

Key for the identification of crustacean nauplii

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Abstract

The nauplius is the earliest free-living stage in the development of most crustaceans, except in the majority of the Malacostraca. Several character states of the nauplius larva are used as constitutive for the Crustacea as a whole. The nauplius shows the following structural characters: a median (nauplius) eye, at least three pairs of head appendages (first and second antennae, where the second antenna bears an arthrite; mandibles), a posteriorly directed fold (the labrum) extending over the mouth, and a cephalic (= nauplius) shield. Extant taxa such as the Cephalocarida, Branchiopoda, Ostracoda, Mystacocarida, Copepoda, Cirripedia, Ascothoracida, Rhizocephala, Facetotecta, Euphausiacea, and Penaeidea are known to develop free-living nauplii. Other Crustacea show at least some vestige of an 'egg-nauplius' during embryonic development. The diversity of nauplii belonging to major crustacean taxa is briefly described, and a key to these nauplii is provided. The key is also available in digital format, as a JAVA program capable of being modified and expanded as new information arises. The programming structure allows uses in dichotomous or multi-branching formats.

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Introduction

A biphasic life cycle alternating between a larval phase and a juvenile/adult phase is common among marine invertebrates. Its ubiquity and presence even in lower metazoans suggests that the earliest phases of metazoan evolution also had such a life cycle (Rieger 1994). Invertebrate larvae have become a focal point of studies on life-history evolution, where the interplay of animal structure, function, ecology, and evolutionary history is investigated (e.g., Jablonski 1986).

The nauplius larva is not only the prevailing hatching larval form of crustaceans, but its morphological organization is a fundamental part of the definition of the Crustacea (Waloszek 1993). However, the hypothesis that nauplii demarcate a plesiomorphic mode among Crustacea has become a controversial issue in recent years (Scholtz 2000). Upon hatching, body segmentation of a nauplius is visible externally in some crustacean taxa only. The presence of three pairs of appendages (first and second antennae, mandibles), however, indicates that at least three body somites are present. A single median eye is usually present. Larval crustaceans carrying three pairs of appendages (= orthonauplii) have been termed nauplii since the

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mid-19th century (Williamson 1982). When postmandibular appendages are indicated externally, the term metanauplius is used for such a larva (Dahms 1990a).

Extant taxa such as the Cephalocarida, Branchiopoda, Ostracoda, Mystacocarida, Copepoda, Thecostraca (Cirripeda, Ascothoracida, Rhizocephala, Facetotoca), Euphausiacea, and Penaeidea are known to develop a free-living nauplius larva (McLaughlin 1980). Other Crustacea show at least some vestige of this type of ‘head larva’ during embryonic development. Besides structural, meristic, and allometric differences, embryonic and postembryonic naupliar stages provide another form of dynamic character, namely developmental allometry and heterochrony. From these character changes, a gradient can be traced. Pre-adult characters that are reminiscent of former character states, or that recapitulate those expressed in the course of ontogeny are particularly valuable for the evaluation of polarity. Dahms (1990a, 2004b) has demonstrated the usefulness of naupliar characters for phylogenetic considerations among the Harpacticoida (Dahms 1994) and Copepoda (Dahms 2004a). Others have applied naupliar characters for phylogenetic considerations in other crustacean taxa (e.g., Olesen 1999).

The crustacean nauplius as a phylotypic stage is characterized to some extent by morphological stasis (cf. Fryer 1985). On the other hand, the life of early postembryonic stages is subject to different selection pressures. Nauplii, therefore, have undergone remarkable adaptive radiation within the limits of their organizational constraints. Early free-living crustacean instars are well adapted for inbenthic, epibenthic, phytal, associated, or pelagic lifestyles and display a variety of specializations within each of these (Dahms 1993, 2000). Besides qualitative and quantitative structural additions, there may also be reductions or functional transformations in the sequence of early postembryonic ontogenies. Lecithotrophy is often accompanied by the atrophy of certain larval structures and by an abbreviated development (Dahms 1989).

The present contribution provides a brief overview of the naupliar development of Crustacea and a key to the identification of crustacean nauplii which shall aid in the determination of nauplii for different applications among the life sciences.

Materials and methods

Nauplii can be collected from the field or hatched in the laboratory. Methods for rearing nauplii in the laboratory can be found in Dahms (1992). In either case samples should be fixed immediately in buffered 4% formaldehyde solution. Then, specimens should be transferred to a sorting solution (95% distilled water,

4.5% propylene glycol, 0.5% propylene phenoxylol; see Fornshell 1994).

The characters used for this survey are based on our own observations, or are compiled from the literature. A selection of helpful papers was chosen to provide a detailed and comprehensive overview for a key to crustacean nauplii. The following contributions—given in systematic order—were particularly useful: Cephalocarida (Sanders 1963a, b), Branchiopoda (Waloszek 1993; Ferrari and Grygier 2003), Mystacocarida (Hessler and Sanders 1966; Cals and Cals-Usciati 1982; Olesen 2001), Ostracoda (Kesling 1951; Swanson 1989), Thecostraca (Lang 1979; Moyses 1987; Korn 1988; Egan and Anderson 1989; Itô and Grygier 1990), Harpacticoida (Dahms 1990a, 1991), Cyclopoida (Dahms and Fernando 1992; Ferrari and Ambler 1992), Poecilostomatoida (Izawa 1986), and Calanoida (Song and Jinchuan 1990; Dahms and Fernando 1993a). The following contributions were used for general information about crustacean nauplii: Bjørnberg (1972, 1986), Boxshall and Huys (1989), Grygier (1987a, b, 1990), Izawa (1987), Koga (1984), Onbé (1984), Sanders (1963a), Scholtz (2000), Schram (1986), and Waloszek (1993).

Terminology

The terms used are in general accord with those provided by Sanders (1963a) and Waloszek (1993). Naupliar stages are operationally defined here as those larval instars of the Crustacea bearing a naupliar arthritic process on the second antenna. This antennal gnathobasal process disappears in postnaupliar stages. This is a useful criterion for crustaceans with a highly anamorphic development, such as the Cephalocarida, Mystacocarida, and in particular the Branchiopoda. An orthonauplius bears three pairs of appendages: the first and second antennae, and the mandibles. Postmandibular appendages (first maxilla, second maxilla, thoracopods = Thp 1, 2, etc.) may develop in metanaupliar stages. These appendages develop successively only if all are present, e.g. in the Calanoida and some Harpacticoida; thoracopods 2&3 usually are present at NVI, but in Siphonostomatoida and in the Cyclopoida the second maxillae and the maxillipeds never develop externally during the naupliar phase, although legs 2 and 3 are present at NVI.

The naupliar body is covered by a shield (= cephalic shield) in the earlier stages. At the posterior end of the body there are indications of caudal rami in later stages. The labrum originates as a lobate flap near the frontal margin of the head, between the bases of the first antennae, and extends posteriorly along the ventral surface of the body. The ventral body wall of the metasome is a tongue-like structure arising near the base of the antennal protopod, and results from the fusion of

sternites. The first antenna is uniramous. The second antenna is noticeably different from postnaupliar or juvenile stages in having a coxal masticatory arthrite (= gnathobase); the latter is called prognathobasal when it is non-functional and indicated only at non-feeding N I stages or in lecithotrophic nauplii. The second antenna consists of a coxa, basis, endopod, and exopod, as does the mandible.

Large cuticular derivatives encompassing a pore through the integument are called setae or spines. A typical seta is a flexible, finely attenuate element that is bare or has a double row of setules. In the latter case it is called pinnate or plumose, or, if the fine spinules are more irregular, the seta is called spinulose. A typical spine is generally short, relatively inflexible, and usually bears a double row of tiny spinules. Very small flexible elements originating from the endocuticle are referred to as setules. Aesthetascs are presumed chemosensory elements which have been shown from naupliar antennules only; they have sclerotized bases and are more transparent than normal setae with blunt or rounded ends and pores. In addition to setae and spines, setules, appendages or the body somites can show a variety of ornamenting cuticular projections.

Peculiarities of crustacean naupliar development

Structural peculiarities

The primitive mode of development in the Crustacea is a regular addition of somites and limbs at each moult (Waloszek 1993). This course of anamorphic development, leading from a naupliar to an adult body form by the successive addition of somites and appendages in regular order, is most closely followed by the Branchiopoda, Cephalocarida, Mystacocarida, and Copepoda. In the Copepoda, only one new somite and limb-pair appears after each molt, whereas in the Branchiopoda three new somites and limbs appear after each molt (Ferrari and Grygier 2003). Ontogenetic information, particularly from early development, is lacking as yet for the Remipedia. Each crustacean taxon has its own characteristics of naupliar development.

The termination of the naupliar phase is most strikingly characterized in the Cephalocarida, Branchiopoda, Mystacocarida, free-living Cirripedia, and Copepoda by the loss of the naupliar arthrite on the coxa of the second antenna. In the Branchiopoda, Cephalocarida and Cirripedia, the end of the naupliar phase is also characterized by the loss of the mandibular palp. The ventral body wall has the form of a tongue-like flap and comprises the floor of the precoxal cavity of the second antenna together with the ventral plate. The paragnaths become externally expressed during later naupliar development.

Stage number

Cirripedia and Copepoda maximally develop six naupliar stages. Rhizocephala have up to four, but their development may have been abbreviated due to lecithotrophy. *Derocheilocaris typicus* (Mystacocarida) also has six naupliar stages (defined by the presence of the gnathobasic process of the second antenna (Hessler and Sanders 1966), but the congeneric *Derocheilocaris remanei* is described as exhibiting ten naupliar stages (Delamare-Deboutteville 1954). Ascothoracida have up to six naupliar stages (Itô and Grygier 1990). The same holds for Facetotecta according to Itô (1990) and Kolbasov et al. (1999).

In Copepoda there are some exceptions to the rule of six naupliar stages. Jacobs (1961, cit. Bjørnberg et al. 1994) described only five naupliar stages for the calanoid *Pseudodiaptomus coronatus*. There are several species of *Pseudodiaptomus* for which development was described from field collections as involving five stages, but based on laboratory cultures these accounts now are generally understood to be wrong. There are four naupliar stages in the calanoid *Chiridius armatus* (Matthews 1964 in Dahms and Qian 2004). In the only report on Misophrioida, Gurney (1933) found only one naupliar stage for *Misophria pallida*. The number of naupliar instars in the Harpacticoida described so far is six (Dahms 1990a). Gurney (1932) reported six stages from the Calanoida without exception, Elgmork and Lange-land (1970) postulated the same number for free-living Cyclopoida, and Izawa (1987) for Poecilostomatoida. However, particularly in some parasitic Copepoda the nauplius phase disappears altogether (e.g. Shotter 1971; Goudey-Perrière 1979; Perkins 1983). Among other characters the occurrence of six naupliar stages implies a close relationship between Copepoda and the thecostracan clade, provided that the number of naupliar instars in the Rhizocephala is reduced secondarily (Dahms 2004a).

Lecithotrophic development

Lecithotrophic larvae, i.e. those that rely only on yolk for their nutritional demands, are usually bigger at hatching than comparable planktotrophic larvae. Larval life tends to be abbreviated in terms of stages, and there is little growth during development. Most yolk (= lecithotrophic) nauplii have a reduced labrum, and show remarkably reduced patterns of the limbs in some cases (cf. Dahms 1989). According to Anderson (1993), lecithotrophic nauplii are a frequent specialization among Scalpellidae and Verrucomorpha (both belonging to the Cirripedia). This specialization has evolved in some tetracitid Balanomorpha (Cirripedia) and is characteristic for the Acrothoracica. In each of these

groups there are also species that retain lecithotrophic naupliar stages in the parental mantle cavity, which are released at the cyprid stage (Anderson 1993).

Nauplii of the Misophrioida (Copepoda) are lecithotrophic, yolk-filled and possess more simply constructed limbs than those of planktotrophic copepod nauplii (Boxshall 1982). Elsewhere in Crustacea, the possession of a lecithotrophic nauplius is typically associated with parasitism or symbiotic relationships. Some parasitic copepods with lecithotrophic nauplii still possess a large number of naupliar stages, e.g. five in the cyclopoid *Notodelphys ophiuris* (see Dudley 1966), but in many the number is reduced to two, as in most Siphonostoma-

toida, and in a few the nauplius phase of development is lost altogether (Izawa, pers. comm.).

An oligomerous first antenna as well as the extreme reduction of the paired caudal armature, both common trade in yolky nauplii of parasitic copepods (cf. Izawa 1987), seem to be secondary acquisitions and possibly are not the result of lecithotrophy. This may leave lecithotrophic nauplii either poorly adapted to meet the functional requirements for feeding, or the limbs may take on additional modifications for swimming efficiency (in planktonic lecithotrophs), no longer needing to balance this behavior with feeding requirements.

Key to crustacean nauplii

Concerning an electronic version of this key, see the corresponding text section below.

- 1 (A) Cephalic shield composed of platelets and a caudal process (Fig. 2G) Facetotecta
- 1 (B) Body visibly segmented in early stages. Predominantly benthic. 2
- 1 (C) Body not visibly segmented in early stages 3
- 2 (A) Antennules with six segments. Found in interstitial waters of subtidal soft substrates (Fig. 2A) Cephalocarida
- 2 (B) Antennules with seven segments. Found in interstitial waters of sandy substrates (Fig. 2E) Mystacocarida
- 2 (C) Antennules with four segments. Trunk eight-segmented and covered by a cephalic shield. Found in plankton Ostracoda: family Punciidae
- 3 (A) With frontal filaments, frontolateral horns, and caudal process (Fig. 2F) Cirripedia-Thoracica
- 3 (B) With frontal filaments and caudal process, but no frontolateral horns (Fig. 2H) Ascothoracida
- 3 (C) With frontal filaments and caudal process. Labrum absent or greatly reduced. Gnathobase on the second antenna, mouth and anal opening absent Rhizocephala
- 3 (D) Not as in 3 (A)–(C) 4
- 4 (A) With bivalved shell (Fig. 2B) (only Punciidae with univalve shield). Ostracoda
- 4 (B) With telson and rostral helmet-like projection (hood) Euphausiacea
- 4 (C) With telson, but lacking a rostral hood (Fig. 2J) Decapoda–Penaeidea
- 4 (D) First antenna not segmented. Protopod of second antenna more than half the length of the limb. Mandible uniramous (Fig. 2C). Primarily in inland waters Branchiopoda
- 4 (E) With five-segmented first antenna. Antennal exopodal segments increase from 6 at N I to a final number of 9 at N VI. A pair of caudal setae at N I is reduced in size at N II Polyarthra, see 4 (E) 1, 4 (E) 2
- 4 (E) 1 Caudal process present. Body pear-shaped Longipediidae
- 4 (E) 2 Body shape rectangular or broadly oval. If caudal process present, then only as a spiniform protuberance Canuellidae
- 4 (F) Not as in 4 (A)–(D) 5
- 5 (A) Body shape ovoid. Caudal armature symmetrical. First antenna uniramous and three-segmented (Fig. 2I). Second antenna biramous, consisting of two-segmented protopod, one-segmented endopod, and five-segmented exopod. Mandible biramous, consisting of two-segmented protopod, two-segmented endopod, and four-segmented exopod without gnathobase Copepoda-Cyclopoida

- 5 (B) Body elongate. Caudal armature often asymmetrical. Body flexed ventrally in many taxa. First and second antenna held forward. First antenna three-segmented with a broad and elongate distal segment. Second antenna biramous, consisting of a two-segmented protopod, two-segmented endopod, and six-segmented exopod. Mandible biramous, consisting of a two-segmented protopod, one-segmented endopod, and four-segmented exopod. Labrum large and spinulose Copepoda-Calanoidea
- 5 (C) First antenna held perpendicular to longitudinal axis of body, one- to three-segmented. Postmaxillar limbs widely spaced. Second antenna and mandibular endopod elongate. Body shape broad and more or less flattened. Mandibular endopod with one or two stout setae terminally on inner process (Figs. 1, 2D) Copepoda-Harpacticoida-Oligoarthra

Crustacean taxa with naupliar development

Cephalocarida

In *Hutchinsoniella macracantha*, a metanauplius hatches from a single embryo present in the ovisac. For this cephalocarid, 18 postembryonic stages have been described by Sanders (1963a), whereas Waloszek (1993) found 18 preadult plus one adult stage. From stage 13 onwards the second antenna lacks the naupliar masticatory process of the coxa. Cephalocarid ontogeny is characterized by a gradual, sequential, and continuous addition of limbs throughout the postembryonic phase of development (Fig. 2A). Cephalocaridan nauplii, like the adults, are benthic and unable to swim. They move substrate-bound, ventral side down.

Branchiopoda

Branchiopod nauplii (with some exceptions in the Conchostraca) have a small and, in most taxa, unsegmented first antenna, with setation only on the distal margin (Fig. 2C; see Ferrari and Grygier 2003). The protopod of the second antenna comprises more than one-half of the total limb length; its setae are subdivided by an articulated zone, and there is a large spine on the medial surface of the distal protopodal segment. The mandible is uniramous (cf. Olesen 1999, 2001).

Ostracoda

According to Kesling (1951), in the Ostracoda there are eight immature stages followed by the adult (Fig. 2B). The presence of only three pairs of appendages at the first stage indicates an orthonauplius. Larval stages of recent ostracods bear a bivalved shield from the first stage onwards (Hartmann and Guillaume 1996), except

in the Punciidae. In the latter family, a univalve cephalic shield has been described for several species of *Manawa* (Swanson 1989). Early nauplii of punciid ostracods are characterized by a segmented trunk and the formation of a non-bivalved, horizontally oriented cephalic shield.

Thoracica

Naupliar development in the Cirripedia-Thoracica departs appreciably from an anameric pattern (Fig. 2F). Neither segments nor limbs are added during the first five stages (six stages being characteristic of the Thoracica). At the final sixth naupliar stage the first maxilla becomes externally expressed. Although six cirriform thoracic limbs can be detected under the cuticle, they belong to the first cyprid stage. In the latter, the somite of the second maxilla and six somites bearing thoracic limbs, as well as abdominal somites plus the telson are added (Lang 1979; Korn 1988). Unique to the Thoracica are nauplii with frontolateral horns and associated glands, forming a complex organ. Thoracica develop through a sequence of naupliar stages that are usually planktic and mostly planktotrophic, followed by a presettlement metamorphosis to a single cypris stage, then by settlement of the cypris and a post-settlement metamorphosis to the juvenile cirriped (Moyses 1987).

Acrothoracica

The nauplii of these boring barnacles are always lecithotrophic. In some species, simple naupliar stages are retained in the mantle cavity and are only released as cyprids. The number of stages is less than six, usually four. The last stage preceding the moult to the cypris is morphogenetically equivalent to the nauplius VI stage of a typical thoracican (Kolbasov et al. 1999).

Rhizocephala

These parasites of other crustaceans exhibit an entirely lecithotrophic development (Høeg and Lützen 1995). The nauplii lack most structures related to feeding, such as antennal masticatory arthrites of the second antenna, mouth, and anal opening; the labrum is reduced to a tiny process. Lecithotrophy probably also accounts for the much reduced setation of the appendages compared to lecithotrophic cirripedes. There is no gut, but large amounts of yolk provide the nutrients for the entire development through implantation into a host. Most species have four naupliar instars; the only exception seems to be *Briarosaccus tenellus* with five instars (Waloszek et al. 1996). The nauplii of most Lernaecodiscidae and Peltogastridae carry an inflated, tube-shaped collar surrounding the whole body, that probably serves as a flotation device; sometimes the collar is reinforced by a dense mesh of cuticular ribs. There is sexual dimorphism in size of rhizocephalan nauplii; male nauplii are larger than female nauplii (Høeg and Lützen 1995).

Ascothoracida

Some ascothoracidan nauplii have cuticular ridges at least on the marginal area of their cephalic shield (Fig. 2H). Planktotrophic nauplii seem to occur in three families of Ascothoracida, but no complete planktotrophic naupliar series has been documented. It appears that Ascothoracida have up to six naupliar stages (Itô and Grygier 1990). Some ascothoracidan nauplii possess cuticular protuberances that are probably homologous to, but are much more plesiomorphic than, frontolateral horns (Grygier 1990). The endopod of the second antenna is clearly three-segmented, contrary to nauplii of Cirripedia, where these fail to separate (Grygier 1993).

Facetotecta

Nauplius larvae first described by Hansen (1899) as “nauplius y” have a heavily reticulated dorsal shield, a dorsocaudal organ of unknown function, and a blind gut (Schram 1970; Elofsson 1971) (Fig. 2G). The cephalic shield is divided by cuticular ridges into many small plates (the supposed NI stage has only about 50 plates; Grygier 1996). It also has paired sensory or secretory organs. Most of the body surface has a very fine, mesh-like texture, but the neck organ (= dorsocaudal organ on the dorsal part of the posterior trunk region) that is present in many taxa is not reticulated (Kolbasov and Hoeg 2003).

Mystacocarida

These tiny, marine interstitial crustaceans hatch as metanauplii with clearly demarcated thoracic somites (Olesen 2001). They lack a nauplius eye but bear a prominent dorsocaudal process (Fig. 2E). The anterior end of the cephalon is separated from the remainder by a deep constriction and carries the first antennae. At hatching, mystacocarid first antennae are eight-segmented (Cals and Cals-Usciati 1982). The exopod of the second antenna is comprised of the final number of segments (= nine) from the first instar; the number of endopod segments (= four) is exceptional for crustacean nauplii. The structure of the mandible is strikingly similar to that of the second antenna, with a seven- or eight-segmented exopod; the endopod is three- or four-segmented, depending on the taxon. A masticatory process projects from the protopod medially beneath the labrum. The first maxilla is uniramous and consists of a four-segmented endopod. Both, larvae and adults are benthic, living in the interstitial realm of littoral sand grains.

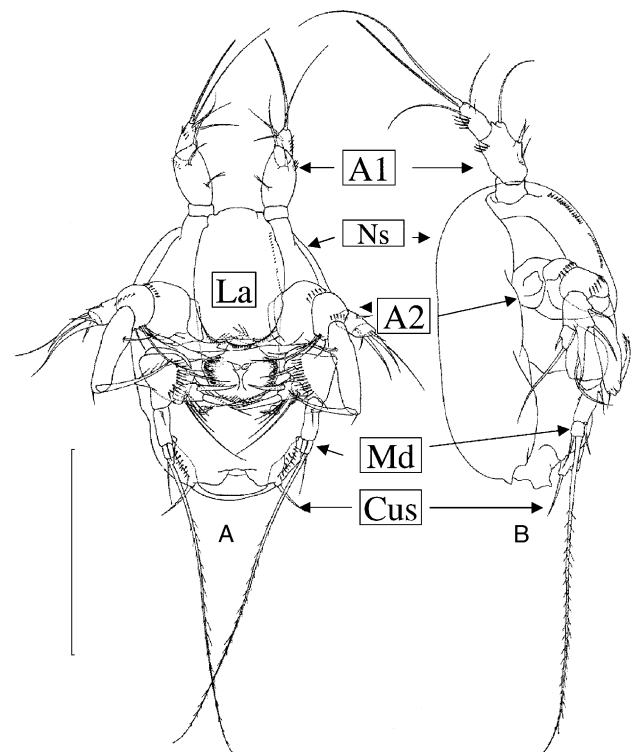


Fig. 1. Semi-schematic illustration of a crustacean nauplius in ventral (A) and lateral (B) views, based on the harpacticoid copepod *Paraleptastacus brevicaudatus* (after Dahms 1990b). Abbreviations: A1 = antennule, A2 = antenna, Cus = caudal setae, La = labrum, Md = mandible, Ns = naupliar shield. Scale bar. 50 μ m.

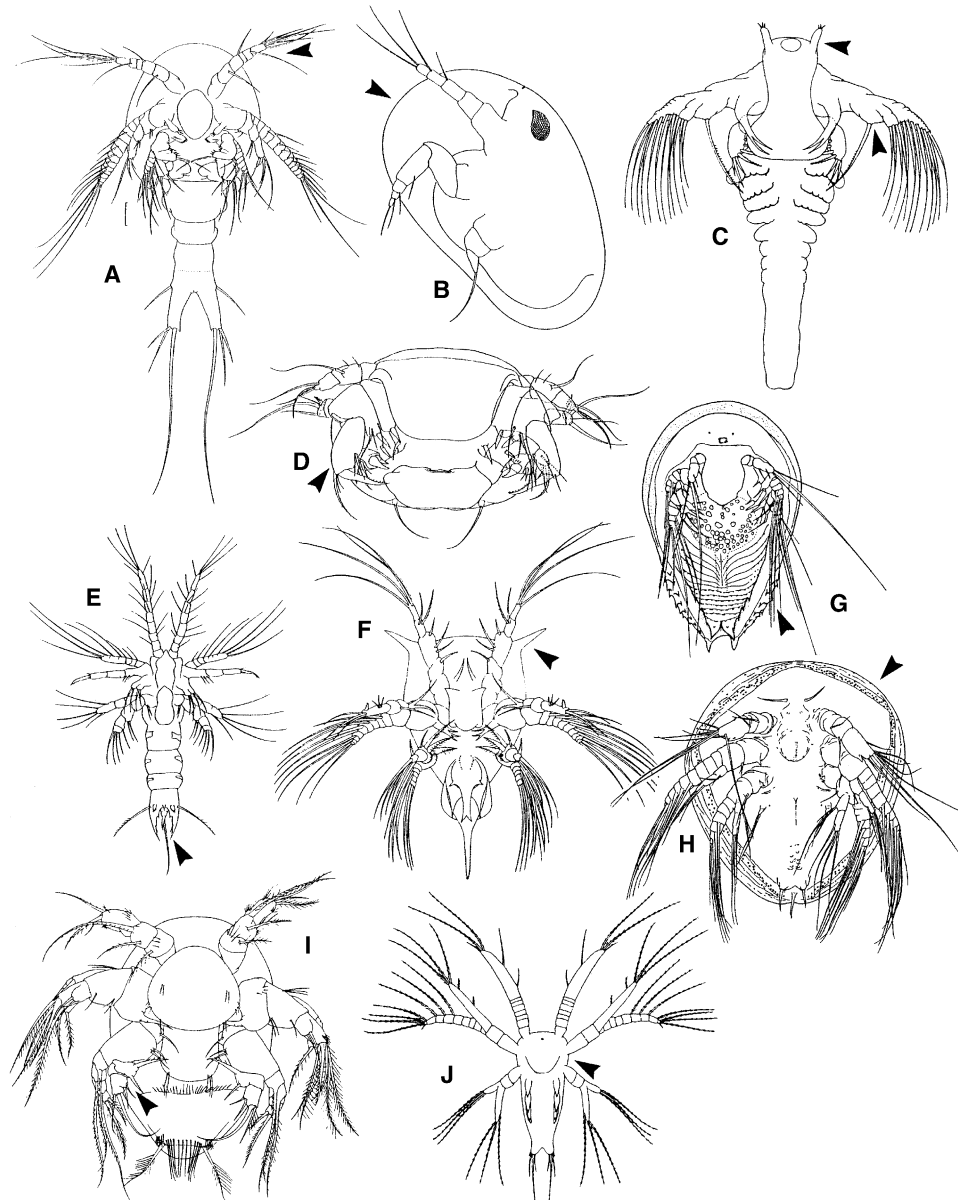


Fig. 2. Pictorial aids for the identification of crustacean nauplii at the level of major taxa; arrowheads point to diagnostic features of the respective taxon, see Key to crustacean nauplii in the text. (A) Metanauplius of *Hutchinsoniella macracantha* (Cephalocarida; after Sanders 1963a). (B) Nauplius I of *Cypris fasciata* (Ostracoda; after Kesling 1951). (C) Metanauplius of *Artemia cf. franciscana* (Branchiopoda-Anostraca; after Sanders 1963b). (D) Nauplius II of *Paramphiascella fulvofasciata* (Copepoda-Harpacticoida; after Dahms 1990a). (E) Metanauplius of *Derocheilocaris remanei* (Mystacocarida; after Delamare-Deboutteville 1954). (F) Metanauplius of *Semibalanus balanoides* (Cirripedia; after Sanders 1963a). (G) Nauplius y I Hansen (Facetotecta; after Schram 1970). (H) Nauplius VI of *Baccalaureus falsiramus* (Ascothoracida; after Itô and Grygier 1990). (I) Nauplius of *Macrocylops fuscus* (Copepoda-Cyclopoida; after Dahms and Fernando 1993b, 1994). (J) Metanauplius of *Penaeus duorarum* (Decapoda-Dendrobranchiata; after Dobkin 1961).

Copepoda

The Copepoda possess at most six naupliar stages, with stage reductions primarily in non-feeding, mostly parasitic taxa (Figs. 1, 2D, I) (cf. Dahms 2004a). Copepod nauplii bear a variable number of first segments of the second antenna: generally three in most taxa, five to six in

Polyarthra (Dahms 2004b), five in some Cyclopoida (Dahms and Fernando 1994), and one to three in the Harpacticoida-Oligoarthra (Dahms 2004b). The coxa of the second antenna bears two setae, the endopod is one-segmented (two-segmented in the Cyclopoida), and the exopod is six-segmented. The mandibular exopod is four-segmented and the postmaxillar limbs developing in later

naupliar stages are juxtaposed medially. In later stages there are six caudal setae (Dahms 1990a). The Polyarthra bear a five-segmented first antenna, the exopodal segments of the second antenna increase from six at N I to a final number of nine at N IV; a dorsocaudal process is present in the Longipediidae and most Canuellidae (Nicholls 1935; Dahms 2004b). Nauplii and juveniles/adults are suspension feeders, and the nauplii are pelagic (Dahms and Qian 2004).

Malacostraca

Development of *Penaeus aztecus* (Penaeidae) (Fig. 2J) provides an example for the Decapoda-Dendrobranchiata. Its postembryonic development begins with two orthonauplius stages (Cook and Murphy 1971); at N III some abdominal somite separation is indicated, and at N IV there are four postmandibular pairs of limb buds (probably representing the first and second maxillae, and thoracopods 1 and 2). At the final N V stage these lobe-like limb buds, the caudal process and the body are more demarcated and more heavily chitinized. The fifth naupliar stage in this species is followed by protozoa I–III stages, mysis I–III, and postlarva I. Since penaeid nauplii are non-feeding, and lack feeding structures on all naupliar appendages, the labrum is poorly developed. Embryos of the Syncarida and Peracarida, despite their direct development, pass through a distinct embryonic nauplius stage (Anderson 1973).

Computer program: keys for the identification of crustacean nauplii (“Nauplius Key”)

This electronic key produces a user-configurable interface for taxonomic identification. The “Nauplius Key” program provides the user with the ability to easily navigate and create either a dichotomous or a multibranching format. The program provides two modes of operation. In the navigate-mode it provides the user with a question and list of answers. Each answer links to a new question. The user may select one of the available answers, choose to move back one step in the process, start the process over, or select another key to browse. In the setup-mode the user may open a question and its answers for review and editing, save it, save it under a different name, add or remove answers, or create a whole new question. Despite its name, the key allows for trees where each node, or question, has more than two descendants, or choices. Each answer in turn is linked to a new question, and each question must be saved with a unique name. The answers, and the subordinate questions they link to, are saved in files named with variations on those of their parent question(s). The program both accepts previously written

complete keys and allows the creation of new keys with ease. The major advantage of producing a key for determination in a digital format is the ease with which a given user may modify it as new knowledge becomes available. Also, it may be modified easily to fit the particular electronic environment in which it is being used.

“Nauplius Key” is written in Java and is platform independent. The program form is available from one of the authors (B.J.F.).

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