Copyright © 2008 · Magnolia Press



A new genus and species of Brychiopontiidae Humes, 1974 (Crustacea: Copepoda: Siphonostomatoida) associated with an abyssal holothurian in the Northeast Pacific nodule province*

RADITH MAHATMA¹, PEDRO MARTÍNEZ ARBIZU^{1*} & VIATCHESLAV N. IVANENKO²

¹Deutsches Zentrum für Marine Biodiversitätsforschung, Forschungsinstitut Senckenberg, Südstrand 44, 26382 Wilhelmshaven, Germany. E-mails: rmahatma@senckenberg.de, pmartinez@senckenberg.de * corresponding author ²Department of Invertebrate Zoology, Biological Faculty, Moscow State University, Moscow 119899, Russia. E-mail: ivanenko@soil.msu.ru

*In: Martínez Arbizu, P. & Brix, S. (Eds) (2008) Bringing Light into Deep-sea Biodiversity. Zootaxa, 1866, 1–574.

Abstract

A new genus and species *Neobrychiopontius galeronae* gen. nov. sp. nov. is described based on female specimens from the Pacific nodule province associated with the abyssal holothurian *Oneirophanta* cfr. *setigera* (Ludwig, 1894) (Elasipodida, Deimatidae). The holothurian and copepods were collected at a depth of 4978 m during the cruise "Nodinaut" (Ifremer, 17 May – 28 June 2004) on RV *Atalante* using a spade corer operated from the submersible *Nautile*. The new genus has retained a greater number of plesiomorphic characters, when compared to its closest relative the monotypic genus *Brychiopontius* Humes, 1974 from the abyssal zone of the North Atlantic: proximal 3 segments of antennule articulates (fused in *Brychiopontius*), well developed mandibular palp and inner lobe of maxilla (both absent in *Brychiopontius*). On the other hand the new genus has only 2 outer spines on the third exopodal segment of leg 1 (instead of 3 in *Brychiopontius*). Two plesiomorphic characters hitherto unknown for the order Siphonostomatoida are present in the new genus viz. the inner lobe of the first segment of the maxilla is armed with 2 setae and the first segment of the mandibular palp is armed with 1 seta. *Neobrychiopontius galeronae* gen. et sp. nov. is the second species of Siphonostomatoida found in association with abyssal holothurians (both belonging to the genus *Oneirophanta*) and represents the first record of the family Brychiopontiidae in the Pacific Ocean.

Key words: *Neobrychiopontius* gen. nov., deep-sea, polymetallic nodules, invertebrate symbiosis, phylogenetic systematics

Introduction

A great number of copepods of the order Siphonostomatoida representing 11 families, as well as many cyclopoid and harpacticoid copepods, live in association with echinoderms (Humes 1980, Huys 1988, Boxshall & Ohtsuka 2001, Ivanenko, Ferrari & Smurov 2001). However, only four families have been found associated with holothurians so far. One species each belongs to the speciose families Asterocheridae Giesbrecht, 1899 and Artotrogidae Brady, 1880 and are associated with shallow water holothurians in the Mediterranean Sea (Giesbrecht 1899, Humes 1980). Copepods of the derived family Nanaspididae Humes & Cressey, 1959 appear to be restricted to holothurians. The family Brychiopontiidae Humes, 1974 was represented so far by a single species *Brychiopontius falcatus* Humes, 1974 recovered from washings of the abyssal holothurian *Oneirophanta mutabilis* Theel (Elasipodida, Deimatidae) collected in the eastern North Atlantic at a depth of 4426–4435 m (Hansen, 1975). Most siphonostomadoids from abyssal sites are recorded from deep-sea hydrothermal vents or from deep-sea plankton (Heptner 1968, Humes 1987, Ivanenko & Defaye 2006). The present paper describes a new genus and species *Neobrychiopontius* gen. nov., sp. nov. from the Pacific nodule province found associated with the holothurian *Oneirophanta* cf. *setigera* (Ludwig 1894, Veillette et al. 2007).

Material and Methods

A holothurian was collected together with sediment using a spade corer (Fig. 1) operated from the submersible *Nautile* during the cruise "Nodinaut" on board of the French RV *L'Atalante* (Dive number PL1595/03, gear: CL 05, from 26/05/2004 at 4978 m depth, coordinates: 14°02.37'17N; 130°06.93'62W). On board the holothurian was removed from the sample, photographed (Fig. 2) and fixed for further studies. The sediment together with the supernatant water was fixed in formalin at a final concentration of 4% for infaunal studies. In the laboratory, all organism were sorted from the sediment. The copepods were transferred to glycerin and dissected under a Leica MZ12 microscope. All specimens or appendages were studied with a Leica DMR compound microscope with bright-field and differential interference optics. Drawings were made with the aid of a drawing tube mounted on the compound microscope. For long-term preservation, the dissected copepods were mounted on slides in glycerol and sealed with paraffin.



FIGURE 1. In situ photograph of the sample taken for this study showing the spade corer with a specimen of the holothurian *Oneirophanta* cfr. *setigera*. Depth 4978 m. Copyright Ifremer.

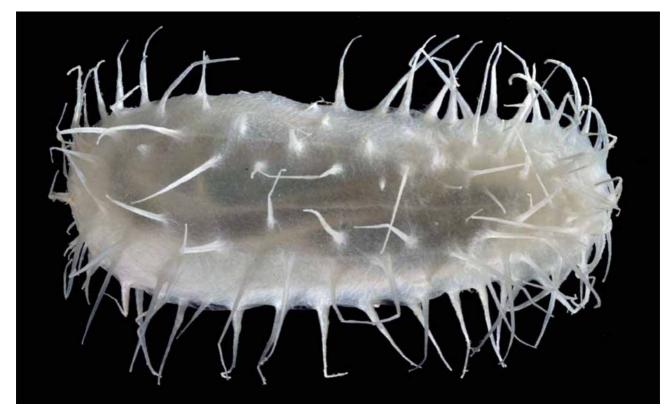


FIGURE 2. Oneirophanta cfr. setigera, the host of Neobrychiopontius galeronae gen. et sp. nov. Copyright Ifremer.

Description Class Copepoda Order Siphonostomatoida Burmeister, 1835 Family Brychiopontiidae Humes, 1974

Neobrychiopontius gen. nov.

Diagnosis—Female. Prosome 4-segmented, with rounded epimeral areas; urosome 5-segmented, consisting of leg 5 bearing somite, genital double-somite, 2 abdominal somites and telson; telson 2 times longer than second abdominal somite. Rostral area projecting ventrally. Oral cone with distal disk formed by labrum and labium. Furca with 7 setae, 12 times longer than wide. Antennule 21-segmented with aesthetasc on segment 18. Antenna and maxilliped with elongate, blunt-pointed, toothed terminally terminal seta. Mandible with 2-segmented palp, each segment armed with 1 seta. First segment of maxilla with inner lobe bearing 2 setae (1 small) near joint with second claw-like segment. Legs 1 to 4 with 3-segmented rami, formula of armature as for the type species. Leg 5 1-segmented, on ventro-lateral side, with 4 setae. Leg 6 represented by 2 setae. Male unknown.

Etymology—The genus name is a combination of the Greek word "neo" (= new) and the name of the type genus.

Type and only species—Neobrychiopontius galeronae sp. nov.

Distribution—Only known from the type locality in the Northeast Pacific nodule Province.

Neobrychiopontius galeronae sp. nov.

Type material —Holotype 9 (SMF 31444) dissected and mounted on 14 slides and 2 paratype females (SMF

31445) preserved in ethanol, locality as below. The type material is deposited in the collection of the Senckenberg Museum, Frankfurt (SMF), Germany.

Type locality—The nodule province in the northeast Pacific Ocean, 14°02.37N; 130°06.93W, depth 4978 m, date 26/5/2004.

Etymology—The species is dedicated to the chief scientist of the cruise Joëlle Galéron (Ifremer, France) in recognition of her scientific achievements.

Description—Adult female (Fig. 3 A). Total length excluding furca 1.4 mm, greatest width 0.74 mm. Prosome 4-segmented, flattened, narrowing anteriorly; epimeral areas of shield and tergites rounded. Urosome (Fig. 3 B) 5-segmented, consisting of somite bearing leg 5, genital double-somite and 2 abdominal somites plus telson. Genital double-somite slightly wider than long; lateral expansions in the anterior part; gonopores located in a dorsolaterally covered by leg 6 bearing 2 small setae (Fig. 3 C). Telson 2 times longer than second abdominal somite; anus located dorsally.

Rostrum (Fig. 3 E) weakly developed, slightly projecting ventrally.

Oral cone (Fig. 3 E, F) short and robust, with distal disk formed by labrum and labium and ornamented with setules.

Egg sacs not observed.

Furca (Fig. 3 B, D) elongate, longer than 2 free abdominal somites and telson together, about 12 times longer than wide, ornamented with rows of spinules, and bearing 7 setae of different lengths (2 setae lost in holotype), one seta is small (see Fig. 3 B).

Antenna (Fig. 4 E, F; 5 A, B): small coxa without ornamentation and setation, elongate basis with spinules on outer margin. Exopod 1-segmented, with 3 smooth setae. Endopod 2-segmented; segment 1 elongate, with spinules along outer and inner margins; segment 2 short, ornamented with setules, armed with 4 setae, 1 seta long and thick, blunt-pointed and toothed terminally.

Mandible (Fig. 5 C): gnathobase long and slender, toothed terminally; palp 2-segmented, each segment with one seta.

Maxillule (Fig. 5 D) bilobed, ornamented with spinules; smaller outer lobe bearing 4 setae, three terminal and one sub-terminal; inner lobe with five terminal setae.

Maxilla (Fig. 5 E, F) 2-segmented: segment 1 wide; segment 2 elongate, with claw-like distal part; inner lob of the first segment armed with 2 setae (1 small).

Maxilliped (Fig. 6 A) syncoxa with 1 long inner seta; basis with inner seta along inner margin of the segment. Endopod 3-segmented: segment 1 with 2 short posterior setae; segment 2 with 2 longer posterior setae; segment 3 bearing 2 terminal setae, 1 seta long and thick, blunt-pointed and toothed terminally.

Legs 1–4 biramous (Figs. 6 B; 7 A, B; 8 A) with 3-segmented rami ornamented by spinules and scales, as illustrated. Formula for the armature of legs 1–4 in Table 1. Leg 1: first segment of exopod with falcate, strong outer spine curved inward; third exopodal segment with 2 outer spines.

TABLE 1. Formula of the armature of swimming legs 1–4, holotype female of *Neobrychiopontius galeronae* gen. nov., sp. nov. Roman numerals indicate spines, Arabic numerals indicate setae.

	Coxa	Basis	Exopod	Endopod	
Leg 1	0-1	1-1	I-1;I-1;II,4	0-1;0-2;1,2,3	
Leg 2	0-1	1-0	I-1;I-1;III,I,4	0-1;0-2;1,2,3	
Leg 3	0-1	1-0	I-1;I-1;III,I,4	0-1;0-2;1,I,3	
Leg 4	0-1	1-0	I-1;I-1;III,I,4	0-1;0-2;1,I,2	

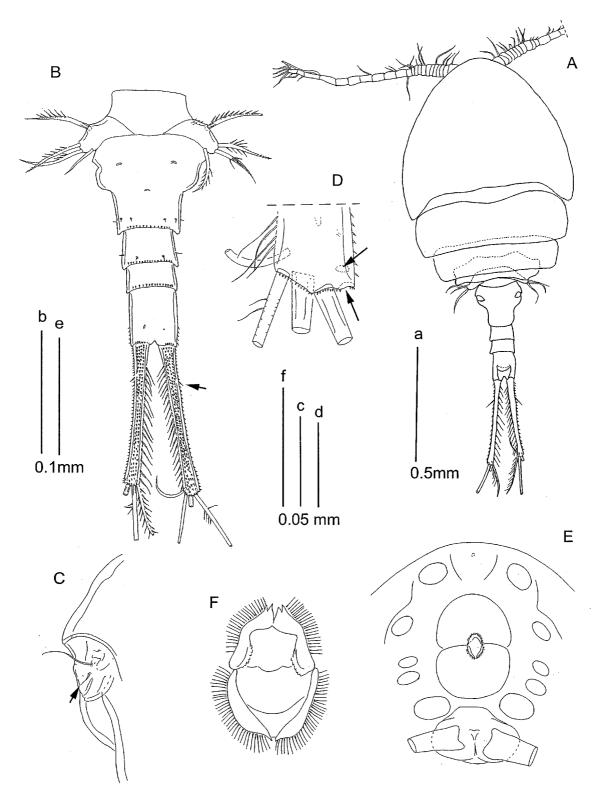


FIGURE 3. *Neobrychiopontius galeronae* gen. nov., sp. nov., holotype female. A, habitus, dorsal; B, urosome, ventral, arrow to small seta; C, left leg 6 and area with gonopores, genital double-somite, dorsal, arrow to small seta; D, distal part of furca bearing 6 setae, arrow to location of missing setae; E, rostral area and oral cone, ventral. F, distal part of oral cone formed by labrum and labium, ventral.

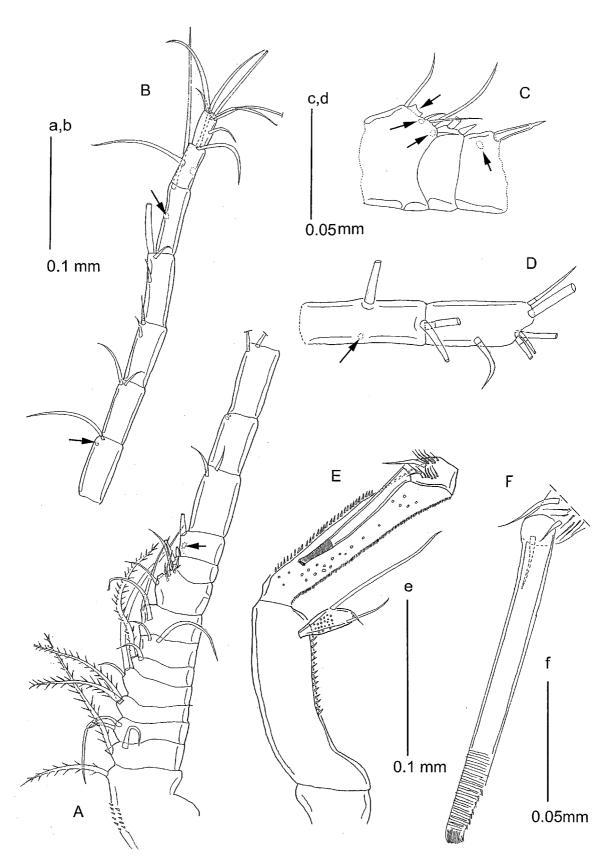


FIGURE 4. *Neobrychiopontius galeronae* gen. nov., sp. nov., holotype female. A, antennule, segments 1 to 14; B, antennule, segments 15 to 21; C, antennule, segments 9 to 11; D, antennule, segments 20 to 21; E, antenna; F, antenna, terminal element and distal part of second endopodal segment. Arrows to location of missing setae.

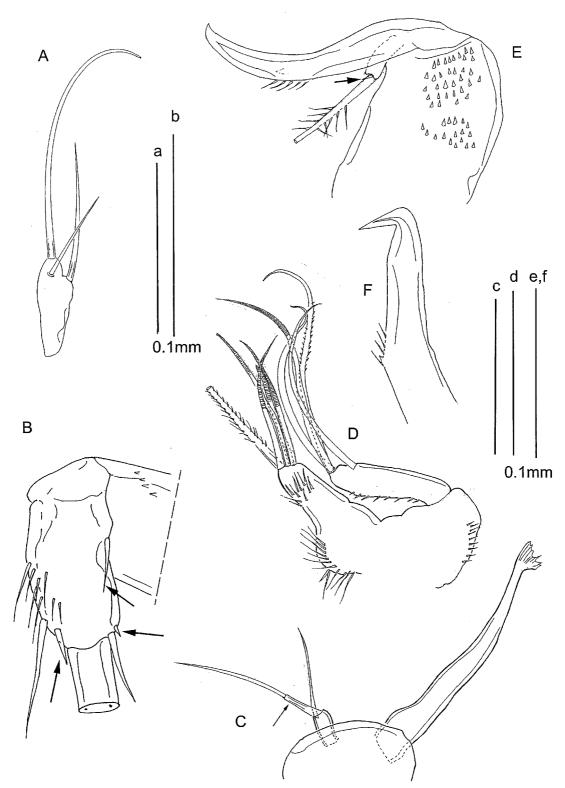


FIGURE 5. *Neobrychiopontius galeronae* gen. nov., sp. nov., holotype female. A, exopod of antenna; B, second segment of antennal endopod, arrows to small setae; C, mandible, arrow to second segment of palp; D, maxillule; E, maxilla, arrow to small seta; F, distal part of second segment of maxilla.

Leg 5 (Figs. 8 B): latero-ventral, 1-segmented, ornamented with spinules and armed with 4 setae. Leg 6 (Fig. 3 C) represented by genital flap bearing 2 setae. Colour unknown. Male unknown.

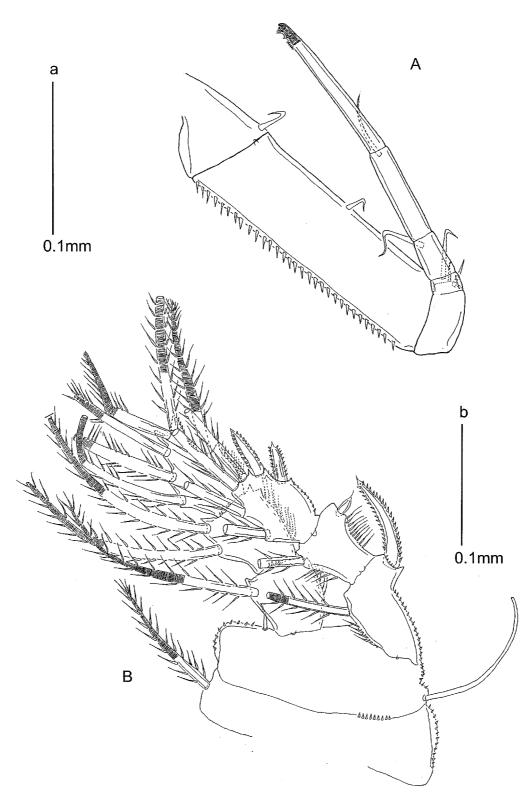


FIGURE 6. *Neobrychiopontius galeronae* gen. nov., sp. nov., holotype female. A, maxilliped, anterior; B, leg 1, posterior.

Discussion

Brychiopontiidae displays a number of primitive characters within Siphonostomatoida such as the urosome of females being 5-segmented, the presence of 3 additional distal segments after the distal aesthetasc of the antennule in female ("mark A" in Ivanenko, 1999), and the presence of a mandibular palp. Representatives of

10 genera of polyphyletic family Asterocheridae Giesbrecht, 1899, viz. *Bythocheres* Humes, 1988; *Chera-momyzon* Humes, 1989; *Collocheres* Canu, 1893; *Collocherides* Stock, 1971; *Dermatomyzon* Claus, 1889; *Gerulusosacculus* Ivanenko & Defaye, 2004, *Glyptocheres* Humes, 1987a; *Ophiurocheres* Humes, 1998; *Rhynchomyzon* Giesbrecht, 1895 share some or all of these plesiomorphic characters.

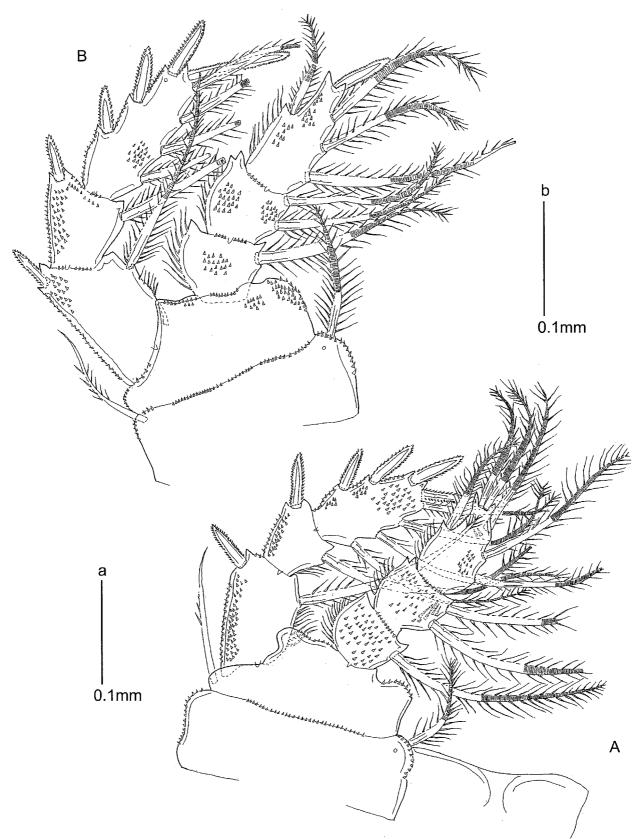


FIGURE 7. Neobrychiopontius galeronae gen. nov., sp. nov., holotype female. A, leg 2, anterior; B, leg 3, anterior.

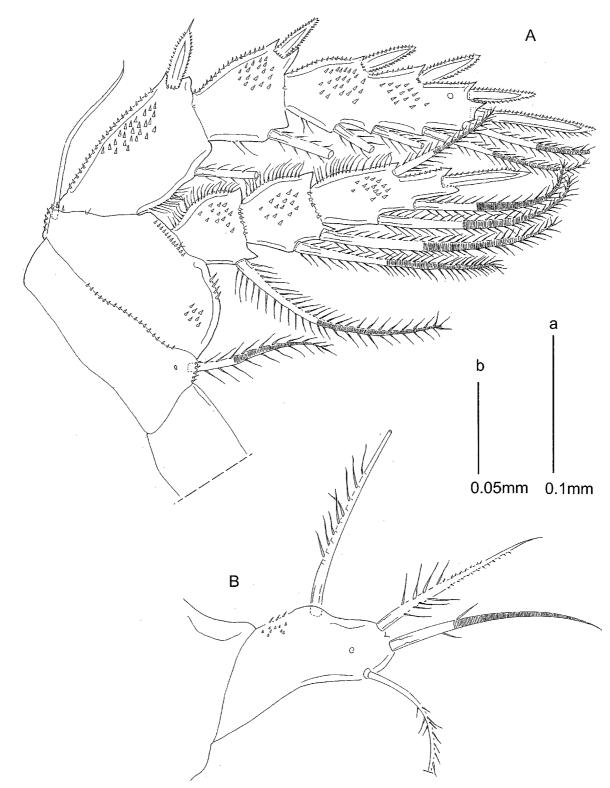


FIGURE 8. Neobrychiopontius galeronae gen. nov., sp. nov., holotype female. A, leg 4, anterior; B, leg 5.

The presumably apomorphic characters of the family Brychiopontiidae are (1) the falcate, strong inwardly-curved outer spine on the first segment of the exopod of leg 1 (but a similar stout spine is shown for 2 species of asterocherids (see Stock, 1966) and (2 & 3) the blunt-pointed terminal element on the antenna and maxilliped (but also shown for the derived siphonostomatoid family Calverocheridae Stock, 1968, Nanaspid-idae and Stellicomitidae Humes & Cressey, 1958 associated with echinoderms). Appearance of the modified

spine on leg 1 in different groups of genera can be explained by convergence, while presence of the bluntpointed terminal element on the antenna and maxilliped in different siphonostomatoid families requires additional investigation. All these indicate that a revision of characters and phylogenetic analysis of Asterocheridae and related families including Brychiopontiidae, as well as Scottomyzontidae and Coralliomyzontidae Humes & Stock, 1991 is urgently needed. Meanwhile, the proposed synonymization of Scottomyzontidae and Coralliomyzontidae with Asterocheridae by Boxshall & Halsey (2004) is not based on a phylogenetic analysis and is therefore not adopted here. The genus *Bythocheres* Humes, 1988 was tentatively placed in Asterocheridae by Boxshall & Halsey (2004), but remains in our view a genus with uncertain phylogenetic and unresolved family position.

Neobrychiopontius gen. nov. is the second genus of siphonostomatoid copepods found in association with abyssal holothurians and the first record of the family Brychiopontiidae in the Pacific Ocean. The new genus can be easily distinguished from *Brychiopontius* by the presence of only 2 (instead of 3) outer spines on the third exopodal segment of leg 1. Besides this, Neobrychiopontius has retained a number of plesiomorphic characters when compared with its closest relative (character states present in *Brychiopontius* in brackets), viz. i.) 3 well-articulated proximal segments on female antennule (proximal 3 segments fused to form a long compound segment), ii.) mandibular palp present, 2-segmented (absent), and iii.) inner conical lobe of the first segment of maxilla present (absent). In addition *Neobrychiopontius* differs from the type genus *Brychi*opontius in the following characters: i.) anterior part of prosome is narrow (wide), ii.) rostral area slightly projecting ventrally (slightly projecting anteriorly), iii.) epimeral areas of prosome are rounded (pointed posteriorly), iv.) anal opening located near the middle of the telson (near the posterior margin), v.) furca 12 times longer than wide (6.4 times), with 7 setae (6), ornamented with spinules (not ornamented), longer than posterior 2 free abdominal somites and telson together (shorter), vi.) oral cone with distal disk ornamented with setules (lacking distal disk and ornamentation of the oral cone), vii.) antenna and maxilliped with terminal endopodal element elongate, toothed terminally (the element is short and stout, with lamelliform distal part, toothless), viii.) maxilla first segment with an inner conical expansion (without expansion), ix.) maxilliped with 2 setae on the second endopodal segment (no setae), x.) leg 5 without inner process (with inner conical process), and xi.) leg 6 with 2 setae (1 seta).

Two important primitive characters found in *Neobrychiopontius* are unique for the order Siphonostomatoida. Until now the inner lobe of the first segment of the maxilla was represented by a single seta in Dirivultidae Humes and Dojiri, 1980 and Ecbathyriontidae Humes, 1987b. The new genus displays a lobe with 2 setae. The second character refers to the first segment of the mandibular palp which is armed with 1 seta, while it is unarmed in all other known members of the order. The diagnosis of the order has to be amended accordingly.

Ecology

Specimens were recovered from deep-sea sediments of a sample which had previously contained a specimen of the holothurian *Oneirophanta* cfr. *setigera*. We conclude that the specimens in question detached from the holothurian host during sample manipulation on board. Both *Brychiopontius falcatus* and *Neobrychiopontius galeronae* gen. et sp. nov. were found associated with deep-sea holothurians belonging to the genus *Oneirophanta*. The diversity of siphonostomatoid copepods associated with other abyssal holothurians remains largely unexplored so far. Only the cyclopoid copepod *Gomphopodarion byssoicum* Humes, 1974, presumably an endoparasite, was found associated with the holothurian *Oneirophanta mutabilis* Theel together with the siphonostomatoid *Brychiopontius falcatus*. It is likely that most macroinvertebrates present in the abyssal plains will host a variety of associated and parasitic copepods. Study of these animals should provide important additional evidence about phylogenetic affinities and biogeographic distributions.

Acknowledgments

The copepods were collected during the cruise "Nodinaut". We are indebt to the captain of RV *L' Atalante* to Joëlle Galéron (Ifremer, Departement Etude des Ecosystemes Profonds, Brest) the chief scientist of the cruise for inviting Pedro Martínez Arbizu to participate and to the crew of the submersible *Nautile* for taking the samples. The research of Viatcheslav N. Ivanenko was supported by the Census of Diversity of Abyssal Marine Life (CeDAMar), a Census of Marine Life project (www.coml.org), and the Russian Foundation for Basic Research (Grant 06-04-48918-a). The contribution of Radith Mahatma was supported by a TPSDP grant of the Ministry of National Education of Indonesia.

References

- Boxshall, G.A. & Halsey, S.H. (2004) An Introduction to Copepod Diversity. The Ray Society, London, 966 pp.
- Boxshall, G.A., Ohtsuka, S. (2001) Two new families of copepods (Copepoda: Siphonostomatoida) parasitic on echinoderms. *Journal of Crustacean Biology*, 21(1), 96–105.
- Brady, G.S. (1880) A monograph of the free and semi-parasitic Copepoda of the British Islands. The Ray Society, London, 3, 83 pp.
- Burmeister, H. (1835) Beschreibung einiger neuer oder weniger bekannter Schmarotzerkrebse, nebst allgemeine Betrachtungen über die Gruppe, welcher sie angehören. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum (Acta der Kaiserlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher), 17, 269–336.
- Canu, E. (1893) Un Copépode ascomyzontide sur une algue pélagique. Annales de la Station Aquicole de Boulogne-sur-Mer, 1(2), 100–107.
- Claus C. (1889) Über neue oder wenig bekannte halbparasitische Copepoden insbesondere der Lichomolgiden- und Ascomyzontiden-Gruppe. Arbeiten aus dem Zoologischen Institut der Universitat Wien und der Zoologischen Station in Triest. 8, 327–370.
- Giesbrecht W. (1895) The subfamilies, genera, and species of the copepod family Ascomyzontidae Thorell: diagnosis, synonymy, and distribution. *Annals and Magazine of Natural History*, 6(16), 173–186.
- Giesbrecht, W. (1899) *Die Asterocheriden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte*. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte, 25, 217 pp.
- Hansen, B. (1975) Systematics and biology of the deep-sea holothurians. Galathea Report, 13, 1-262.
- Heptner, M.V. (1968) Description and functional morphology of *Megapontius pleurospinosus* sp. n. from the Pacific with some remarks on the status of genus *Megapontius* within the system of families of Siphonostoma group (Copepoda, Cyclopoida). *Zoologicheskii Zhurnal*, 47 (11), 1628–1638.
- Humes, A. G. (1974) New cyclopoid copepods associated with an abyssal holothurian in the eastern North Atlantic. *Journal of Natural History*, 8, 101–117.
- Humes, A. G. (1980) A review of the copepods associated with holothurians, including new species from the Indo-Pacific. *Beaufortia*, 30, 31–123.
- Humes, A.G. (1987a) Copepoda associated with crinoid echinoderms in the western Pacific. *Publications of the Seto Marine Biological Laboratory*, 32(1–3), 63–108.
- Humes, A.G. (1987b) Copepoda from deep-sea hydrothermal vents. Bulletin of Marine Science, 41, 645-788.
- Humes, A.G. (1988) *Bythocheres prominulus*, a new genus and species (Copepoda: Siphonostomatoida) from deep-water cold seeps at the West Florida Escarpment. *Proceedings of the Biological Society of Washington*, 101 (3), 568–575.
- Humes, A.G. (1989) Copepoda from deep-sea hydrothermal vents at the East Pacific Rise. *Bulletin du Museum national d'Histoire naturelle, Paris, 4e série, section A*, 4, 829–849.
- Humes A.G. (1998) Copepoda (Siphonostomatoida) associated with Ophiuroidea in Jamaica, Puerto Rico, and Barbados. *Zoologische Verhandelingen*, 323, 365–382.
- Humes, A.G. & Cressey, R.F. (1958) A new family containing two new genera of cyclopoid copepods parasitic on starfishes. *Journal of Parasitology*, 44 (4), 395–408.
- Humes, A.G. & Cressey, R.F. (1959) A new family and genus of cyclopoid copepods parasitic on a holothurian. *Journal* of *Parasitology*, 45 (2), 209–216.
- Humes, A.G. & Dojiri, M. (1980) A new siphonostome family (Copepoda) associated with a vestimentiferan in deep water off California. *Pacific Science*, 34, 143–151.
- Humes, A.G. & Stock, J.H. (1991) Coralliomyzontidae, fam. n. (Copepoda: Siphonostomatoida), associated with scleractinian corals in Madagascar. *Bull. Zool. Univ. Amsterdam*, 13, 17–24.

- Huys, R. (1988) On the identity of the Namakosiramiidae Ho & Perkins 1977 (Crustacea, Copepoda) including a review of harpacticoid associates of Echinodermata. *Journal of Natural History*, 22(6), 1517-1532.
- Ivanenko V.N. (1999) Comparative analysis of the antennules of the asterocherid females (Copepoda, Siphonostomatoida) - symbionts of marine invertebrates. In F.R. Schram and J.C. von Voupel Klein (Eds.) Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20-24, 1998, Vol. I. Koninklijke Brill, Leiden, pp. 207–216.
- Ivanenko V.N., Ferrari F.D., Smurov A.V. (2001) Nauplii and copepodids of Scottomyzon gibberum (Copepoda: Siphonostomatoida: Scottomyzontidae, new family), a symbiont of Asterias rubens (Asteroidea). Proceedings of the Biological Society of Washington, 114 (1), 237–261.
- Ivanenko, V.N. & Defaye, D. (2004) A new genus and species of the family Asterocheridae (Copepoda: Siphonostomatoida) from the East Equatorial Atlantic (Angola margin). *Crustaceana*, 77 (9), 1131–1144.
- Ivanenko, V.N. & Defaye, D. (2006) Copepoda. In: Desbruyères, D. Segonzac, M. & Bright, M. (Ed.) Handbook of Deep-Sea Hydrothermal Vent Fauna. Second completely revised edition. Denisia, 18, pp. 318–355.
- Ludwig, H. (1894) Reports on a exploration of the west coast of Mexico, Central and South America, and off the Galapagos Islands in charge of Alexander Agassiz by the U.S. Fish Commission Steamer "Albatross" during 1891. XII. The Holothurioidea. *Memoirs of the Museum of Comparative Zoology at Harvard College*, XVII (3), 1–183.
- Stock, J.H. (1966) Cyclopoida siphonostoma from Mauritius (Crustacea, Copepoda). Beaufortia, 13 (159), 145–194.
- Stock, J.H. (1968) The Calvocheridae, a family of copepods inducing galls in sea-urchin spines. *Bijdragen tot de Dierkunde*, 38, 85–90.
- Stock, J.H. (1971) *Collocherides astroboae* n. gen., n. sp., a siphonostome cyclopoid copepod living in the stomach of basket stars. *Bijdragen tot de Dierkunde*, 41, 19–22.
- Veillette, J., Sarrazin, J., Gooday, A.J., Galéron, J., Caprais, J.-C., Vangriesheim, A., Étoubleaub, J., Christiand, J.R.
 & Junipera S.K. (2007) Ferromanganese nodule fauna in the Tropical North Pacific Ocean: Species richness, faunal cover and spatial distribution. *Deep Sea Research Part I: Oceanographic Research Papers*, 54 (11), 1912-1935.