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THE TANTULOCARIDAN LIFE CYCLE: THE CIRCLE CLOSED?

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ABSTRACT

The discovery of a new stage in the life cycle of the Tantulocarida is reported. A sexual female, collected from a deep-sea harpacticoid copepod host, was removed from the trunk sac of the preceding tantulus larva. This female is a free-living and nonfeeding stage which presumably mates with the free-swimming adult male previously described. The female comprises a cephalothorax, probably incorporating 2 limbless thoracic somites, 2 free pedigerous trunk somites, and 3 limbless trunk somites. It also possesses paired antennules, the only well-defined cephalic appendages present at any stage in tantulocaridan life history. There is a median genital aperture, the copulatory pore, located ventrally on the cephalothorax at about the level of the incorporated first thoracic somite. This is interpreted as further evidence of a sister-group relationship between the Tantulocarida and the Thecostraca. The known life-cycle stages of the Tantulocarida are now interpreted as forming two cycles, one sexual, the other parthenogenetic.

Tantulocaridans are minute ectoparasitic crustaceans that utilize a variety of other crustacean groups as hosts (Boxshall and Lincoln, 1983). The known life cycle of the Tantulocarida, as described by Boxshall and Lincoln (1987), is remarkable for the complete lack of any typical crustacean molting process. The adult female described by Boxshall and Lincoln (1987) has a saclike trunk which develops immediately behind the head; the larval trunk is sloughed, leaving an abscission scar. This adult female is permanently attached to its host via the adhesive oral disc on the larval head. The female produces relatively large numbers of eggs which develop within the female's body and hatch directly as tantulus larvae. The life cycle is also unique in the bizarre metamorphosis that takes place in the development of the male, during which a large, free-swimming adult differentiates within the expanded trunk sac of the preceding tantulus larva. This adult male is supplied with nutrients via a tissue connection with the permanently attached larval head and it is nonfeeding after hatching.

Boxshall and Lincoln (1987) considered the relative size of the penis of male tantulocaridans and the tantulus larva and concluded that mating could not take place between these two stages. They therefore suggested that fertilization might be achieved by injection of sperm through the body wall of the developing saclike female. However, they also suggested that a second, sexual, female developmental pathway might exist, leading to a large, free-swimming adult which would be capable of mating with the known adult male. Huys (1991) interpreted the significant variation in penis structure in known male tantulocaridans (Huys, 1990) as evidence in support of the existence of a sexual female with complementary copulatory structures. He suggested that there might be both parthenogenetic and sexual cycles within the tantulocaridan life cycle.

This paper records the discovery of the sexual female of a tantulocaridan. A single specimen, attached to a deep-sea harpacticoid copepod, was found in a sample of copepods from off the Philippines. The harpacticoid host represents a new family and is described in a separate account (Huys, in press). The sexual female is described in detail and a fuller interpretation of the tantulocaridan life cycle is presented. The phylogenetic implications of the new information on tantulocaridan morphology are discussed.

MATERIAL AND METHODS

A single tantulocaridan was found attached to the exopod of the third swimming leg of a female harpacticoid copepod, *Styracothorax gladiator* Huys, 1993 (Huys, in press, fig. 1), collected during the ESTASE II expedition (14 November–8 December 1984) to the deep waters off the Philippines on board the RV *Jean Charcot* (coordinators: L. D. Labeyrie and B. Metivier). Locality: Station CP02 (14°05.40′N, 120°02.46′E) to the northwest of Manila, 14 November 1984, at a depth of 2,050 m. Material sorted in CENTOB, Brest (coordinator: M. Segonzac). The specimen is stored on an electron microscope stub in the Natural History Museum, London: BM(NH) Reg. No. 1992.1070.

The specimen was prepared for examination using light microscopy by mounting temporarily in lactophenol. Observations were made using oil immersion on a Leitz Diaplan microscope with Nomarski differential interference contrast. Drawings were made using a camera lucida. After light microscopy, the specimen was washed in alcohol to remove the lactophenol and transferred to 50% acetone ready for preparation for Scanning Electron Microscopy (SEM). It was dehydrated through graded acetone, critical-point dried, mounted on a stub, and sputter-coated with palladium. Observations were made using a Hitachi S–800 FSEM. The pore pattern nomenclature follows Boxshall and Vader (in press).

DESCRIPTION

Sexual Female

Body comprising large cephalothorax, 2 free pedigerous somites and 3 limbless somites (Fig. 1A). Body cuticle weakly chitinized. Body length measured around curved dorsal surface, about 435 μm from frontal margin of cephalothorax to rear margin of caudal rami. Cephalothorax without defined dorsal shield; with conspicuous, paired, lateral zones of longitudinally folded cuticle (Figs. 1A, 3C). Surface of cephalothorax entirely lacking integumental pores and sensilla (Fig. 4A). No epicuticular ornamentation apparent on cephalothorax, although 2 transverse furrows (arrowed in Fig. 3D) present posteriorly, possibly representing vestigial boundaries marking position of incorporated first and second thoracic somites. Frontal margin of cephalothorax bearing paired antennules (Figs. 1B, 4A), located dorsal to large median aperture into which umbilical cord passes (Fig. 1D).

Cephalothorax bearing median aperture, referred to here as copulatory pore, posteriorly on ventral surface (Fig. 1E, G). Copulatory pore surrounded by fine cuticular ridges, arranged radially (Fig. 4C, D); pore extending internally, via short cuticle-lined duct, into poorly defined sac. Most of space inside cephalothorax occupied by 14 eggs, about 32 μm in diameter.

Antennules unsegmented, anteriorly directed; fused together basally and fused to frontal margin of cephalothorax (Fig. 1C). Antennule armed with 5 setal elements, 1 located dorsally about at midlength, 1 subapically, and 3 around distal margin. Each seta with parallel sides and brushlike apex (Figs. 1B, 4B).

Postcephalothoracic trunk comprising 2 pedigerous somites (probably representing third and fourth thoracic somites) and 3 limbless somites (Fig. 2D), the last bearing paired caudal rami but lacking anus or anal operculum. Pedigerous and limbless somites without defined tergites, lacking surface ornamentation. Caudal rami (Fig. 2G) elongate, about 100 μm in length by 10 μm in width; ornamented with numerous irregular rows of denticles. Each ramus bearing 2 distal setae, set in a concavity formed by dorsal and ventral marginal membranes with serrated edges. Caudal setae curved at tip and provided with serrated membrane along concave surface.

Legs 1 and 2 biramous, similar in segmentation; protopod 2-segmented, comprising small coxa and large basis separated by well-developed articulation; both rami 1-segmented. Leg 1 (Fig. 2E) slightly larger than leg 2; coxa unarmed, basis unarmed but ornamented with few denticles. Exopod and endopod both elongate, each armed with single seta distally; posterior margins of both rami bearing toothlike spinous processes. Setae curved at tip, irregularly serrate along posterior margin. Leg 2 (Fig. 2F) with unarmed coxa, basis unarmed but ornamented with several surface denticles. Rami each armed with single seta distally, with base of seta protected anteriorly by marginal membrane with serrated edge. Posterior margin of both rami ornamented by numerous denticles; setae irregularly serrate along posterior margin, more slender than those of leg 1.

Tantulus Larva

The adult female was contained, in the reflexed position typical for adult males, within the expanded trunk sac of the preceding tantulus larval stage (Fig. 3A). The postcephalic trunk of the tantulus had already been sloughed, leaving an abscission scar (Figs. 1D, 2B, C, 3B).

Dorsal shield of tantulus larva (Figs. 2A, C, 3B) slender, tapering anteriorly; shield length about 58 μm, maximum width about 30 μm; about 1.9 times longer than wide. Cephalic shield with 13 pairs of pores and 2 unpaired median pores: pore formula A_{I-V}, D_{I-IV}, L_{I-III}, M. Pores A_I, D_I and L_I all sensillate. Median pores (M) arranged asymmetrically, on either side of midline,

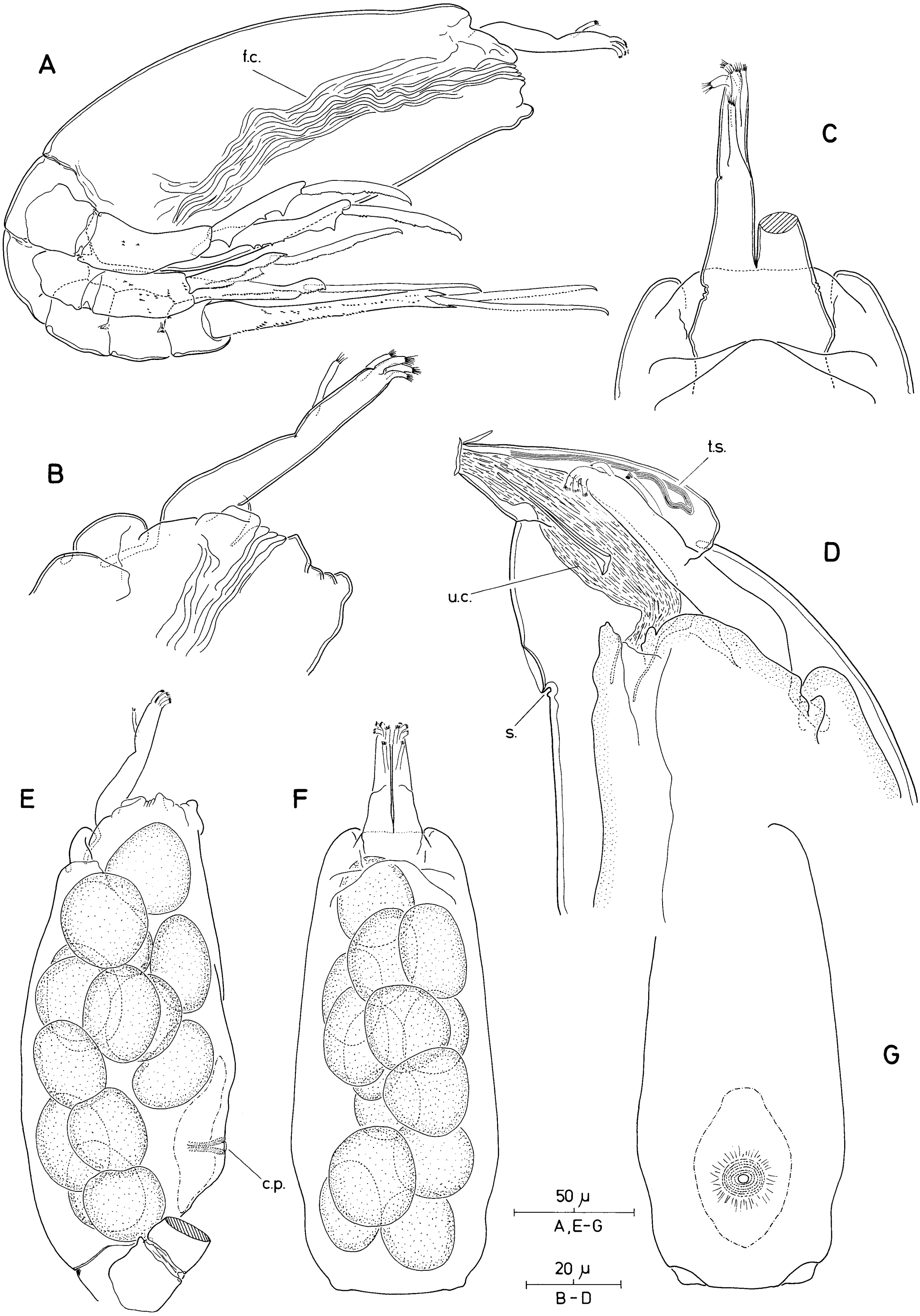

Fig. 1. *Itoitantulus misophricola,* sexual female. A, lateral view; B, anterior margin of cephalothorax, lateral; C, same, dorsal; D, anterior part of tantulus sac, showing umbilical cord leading to sexual female, lateral; E, cephalothorax, showing eggs and copulatory pore, lateral; F, same, dorsal; G, ventral surface of cephalothorax, showing copulatory pore. [Abbreviations: c.p. = copulatory pore, f.c. = folded cuticle, s. = abscission scar, t.s. = tubular structure, u.c. = umbilical cord.]

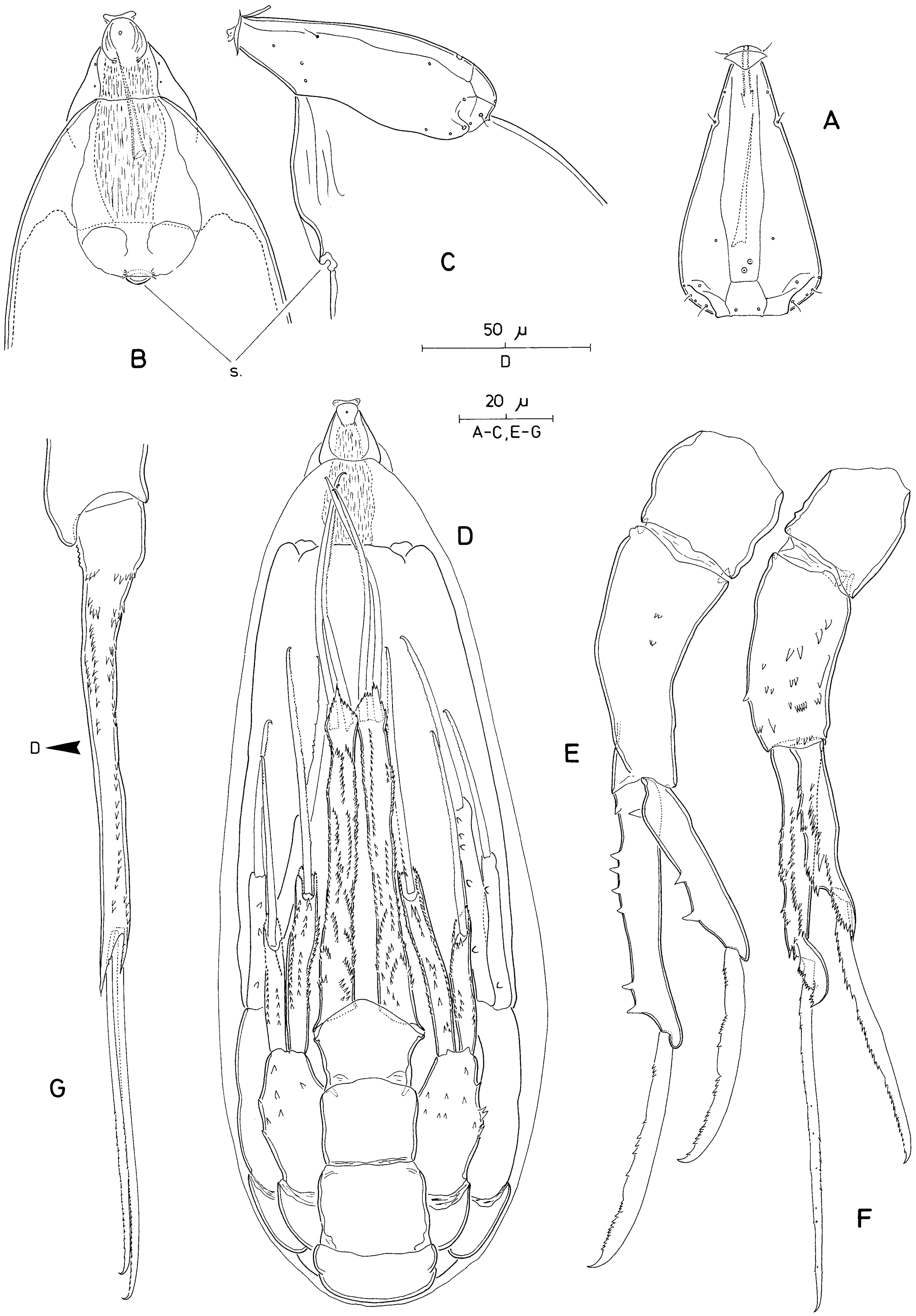

Fig. 2. *Itoitantulus misophricola.* A, cephalic shield of tantulus, dorsal; B, anterior part of attached tantulus, ventral; C, same, lateral; D, sexual female within trunk sac of preceding tantulus stage, ventral; E, first thoracopod, lateral; F, second thoracopod, lateral; G, caudal ramus, lateral view with arrow indicating dorsal surface. [Abbreviations: s. = abscission scar.]

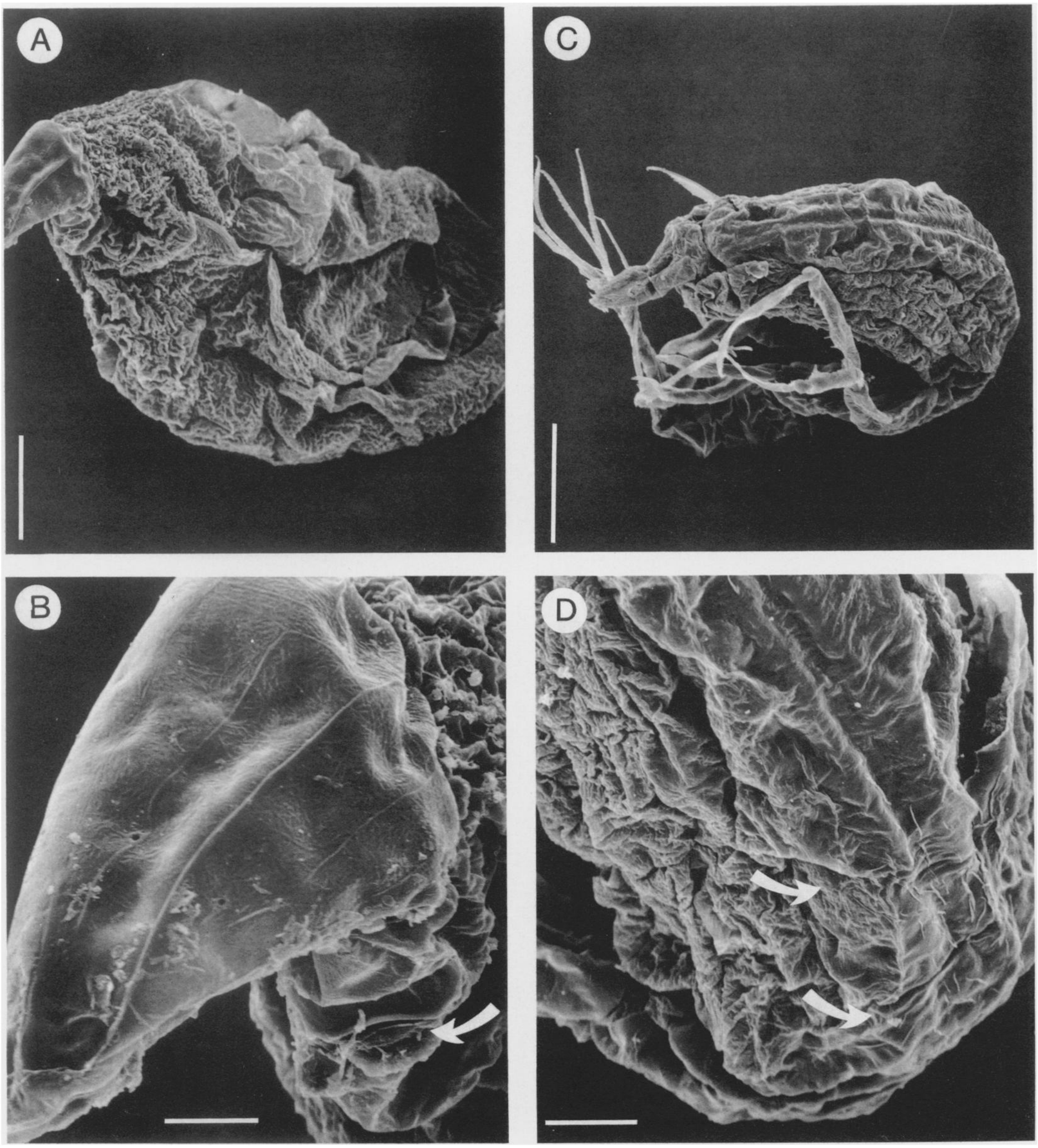

Fig. 3. Scanning electron micrographs of *Itoitantulus misophricola*. A, tantulus larva with trunk sac, after removal of sexual female; B, cephalic shield of tantulus, lateral, with arrow marking abscission scar formed by sloughing of larval trunk; C, sexual female, lateral; D, posterior part of cephalothorax of sexual female, with arrows marking possible sutures between cephalon and first thoracic somite and between first and second thoracic somites. Scale bars: A = 25 μm, B = 5 μm, C = 40 μm, D = 10 μm.

just posterior to A_V pair. Pair of complete dorsal, longitudinal epicuticular lamellae present on shield, plus additional transverse lamellae near posterior margin. Oral disc about 10 μm in diameter. Cephalic stylet straight, about 29 μm in length.

Identification of the Tantulocaridan

Most of the taxonomic characters used to distinguish between tantulocaridan taxa, particularly at the species level, have been based on the head shield, thoracopods, and apparent abdominal segmentation of the tantulus larvae. The only specimen available for the present study lacks the entire postcephalic larval trunk, leaving only head shield characters available for comparison. Fortunately, the specimen possesses a pair of asymmetrical pores (the "M" pores), on either side of the dorsal midline. These pores

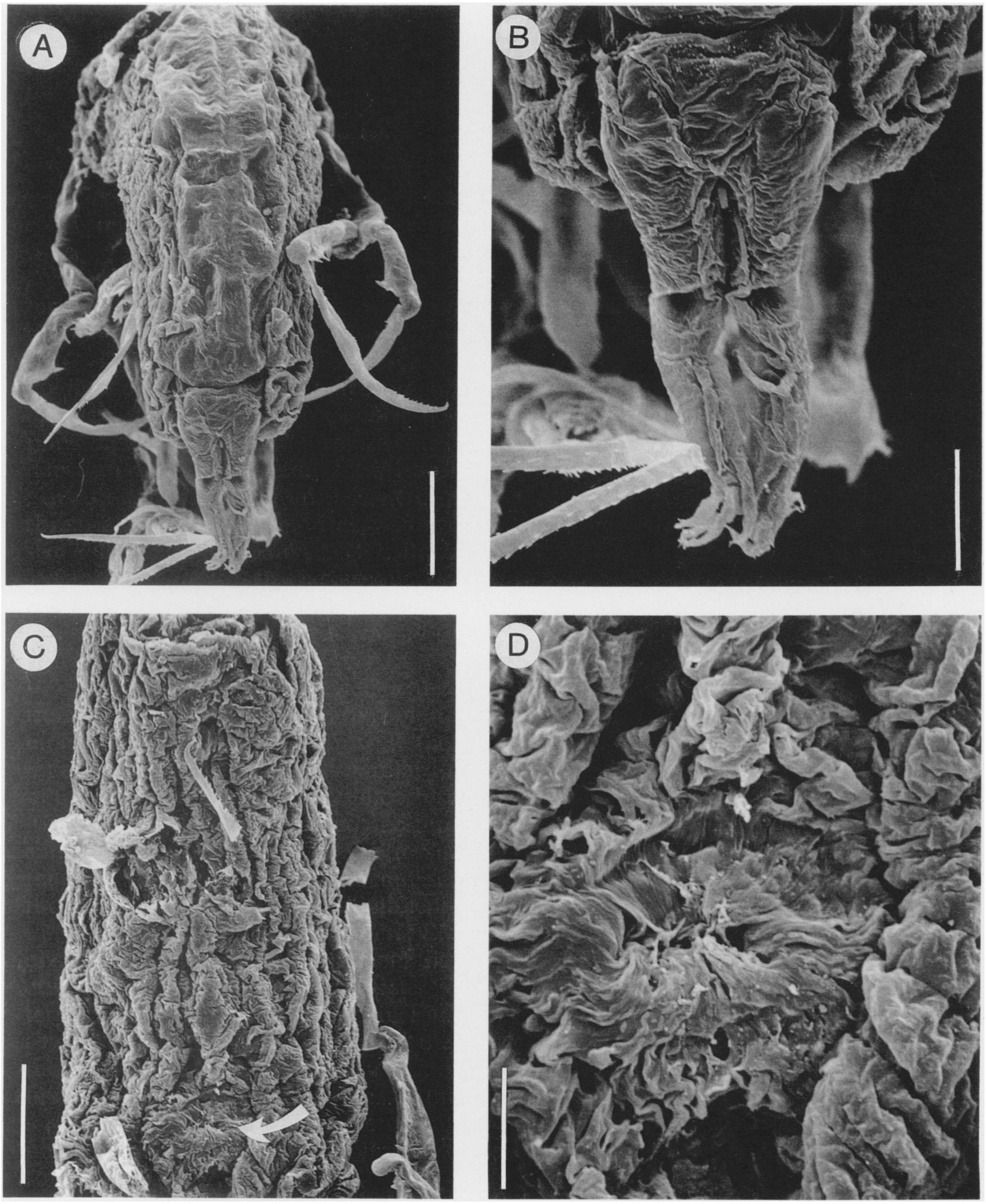

Fig. 4. Scanning electron micrographs of sexual female of *Itoitantulus misophricola*. A, dorsal view; B, antennules, dorsal; C, ventral view of cephalothorax, with arrow marking median copulatory pore; D, copulatory pore. Scale bars: A = 25 μm, B = 10 μm, C = 20 μm, D = 5 μm.

are known only in the newly described deoterthrid *Itoitantulus misophricola* Huys, Ohtsuka, and Boxshall (Huys *et al.*, 1992). This species has been reported only on a misophrioid copepod host collected at a depth of 167 m in Japanese waters off Okinawa. Detailed comparison between the dorsal shields of the tantulus larvae of the present specimen and of *I. misophricola* revealed no significant differences. The cephalic shield of the present specimen is smaller than *I. misophricola* from Japan, but the proportions are similar. On the basis of the similarities in cephalic shield shape

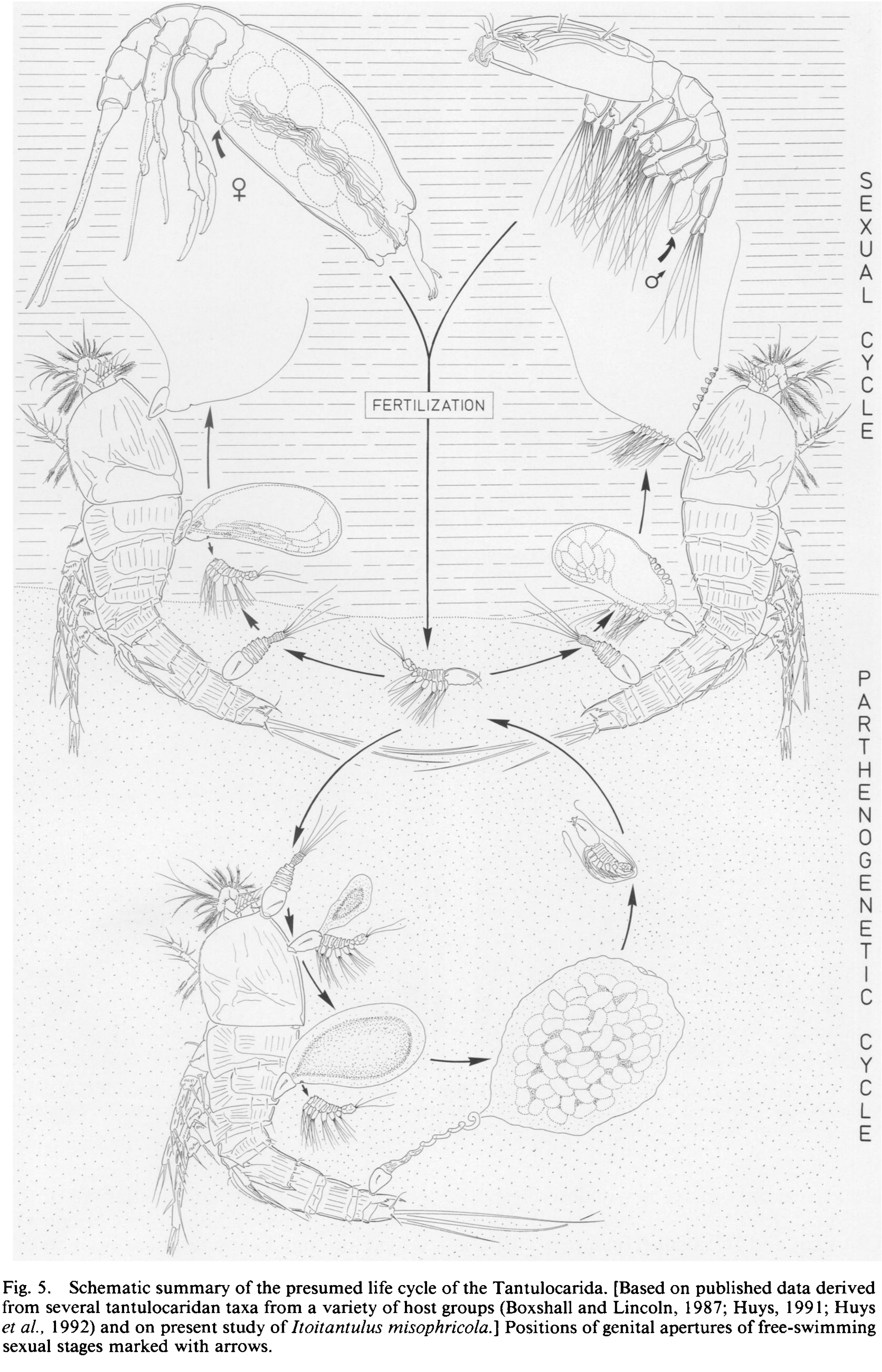

Fig. 5. Schematic summary of the presumed life cycle of the Tantulocarida. [Based on published data derived from several tantulocaridan taxa from a variety of host groups (Boxshall and Lincoln, 1987; Huys, 1991; Huys *et al.*, 1992) and on present study of *Itoitantulus misophricola*.] Positions of genital apertures of free-swimming sexual stages marked with arrows.

and in the arrangement of pores, in particular the presence of the unique median asymmetrical (M) pores, we provisionally identify the present specimen as *I. misophricola* despite the separation, both horizontally and vertically, of the two localities. This identification is provisional, because it is based solely on the characters of the larval head. The presence of the same tantulocaridan on hosts representing two different orders of copepods is remarkable, as are its wide depth and geographical distributions.

DISCUSSION

The Life Cycle

The description of the new life-history stage in the Tantulocarida may bring to a close the basic discovery phase for this taxon. The known life-history stages of tantulocaridans now appear to form two cycles, summarized in Fig. 5. The sexual male, first described by Boxshall and Lincoln in 1987, now has a sexual partner with which to mate. The sexual adults of both sexes are free swimming and nonfeeding. The male possesses a well-developed intromittent organ, the penis, and fertilization is almost certainly internal, with the male depositing sperm directly into the median copulatory pore of the female. The large saclike females which remain permanently attached to their host probably represent a parthenogenetic, multiplicative phase in the life cycle. On the assumption that the eggs inside the sexual female hatch as tantulus larvae, these larvae presumably form the link between the sexual and parthenogenetic cycles.

No information is currently available on the relationship between the two cycles. We do not know whether there is a simple alternation between the cycles or whether there is some kind of genetic switch mechanism. Similarly, we have no data available on the nature of any environmental cues which might be involved in stimulating such a switch, although the presence of sexual males, parthenogenetic females, and tantulus larvae all on the same host individual (see e.g., Huys, 1990) indicates that it is not a simple seasonal switch from one cycle to the other.

Tantulocaridans are widely distributed and can be locally common in well-studied areas, such as the North Sea and the Scandinavian coast. It is, therefore, remarkable that relatively large, free-swimming, sexual stages have not been reported from plankton samples. This may indicate that they are extremely short lived, or that they inhabit the hyperbenthic community, which is difficult to sample by traditional methods.

The sexual male is well adapted for swimming, having six pairs of powerful, setose thoracopods. It also carries an array of sensors on the cephalothorax, comprising the paired clusters of chemosensory aesthetascs and the numerous, probably mechanosensory, sensilla on the surface of the dorsal shield. This sensory apparatus presumably enables it to locate the receptive sexual female. The sexual female, by comparison, seems poorly adapted for a free-swimming existence. It has only two pairs of biramous thoracopods, each bearing only a single seta per ramus. We interpret the form of these thoracopods as indicative of a raptorial, rather than a locomotory role. Since the male is conspicuously lacking in any structures that could be interpreted as specialized for grasping its partner during mating, it seems probable that, after the sexes make contact, the female grasps the male using the modified thoracopods.

The sexual female possesses antennules. This is the only cephalic appendage present at any stage in the dual life cycle of the Tantulocarida. Boxshall and Lincoln (1987) suggested that the paired clusters of aesthetascs in the adult male probably represent the vestigial antennules. The discovery of a distinct antennule in the sexual female provides comparative evidence in support of this interpretation. Each female antennule carries five setae with brushlike tips. These elements appear to constitute the entire sensory array of the adult female, which lacks the surface sensilla present on the cephalothorax in males.

The single specimen available was in an advanced state of development, with all aspects of its external morphology appearing well defined. It was, however, still in contact with the host via the larval head and umbilical cord which had not yet atrophied, as it does prior to release of the adult male (Boxshall and Lincoln, 1987). The retention of a functional umbilical cord indicates that nutrients were still required by the female, presumably for the further development of the eggs. The 14 eggs present were only about

32 μm in diameter, smaller than the 37–50-μm diameter eggs reported from parthenogenetic females of *Onceroxenus curtus* Boxshall and Lincoln (Boxshall and Lincoln, 1987). The 30-μm diameter eggs found in the only known parthenogenetic female of *I. misophricola* (Ohtsuka, unpublished data) were at an early stage of development. The small egg size reinforces the interpretation that the eggs had not yet attained maturity. The areas of longitudinally furrowed cuticle along the lateral margins of the cephalothorax provide a ready mechanism by which the cephalothorax can expand to accommodate the continued growth of the eggs.

The difference in the site of trunk sac formation in males and females is well known, but has never been discussed. In the male the genital aperture is located on the seventh trunk somite and the trunk sac is formed toward the posterior end of the larval trunk, whereas in female development the trunk sac is formed immediately behind the larval cephalon in both sexual and parthenogenetic cycles. In the light of the new data on the position of the female gonopore, it seems likely that this difference reflects a difference in the position of the primordia of the gonads in the sexes.

Parthenogenesis is extremely rare in crustaceans, occurring in a few ostracods (see review by Cohen and Morin, 1990), a few copepods (e.g., Roy, 1931; Sarvala, 1979) and, more widely, in branchiopods, especially cladocerans (Calman, 1911). Sexual reproduction is, however, typical in crustaceans and it is reasonable to assume that the sexual cycle is the ancestral cycle and the parthenogenetic cycle is the more recent addition. How did parthenogenesis evolve? In the sexual cycle the female containing a brood of eggs develops within the trunk sac of the preceding stage, and is released for a brief free-living existence. If this female were not released, but instead became extremely simplified, being represented only by the germinal layers within the trunk sac, and if the eggs contained within the female developed without fertilization, then the resulting parthenogenetic female could be regarded as equivalent to a secondarily reduced sexual female. The tissues within the neck of the parthenogenetic female that are responsible for transporting nutrients from the larval head to the developing eggs are then equivalent to the umbilical cord of the sexual stages.

Phylogenetic Implications

The sexual female of tantulocaridans is very specialized, but it provides at least one character of immense phylogenetic significance—the position of the female genital aperture. The location of the genital apertures in both sexes is important in the maxillopodan groups (Newman, 1982; Grygier, 1983; Boxshall, 1983). The presence of a median penis, derived from thoracopods, on the seventh trunk somite in male tantulocaridans has already been used as evidence of the thecostracan affinities of the Tantulocarida within the Maxillopoda (Boxshall and Lincoln, 1987; Newman, 1987; Boxshall and Huys, 1989; Boxshall, 1991; Newman, 1992). The discovery of the median copulatory pore on the ventral surface of the cephalothorax is worthy of detailed analysis.

The copulatory pore is located on the ventral midline, about three-quarters of the distance along the cephalothorax. If the tagmosis of the sexual female is similar to that of the male, this position would correspond to the level of the incorporated first thoracic somite. There is some evidence to suggest that, as in the male, the first and second thoracic somites are fused with the cephalon to form a cephalothorax. Under SEM we observed two transverse furrows in the otherwise longitudinally creased cuticle. We interpret these furrows, arrowed in Fig. 3D, as marking the planes of fusion of the first thoracic somite to the cephalon and of the first and second thoracic somites. If this interpretation is correct, then the copulatory pore lies on the incorporated first thoracic somite.

In the ancestors of the core maxillopodan taxa the genital apertures of both sexes were probably located on the seventh postcephalic trunk somite (Newman, 1982; Grygier, 1983; Boxshall, 1983). This condition is retained in both sexes in the Copepoda (Huys and Boxshall, 1991) and possibly also in the Ostracoda (Schulz, 1976). It is retained only in males of the Tantulocarida and Thecostraca. The thecostracans are characterized by the apomorphic position of the female gonopores on the first thoracic somite, the most anterior position occupied by genital apertures in any crustacean (Newman *et al.,* 1969). The discovery of the sexual female of tantulocaridans reveals this character state to be a synapomorphy between the Tantulocarida and Thecostraca. This is powerful new evidence in support of a sister-group relationship between the Tantulocarida and the Thecostraca. We stress that it is the location of the female gonopore(s) on the first thoracic somite that provides the synapomorphy. The presence of a single median aperture in female tantulocaridans is autapomorphic relative to the retention of paired apertures in thecostracans. It is reasonable to assume that female genital apertures of maxillopodans originally performed the dual functions of receiving sperm and releasing eggs, as in primitive copepods (Huys and Boxshall, 1991). Only the former function appears to be retained in female tantulocaridans, since eggs are probably released by rupture of the cephalothorax.

We hypothesize that the common ancestor of the Tantulocarida-Thecostrâca clade possessed a somewhat generalized larval stage, bearing six pairs of thoracopods, preceding the adult. Since there is no evidence that either the cyprid stage has been secondarily lost from the tantulocaridan life cycle or the tantulus stage has been secondarily lost from the thecostracan cycle, we also suggest that the thecostracan cyprid larva and the tantulocaridan tantulus larva are independently derived from this generalized ancestral larva. The alternative hypothesis, that one of these larvae is derived from the other, appears extremely unlikely when the highly specialized nature of each is considered. The tantulus, which lacks all trace of cephalic appendages, is an improbable ancestor of the cyprid, which has well-developed antennules and mouthparts. The cyprid, in which the first thoracic somite is almost completely incorporated into the cephalon and lacks a tergite, is equally improbable as ancestor of the tantulus larva, which retains a well-developed, functional articulation between the head and the tergite-bearing, first thoracic somite. The evolution of different attachment mechanisms in these two larvae (modified antennules in the cyprid larva and an oral disc in the tantulus) can be interpreted as further support for the hypothesis that these specialized larvae are independently derived from a generalized ancestral larva. The difference in number of trunk somites between tantulus larvae and thecostracans is not a reliable character; we are currently reinterpreting the apparent trunk segmentation of tantulus larvae.

The suite of characters that constitutes the cyprid larva is the most powerful synapomorphy of the Thecostraca, linking the plesiomorphic Ascothoracida with the more apomorphic Facetotecta, Cirripedia, and Rhizocephala. Inclusion of the Tantulocarida in the Thecostraca, as proposed by Newman (1992), would significantly dilute the otherwise robust concept of the Thecostraca. We recognize the close phylogenetic relationship between tantulocaridans and thecostracans, based on the cephalothoracic location of the female gonopore and on the median penis on the seventh trunk somite of the male. However, we consider that the presence of the independently derived tantulus larva, rather than a cyprid larva, and the persistence of plesiomorphic character states, such as reduced endites on the thoracopods, indicates that the Tantulocarida should be classified as the sister group of the Thecostraca.

In the most plesiomorphic crustacean classes, the Cephalocarida and Branchiopoda, the genital apertures are located on the same trunk somite in males and females (although the particular somite differs from group to group). We regard this as the probable ancestral state of the Crustacea. The Tantulocarida-Thecostraca clade is one of only three crustacean taxa in which male and female apertures are located on different trunk somites. In the Malacostraca the female aperatures lie on the sixth trunk somite and the male on the eighth (Calman, 1909); in Remipedia the female apertures lie on the eighth trunk somite and the male on the fifteenth (Itô and Schram, 1988; Yager, 1991); and in the Tantulocarida-Thecostraca clade the female aperture is on the first trunk somite and the male on the seventh. In all three taxa it is the female apertures that are located anterior to those of the male. However, the differences in position along the trunk indicate that these are not homologous character states. All three represent uniquely derived character states.

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