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ORIGINAL ARTICLE

Lecithotrophic nauplius of the family Dirivultidae (Copepoda; Siphonostomatoida) hatched on board over the Mid-Atlantic Ridge (5°S)

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Abstract

A copepod nauplius of the family Dirivultidae Humes & Dojiri 1980 is described for the first time. The lecithotrophic nauplius of the widespread symbiotic copepod *Stygiopontius pectinatus* Humes 1987 was released from females bearing paired egg sacs that included only one yolky embryo each. The ovigerous females of *S. pectinatus* were washed from the branchial chamber of alvinocaridid shrimps (*Rimicaris exoculata* Williams & Rona 1986) collected at a deep-sea hydrothermal field on the Mid-Atlantic Ridge at 5° S (Red Lion site, chimney 'Shrimps Farm', depth 3,048 m) by *ROV Quest 4000* and maintained in a laboratory on the *R/V METEOR* (cruise M64/1, 2005). The nauplius of *S. pectinatus*, appears to be a stage I nauplius because it bears only one pair of caudal setae and the setose bud of maxilla 1 is absent. Like nauplii of other copepods of the order Siphonostomatoida, this nauplius of *S. pectinatus* possesses a reduced labrum and the body is filled with yolky granules; it also lacks a masticatory process on the antennal coxa. The presence of two inner setae (instead of one seta) on the mandibular endopod is hypothesized to be a primitive character of dirivultids that distinguishes them from the remaining siphonostomatoid genera. The Dirivultidae is a widespread and diverse family of copepods endemic to the deep-sea hydrothermal vents of the Pacific and Atlantic Oceans. Morphological features of the planktonic nauplius of *S. pectinatus* suggest nutritional independence during their dispersal.

Problem

Dirivultidae Humes & Dojiri 1980 is the most diverse family of copepods (49 species in 13 genera) found in deep-sea hydrothermal vents of the Mid-Atlantic Ridge (MAR) and the Pacific Ocean (Ivanenko 2006; Ivanenko & Defaye 2006a; Ivanenko *et al.* 2006). This family belongs to the order Siphonostomatoida, which includes many families of copepods whose species usually parasitize fishes and invertebrates (Martin & Davis 2001). In contrast, morphological observations and ecological data suggest that most dirivultids are free-living or associated with invertebrates, and that they feed on small particles and bacterial films (Humes & Lutz 1994; Heptner & Ivanenko 2002; Tsurumi *et al.* 2003). Some dirivultids live in association with invertebrates (polychaetes, shrimps, bivalves *etc.*); a few, such as copepods of the type genus *Dirivultus* Humes & Dojiri 1980, are found on vestimentiferan polychaetes and are considered parasites (Humes & Segonzac 1998; Heptner & Ivanenko 2002).

The symbiotic dirivultid *Stygiopontius pectinatus* Humes 1987 has been recovered from several sites on the MAR; they have been collected from the branchial chamber of alvinocaridid shrimps and from the plankton over the hydrothermal field (Humes 1987, 1996; Ivanenko 1998; Ivanenko *et al.* 2006). The species also has been found in hydrothermal fields of the Mariana Back-Arc Basin (West Pacific) where it was associated with the polychaete *Alvinella pompejana* (Humes 1990). Thousands of adult females have been collected, but males of *S. pectinatus* are unknown. Observations of the feeding apparatus of the females suggest that *S. pectinatus* can ingest chemoautotrophic bacteria growing on the inner surface of the branchial chamber and on the feeding appendages of alvinocaridid shrimps (Humes 1996; Ivanenko *et al.* 2006).

This paper describes a naupliar stage of the family Dirivultidae for the first time.

Material and Methods

Alvinocaridid shrimp and dirivultid copepods associated with them were collected by the *ROV Quest 4000* (Marum University of Bremen) operating from the *R/V METEOR* during cruise M64/1 on the MAR at 5° S (Red Lion site, chimney 'Shrimps Farm', depth 3,048 m; 14°47.824′ S, 12°22.595′ W) on April 16, 2005 (Devey *et al.* 2005). The vent site and the methods used for collecting shrimp are described by Ivanenko *et al.* (2006). All specimens were washed from alvinocaridid shrimp (*Rimicaris exoculata* Williams & Rona 1986) in filtered seawater and sieved through 40 μm mesh. The live copepods were kept in Petri dishes for 2 h then preserved with 72% ethanol. The nauplii described here were found in a sample (146 ROV#6) containing 316 adult females and two first copepodites of the dirivultid species *Stygiopontius pectinatus* Humes 1987 (Ivanenko *et al.* 2006).

The copepods were studied applying the 'hanging drop method' described in detail by Ivanenko & Defaye (2004). The copepods were dissected under a Leica MZ12 microscope and studied with a Leica DMR compound microscope having bright-field and differential interference contrast optics. Drawings were made with a *camera lucida* mounted on the microscope. For long-term preservation, the dissected copepods were mounted on slides in glycerol and sealed with paraffin.

The copepods are in the DZMB – Forschungsinstitut Senckenberg, Wilhelmshaven, Germany.

Results

Most of the females carried two egg sacs, each of them containing a single ovoid embryo whose body was filled with yolk granules.

We studied three stage I nauplii (Fig. 1), one of which was found inside a broken embryo sac. The description is as follows. Body (Fig. 1A,B) ovoid, filled with spherical granules of yolk. Length: 0.24 mm, maximum width 0.18 mm. Caudal rami represented by one pair of fine setae. Naupliar eye not observed. Labrum, mouth and anal opening not present. Antennule (Fig. 1C): one-segmented, armed with three terminal and two midventral setae. Antenna (Fig. 1D): short coxa without masticatory process, separate from elongate basis, both coxa and basis unarmed. Exopod of antenna five-segmented, armed with 1, 1, 1, 1, and 2 setae; first segment elongate, fused with basis. Endopod of antenna two-segmented, first segment unarmed, indistinctly separate from basis, second segment armed with three setae, two terminal and one midventral. Mandible (Fig. 1E): coxa separate from elongate basis, both coxa and basis unarmed. Exopod of mandible four-segmented, armed with 1, 1, 1, and 2 setae; first segment elongate, fused with basis. Endopod of mandible one-segmented, indistinctly separate from basis, armed with four setae, one proximoventral, one distoventral and two terminal.

Discussion

The nauplius of *Stygiopontius pectinatus* possesses features common to nauplii of copepods of the order Siphonostomatoida, as well as to many nauplii of parasitic copepods in other orders (Giesbrecht 1899; Lang 1949; Changeux 1961; Carton 1968; Röttger *et al.* 1972; Johnson & Albright 1991; Lin *et al.* 1997; Ivanenko *et al.* 2001). The body is full of yolky granules, lacks a masticatory process on the antennal coxa, and the labrum is reduced in size. Correspondence of this dirivultid nauplius to the nauplius I of the free-living copepods with six naupliar stages is uncertain because the number of naupliar stages of dirivultid copepods remains unknown. At most, four morphologically distinguishable naupliar stages have been described for other copepods of the order Siphonostomatoida (Ivanenko *et al.* 2001). The better studied siphonostomatoid copepods that parasitize fishes have at most two naupliar stages (Johnson & Albright 1991; Lin *et al.* 1997). However, a single pair of caudal setae and the absence of the setose bud of maxilla 1 suggest that this nauplius of *S. pectinatus* corresponds to an orthonauplius.

The presence of two inner setae (instead of one seta) on the mandibular endopod of the dirivultid nauplius I is a primitive character of dirivultids distinguishing them from other siphonostomatoids. The other characters of the dirivultid nauplius I distinguishing it from the nauplius I of *Scottomyzon gibberum* (Scottomyzontidae), a parasite of the shallow-water starfish *Asterias rubens* (see Ivanenko *et al.* 2001), are the completely reduced labrum and two ventral setae (instead of one seta) on the antennule. The dirivultid nauplius differs from the first nauplius of derived caligid siphonostomatoids (Johnson & Albright 1991; Lin *et al.* 1997) in having an ovoid body (instead of slightly elongate), thin caudal setae (instead of stout

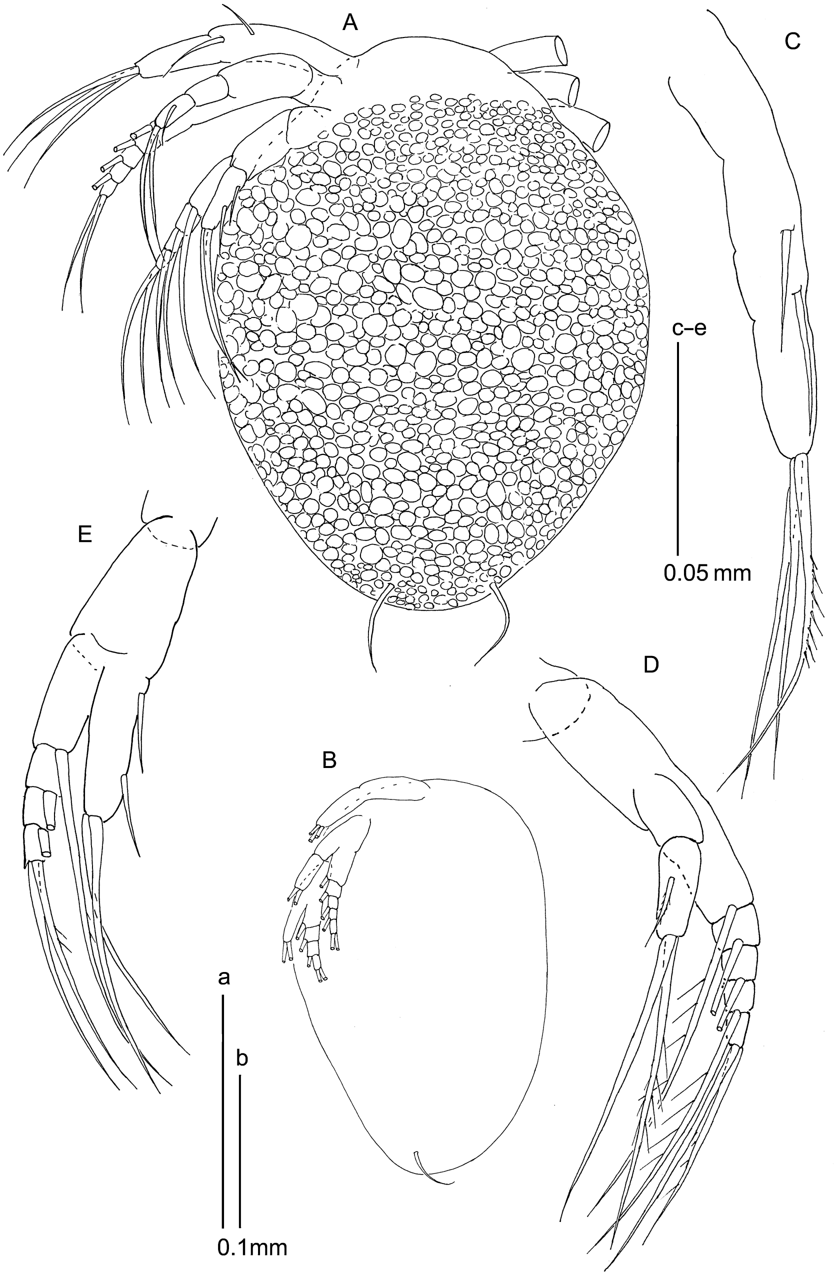

Fig. 1. *Stygiopontius pectinatus* Humes 1987, nauplius of stage I: A, habitus, ventral; B, habitus, lateral, left side; C, antennule, ventral; D, antenna, ventral; E, mandible, dorsal.

obtuse balancers), absence of a terminal aesthetasc (present in caligids) and with three long terminal setae (instead of two setae) on the antennule, two long terminal setae (instead of one seta) on the distal exopodal segment of both antenna and mandible, and five segments of the antennal exopod armed with seta(e) (instead of four segments).

Little is known of the development and life cycle of copepods of the family Dirivultidae (Ferrari & Dahms 2007). Depending on the species, females of dirivultids carry one to three (typically two, rarely more) large yolky embryos in each of two sacs (Heptner & Ivanenko 2002). Different stages of dirivultids (adults of three species, including *S. pectinatus*, lecithotrophic nauplii and juvenile copepodids) were captured at 80–300 m above a deep-sea hydrothermal vent on the MAR (Broken Spur, 29° N) by a slurp gun deployed on the Russian submersible *MIR* (Ivanenko 1998). A stage I copepodid with a cephalothorax including the first and second thoracic somite, three articulating thoracic somites plus anal somite, swimming legs 1 and 2 with one-segmented rami, and swimming leg 3, a bilobe bud, was identified as a Dirivultidae.

The co-occurring lecithotrophic nauplii were not described because their identification as dirivultid nauplii was in question at the time. This finding and an absence of records of subadult copepodid stages of dirivultids in many benthic samples suggested that adults of some dirivultid species might ascend to the pelagic zone to copulate, that females release their embryos in the pelagic zone and that juveniles also develop there (Ivanenko 1998). Recent investigation of samples obtained by sediment traps deployed over a hydrothermal field on the East Pacific Rise (13° N, IFREMER samples) revealed nauplii and stage I copepodids identified as dirivultids (Ivanenko & Defaye 2006b; personal observations of V. N. Ivanenko). Additionally, our observation of meiofauna associated with vestimentiferans from hydrothermal fields on the East Pacific Rise (9° N, C. Fisher samples) revealed dirivultids of different copepodid stages (Heptner & Ivanenko 2002; personal observations of V. N. Ivanenko). These observations suggest that adults of some dirivultid species copulate, hatch and develop to subadult copepodid stages in the benthic environment, although stage I copepodids of dirivultids can live in plankton associated with bacterial films floating over deep-sea hydrothermal fields.

Morphological features of the planktonic nauplius of *S. pectinatus* suggest that these larvae are lecithotrophic at least during the early dispersal phase. It is possible that physiologically inactive nauplii released by dirivultid females in hydrothermal fields are carried away by water currents, and that these dirivultid nauplii remain in the plankton until they reach a habitat with appropriate environmental conditions, at which time molting of nauplii is initiated and the copepodids settle out of the plankton.

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