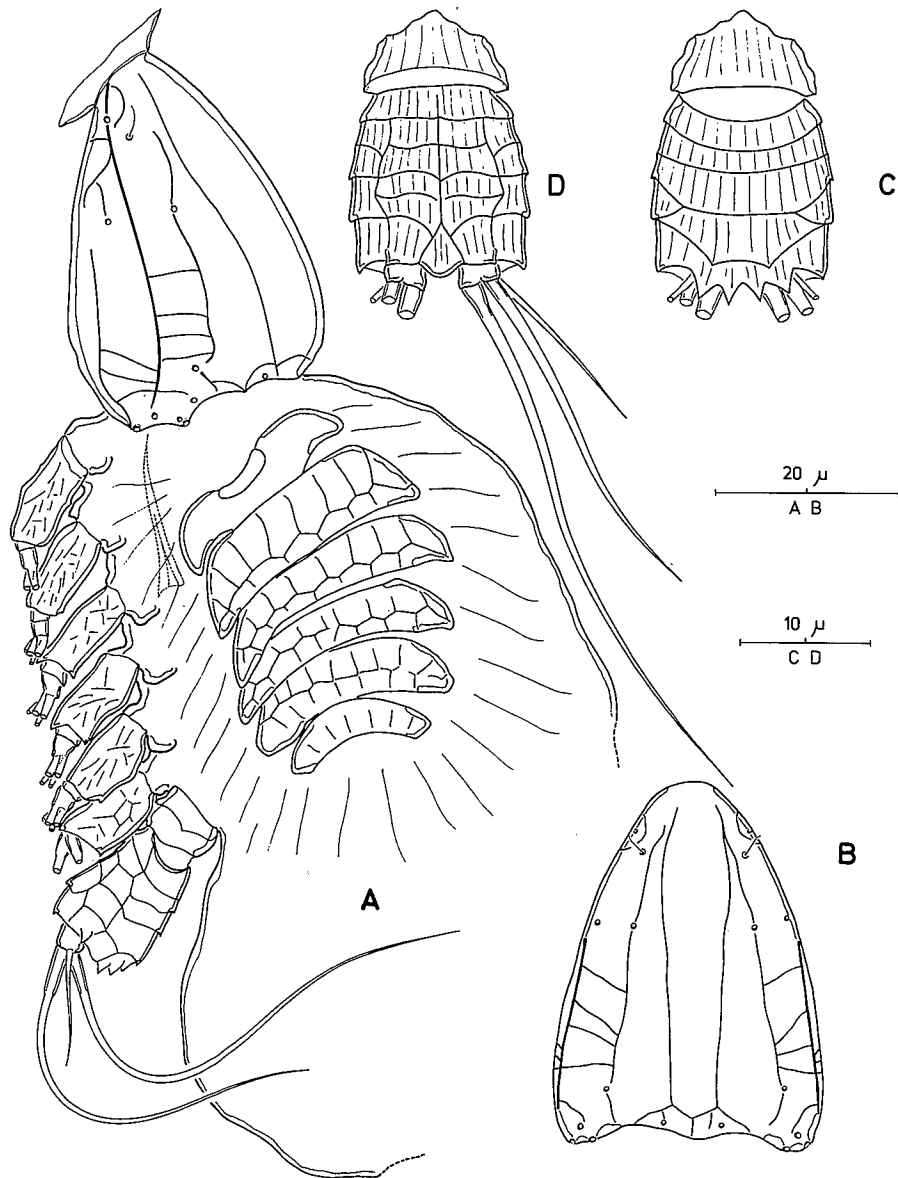


Fig. 2. *Coralliotantulus coomansi* gen. et sp. n.: A, holotype tantulus (after having dissected the adult male out of the trunk sac), lateral view; B, cephalic shield of tantulus, dorsal view; C, abdomen of tantulus, dorsal view; D, abdomen of tantulus, ventral view.

shield, 6 free thoracic somites, and a 2-segmented abdomen. Total body length about $94 \mu\text{m}$, measured from the tip of the cephalon to the posterior margin of the caudal rami. Cephalon (Figs. 2A–B; 7B) tapering anteriorly towards the oral disc; dorsal posterior margin concave at both sides of midline, with posterolateral angles represented by slightly pronounced lobes; ventrolateral margins without oblique lamellae. Cephalic shield about 1.33 times

longer than wide ($40 \mu\text{m} \times 30 \mu\text{m}$); four dorsal and two lateral, longitudinal epicuticular lamellae extend to the basis of the oral disc; lateral areas also with two shorter longitudinal surface lamellae and several transverse ones. The rostrum is absent. The oral disc is about $16 \mu\text{m}$ in diameter and is located ventrally at anterior margin of head; it is sheathed by a short outer membrane, closely adpressed onto the surface of the disc (Fig. 7B). There are 11 pairs

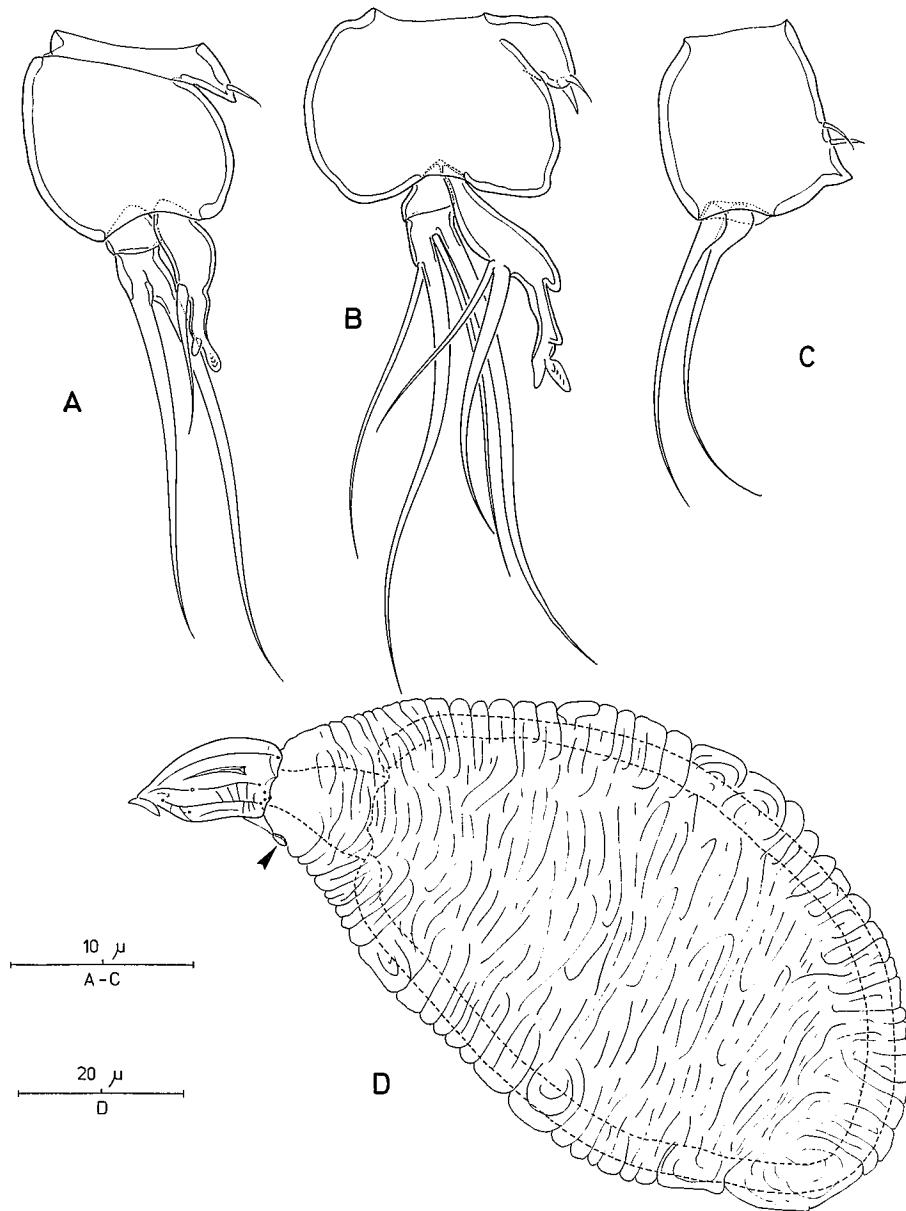


Fig. 3. *Coralliotantulus coomansi* gen. et sp. n.: A, thoracopod 1 of tantulus; B, thoracopod 2 of tantulus; C, thoracopod 6 of tantulus; D, female stage of development (arrow indicating scar of sloughed larval trunk).

of simple pores on the shield; 4 pairs in the anterior part (on both sides arranged in the typical deuterthrid L-pattern) and 7 pairs around the posterior margin of which 1 pair is located subdorsally and another posterolateral one surrounds a tiny sensillum. The ventral surface of the shield lacks pores and lamellae altogether. There are no cephalic appendages.

The cephalic stylet is visible through the integument, about $18\ \mu\text{m}$ long and slightly curved both in dorsal and in lateral aspect; the tip of the stylet does not taper to a very fine point; the base is hollow but well developed lateral barbs could not be observed. In swollen tantuli the stylet is often found inside the trunk sac due to atrophy of associated musculature (Fig. 2A). The tubular organ, striated organ, chi-

tinous collar and glandular lobes reported in previous descriptions were not found in the present material.

The six free thoracic somites each have a well developed tergite (Figs. 2A; 7B), that of first somite largely concealed beneath posterior rim of cephalic shield; others ornamented with a distinct pattern of conspicuous epicuticular lamellae and with setulate posterior margin (visible only with SEM). Each thoracic somite bears a pair of well developed thoracopods.

Thoracopod 1 (Fig. 3A) biramous, with protopod divided in proximal, thin-walled praecoxa, bearing a lobate medial endite at the proximal rim, and a large coxa-basis. Endite armature visible as one spinous element (using light microscopy). The exopod is two-segmented, distal segment armed with two strong setae. Endopod represented by a digitiform segment bearing a spatulate spinule at its distal end, and a short outer-margin seta.

Thoracopods 2 to 5 (Fig. 3B) similar, biramous; each with large one-segmented protopod bearing lobate, medial endite proximally. Under light microscope a subapical spine and a spiny process are visible on the endite. Exopod two-segmented, short, with two strong and two slender naked setae. Endopod one-segmented, long, with conspicuous bulb at midway inner margin; distal part tapering and thin-walled, armed with two outer-margin setae laterally, the distal one being swollen and spini-form; apex with two processes, one of which being spatulate.

Sixth thoracopod (Fig. 3C) with simple protopod lacking medial endite, but bearing two coupling spines on the medial margin; inner distal corner with one spinous process. Rami not distinct but possibly represented each by a vestige bearing a strong naked seta.

The abdomen (Figs. 2A, C, D) is 20 μm in length and two-segmented. The first abdominal somite is 2.4 times wider than long (9.5 μm \times 4 μm), the second 1.3 times longer than wide (16.5 μm \times 12.5 μm). First somite with one lateral surface lamella. Second somite tapering anteriorly; ornamented with complex pattern of transverse and longitudinal epicuticular lamellae both ventrally and laterally. Ventral posterior border of abdomen with median

lobe, but without paired combs; dorsal hind margin armed with two pairs of minute spinous processes; two additional spiny processes can be discerned laterally. Caudal rami very small, wider than long; armed each with one short lateral seta and two long medial setae.

Male metamorphosis (Figs. 2A; 7C; 8A–C)

Adult male formed in reflexed position within grossly expanded trunk sac of preceding tantulus stage. The huge sac-like swelling is produced at the rear end of the thorax, posterior to the tergite of the sixth thoracic somite (Figs. 8A, C). No additional swelling discernible in front of the first thoracic tergite, nor between tergites of fourth to sixth thoracic somites (Fig. 8B). The head and the rest of the thorax and abdomen remain unchanged from the larval condition (Fig. 2A). The larval limbs are separated by slight thoracic expansion. The male is connected to the larval cephalon via a tissue strand (umbilical cord) entering the male cephalothorax mid-ventrally in the anterior half. The full-grown male was successfully dissected out of the trunk sac (Fig. 4A).

Adult male (Figs. 4A–B; 5A–F; 6A–E)

Body comprising cephalothorax incorporating first and second pedigerous somites, four free thoracic somites and a two-segmented abdomen (Fig. 4A). The total body length is 320 μm measured from the anterior tip of the cephalothorax to the posterior margin of the caudal rami. Dorsal shield of cephalothorax with produced posterolateral angles and slightly incised bilaterally in the anterior half (Fig. 4B). Cephalothoracic shield highly ornamented, showing almost symmetrical pattern of ornamentation consisting primarily of strong, longitudinal epicuticular lamellae interspersed with short transverse ridges. Sensory apparatus consisting of 3 pairs of aesthetascs and 7 pairs of sensillae. Aesthetascs arranged in a cluster on each side of anterior margin of head, the inner one being bilobed; these structures probably represent reduced anten-

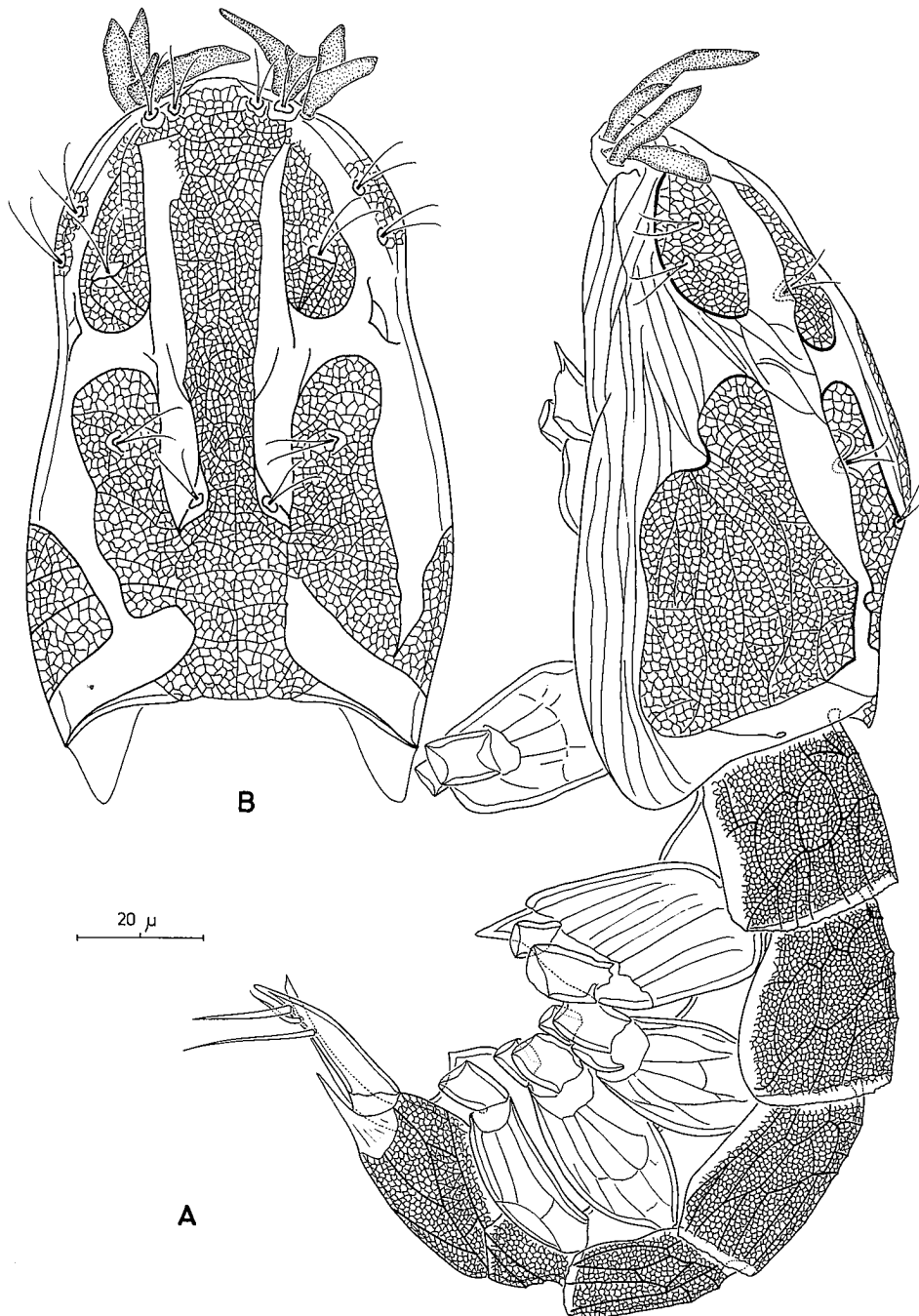


Fig. 4. *Coralliotantulus coomansi* gen. et sp. n.: A, male dissected out of trunk sac of preceding tantulus, lateral view; B, cephalothorax of male, dorsal view.

nules. The sensillae are bifid and each located in a cup-shaped depression. No other cephalic appendages represented. Anterior third of ventral surface of cephalothorax also ornamented with transverse and longitudinal surface ridges (Fig. 6A). Opening

marking connection with umbilical strand circular, lacking any associated structures. Cephalothorax bearing two pairs of well developed thoracopods posteriorly.

Each of the four free thoracic somites has slight-

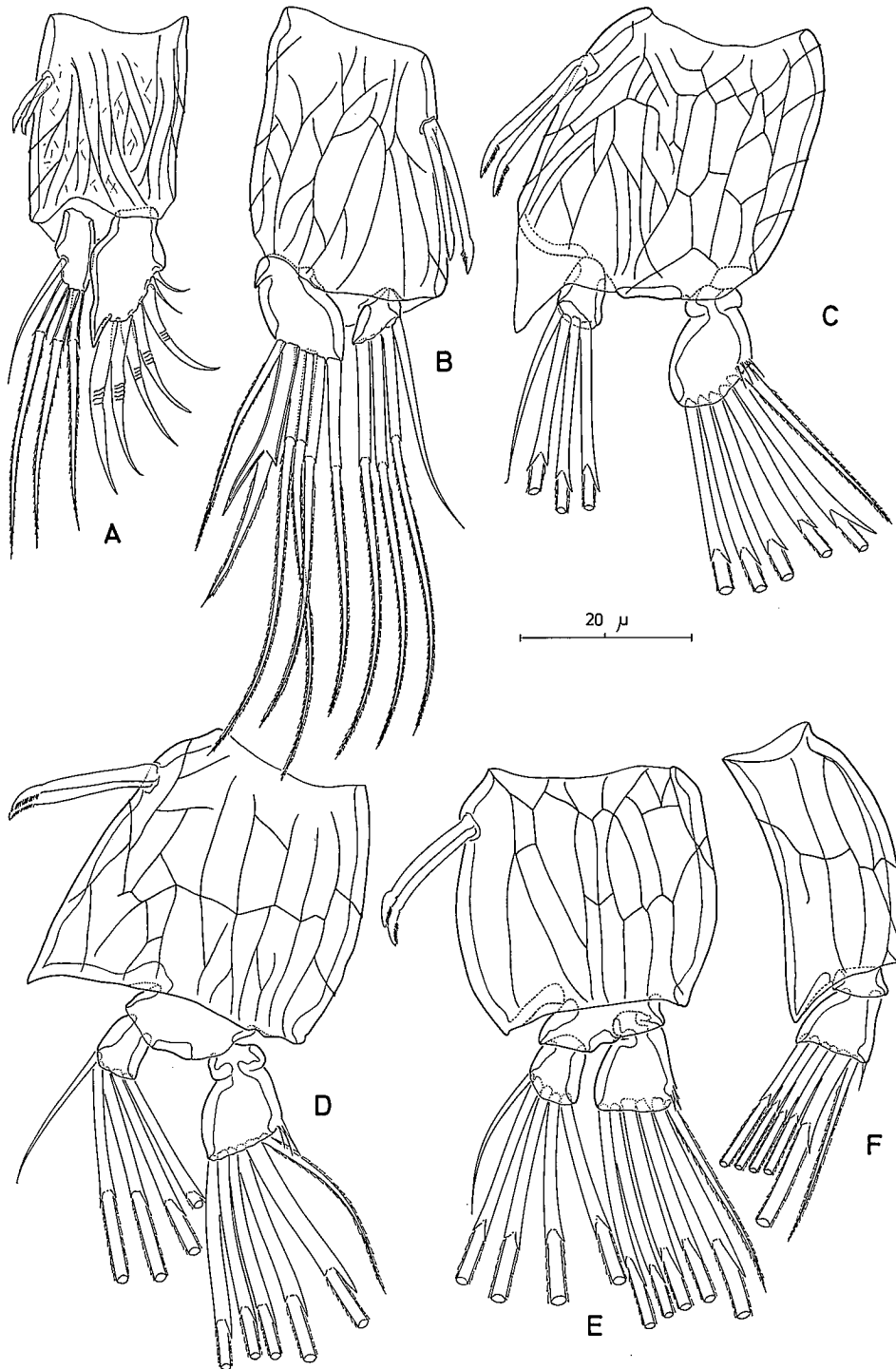


Fig. 5. *Coralliotantulus coomansi* gen. et sp. n., adult male: A, thoracopod 1; B, thoracopod 2; C, thoracopod 3; D, thoracopod 4; E, thoracopod 5; F, thoracopod 6.

ly produced posterolateral angles and each is narrower than the preceding one so the body tapers markedly from cephalothorax to abdomen. The

free thoracic somites are covered by a well developed tergite ornamented with conspicuous transverse and longitudinal surface lamellae (Fig. 6B);

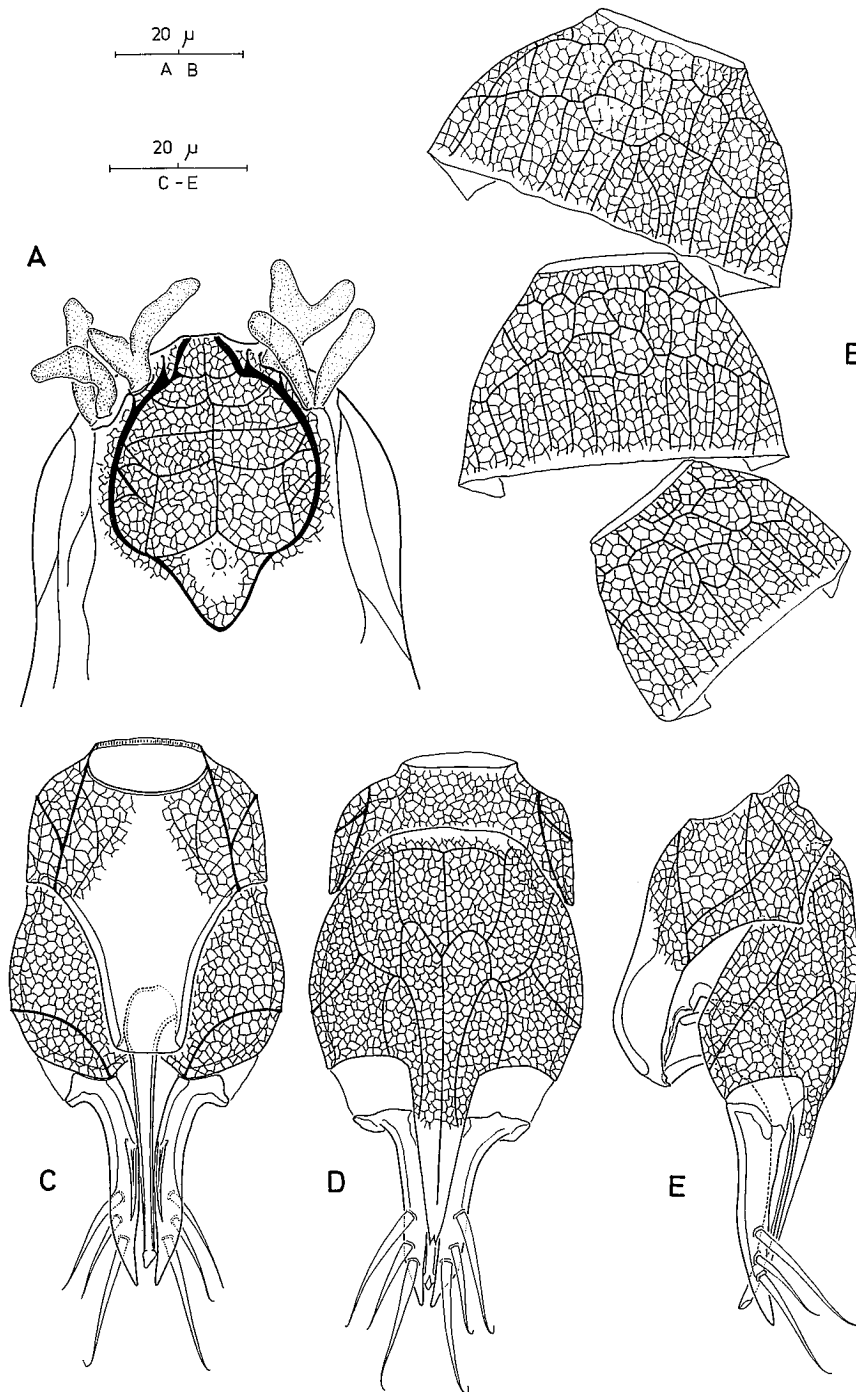


Fig. 6. *Coralliotantulus coomansi* gen. et sp. n., adult male: A, anterior half of cephalothorax, ventral view; B, tergites of third to fifth thoracic somites, dorsal view; C, abdomen, ventral view; D, abdomen, dorsal view; E, abdomen, lateral view

each somite bears a pair of well developed thoracopods.

Thoracopods 1 to 3 (Figs. 5A–C) each compris-

ing large, unsegmented protopod bearing a pair of brush setae (short in P1) proximally on medial margin, and unsegmented rami. Anterior and posterior

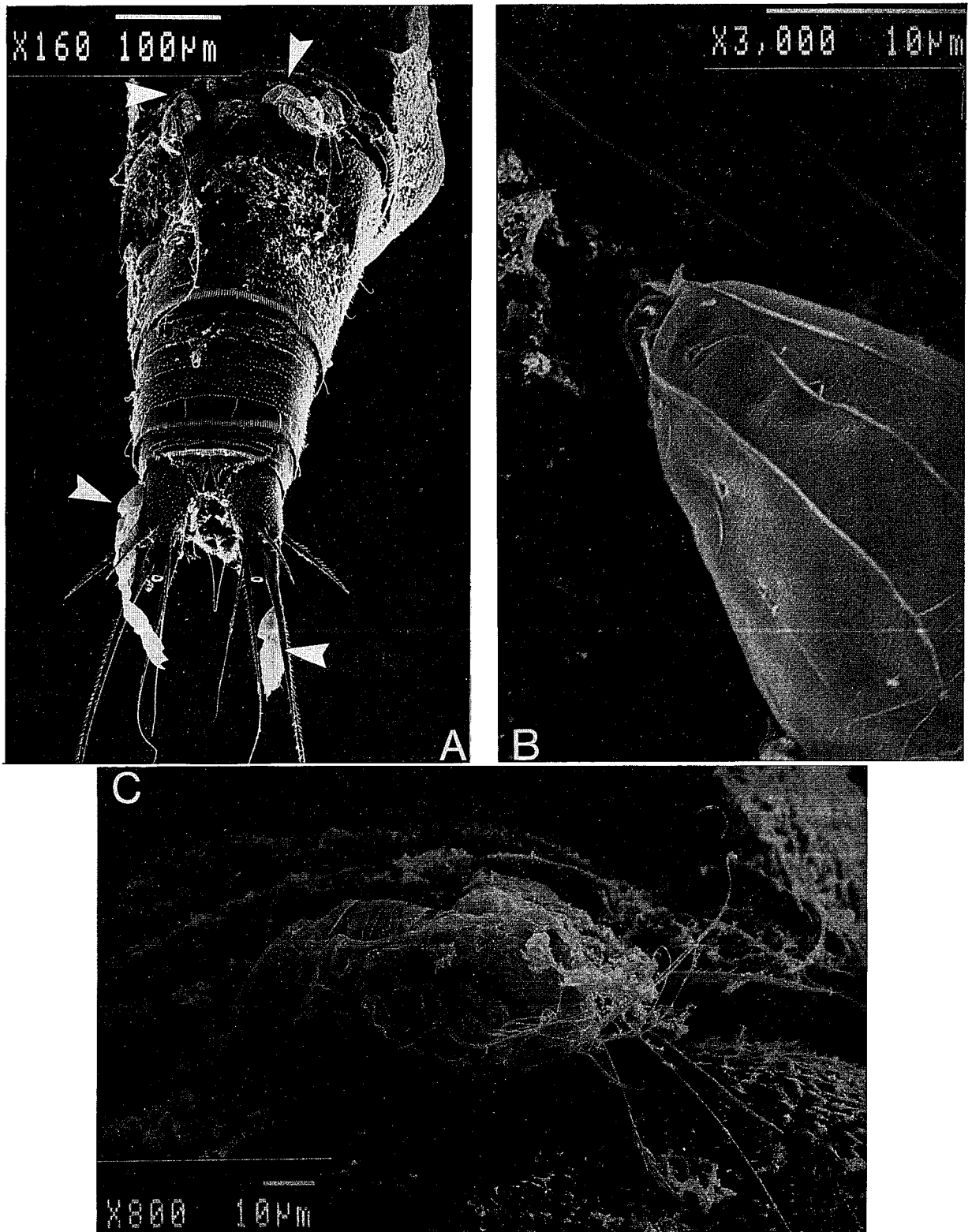


Fig. 7. *Coralliotantulus coomansi* gen. et sp. n., SEM micrographs: A, tantuli (arrowed) attached to genital double somite and caudal rami of *Longipedia scotti* G.O. Sars; B, epicuticular ornamentation on cephalic shield of tantulus; C, tantulus belonging to male sequence with empty trunk sac, lateral view.

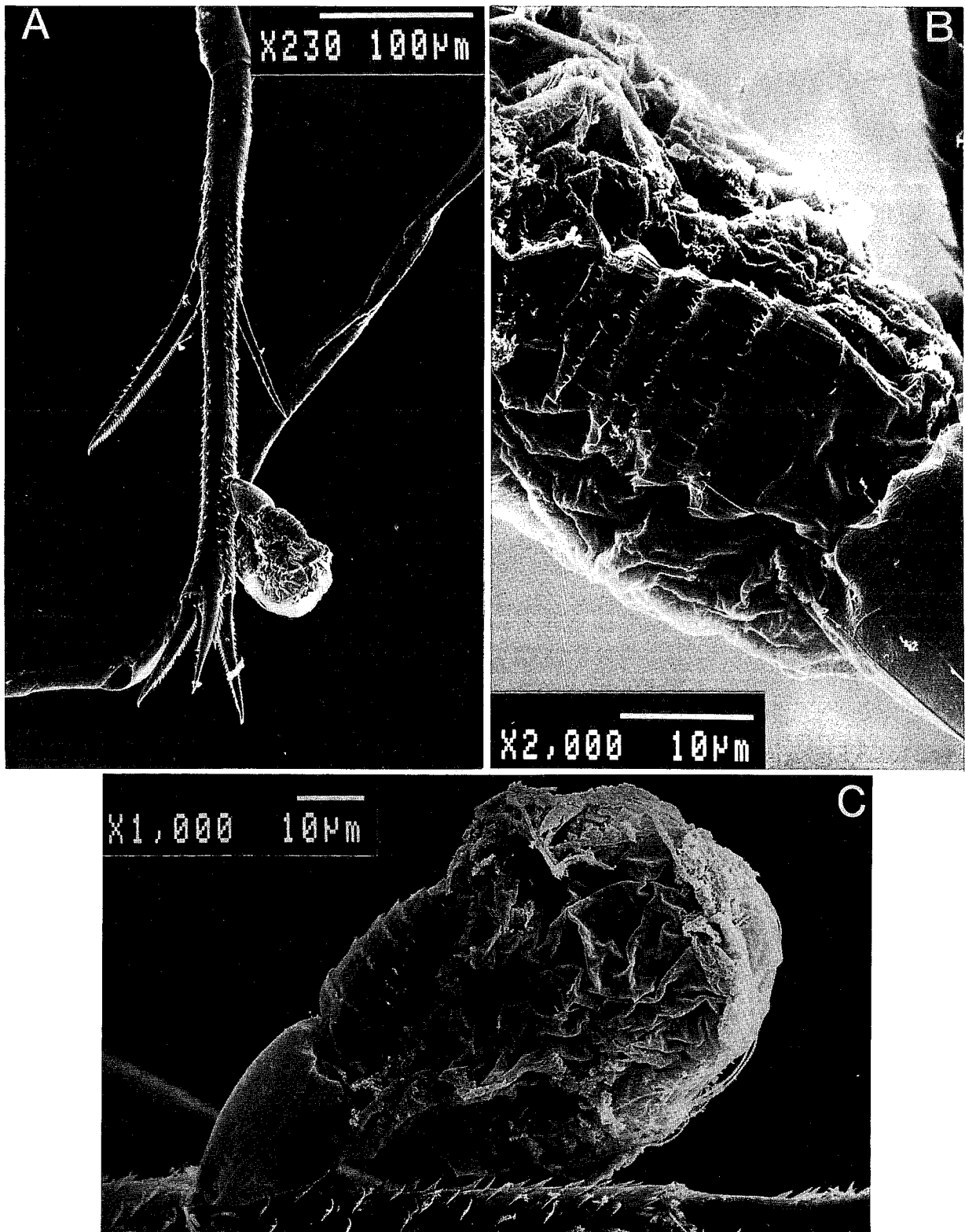


Fig. 8. *Coralliotantulus coomansi* gen. et sp. n., SEM micrographs: A, male precursor attached to distal segment of right endopod P2 of host harpacticoid; B, posterior margin of cephalic shield and thoracic tergites of expanded trunk sac of male precursor, dorsal view; C, male precursor with empty trunk sac, lateral view.

surfaces of protopod ornamented with fine epicuticular lamellae. Protopod of leg 3 with large hyaline process at the inner distal corner. Endopod small, longer than wide, with oblique apical margin; armed with a short, naked inner seta and 3 articulated setae which are bilaterally serrate distal to articulation. Exopod of thoracopod 1 large, forming a spinous process at the inner distal corner and armed with 5 short, geniculate (increasing in length adaxially) and 2 smaller, simple setae. Exopod of legs 2–3 seemingly 2-segmented but separation between minute proximal lobe and large distal lobe only marked by superficial constriction and not by articulation; armed with 5 articulated setae (outermost one of P2 swollen and bearing a long outer spinous projection proximal to articulation; this feature is also present on other setae and on other legs but is only slightly developed), an outer, short, serrate seta and a few spiniform structures at the outer corner (in leg 3).

Thoracopods 4 and 5 (Figs. 5D–E) similar to thoracopod 3 in segmentation and exopodal ornamentation, except protopod is 2-segmented, comprising a large proximal syncoxa and a small distal basis; the endopod is armed with a short, inner seta and 4 articulated, distally serrate setae. The syncoxa of P4 shows a spinous projection at its inner distal corner. Thoracopod 6 (Fig. 5F) uniramous, 3-segmented. Syncoxa large, forming a distinct inner process distally; ornamented with conspicuous surface lamellae; lacking brush setae. Second segment (basis) minute, without ornamentation. Distal segment representing exopod, bearing an outer spinule, an outer serrate seta and 5 articulated, distally serrate setae.

The two-segmented abdomen has a complex morphology (Figs. 6C–E). The first somite is smallest, measuring $10 \mu \times 32 \mu$ in dorsal aspect, but largely produced posteroventrally. The dorsal surface is ornamented with an irregular pattern of minute surface ridges but conspicuous longitudinal lamellae are found on both lateral surfaces. The median posteroventral projection of the somite narrows posteriorly, overlaying the ventral surface of the second abdominal somite. A robust, curved abdominal stylet (penis) is attached to the dorsal face of the median projection so that its base is only visi-

ble in lateral aspect. The second abdominal somite, measuring $35.5 \mu \times 37.5 \mu$, is slightly longer than wide but produced a long middorsal process, tapering posteriorly and bifid apically. The dorsal and lateral surfaces of the somite are ornamented with distinct longitudinal and transverse lamellae and minute epicuticular ridges. The somite is strongly incised ventrally, forming a median concavity in which the penis fits. The caudal rami are slender, curved adaxially and borne on the outer posterolateral corners of the second abdominal somite. Each ramus tapers to a fine tip which is slightly directed adaxially and dorsally. The ornamentation consists an inner spinous process ventrally and three short setae, all arising from the distal half of the outer margin. The penis is broad at its attachment base and tapers posteriorly to a slight apical swelling which bears a large opening. It extends nearly to the posterior margin of the caudal rami and is well protected by various surrounding structures. The curved posterodorsally directed penis is enclosed in the midventral concavity of the second abdominal somite; the distal half of the penis is flanked by the caudal rami and concealed beneath the middorsal, posterior process so that only the apical part of the penis is visible in dorsal view. The penis becomes fully exposed (during fertilization) by lifting of the second abdominal somite in dorsal direction and by ventral flexure of the penis itself, this being facilitated by the area of thin integument around the articulation with the midventral process of the first abdominal somite.

Adult female (Figs. 1C; 3D)

The only female that is available represents an early stage of development in which the sac contents remained undifferentiated other than into an outer layer of columnar cells and a central, cellular mass which is connected via a broad tissue strand with the larval cephalon (Fig. 3D). The total length of the specimen measured about 105μ but the highly folded and wrinkled integument suggests that this stage might expand further to a larger sac. The larval thorax and abdomen are sloughed, leaving a minute ventral scar immediately behind the ce-

phalic shield. The latter remained unchanged and shows the same surface ornamentation as well as the internal stylet as described for the tantulus.

Discussion

The class Tantulocarida currently comprises five families (Boxshall & Lincoln 1983, 1987; Huys in press a) but only the Microdajidae Boxshall & Lincoln, the Deoterthridae Boxshall & Lincoln and the Doryphallophoridae Huys exhibit a two-segmented abdomen in the tantulus larva. The latter two families also have well developed thoracopods with rich setation on the respective rami, this being in contrast to the Microdajidae which have strongly reduced legs in the tantulus. On the basis of the cephalic pore pattern, the absence of a rostrum and the presence of only 2 setae on the exopod of thoracopod 1, *Coralliotantulus* is assigned to the Deoterthridae. The discovery of *Deoterthron lincolni* (Boxshall 1988) already represented an opportunity to compare the male trunk sac formation between *Deoterthron* Bradford & Hewitt and *Doryphallophora* Huys. The difference noted in the position of the male trunk sac between two species of the same family was reckoned by Boxshall (1988) as a possible result of prematurely having established the Deoterthridae. Huys (in press a) compared the various deoterthrid species also on the basis of larval characters (rostrum, cephalic pore pattern, setation on exopod of leg 1) and concluded that *Deoterthron* represented a mixture of two genera belonging to different families. This resulted in the establishment of the Doryphallophoridae but apart from the position of the trunk sac, an in-depth comparison of the male morphology turned out to be impossible because the only deoterthrid male (Boxshall 1988) known at that time represented an early stage of development.

The position of the male trunk sac in *C. coomansi* corroborates the exclusion of the isopod-infesting species *D. harrisoni*, *D. megacephala* and *D. aseloticola* from the genus *Deoterthron* and their removal to a separate genus and family. Both in *Deoterthron* (cf. Boxshall 1988) and in *Coralliotantulus* the huge sac-like swelling containing the male

is found posteriorly to the sixth tergite and no additional expansion between the cephalon and the thorax, nor between the other tergites could be detected. In the Doryphallophoridae the trunk sac is produced primarily by swelling between tergites 5 and 6 and by minor expansion between tergites 4 and 5 (Boxshall & Lincoln 1987). The description of other males (Boxshall & Lincoln 1987; Grygier & Sieg 1988; Boxshall & Huys 1989; Boxshall *et al.* 1989) indicated already that the Doryphallophoridae have a unique, strongly reduced male. The most significant character is the unsegmented abdomen which bears a midventral, rigid, posteriorly directed stylet and a pair of long caudal setae which probably represent the vestigial caudal rami. None of these features were found in the male of *C. coomansi* reinforcing the different familial position of *Doryphallophora*.

The shape and orientation of the male abdominal stylet differs among the various families and the penis of *C. coomansi* represents yet another type. In *Stygotantulus stocki* (Basipodellidae) the penis comprises a swollen, basal part and a curved, tapering distal part of which the tip is anteriorly directed (Boxshall & Huys 1989). In the Microdajidae the stylet is divided by a surface furrow into a rectangular proximal portion and a slightly curved, posteriorly directed, robust distal part (Boxshall & Lincoln 1987; Boxshall *et al.* 1989). The male of *D. harrisoni* (Doryphallophoridae) has a spear-like, probably immobile penis since there is no articulation present, nor are there any associated muscles (Boxshall & Lincoln 1987). The penis of *Coralliotantulus* differs from all these types because the curved distal part inserts at the dorsal face of the basal portion and because it is sheathed by the second abdominal somite and the caudal rami. Regarding this type as being typical for the Deoterthridae would probably be a premature statement, but the high diversity in penis morphology noted in the few tantulocaridan males described thus far suggests that it might serve as a significant character in diagnosing suprageneric taxa.

Tantulocaridan males often have long, cylindrical caudal rami bearing 3 (sometimes 2; cf. *Microdajus langi*) long setae at the distal margin. Only the doryphallophorid male lacks well developed

caudal rami and their homologue might be found in the paired caudal seta arising from the posterior margin of the unsegmented abdomen. The male of *C. coomansi* differs from these two conditions by the shape of the rami which are curved adaxially and dorsally, and by their ornamentation which consists of 3 short, laterodorsal setae and a ventral spinous process.

The new genus is also unique in the morphology of thoracopod 1. The exopodal ornamentation of this leg consists of 5 short, geniculate setae and 2 minute setules instead of the articulated, distally serrate setae typically found in other males. Unlike other species, *C. coomansi* shows only 4 setae (instead of 5) on the endopod of thoracopods 1 to 3. It further can be differentiated by the ornamentation of leg 6, exhibiting 6 setae on the exopod but lacking brush setae on the syncoxa. *Doryphallophora harrisoni* also has 6 setae on the exopod but shows 1 brush seta on the syncoxa. The absence of syncoxal brush setae is shared with the Microdajidae, however these species have only 5 exopodal setae. Finally, a combination of 2 syncoxal brush setae and 5 exopodal setae is found in *S. stocki*.

Comparison of the sensory apparatus on the male cephalothorax reveals only little variation among the various families. Males typically display 4 pairs of aesthetascs located on either side of the rostrum and arising directly from the surface of the cephalothorax; often the innermost aesthetasc is bilobed. Only *C. coomansi* is exceptional in having but 3 pairs of aesthetascs. The cephalothoracic sensillae could not be discerned in *S. stocki* because the cephalothorax was damaged during removal from the sac. The other males show a remarkable consistency in the number and relative position of these sensillae, indicating that 7 pairs of bifid sensillae might be the ancestral condition. In *D. harrisoni* only 6 pairs could be detected and the distribution pattern indicates that it is the anterior one of the two pairs found in the posterior half of the cephalothorax of other males, that is absent.

The pore pattern found on the tantulus' cephalic shield shows a higher level of diversity among the various families, but genera belonging to the same family usually exhibit the same configuration (Huys in press a). The basic pattern of the Deoter-

thridae consists of 4 pairs of anterior pores and 6 pairs distributed along the posterior margin of the shield; one pair of posterior pores is always subdorsal in position. The latter pores are also found in *Coralliotantulus* but the shield shows a 4 + 7 configuration which represents a slight deviation from the general pattern.

As in the tantuli of *Boreotantulus* Huys & Boxshall and *Deoterthron*, the endopod of thoracopod 1 in *Coralliotantulus* is represented by a digitiform segment bearing one seta. Other Deoterthridae either lack this tiny seta as in the mediterranean species *Dicrotrichura tricincta* (cf. Huys in press b) or have, as exemplified by the bathyal genus *Campyloxiphos* Huys, no endopod at all. The new genus can be differentiated from *Deoterthron* by the presence of only 4 setae on the exopod of thoracopods 2 to 5, the conspicuous epicuticular lamellae on the abdomen, and the slender lateral seta on the caudal rami. Both *Deoterthron* species have 5 setae on the exopod of legs 2–5, lack distinct surface lamellae on the abdomen and have a serrate lateral spine on the caudal rami. They also exhibit oblique lamellae on the ventrolateral margins of the cephalic shield, which are definitely absent in *Coralliotantulus*. *Boreotantulus* is similar to the new genus in the presence of transverse and longitudinal surface lamellae on the second abdominal somite, but none of these could be traced on the cephalic shield of *B. kunzi* whilst *C. coomansi* has rich epicuticular ornamentation on the cephalon. The Scandinavian species also differs in the setation of the exopods of thoracopod 1 (3 setae) and 2 to 5 (2 setae). The bulbous inner process and the swollen distalmost seta on the endopod of legs 2 to 5 are also typical for *C. coomansi*. The presence (on thoracopod 1) of a discrete precoxa bearing the medial, lobate endite was already documented for other species (Huys & Boxshall 1988; Boxshall *et al.* 1989). *C. coomansi* is the seventh tantulocaridan known to parasitize harpacticoid copepods.

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