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Ascothoracida

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GENERAL: The Ascothoracida are ecto-, meso- or endoparasites in echinoderms and anthozoans (Grygier and Høeg 2005). Except for the secondarily hermaphroditic species of the Petrarciidae, they have separate sexes. The larger female is accompanied by dwarf cypridiform-like males, often living inside her mantle cavity. Ascothoracidans use their piercing mouthparts for feeding on their hosts, although in some advanced forms nutrient absorption may also take place through the integument. The approximately 100 described species are classified in 2 orders, the Laurida and Dendrogastrida (Grygier 1987; Kolbasov et al. 2008b). The life cycle includes up to six free-swimming naupliar instars (fig. 19.1A–C, F, G), an a-cypris larva (fig. 19.1D, E, H–J), a juvenile, and an adult. The larval stages are free living or brooded. Juveniles and adults are parasitic on different taxa of cnidarians and echinoderms.

LARVAL TYPES:

Nauplius and A-Cyprid: Some Ascothoracida retain the thecostracan ground pattern, with six instars of planktotrophic nauplii, but most species either release lecithotrophic nauplii or brood their offspring inside the mantle cavity until their release as a-cyprids, also called ascothoracid larvae (Itô and Grygier 1990). The a-cyprid locates and attaches to the host, using its prehensile antennules.

MORPHOLOGY

Nauplii: The nauplii have an oval bowl-shaped head shield that is broader anteriorly. The head shield can carry short setae, small pores, and feeble ridges (Itô and Grygier 1990; Grygier 1992). Nauplii have a nauplius eye and a pair of setiform frontal filaments (fig. 19.1A, B). The labrum is small and slightly protruding (fig. 19.1G). There are three pairs of natatory limbs: uniramous antennules, and biramous antennae and mandibles, all armed with long setae (fig. 19.1A, B, K, L). Beginning with nauplius instar II, there are also setiform vestiges of the maxillules. Under the hindbody, the last nau-

pliar instar stages have small vestiges of the thoracopods of the ensuing a-cyprid. The hindbody ends in an unpaired terminal spine and a pair of caudal setae or spines (fig. 19.1A, B).

A-Cyprid: The a-cyprid (or ascothoracid larva) has a bivalved carapace that surrounds the body, although the hindbody will normally protrude posteriorly (fig. 19.1D, E, I, J). The carapace surface can be almost smooth (fig. 19.1I) or covered by prominent polygonal cuticular ridges (fig. 19.1J). There are five pairs of lattice organs (without a pore field) along the dorsal hinge line. The prehensile antennules are Z-shaped and composed of four to six segments, whose precise homology to the antennular segments in facetotectan y-cyprids and cirripe de cyprids is uncertain. The distal segment bears a hooked claw (for mechanically grasping the host) and different types of setae, including long aesthetascs (fig. 19.1D, M, N). The compound eyes are often reduced, but their vestiges may be present (Hallberg et al. 1985; Grygier 1992). Frontal filaments are attached at the borderline between the anterior part of the larval body and the inner surface of the carapace. Behind the antennules, the mantle cavity houses a conspicuous oral pyramid, with vestiges of piercing mouthparts (fig. 19.1D, E). The thorax carries six biramous and natatory thoracopods (fig. 19.1D, E, H, N). The long abdomen consists of five segments, including an elongated telson that terminates with unsegmented furcal rami (fig. 19.1D, E, H, I).

MORPHOLOGICAL DIVERSITY: The a-cypris larvae of the Ascothoracida differ in the shape and ornamentation of the carapace and in the segmentation of the antennules. The a-cyprids of the Laurida (fig. 19.1J) normally have a more sculptured (reticular ornamentation) carapace, with five pairs of the lattice organs, while those of the Dendrogastrida (fig. 19.1I) have less carapace ornamentation and only four pairs of lattice organs (Kolbasov et al. 2008b). In addition, the laurid a-cyprids normally have six-segmented antennules, as opposed to the four-segmented antennules in dendrogastrid a-cyprids. The Dendrogastrida brood their larvae until the a-cypris stage,

whereas the Laurida release their larvae as free-swimming planktotrophic or lecithotrophic nauplii.

NATURAL HISTORY: Free-swimming lecithotrophic nauplii may be reared in culture to the a-cypris stage (Itô and Grygier 1990; Grygier 1992). Development from nauplius I to the a-cypris seems to last approximately one month in warm waters (Itô and Grygier 1990). Species of the Dendrogastrida brood their larvae inside the female's mantle cavity until the cypridoid stage, which consists of two a-cypris instars (Brattström 1948; Wagin 1976; Kolbasov et al. 2008b). The first a-cypris instar has an infantile morphology. The carapace is smooth, without pores, setae, and lattice organs. The antennules have only a rudimentary armament, and the abdomen has only four of the five segments present in the second a-cypris instar. The first a-cypris instar is normally retained within the mantle cavity, while the second instar has the definitive morphology for host location and attachment and is released into the plankton. The a-cyprids of the Laurida (called Tessmann's larvae) can be found in the plankton. Settlement and metamorphosis of the a-cyprid have never been observed, so a full life cycle is not known for any species, but a tentative life cycle is proposed for *Ulophysema oeresundense* in Grygier and Høeg (2005). Primitively, there seems to be little change from an a-cyprid to an adult. This is especially true for the males, where it is questionable whether any molt separates the a-cyprid from the sexually mature form. In advanced species (dendrogastrids), the adult females can grow into elaborate forms, with bizarre extensions from the body.

PHYLOGENETIC SIGNIFICANCE: Ascothoracidans constitute one of the 3 subclasses of the Thecostraca. Historically, the study of relationships within this group has relied

heavily on developmental features (e.g., see Høeg 1992; Høeg and Møller 2006; Høeg et al. 2009a). Modifications to accommodate their parasitic lifestyle separate most ascothoracidan larvae from those of other thecostracans.

HISTORICAL STUDIES: The larval development of *Ulophysema öresundense* was studied in detail by Brattström (1948). Thorough studies of the larval development of laurid ascothoracidans, using SEM, were published by Itô and Grygier (1990) and Grygier (1992). The morphology of both the first and second a-cyprid larvae were studied with SEM by Kolbasov et al. (2008b). Wagin (1976) published a monograph on the Ascothoracida, including their development.

Selected References

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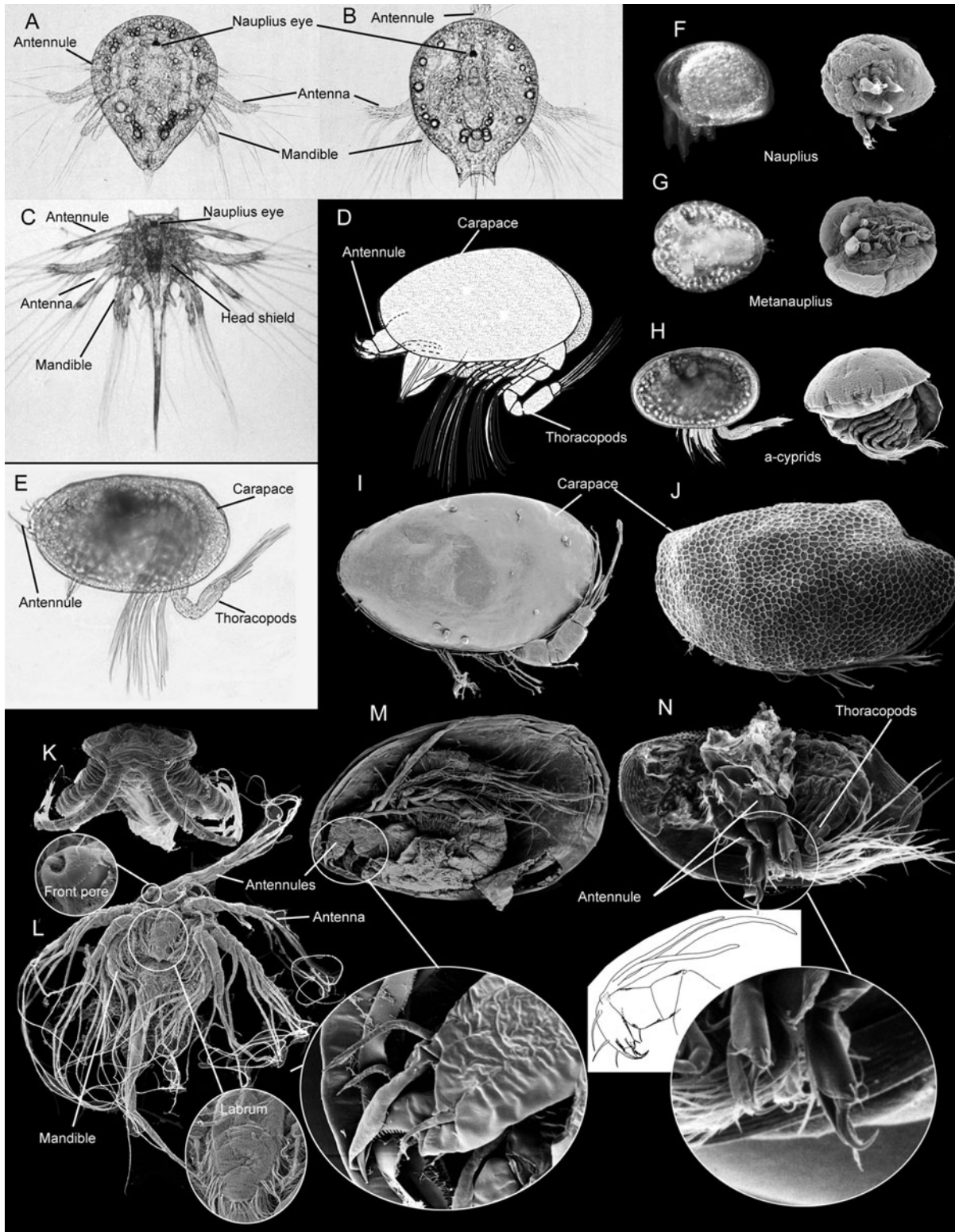


Fig. 19.1 Nauplii and a-cyprids of the Ascothoracida. A and B: lecitotrophic nauplii of *Baccalaureus falsiramus*, light microscopy, dorsal view. C: planktotrophic nauplius of *Zibrowia* sp., light microscopy, ventral view. D: schematic drawing of an a-cyprid. E: a-cyprid of *Dendrogaster rimskykorsakowi*, light microscopy, lateral view; note the mouth cone protruding ventrally. F–H: *D. rimskykorsakowi*. F and G: nauplii, light microscopy (left) and SEMs (right). H: a-cyprids, light microscopy (left) and SEM (right). I: a-cyprid of *Ulophysema oeresundense*, SEM, lateral view. J: a-cyprid of *Baccalaureus falsiramus*, SEM, lateral view. K and L: nauplius I of *Zibrowia* sp., SEMs. K: frontal view. L: ventral view. M and N: a-cyprid of *U. oeresundense*, SEMs; note the claw, used for mechanical attachment, at the tip of the antennules in the closeups and the drawing. M: right half of the carapace removed to reveal the body and appendages (ventral side is up). N: left half of the carapace removed (ventral side is down). A–H, K original, of material from Japan and Okinawa; I, M, and N original, of material from the Sound (Øresund) in Denmark.