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23. Tantulocarida

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GENERAL: The Tantulocarida is a small group of microcrustaceans that exhibits a unique protean life cycle, composed of obligatory ectoparasitic larvae and free-swimming non-feeding adults. Larval tantulocaridans utilize other marine crustaceans as hosts, including copepods, amphipods, tanaidaceans, isopods, cumaceans, and ostracods (Huys 1991; Boxshall and Vader 1993). The Tantulocarida was established as a new class of Crustacea by Boxshall and Lincoln (1983), but the roots of its taxonomic history reach back to the beginning of the twentieth century. The first genera to be formally described were *Cumoniscus* and *Microdajus*, both of which were originally classified as epicaridean isopods (Bonnier 1903; Greve 1965). Currently, the group accommodates 34 described species assigned to 22 genera (Knudsen et al. 2009; Kolbasov and Savchenko 2009; Savchenko and Kolbasov 2009; Mohrbeck et al. 2010). The most widely used classification (Huys 1990a) recognizes 5 families, but recent contributions suggest that the Deoterthridae and Basipodellidae are possibly paraphyletic or polyphyletic (Kolbasov et al. 2008a; Savchenko and Kolbasov 2009; Petrunina and Kolbasov 2012). Tantulocaridans have been recorded from abyssal depths to the intertidal zone and from polar to tropical waters, including unusual habitats like anchialine cave pools (Boxshall and Huys 1989), coral reefs (Huys 1990b) and hydrothermal vents (Huys and Conroy-Dalton 1997). Recent contributions (Gutzmann et al. 2004; Mohrbeck et al. 2010) suggest that the current number of described species greatly underestimates their actual diversity. Tantulocaridans exhibit no recognizable cephalic limbs at any stage of their intricate life cycle (except for the antennules in the sexual female), but the shared position of the female copulatory pore (ventrally on the cephalothorax, at about the level of the incorporated first thoracic segment) and the male genital apertures (on the seventh post-cephalic trunk segment) is interpreted as evidence that their affinities lie with the Thecostraca (the Facetotecta, Ascothoracida, and Cirripedia) (Huys et al. 1993; also see Petrunina et al. 2013).

The known life-history stages appear to form a complex dual life cycle, combining a sexual phase (with free-swimming adults) and a presumed parthenogenetic multiplicative phase that takes place on the host (fig. 23.1) (Huys et al. 1993).

LARVAL TYPES

Tantulus Larva: The infective stage, or tantulus larva (figs 23.2C; 23.3A, B), is the only stage that occurs in both cycles. Prior to mate location, the larva goes through a benthic non-feeding phase—probably at the sediment-water interface—as part of the temporary meiofauna (Huys 1991). Attached larvae undergo development on the host without conventional molting. In the parthenogenetic pathway, the tantulus forms a large dorsal trunk sac immediately behind the cephalon, causing the ventral deflection of the larval trunk, which is subsequently sloughed (fig. 23.2A, B). The contents of the sac differentiate into eggs that are later released as fully developed tantulus larvae (fig. 23.3I). The sexual cycle involves a unique type of metamorphosis in which a free-swimming adult is formed within the expanded trunk sac of the preceding tantulus larva. In the female pathway the trunk sac forms immediately posterior to the cephalic shield, and the larval trunk is sloughed (fig. 23.3F–H, K). In the male pathway the site of trunk sac formation is at or near the back of the larval thorax, causing the ventral deflection of the urosome and thoracopods (figs. 23.2A, D, E; 23.3J). Throughout metamorphosis the developing sexual females and males are supplied with nutrients via an umbilical cord (fig. 23.3F, G).

Nauplius: A benthic non-feeding stage that can be recognized as a nauplius has been reported recently but not formally described (Martínez Arbizu 2005; Mohrbeck et al. 2010), suggesting that eggs produced by the sexual female hatch as nauplii rather than as tantulus larvae.

MORPHOLOGY: The tantulus larva (body size 75–195 μm) (figs. 23.2A–C; 23.3A, B) is composed of an anterior tagma

(prosoma), consisting of the cephalon and a thorax of six pedigerous segments, and a limbless tagma (urosoma), consisting of the last thoracic segment and a one-segmented abdomen that bears paired caudal rami (fig. 23.2F, J). The cephalon is covered with a dorsal shield bearing pores, sensilla, and (usually) epicuticular lamellae (figs. 23.2C; 23.3A, B). The tantulus has no cephalic appendages and is permanently attached to the host by a frontal oral disc (figs. 23.2C; 23.3A); in free-swimming larvae this disc is often accompanied by several pairs of sensilla and a funnel-shaped organ or proboscis (fig. 23.3B, E). The larva has six pairs of thoracopods (fig. 23.2G, H). The first five pairs are biramous and typically have a well-developed precoxal endite (figs. 23.2I; 23.3C, D); the sixth pair is uniramous and lacks an endite. The endites carry palmate spines apically and function as coupling devices, holding the two members of a leg pair together. Each endopod typically has a grappling apparatus at its tip, which may either act as an additional coupling apparatus for synchronizing thoracopod movements (Huys 1991), or as an attachment device, enabling the tantulus to hold onto the host prior to cementing down the oral disc (Boxshall 1991). Near the center of the disc is a tiny (0.5–2.0 μm) aperture (the stylet pore), through which the tantulus punctures the host's integument with its cephalic stylet. The stylet is operated by paired protractor and retractor muscles (fig. 23.3E) (Huys 1991). Host penetration may be purely mechanical, but large secretory glands inside the cephalon may assist this process. Little of the internal anatomy of the tantulus can be discerned once it has attached itself to the host.

MORPHOLOGICAL DIVERSITY: Tantulocarid taxonomy is largely based on larval characters, such as the cephalic pore pattern, stylet shape, thoracopod morphology and armature, cephalic and abdominal surface ornamentation (fig. 23.2C, F, J), and caudal ramus structure. The mode of male trunk-sac formation in the preceding tantulus larva is diagnostic at the family level, with swelling occurring either posterior to the sixth thoracic tergite and additional expansion between the cephalon and the first tergite (the Basipodellidae); or exclusively posterior to tergite 6 (the Onceroxenidae, Microdajidae, and Deoterthridae); or between tergites 5 and 6, with secondary expansion between tergites 4 and 5 (the Doryphallophoridae) (Huys 1991). Microdajid tantulus larvae that develop into parthenogenetic females produce a long drawn-out neck region, which has not yet been recorded in females of other families (Ohtsuka 1993).

NATURAL HISTORY: The infective tantulus larva attaches permanently to a crustacean host, which supplies all the nutrients it requires throughout its entire life. Nutrients are absorbed and transported back into the larval cephalon by a tubular rootlet system that penetrates the host and appears to be continuous with the umbilical cord that supplies a sexual adult developing within its trunk sac. The non-feeding sexual male must store sufficient food reserves during development to maintain it during the free-swimming mate-location phase.

The sexual female must obtain sufficient nutrients to allow the fertilized eggs to complete their development. Reproduction is semelparous, with each female (sexual or parthenogenetic) producing a single batch of larvae that are probably all released simultaneously. Thus heavily infested hosts may have encountered a swarm of newly released larvae (Huys 1990b; Boxshall and Vader 1993). The larvae do not appear to suppress host molting hormonally, but they may slow host growth by diverting resources into their own development (Huys 1991). Mating between free-swimming adults, as well as the hatching and development of larvae produced by the sexual female, have never been observed. Similarly, it is not known whether there is a simple alternation between the sexual and parthenogenetic cycles, or whether there is some kind of genetic switch mechanism. The presence of sexual males, parthenogenetic females, and tantulus larvae all on the same host individual (fig. 23.2A) (e.g., see Huys 1990b; Knudsen et al. 2009) indicates that it is not a simple seasonal switch from one cycle to the other.

PHYLOGENETIC SIGNIFICANCE: Tantulocarids are assumed to be allied to the thecostracans (the Facetotecta, Ascothoracida, and Cirripedia), based largely on the placement of the adult genital openings (Huys et al. 1993) and 18S rDNA sequence data (Petrunkina et al. 2013). Larval morphology plays an important role in tantulocarid taxonomy and systematics.

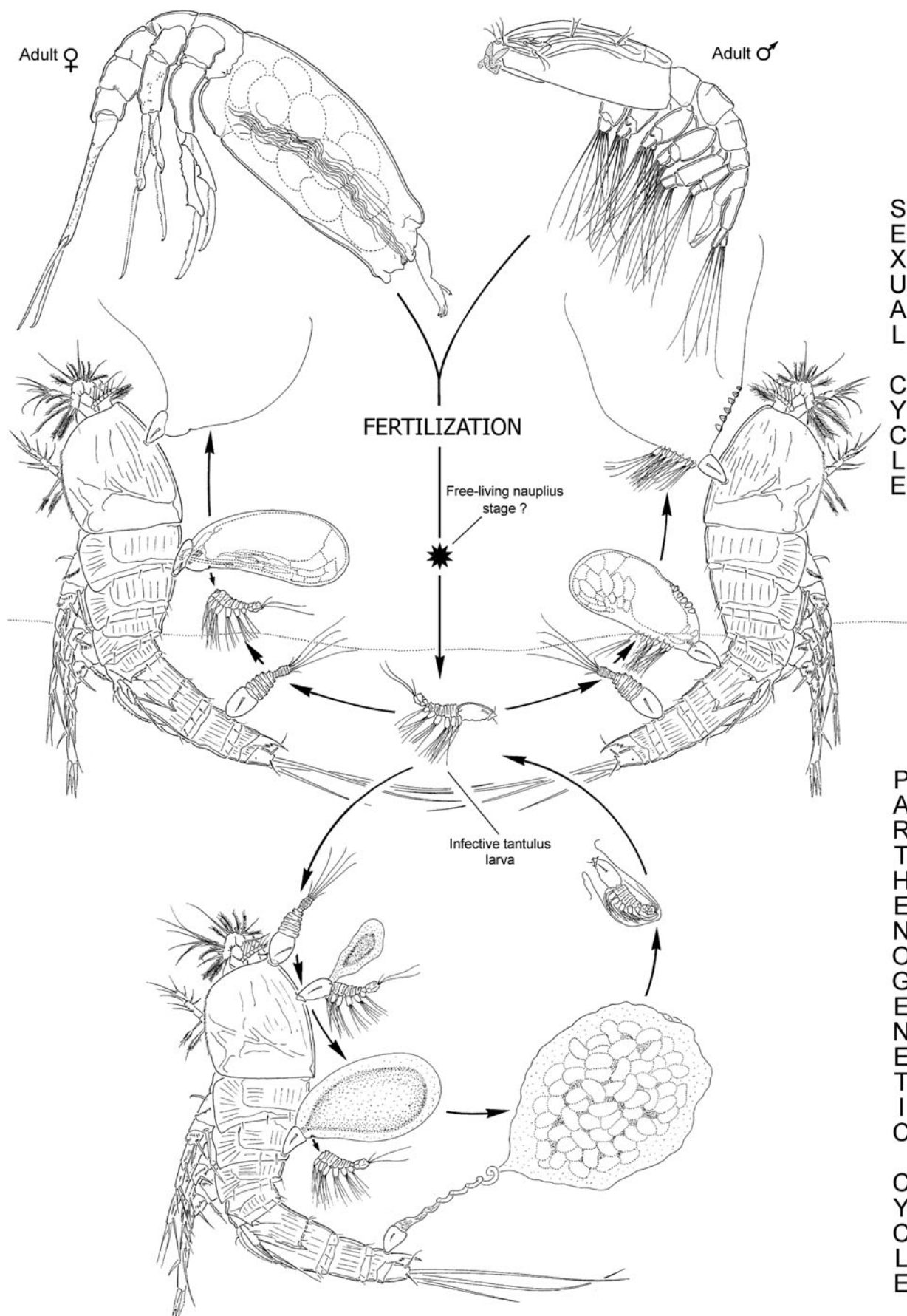
HISTORICAL STUDIES: Boxshall and Lincoln (1987), Huys (1991), and Huys et al. (1993) described aspects of the dual life cycle. Huys (1991) described the internal anatomy of the cephalon, as well as the musculature of the trunk and legs of free tantulus larvae of *Xenalytus scotophilus* prior to their attachment to the host. Tantulus larvae of a number of genera have been examined with SEM, including *Amphitantulus* (Boxshall and Vader 1993), *Arcticotantulus* (Kolbasov et al. 2008a; Knudsen et al. 2009), *Coralliotantulus* (Huys 1990b), *Doryphallophora* (Boxshall and Lincoln 1987), *Itoitantulus* (Huys et al. 1992b), *Microdajus* (Boxshall and Lincoln 1987; Boxshall et al. 1989; Kolbasov and Savchenko 2009), *Onceroxenus* (Boxshall and Lincoln 1987), *Serratotantulus* (Savchenko and Kolbasov 2009), and *Tantulacus* (Huys et al. 1992a). Knudsen et al. (2009; Petrunkina et al. 2013) also published the first photographs of live tantulus larvae, developing males, and parthenogenetic females of *Arcticotantulus kristenseni*, and they presented an overview of the subclass. Petrunkina et al. (2013) published TEM sections of newly settled tantulus larvae of *Arcticotantulus pertzovi* and also provided complete 18S rDNA sequences for this species and *Microdajus tchesunovi*.

Selected References

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Fig. 23.1 (opposite) Schematic summary of the presumed dual life cycle of the Tantulocarida. A solid star indicates the presumed position of free-living nauplius stage(s) in the sexual life cycle. The sediment-water interface is indicated by a dotted line (modified after Huys et al. 1993). Drawing based on published data derived from several taxa and a variety of host groups (Boxshall and Lincoln 1987; Boxshall et al. 1989; Huys 1991; Huys et al. 1992b, 1993).



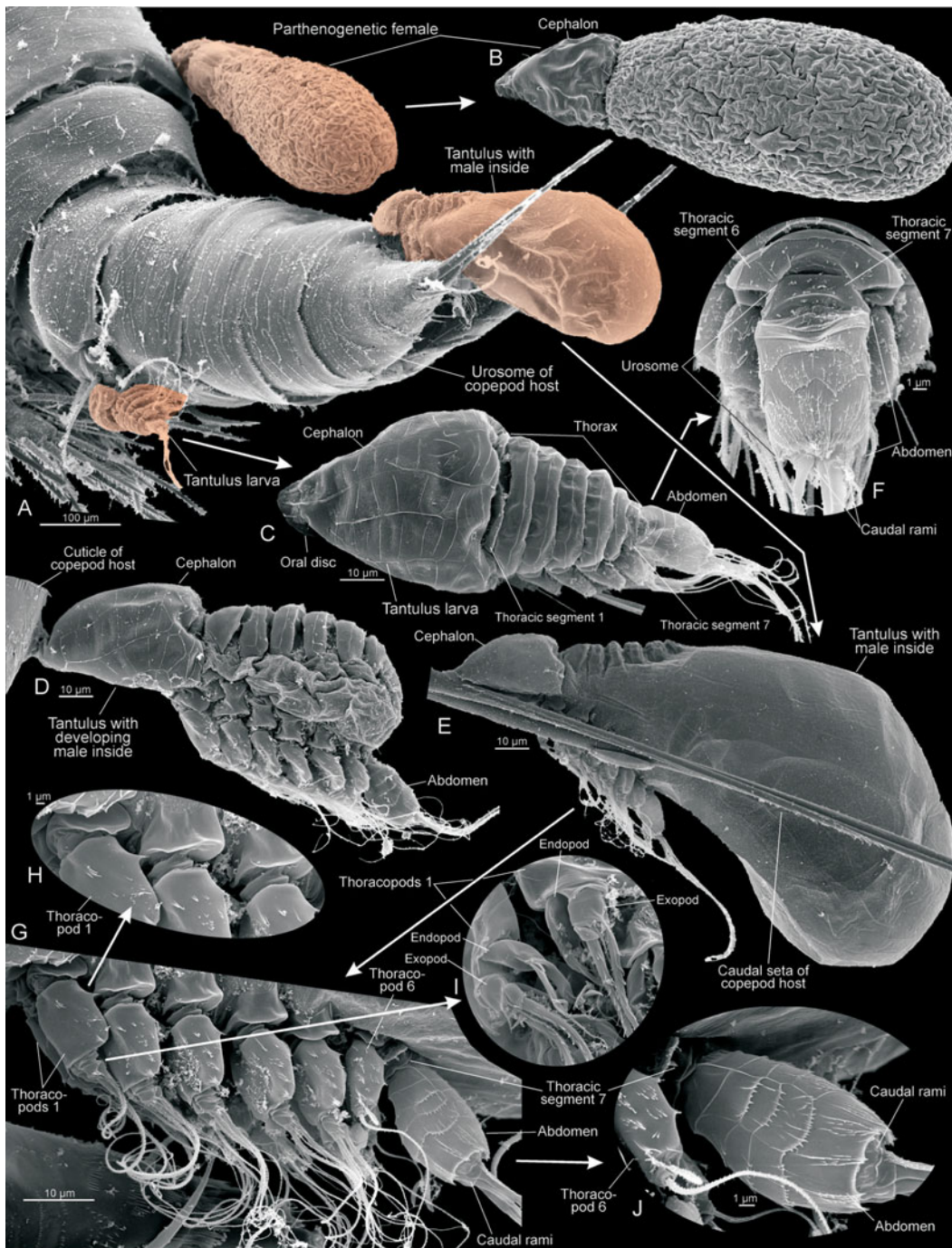


Fig. 23.2 Tantulus larvae of *Arcticotantulus kristenseni* at different stages of development, SEMs. A: recently attached, unmodified tantulus larva (prior to metamorphosis), young parthenogenetic female, and tantulus with a developing male inside an expanding trunk sac; stages are attached to a harpacticoid copepod host (*Bradya* sp.). B: parthenogenetic female at an early stage of trunk-sac formation; note the absence of the postcephalic trunk and thoracopods of the tantulus, and the highly wrinkled integument (which will stretch as the trunk sac enlarges and the eggs develop inside), lateral view. C: premetamorphic tantulus larva, showing the oral disc and basic tagmosis, dorsolateral view; note that the first thoracic tergite is largely concealed beneath the posterior margin of the cephalic shield. D: tantulus, with a developing male inside, showing the initial onset of trunk-sac formation posterior to the sixth thoracic tergite, causing the downward deflection of the urosome and thoracopods, lateral view. E: large metamorphosed tantulus containing a male at an advanced stage of development, attached to the caudal ramus seta of a harpacticoid host, lateral view. F: posterior end of the tantulus, showing the position of the major body articulation between the sixth thoracic segment and the urosome (encompassing thoracic segment 7 and the one-segmented abdomen), dorsal view; note the surface sculpturing on the abdomen. G: thoracopods 1–6 and the abdomen of a metamorphosed tantulus (containing a developing male; see D), lateral view. H–J = closeups of G. H: protopods of thoracopods 1–3, lateral view. I: first pair of thoracopods, showing the biramous structure, ventral view. J: abdomen and caudal rami, lateral view; note the surface ornamentation. A and C–E modified after Knudsen et al. (2009); B and F–J original.

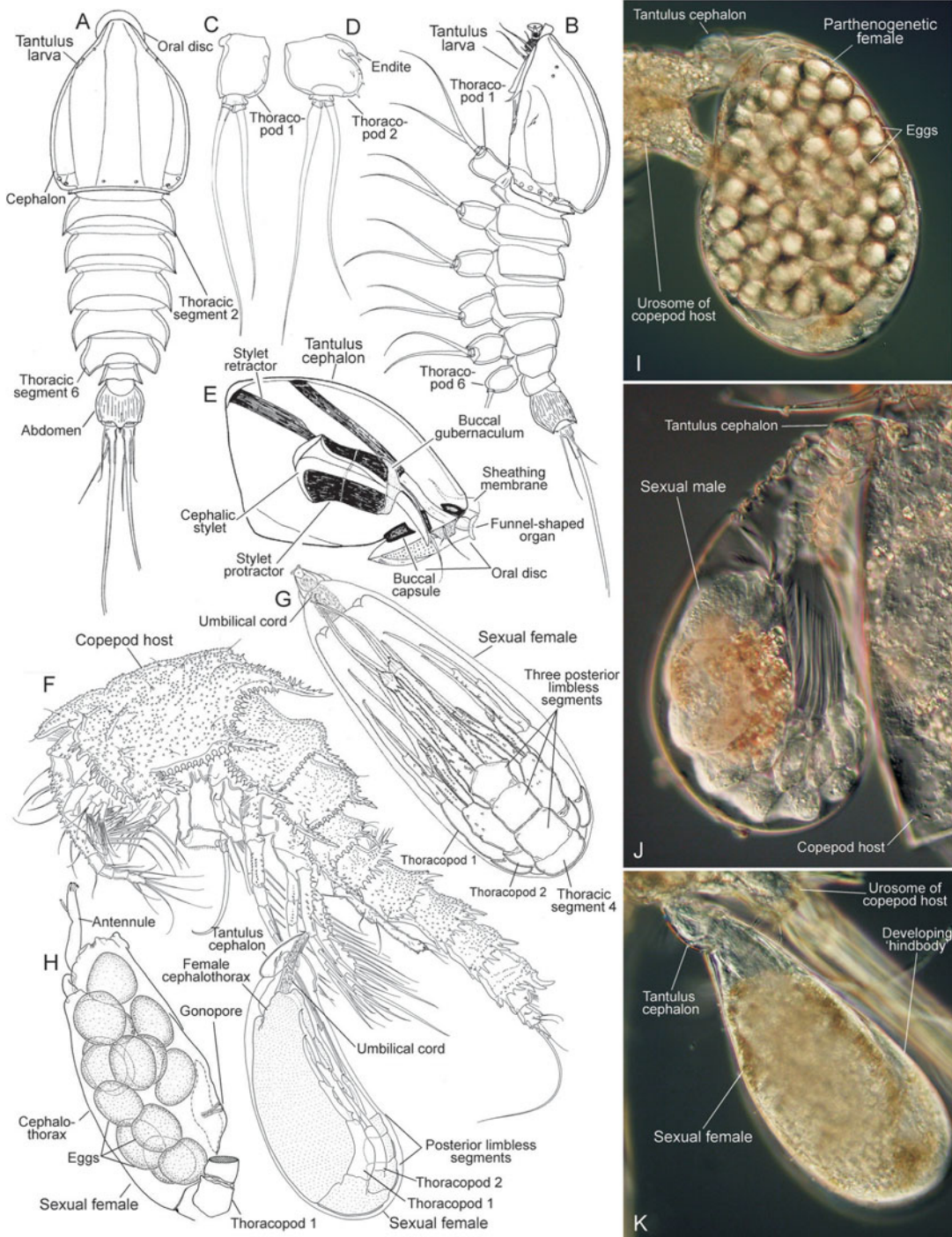


Fig. 23.3 Morphological details of tantulus larvae and other aspects of the life cycle of the Tantulocarida. A–E: drawings of *Xenalypus scotophilus*. A: tantulus larva, dorsal view. B: tantulus larva, lateral view. C: thoracopod 1 of the tantulus, anterior view. D: thoracopod 2 of the tantulus, anterior view. E: sagittal section through the cephalon of a free-living tantulus (prior to infection), revealing the cephalic stylet and associated musculature. F–H: drawings of *Itoitantulus misophricola*. F: harpacticoid host (*Styracothorax gladiator*) with an attached metamorphosed tantulus containing the sexual female stage of *I. misophricola* at an advanced state of development, lateral view. G: sexual female of *I. misophricola* developing within the trunk sac of the preceding tantulus stage, ventral view. H: cephalothorax of a developing sexual female of *I. misophricola*, showing the eggs and gonopore position. I: live parthenogenetic female of *Arcticotantulus kristenseni*, containing eggs, attached to the urosome of a copepod host, light microscopy. J: live tantulus of *A. kristenseni*, containing a male at a late stage of development, attached to the cephalothorax of a harpacticoid host, light microscopy. K: live tantulus of *A. kristenseni*, containing a sexual female at an early stage of development, light microscopy; note the developing postcephalothoracic trunk (hindbody). A–E modified after Huys (1991); F modified after Huys (1993); G and H modified after Huys et al. (1993); I–K modified after Knudsen et al. (2009).