

Telestacicola xenophiothricis n. sp. (Copepoda, Poecilostomatoida), a remarkably well adapted commensal of the brittlestar *Ophiothrix purpurea* (Echinodermata)

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ABSTRACT. A study of the turbellarian commensal fauna of the brittlestar *Ophiothrix purpurea* in Hansa Bay (Papua New Guinea) revealed the presence of a remarkably well-adapted lichomolgid copepod : *Telestacicola xenophiothricis* n. sp. (Rynchomolgidae, Poecilostomatoida). Fourteen out of 118 (12%) ophiuroids inspected were infested by one to three copepods (a total of 18 specimens observed). The body colour of this commensal crustacean mimics perfectly the pattern of orange-red and pink lines of the central disk of the host, and this complex and uncommon mimicry could indicate a high host specificity. *T. xenophiothricis* is the fourth member in this genus, but is the first encountered on ophiuroids (Echinodermata), while it is the tenth species of Poecilostomatoida amongst the 46 known species of Copepoda associated with ophiuroids (others are 22 Siphonostomatoida, 13 Cyclopoida and one Harpacticoida). Furthermore, the generic assignment of *Doridicola claudus* Humes & Stock is discussed, and the species is allocated to the genus *Telestacicola*.

KEY WORDS : Copepoda, new species, host preference, mimicry, Papua New Guinea.

INTRODUCTION

Since the establishment of the first lichomolgid genus *Doridicola* by Leydig in 1853, our knowledge about the lichomolgid complex has expanded tremendously (HUMES, 1994). In recent years two basic revisions of this taxon have been published (HUMES & STOCK, 1973; HUMES & BOXSHALL, 1996), inclusive in the latter, a phylogenetic analysis of the relationships between the several families. Today, the lichomolgid complex comprises ten families with hundreds of species distributed over 122 genera. Despite this exponential growth of our knowledge of the species richness of this group, the cited figures certainly represent only the tip of the iceberg (HUMES, 1994). However, where we have now a sound systematic framework for this superfamily, the study of their behaviour and their impact on the hosts is a vast open field of research (GOODING, 1957; HUMES, 1982).

During a study of the symbiont polyclad *Discoplana* spec. (Turbellaria) in the brittlestar *Ophiothrix purpurea* von Martens, 1867 (Ophiotrichidae, Echinodermata), an interesting lichomolgoid copepod was detected living on the central disc of the host. The present contribution deals with the description of this new species, with some information on its behaviour and its remarkable colour pattern.

MATERIAL AND METHODS

Ophiuroids *Ophiothrix purpurea* von Martens, 1867 were collected from the coral reefs surrounding Laing

Island (4°10'S, 144°52'E), Hansa Bay and Durangit Reef (Madang Province, Papua New Guinea). All specimens were collected by Scuba diving between 3 to 20 m deep during three missions performed between 1994 and 1996. During collections, echinoderms were placed individually in plastic bags. Once in the laboratory at the Biological Station King Leopold III on Laing Island, they were immediately observed and dissected under a stereomicroscope. Copepods found were counted, photographed and fixed in 100% ethanol or in Bouin's fluid for morphological studies. After 24h, the latter were transferred to 75% ethanol for preservation.

The dissected specimens were mounted in glycerine with Euparal®-sealed cover glasses. Preserved specimens were stored in 75% ethanol. Observations were made on a Leitz Diaplan light microscope equipped with phase contrast and a drawing tube. Descriptive terminology follows HUMES & BOXSHALL (1996). All specimens were incorporated in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (labeled COP).

SYSTEMATICS

Family Rynchomolgidae Humes & Stock, 1973
Telestacicola xenophiothricis n. sp.

Material : Holotype : 1 dissected female, labeled COP 4580A-E; allotype : 1 dissected male, labeled COP 4581A-D; paratype : 1 dissected female (COP 4582A-

B); 2 females and 1 male, preserved in alcohol, labeled COP 4583.

Type locality : Lagoon of Laing Island, Madang Province, Papua New Guinea.

Host : *Ophiothrix purpurea* von Martens, 1867 (Echinodermata : Ophiotrichidae).

Etymology : The specific epitheton, *xenophiothricis*, is a conjunction of the Greek words *Xeno*, meaning guest, and *Ophiothrix*, brittlestar.

Description

Female

Body (Figs 1A & B) graceful cyclopoid shaped, 1.75 mm long (including caudal rami, but without setae). Head with dorsal trace of separation between head and first pedigerous somite. Third and fourth pedigers slightly expanded laterally.

Genital double somite expanded laterally in anterior part (190 µm wide) and nearly cylindrical in posterior half (115 µm wide). Length of somite : 210 µm. Leg 6 with setiform lateral element (± 45 µm long) and two

spiniform processes. Valves ovate. The three postgenital somites are (LxW, in µm) 67x90, 67x80, 100x73. Leg 5 bearing somite 163x86 µm, with lateral seta 38 µm long. Dorsal integument with pattern of minute perforations in proximal half.

Caudal rami cylindrical, 96 x 16 µm (6.4/1) with six setae. Dorsal seta 28 µm long, proximal lateral seta 56 µm, outer terminal seta 150 µm, and median terminal seta 170 µm long. Proximal lateral and dorsal setae smooth, all others feathered. Inner terminal seta and distal lateral one broken.

Antennule (Fig. 2A) 7-segmented. Segments with following lengths (measured along median axis) : 55, 85, 30, 45, 50, 40, 40. Setal complement (Aesth. means aesthetasc) : 4-13-6-3-5-2+Aesth-7+Aesth.

Antenna (Figs. 3A, B & C) 4-segmented with following armature : 1, 1, 3, 5+2. First endopodal segment with field of spinules in proximal half and row of spinules along inner margin. Terminal segment spinulose along inner margin. Elements of third segment long, reaching far beyond middle of fourth segment. Claws with pinnate proximal half, and serrate distal one.

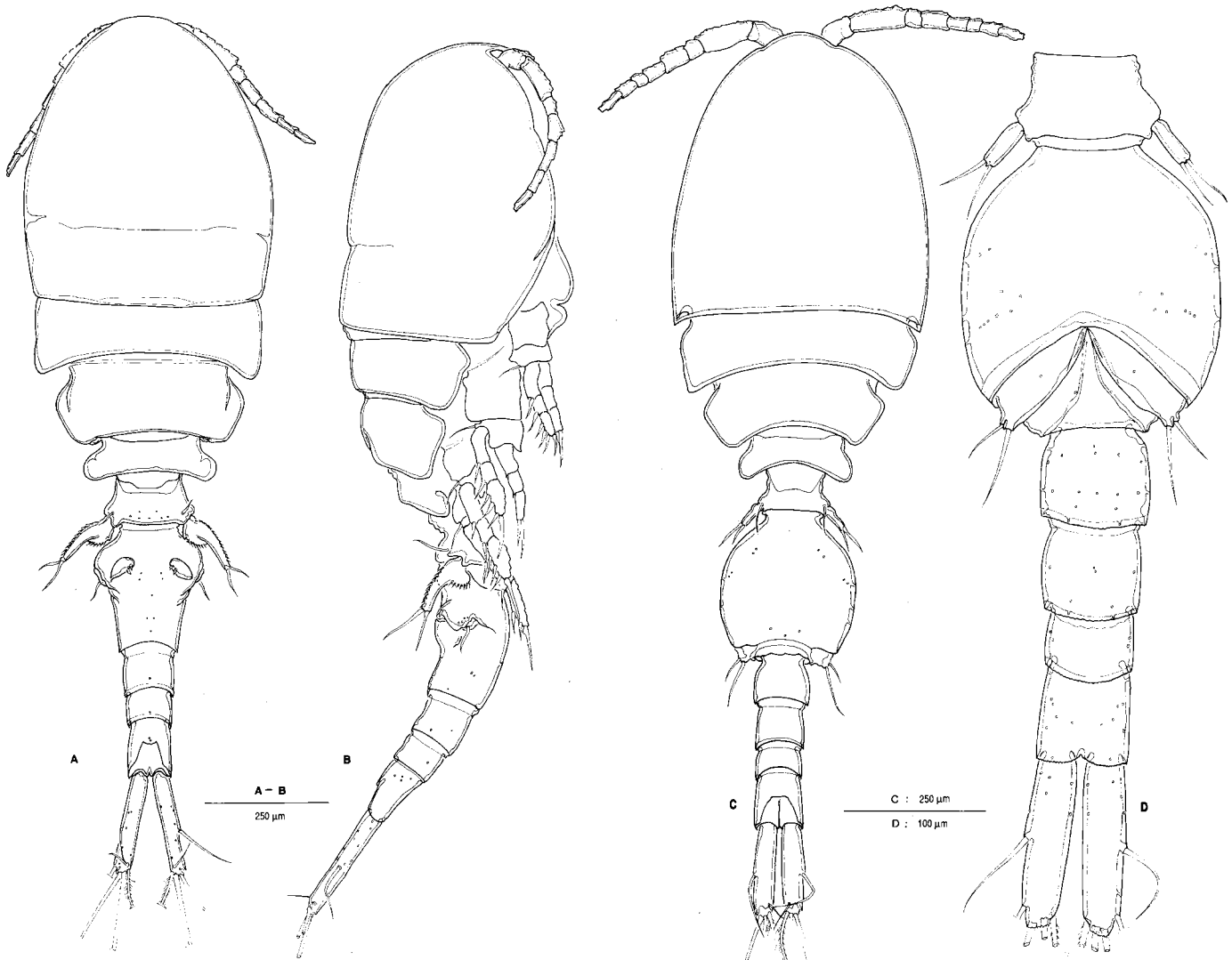


Fig. 1. – *Telestacicola xenophiothricis* n. sp., female. A, Habitus in dorsal view; B, Habitus in lateral view; Male. C, Habitus in dorsal view; D, Urosome, in ventral view.

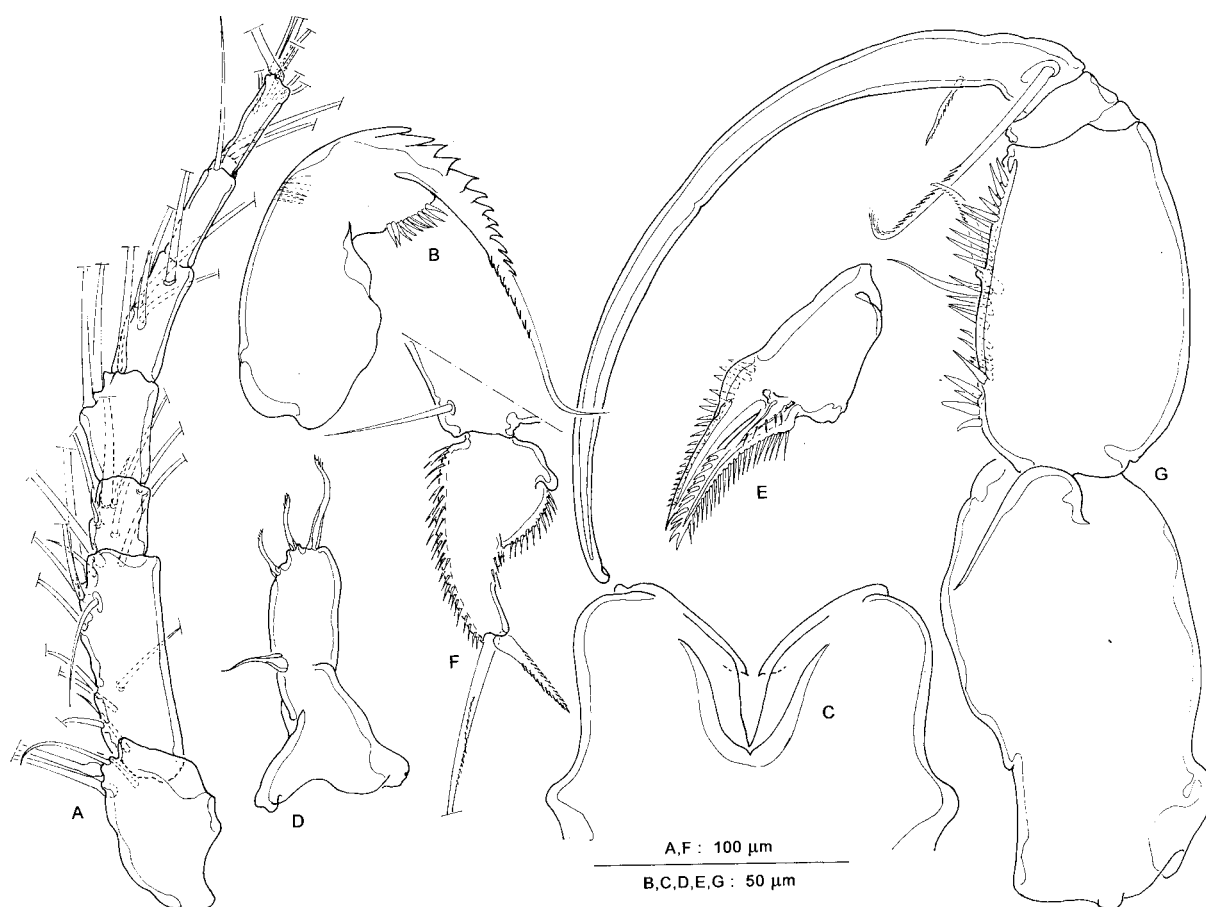


Fig. 2. – *Telestacicola xenophiothricis* n. sp., female. A, Antennule; B, Mandible; C, Labrum; D, Maxillule, E, Maxilla; F, Leg 5; Male : G, Maxilliped.

Mandible (Fig. 2B) with slender lash, having 12 medial teeth (those along the convex side) and eight teeth in the middle of the concave side. Maxillule (Fig. 2D) short, with four setae. Lateral seta thickened at base. Terminal 3 setae robust, pinnate apically. Maxilla (Fig. 2E) with stout, unarmed, basal segment (not drawn). Distal segment attenuated into short lash armed with about 20 teeth. Auxiliary lash with nine teeth along outer margin, and densely armed with long and slender spinules along the entire medial margin. Additional seta short, arising near insertion of auxiliary lash. Maxilliped (Fig. 3D) with robust basal segment devoid of elements. Second segment twice as long as wide with two setae at midlength of medial margin. Terminal segment short with two terminal claw-like confluent elements.

Legs 1-4 with large square and smooth coxa. Outer distal region somewhat protruded and medial distal edge with feathered seta. Intercoxal sclerite in all legs with smooth surface. Basis of all legs with short and naked outer seta. Medial margin of basis rounded and smooth. Rami 3-segmented except for the fourth leg endopod, which is one-segmented (Fig. 3I). Distal outer edge of terminal exopodal segment of legs 2-4 protruded into a small hyaline lobe with a bifid distal margin (Fig. 3H). Endopodite of leg 4 just reaching to the middle of the second exopodal segment. Proximal part slightly expanded laterally. Inner lateral seta pinnate, terminal elements

spiniform (Fig. 3E). Inner terminal one 51 μ m, outer one 38 μ m (outer/inner : 0.74/1).

Leg 5 (Fig. 2F) with inflated proximal part and sub-squarish distal half. Inner margin of proximal part with a distinct supplementary notch. Inner and outer margin of segment densely ornamented with rigid spines. Outer terminal setiform, broken in all specimens, but at least 2.5 times longer than inner spiniform element.

Male

Habitus (Fig. 1C) cyclopid, 1.25 mm long. Cephalothorax without trace of separation between head and first pedigerous somite. Third and fourth pedigerous somite slightly expanded laterally. Second urosomal somite large and ovate (194x195 μ m), bearing well-developed sixth legs. Third to last urosomal somites narrow, respectively (LxW, in μ m) : 69x77, 66x69, 39x61, 69x61.

Caudal rami 3.8 times as long as wide, with six setae. Ventrodistal margin slightly protruded, and serrate. Proximal lateral seta (75 μ m) arising in middle of outer margin, distal lateral one implanted close to distal outer edge. Dorsal seta 75 μ m long, located near distal inner edge. Outer distal and all terminal setae broken.

Antennule 7-segmented with following complement : 4 – 12+Aesth. – 6 – 3+Aesth – 4+Aesth – 2+Aesth – 7+Aesth.

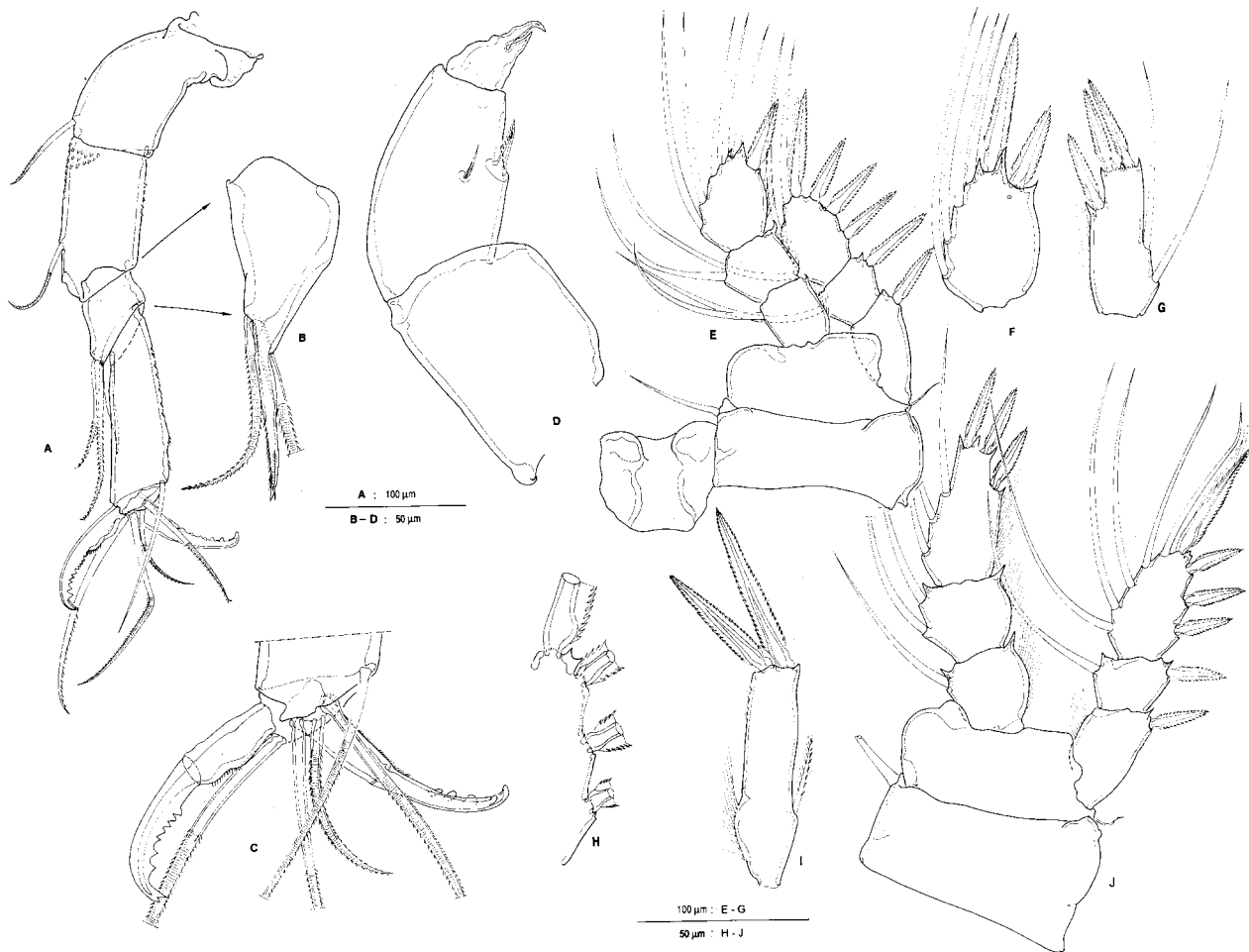


Fig. 3. – *Telestacicola xenophiothricis* n. sp., female. A, Antenna, B, Third antennal segment, enlarged; C, Distal margin of terminal antennal segment, enlarged; D, Maxilliped; E, Leg 1; F, Distal endopodal segment of male leg 1; G, Distal endopodal segment of leg 2; H, Detail of distal exopodal segment of leg 2; I, Leg 4 endopodite; J, Leg 3.

Maxilliped (Fig. 2G) with long, unarmed basal segment. Second segment with long ovate appearance, densely armed with robust spinules along the medial margin, and bearing two elements near the middle of the medial margin. Third segment small, unarmed. Claw long, blunt and with two elements. Proximal one four times longer than distal one.

Leg 1 (Fig. 3F) typically sexually dimorphic: terminal endopodite segment with four medial setae, one terminal and one subdistal outer spine.

Leg 5 (Fig. 1D) short ($36 \times 12 \mu\text{m}$) and cylindrical, bearing two subequal setiform elements: outer one $44 \mu\text{m}$, inner one $38 \mu\text{m}$. Leg 6 (Fig. 1D) as a triangular plate with two setiform elements: outer one $36 \mu\text{m}$, inner one $58 \mu\text{m}$.

Affinities

Within the key to the genera of the Rynchomolgidae (HUMES & BOXSHALL, 1996), the specimens at hand key out to the genus *Telestacicola* Humes & Stock, 1973 in which nowadays three species are assembled: *T. angoti* Humes & Stock, 1973 (type-species), *T. sertus* Humes, 1977 and *T. lobophyti* Humes, 1990. *T. xenophiothricis* n. sp. is at once distinguishable from *T. lobophyti* by the longer caudal rami in the male ($3.8/1$ versus $3.17/1$) and

female ($6.5/1$ versus $4.8/1$), the serrate antennal claws, and the much longer and wider articulating segment of the fifth leg. *T. sertus* differs from the here described species by its short caudal rami (only 1.6 times longer than wide) and the dentate nature of the antennal claws.

T. xenophiothricis resembles most closely *T. angoti*. Both species share the graceful cyclopid body shape with long caudal rami, a proximally inflated female fifth leg, and the long outer terminal spine on the fourth leg endopodite, reaching far beyond the middle of the inner element. The former has, however, longer caudal rami (female: $6.4/1$ versus $4.8/1$; male: $3.8/1$ versus $3.19/1$), and a much more compact endopodite in the fourth leg, reaching only to the middle of the second exopodal segment. *T. xenophiothricis* differs significantly from its congeners in the elements on the antenna. Whereas *T. angoti* has terminal claws, which are serrate along the entire concave part of the stem, *T. xenophiothricis* is only serrate in the distal half of the stem of the claw, whilst the proximal part of the stem is finely dentate. Moreover, the elements on the third antennal segment in *T. angoti* are clearly much shorter than in *T. xenophiothricis* where the three elements reach far beyond the middle of the terminal segment.

The previously known species of this lichomolgid genus have been found as associates on Telastacea (*T. angoti*, *T. sertus*) and Alcyonacea (*T. lobophyti*). *T. xenophiothricis* is the first representative of the genus known to live on an echinoderm. Among the 41 genera recognised within the family, *Telestacicola* is the third genus besides *Critomolgus* Humes & Stock, 1983 and *Doridicola* Leydig, 1853 known to include species that live in association with cnidarians as well as with other invertebrates (Nudibranchia, Porifera, Bivalvia, Gastropoda, Cephalopoda, and Echinodermata) (HUMES & BOXSHALL, 1996; HO & KIM, 2001).

We cannot ignore the close resemblance between the genus *Telestacicola* and the genera *Doridicola* and *Critomolgus*. As a matter of fact the three genera are only discriminated by the morphology of the fourth leg. *Critomolgus* differs from the two other genera by the (plesiomorph) chaetotaxy of the terminal segment of the exopodite in the fourth leg. With a complement of III,I,5 it differs significantly from its sister taxa (*Doridicola* and *Telestacicola*), which possess a II,I,5 complement on this segment. *Telestacicola* is distinguishable from *Doridicola* because of the one-segmented condition of the endopodite in the fourth leg. Among the 45 species possessing a two-segmented endopodite in the fourth leg and which are consequently attributed to the genus *Doridicola*, one species, namely *D. claudus* Humes & Stock, 1973, has a short and functionally 1-segmented endopodite in the fourth leg. An indistinct and incomplete transversal line is located where the other *Doridicola* species show the articulation between the proximal and distal segments. Without enlarging the generic diagnosis of *Doridicola*, *D. claudus* cannot be maintained in it and should be transferred to *Telestacicola* and referred to as *T. claudus* (HUMES & STOCK, 1973) comb. nov.

Without doubt the herein described *T. xenophiothricis* and *T. claudus* resemble each other in many characteristics, but the former differs from the latter by its longer caudal rami, the longer armature on the second antennal segment and the serrate nature of the terminal antennal claws.

THE COPEPOD-HOST RELATIONSHIP

In comparison with the three other associates (the polyclad *Discoplana* spec., the polynoid annelid *Hololepidella nigropunctata* and the phyllodocid annelid *Eumida ophiuricola*; DOIGNON, pers. obs.; BRITAYEV et al., 1999) of which the first two showed a much higher infestation rate of the host in the study area, *T. xenophiothricis* was found only in one station in some abundance. In this station, 11 out of 30 host specimens (37%) were infested with the copepod. In the other three stations infestation rates never exceeded 4%.

In most cases only a single copepod specimen was detected on the ophiurid central disc, but some brittlestars carried up to three copepod specimens on their body. The copepods seem to be explicitly located on the central disc, as they were never detected on the arms of the host.

The ophiurid host is, like so many of its congeners, a colourful animal with a magnificent and complex pattern of reddish lines (Fig. 4). The animals are commonly

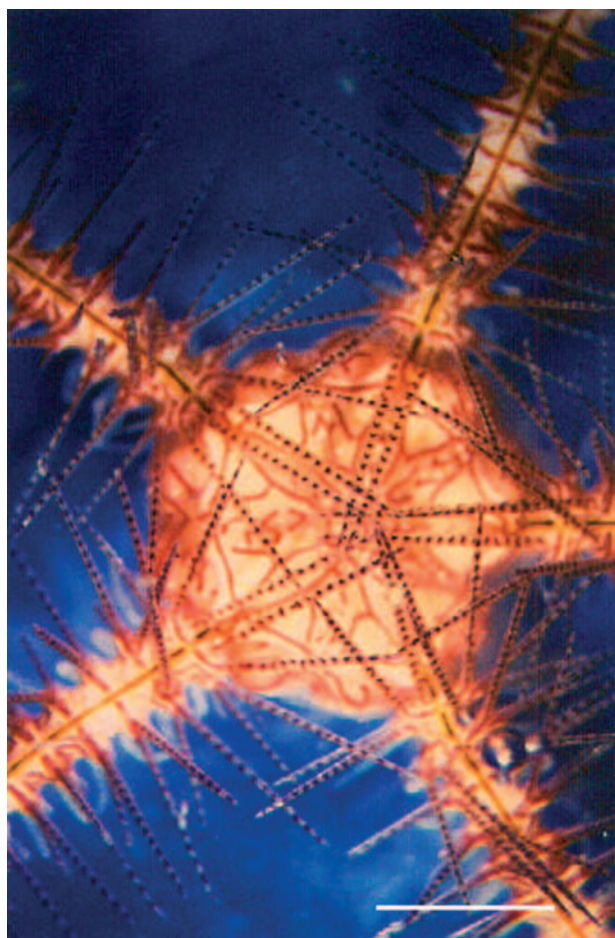


Fig. 4. – Central disc of *Ophiothrix purpurea* von Martens, 1867 showing colour pattern (Scale : 5 mm).

encountered aggregated on top of a wide diversity of branched scleractine and alcyonarian corals. Within the study area, *O. purpurea* was found on ten different scleractine corals (Acroporidae, Pocilloporidae and Poritidae) and on one species of Alcyoniidae.

The low infestation rate of the copepod, and the fact that three congeners are known from hydrozoan and anthozoan hosts led at first to the suggestion that the copepods were in fact strays from the populations living on the corals over which the ophiurid was crawling. However, the presence of a copepod associate was not readily detected during the in situ observations of the ophiurid by one of the authors (G.D.). As the copepod body has a particular colouration pattern of reddish lines dorsally and laterally on the prosome and laterally along the urosome on a creamy white background (Fig. 5), it mimics perfectly the colouration pattern of its host. The fact that the copepod remains attached with its buccal pieces fixed on the spiniform projections of the host's disc over a long period of time, made it difficult to locate the animal.

At the dawn of copepodology, researchers were already fascinated by the fact that several copepods living in association with other invertebrates were often colourful, and the bright illustrations, for example, in CANU (1892) are well known among those working in this field of research. The body colour in life of several lichomolgid copepods has been described (HUMES & STOCK 1973; HUMES,

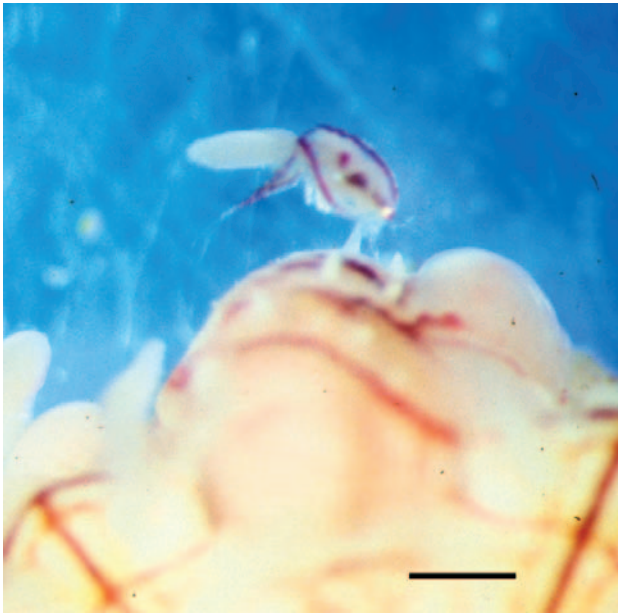


Fig. 5. – Part of the central disc of *Ophiothrix purpurea* with an ovigerous specimen of *Telestacicola xenophiothricis* n. sp. (Scale : 1 mm).

1982; HUMES, 1990). If colouration is present, the overwhelming majority have a uniform body colouration (light opaque gray to light brown) with the egg sacs somewhat darker. Others are transparent but have brightly coloured inner organs. *Herrmannella bullata* Humes & Stock, 1973 (Lichomolgidae) living in association with scallops, is in this context remarkable. Scallops show a clearly defined sexually-dimorphic colour of the tissues. Males are deep orange while females are white. According to the sex of the host, the copepod associate mimics the background on which it lives.

Among the Rynchomolgids, the red body color of *Acanthomolgus astrictus* Humes & Stock, 1973 has been said to imitate the color of the host gorgonian on which it lives, and species of the genus *Metaxymolgus* Humes & Stock, 1973 living on certain sea anemones are known to be vividly coloured with a dark red or dark green digestive cross resembling the coloured spots on the column of the host (HUMES, 1982).

Apparently the associated copepods, with a total body length of slightly more than 1 mm, may have advantage in their body colouration.

Brittlestars, and Echinodermata in general, are known to provide refuge for a wide array of invertebrates. JANGOUX (1990) listed 19 species of copepods parasitic on or in ophiuroids. If we include the species for which the parasitic nature has not been proved (quoted as “commensal” or “associates”) and the species described since that review, there are actually 46 species of Copepoda associated with ophiuroids. Most of them are Siphonostomatoida (22 species), which are ectosymbiotic, little modified and generally quite harmless to their hosts (genera *Astrocheres*, *Collocheres*, *Collocherides* and *Ophiurocheres* from the family Astrocheridae (HUMES, 1986; GOTTO, 1993; HUMES, 1998); *Cancerilla*, *Cancerillopsis*, *Ophiopsyllus*, *Parartotrogus* and *Parophiopsyllus* from the family Cancerillidae (BARTSCH, 1994; HUMES & HEN-

DLER, 1999)). *Codoba discoveryi* from the new family Codobidae (BOXSHALL & OHTSUKA, 2001), the cancerillid *Ophiopsyllopsis indicus* and the astrocherid *Collocherides astroboae* are the only Siphonostomatoida endosymbiotic on ophiuroids, the first two being found in the genital bursae of their hosts and the latter being found in their stomach (JANGOUX, 1990; HUMES & HENDLER, 1999). The Cyclopoida associated with ophiuroids (13 known species) are endosymbiotic, highly modified and induce galls on their hosts (genera *Arthrochordeumium*, *Chordeumium*, *Lernaeosaccus*, *Ophioicodes*, *Ophioika* and *Parachordeumium* from the family Chordeumiidae (BOXSHALL, 1988; BARTSCH, 1996)). The cyclopoid *Thespesiopsyllus* (*Thaumatopsyllus*) *paradoxus*, classified as Monstrilloida for a long time, is reported from the stomach of five species of ophiuroids (BAREL & KRAMERS, 1977; JANGOUX, 1990; HUYS & BOXSHALL, 1991). One Harpacticoida, *Thalestris longimana*, is known as ectosymbiotic on *Ophiopholis aculeata* and *Ophiothrix fragilis* (DAHMS, 1990). Among Poecilostomatoida, *Telestacicola xenophiothricis* is the tenth known species associated with ophiuroids. With the exceptions of *T. claudus* found in the stomach of *Euryale aspera* and *Critomolgus astrophyticus* occasionally found in the same compartment in *Astrophyton muricatum* (HUMES & STOCK, 1973; WILLIAMS & WOLFE-WATERS, 1990), all these poecilostomatoids (genera *Doridicola*, *Presynaptiphilus*, *Pseudanthessius* and *Telestacicola*) are exclusively ectosymbiotic and display only few anatomical modifications (HUMES, 1986; HUMES, 1998; HUMES & HENDLER, 1999; KIM, 2000; HO & KIM, 2001). As pointed out above, *T. xenophiothricis* is the only one amongst them to show a particular colouration that mimics perfectly that of its host; this complex and uncommon mimicry could be indicative of high host specificity.

ACKNOWLEDGEMENTS

The authors thank Dr I. Eeckhaut (UMH), Dr D. Van den Spiegel (UMH) and Mr G. Seghers (ULB) for their valuable help during sampling and for technical assistance on Laing Island. We also thank Prof. M. Jangoux (ULB & UMH) for permitting work in his laboratories. Funding for this research was provided by an FNRS (Fonds National pour la Recherche Scientifique, Belgique) grant to G. Doignon and by an FRFC convention (contract number 2.4560.96F). Contribution of the Centre Interuniversitaire de Biologie Marine (CIBIM), Belgium.

REFERENCES

- BAREL, C.D.N. & P.G.N. KRAMERS (1977). A survey of the echinoderm associates of the north-east Atlantic area. *Zool. Verh., Leiden*, 156 : 1-159.
- BARTSCH, I. (1994). Siphonostomatoida copepoden auf Ophiacanthiden (Ophiuroidea). Beschreibung von drei *Cancerilla*-arten (Cancerillidae, Copepoda) aus der Antarktis. *Mitt. Hamb. Zool. Mus. Inst.*, 91 : 61-76.
- BARTSCH, I. (1996). Parasites of the Antarctic brittle star *Ophiacantha disjuncta* (Ophiacanthidae, Ophiuroidea). Redescription of the copepod *Lernaeosaccus ophiacanthae* Heegaard, 1951. *Mitt. Hamb. Zool. Mus. Inst.*, 93 : 63-72.
- BOXSHALL, G.A. (1988). A review of the copepod endoparasites of brittle stars (Ophiuroidea). *Bull. Brit. Mus. Nat. Hist. (Zool.)*, 54 : 261-270.

- BOXSHALL, G.A. & S. OHTSUKA (2001). Two new families of copepods (Copepoda: Siphonostomatoida) parasitic on echinoderms. *J. Crust. Biol.*, 21 : 96-105.
- BRITAYEV, T.A., G. DOIGNON & I. EECKHAUT (1999). Symbiotic polychaetes from Papua New Guinea associated with echinoderms, with the description of three new species. *Cah. Biol. Mar.*, 40 : 359-375.
- CANU, E. (1892). Les Copépodes du Boulonnais. Morphologie, Embryologie, Taxonomie. *Trav. Lab. Zool. Mar. Wimereux-Ambleteuse*, 6 : 1-354, Pl. 1-30.
- DAHMS, H.-U. (1990). The first nauplius and the copepodite stages of *Thalestris longimana* Claus, 1863 (Copepoda, Harpacticoida, Thalestridae) and its bearing on the reconstruction of phylogenetic relationships. *Hydrobiologia*, 202 : 33-60.
- GOODING, R.U. (1957). On some Copepoda from Plymouth, mainly associated with invertebrates, including three new species. *J. Mar. Biol. Ass. U.K.*, 36 : 195-221.
- GOTTO, V. (1993). *Commensal and parasitic copepods associated with marine invertebrates (and whales)*. In : Synopses of the British fauna (new series), Vol. 46. KERMACK, BARNES & CROTHERS (Eds). Linnean Society of London & The Estuarine and Coastal Sc. Associated, Oegstgeest, The Netherlands : 1-264.
- HO, J.-S. & I.-H. KIM (2001). New species of *Doridicola* (Copepoda, Rhynchomolgidae) from Thailand, with a cladistic analysis of the genus. *J. Crust. Biol.*, 21 : 78-89.
- HUMES, A.G. (1982). A review of Copepoda associated with sea anemones and anemone-like forms (Cnidaria, Anthozoa). *Trans. Amer. Phil. Soc.*, 72 : 1-120.
- HUMES, A.G. (1986). Two new species of Copepoda associated with the basket star *Astroboa nuda* (Ophiuroidea) in the Moluccas. *Zool. Scripta*, 15 : 323-332.
- HUMES, A.G. (1990). Synopsis of lichomolgoid copepods (Poecilostomatoida) associated with soft corals (Alcyonacea) in the tropical Indo-Pacific. *Zool. Verh., Leiden*, 266 : 1-201.
- HUMES, A.G. (1994). How many copepods? *Hydrobiologia*, 292/293 : 1-7.
- HUMES, A.G. (1998). Copepoda (Siphonostomatoida) associated with Ophiuroidea in Jamaica, Puerto Rico, and Barbados. *Zool. Verh., Leiden*, 323 : 365-382.
- HUMES, A.G. & G.A. BOXSHALL (1996). A revision of the lichomolgoid complex (Copepoda : Poecilostomatoida), with the recognition of six new families. *J. Nat. Hist.*, 30 : 175-227.
- HUMES, A.G. & G. HENDLER (1999). Biology and taxonomy of species of *Ophiopsyllus* and *Pseudanthessius* (Copepoda) associated with brittle stars (Ophiuroidea) in Belize. *Bull. Mar. Sc.*, 65 : 699-713.
- HUMES, A.G. & J.H. STOCK (1973). A Revision of the Family Lichomolgidae Kossmann, 1877, Cyclopoid Copepods mainly associated with Marine Invertebrates. *Smiths. Contr. Zool.*, 127 : 1-368.
- HUYS, R. & G.A. BOXSHALL (1991). *Copepod evolution*. The Ray Society, London (468 pp).
- JANGOUX, M. (1990). Diseases of Echinodermata. In : *Diseases of Marine Animals (Vol. 3)*. KINNE (Ed.). Biologischen Anstalt Helgoland, Hamburg : 439-567.
- KIM, I.-H. (2000). Poecilostomatoid copepods from an intertidal mud flat in the Yellow Sea. *J. Nat. Hist.*, 34 : 367-432.
- WILLIAMS, E.H. Jr & T.J. WOLFE-WATERS (1990). An abnormal incidence of the commensal copepod, *Doridicola astrophyticus* Humes, associated with injury of its host, the basketstar, *Astrophyton muricatum* (Lamarck). *Crustaceana*, 59 : 302.

