Chaper 27. Copepoda

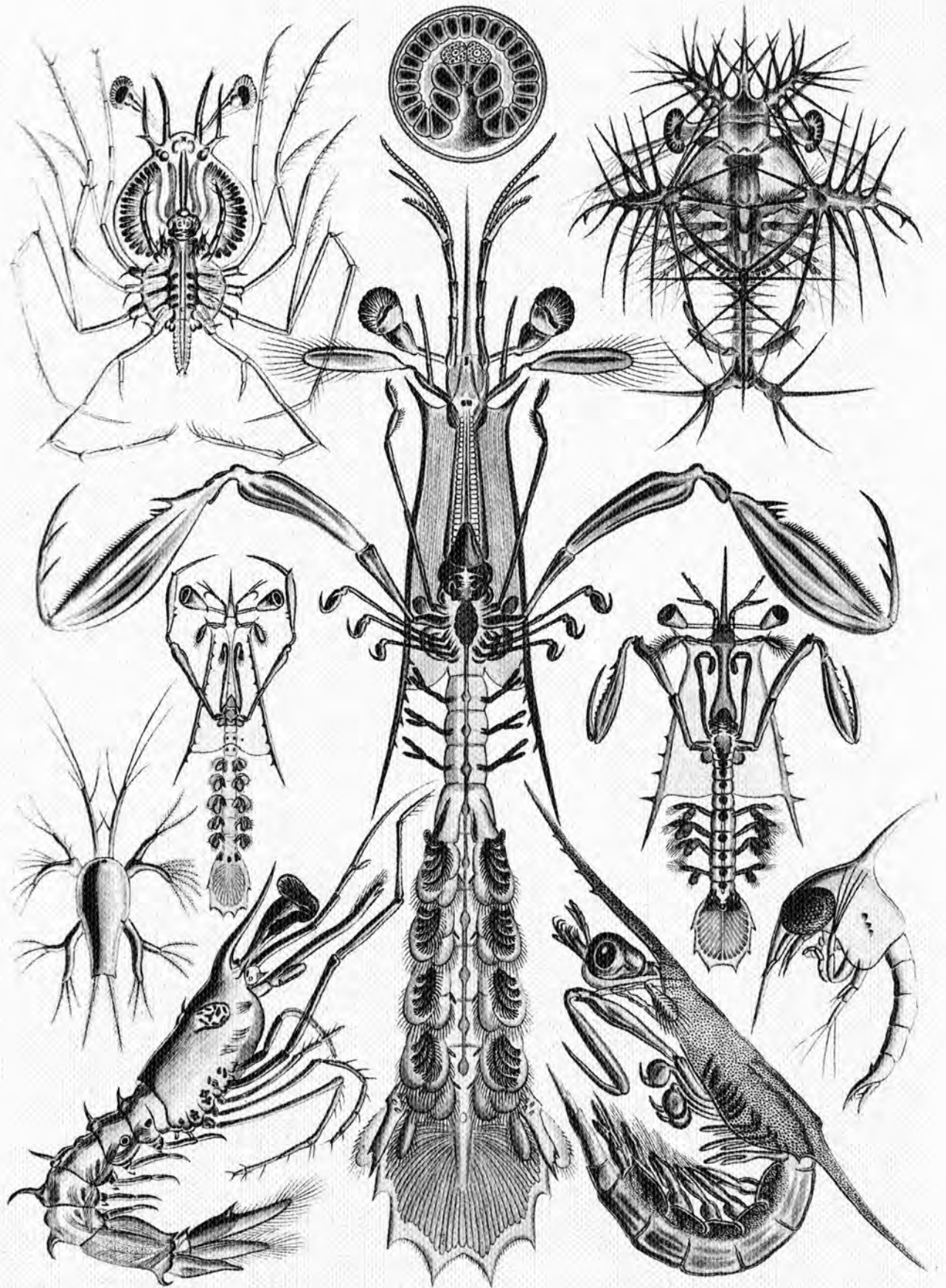**Chapter** · January 2014

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ATLAS OF CRUSTACEAN LARVAE

EDITED BY Joel W. Martin, Jørgen Olesen & Jens T. Høeg

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Frontispiece: Plate number 76 from the 1904 publication *Kunstformen der Natur (Artforms of Nature)* by Ernst Haeckel (1834–1919), depicting various forms of crustacean larvae (classified by Haeckel as Thoracostraca).

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Rony Huys

Copepoda

GENERAL: Copepods outnumber every other group of multicellular animals on earth, including the hyperabundant insects and nematode worms (Hardy 1970; Huys and Boxshall 1991). These small crustaceans are found throughout the world's natural and man-made aquatic environments, spanning the entire salinity range from fresh water to hypersaline water, including the most unusual continental habitats (Reid 2001). Copepods, with more than 12,500 described species, and outnumbering the insects in terms of individuals by up to three orders of magnitude (Schminke 2007), carry a global biological importance that is belied by their generally small size. In the pelagic realm, which encompasses a volume of 1,347 million km³ and is the largest biome on the planet, copepods are the dominant members of the holozooplankton, both numerically and in terms of biomass (Harris et al. 2000). In addition to life strategies that encompass free-living, substrate-associated, and interstitial habits, copepods also have extensive impacts in their role as associates or parasites of the majority of aquatic metazoan phyla, from sponges to chordates, including reptiles and marine mammals. This variety of life strategies has generated an incredible morphological plasticity and disparity in body form and shape that are arguably unrivalled among the Crustacea. Copepods underpin the world's freshwater and marine ecosystems (Costanza et al. 1997). They are sensitive bioindicators of local and global climate change (Richardson 2008), key ecosystem-service providers (Frangoulis et al. 2005; Falk-Petersen et al. 2007), and parasites of economically important aquatic animals (M. Costello 2009). They sustain the majority of the world's fisheries (Costanza et al. 1997) and, through their roles as vectors of disease (Huq et al. 1983; Dick et al. 1991), also have a number of direct and indirect effects on human health and our quality of life.

Copepods are typically small. In planktonic and benthic forms, total body length is usually between 0.2 and 5.0 mm, although some species of *Valdiviella* (Calanoida) can reach 28 mm in length. The real giants amongst the copepods are the parasites, with the largest being members of the siphono-stomatoid family Pennellidae (*Pennella balaenopterae* reaches about 250 mm in length and carries egg sacs that may exceed 350 mm). Most classifications (e.g., Huys and Boxshall 1991; J. W. Martin and Davis 2001; Boxshall and Halsey 2004) recognize 2 infraclasses: the Progymnoplea (containing the single order Platycopioida) and the far more speciose Neocopepoda, which is divided into the superorders Gymnoplea (order Calanoida) and Podoplea (orders Misophrioida, Cyclopoida, Mormonilloida, Harpacticoida, Siphonostomatoida, and Gelyelloida). The ecological adaptability displayed by copepods is reflected in their tremendous morphological plasticity, which makes it difficult to formulate a rigorous diagnosis of the subclass Copepoda that is both informative yet sufficiently comprehensive to cover the bizarre parasites as well as the free-living forms. Virtually all copepods have a stage in their life cycle—either the adult or one of the copepodid instars—exhibiting a cephalosome into which the maxilliped-bearing first thoracic somite is incorporated and possessing at least two pairs of swimming legs, the members of which are linked by an intercoxal sclerite. The life cycle typically consists of nauplii (0–6) and copepodids (1–6), the last copepodid stage being equivalent to the adult (fig. 27.1A).

LARVAL TYPES: Post-embryonic development of copepods is divided into a naupliar phase and a copepodid phase. Primitively, each phase consists of six stages (fig. 27.1A).

Nauplius: Larval development and life cycles are highly variable and can be significantly abbreviated (fig. 27.6A), although most copepods hatch at the (ortho)nauplius stage, a simple larval form described earlier (see chapter 2). Typically, after six naupliar instars (often designated NI, NII, NIII, etc.), the final nauplius stage molts into a copepodid stage.

Metanauplius: Occasionally the first stage in the life cycle is a metanauplius, and some parasitic species are known to hatch as a copepodid.

Copepodid: Copepodid stages are often referred to as CoI, CoII, and so forth (or CI, CII, etc.). The first copepodid re-

sembles the adult but has a simple, unsegmented abdomen and only three pairs of thoracic limbs (maxillipeds and legs 1–2). There are significant changes in body size and shape, as well as in the appendages, in the molt from NVI to CoI, collectively known as metamorphosis (e.g., Gurney 1942; Dahms 1992). Intermolt stages are important for tracing the origin and homology of larval structures between naupliar and copepodid stages; examples are provided by Hulsemann (1991) for calanoids and by Dahms (1992) for harpacticoids.

Chalimus: In some parasitic groups a stage following the infective copepodid (or one of the copepodid stages) is called the chalimus; it differs from the copepodid in its possession of a frontal filament that aids in attachment to the host (e.g., I.-H. Kim 1993; Ohtsuka et al. 2009).

Other Stages: Some parasitic copepods have an onychopodium or (transient) pupal stages in their life cycle.

MORPHOLOGY

Nauplius: Copepods lack any external expression of somites during the naupliar phase of development. The naupliar body usually increases in size from one stage to the next. Early nauplii have three well-developed limbs (antennules, antennae, and mandibles), and the setose buds of the caudal rami. Buds of other limbs between the mandible and caudal ramus may be added during the naupliar phase. During the molt to CoI, the naupliar limb buds, including the caudal rami, appear as functional ("transformed" *sensu* Ferrari and Dahms 2007) limbs. Copepods possess, at most, six naupliar stages (NI–NVI) (virtually all of the Calanoida, the Harpacticoida, and free-living Cyclopoida) (fig. 27.6A), with stage reductions primarily in parasitic taxa (e.g., Izawa 1987) but also in free-living orders (e.g., Gurney 1933a; Matthews 1964). According to Izawa (1987), abbreviated naupliar phases with only five, four, three, or two stages result from the suppression of NII, NII–NIII, NII–NIV, and NII–NV, respectively, but this formula does not seem to be applicable to all parasitic copepods (Ferrari and Dahms 2007). In the lernaeopodid *Salmincola californiensis* (Kabata and Cousens 1973) and some Nicothoidae (*Hansenulus trebax*, see Heron and Damkaer 1986; *Neomysidion rahotsu*, see Ohtsuka et al. 2007), the short-lived nauplius remains inside the egg membrane and hatches direct at the first copepodid stage (figs. 27.5D; 27.9C). Some Pennellidae, such as *Cardiodectes medusaeus* (P. Perkins 1983), *Peniculisa shiinoi* (Izawa 1997), *Peniculus minuticaudae* (Ismail et al. 2013), and *Peroderma cylindricum* (Samia 1993), have lost the naupliar phase completely; the embryo develops directly into the first copepodid stage (fig. 27.9A). In the Cucumaricolidae and some Chordeumiidae (e.g., *Parachordeumium amphiurae*), the life cycle is even more abbreviated, hatching from the egg at the second copepodid stage, with no intervening nauplius stage (fig. 27.6A) (Paterson 1958; Goudey-Perrière 1979). The key below (after Ferrari and Dahms 2007) is useful for copepods in which all six naupliar stages are expressed, particularly for the free-living species.

Metanauplius: Some copepods have a nauplius stage with more than three pairs of functional appendages. The life cycle of thaumatopsyllids includes a parasitic metanauplius that lives in the stomach of its ophiuroid host (Dojiri et al. 2008); it possesses bilobate maxillules and limb buds of legs 1–2 (figs. 27.3A, B; 27.7A–D). Thaumatopsyllid metanauplii usually show sexual dimorphism in their body shape, pigmentation, nauplius-eye morphology, and (occasionally) gonadal structure (Dojiri et al. 2008; Hendler and Dojiri 2009; Hendler and Kim 2010). At least some representatives of the Chordeumiidae have functional maxillules that are subsequently lost in the copepodid stages and in adults (fig. 27.3E, F) (Jungersen 1914). Adult micrallectids have a complete set of functional cephalothoracic appendages but lack all posterior limbs, and their organization is comparable with a metanauplius (fig. 27.3C, D) (Huys 2001).

Copepodid: Copepodid stages usually have their thoracic and abdominal somites separated by an arthrodial membrane, lack the naupliar endite on the antennary coxa, exhibit well-developed post-mandibular appendages, and have their swimming legs united by an intercoxal sclerite (interpodal bar). The antenna shifts from a naupliar paroral to a copepodid pre-oral position and loses its masticatory function. During the copepodid phase, body size and the number of somites usually increase (fig. 27.1A, B), but many exceptions exist. During each molt to a new copepodid stage, one new somite is added from a growth zone that is located in the anterior part of the posterior abdominal (anal) somite. First copepodid stages have five post-cephalosomic trunk somites, and there seems to be a functional tagma boundary between the third and fourth somites in gymnopleans, but not in podopleans (fig. 27.1C). This tagma boundary is not morphologically specialized, but instead is a flexure point defined by the behavior of the animal. At CoII the functional flexure point is located between the fourth and fifth post-cephalosomic somites and remains the definitive prosome-urosome boundary in podopleans; in gymnopleans this boundary is positioned between the fifth and sixth somites and is not attained until CoIII. There are up to nine pairs of well-developed limbs at the first copepodid stage: antennules, antennae, mandibles, maxillules, maxillae,

Three functional limbs (antennule, antenna, mandible); bud of the caudal ramus with one pair of setae ....NI

Bud of the maxillule a simple lobe, with one seta or the posterior part of the body distinctly narrower than the anterior part.. NII

Bud of the caudal ramus with more than one pair of setae .... NIII

Mandibular gnathobase present and/or bud of the maxillule multilobate, with no more than six setae .... NIV

Bud of the maxilla present or bud of the maxillule multilobate, with at least seven setae .... NV

Bud of swimming legs 1 and 2 present.. NVI

Table 27.1 Common pattern of development for legs 1–4 during copepodid phase

	Leg 1	Leg 2	Leg 3	Leg 4
N	1^B	1^B		
CoI	1 + 1	1 + 1	1^B	
CoII	2 + 2	2 + 2	1 + 1	1^B
CoIII	2 + 2	2 + 2	2 + 2	1 + 1
CoIV	2 + 2	2 + 2	2 + 2	2 + 2
CoV	3 + 3	3 + 3	3 + 3	3 + 3
Adult	3 + 3	3 + 3	3 + 3	3 + 3

Note: 1 + 1 = reorganized leg with 1-segmented exopod and endopod; 2 + 2 = leg with 2-segmented exopod and endopod, etc. Abbreviations: N = pre-metamorphic nauplius, Co = copepodid instar, 1^B = primary setose leg bud (Ferrari 1988).

maxillipeds, swimming legs 1–2, and the caudal rami, plus a setose bud of swimming leg 3. The remaining limbs are added as buds during the copepodid phase, one stage later than that in which their respective somites are expressed. Most limbs develop segments during the copepodid phase. Ferrari (1988) identified a common pattern of development for legs 1–4 during the copepodid phase (table 27.1), but he found that there are 23 additional patterns that can produce an adult leg with three-segmented rami. Published studies suggest that all copepods have at least one copepodid stage in their life cycle (usually copepodid I), the only known exceptions being *Parachordeumium amphiurae* and *Cucumaricola notabilis*, which hatch from the egg at the copepodid II stage (see Paterson 1958; Goudey-Perrière 1979). Copepodid I (or, rarely, CoII) is often the infective stage in the life cycle of symbiotic copepods. In some Chitonophilidae, extreme transformation and a gross increase in size (as a result of hypermorphosis) take place at the final molt (fig. 27.11C, D) (Huys et al. 2002). Goudey-Perrière (1979) distinguished up to eight post-naupliar instars in the life cycle of the chordeumiid *Amphiurophilus amphiurae*, which she related to copepodids II–VI (instar 1 = CoII, instar 2 = CoIII, instar 3 = CoIV, instars 4–5 = CoIV; instars 6–8 in females or 6–7 in males = CoVI). The process of setal formation during copepodid molting was described by B. Dexter (1981).

Chalimus: The chalimus is one of up to four stages in the copepodid phase of development that attach themselves to the host by means of a frontal filament (figs. 27.4B, C; 27.9A, B). The possession of a frontal filament is a feature of several families within the large fish-parasitic clade of siphonostomatoid copepods, including members of the Caligidae, Pandaridae, Cecropidae, Pennellidae, and Lernaeopodidae (C. Wilson 1907a; Sproston 1942; Kabata and Cousens 1973; Grabda 1974; T. Schram 1979); its presence in the Hatschekiidae was inferred by T. Schram and Aspholm (1997), who recorded a frontal filament–secreting organ in *Hatschekia hippoglossi*. The pre-formed frontal filament carried within the frontal region of the infective copepodid is everted and attached to the host before the molt to chalimus I. This filament is a discrete structure and remains permanently attached to the host. At the subsequent molt to chalimus I, an additional bulb of material is secreted at the origin of the filament, around its base. At

each of the next three molts, a further bulb of material (an extension lobe) is secreted at the origin of the filament, so chalimus II has two lobes at the base of its filament, chalimus III has three lobes, and chalimus IV has four lobes (fig. 27.4A, C). The nature of development between first copepodid and adult caligids has caused considerable confusion in determining the number of true instars (stages separated by true molts). Ohtsuka et al. (2007) reviewed the dissenting views on *Lepeophtheirus*, which is the only example in the entire Copepoda where the number of stages in copepodid-phase development has been reported to exceed five (four chalimus stages and two pre-adults) before the adult. Their reinterpretation suggests that *Lepeophtheirus* conforms to the basic caligid life cycle, consisting of two naupliar, one copepodid, and four chalimus stages (corresponding to the second to fifth copepodid stages) preceding the adult (see also Venmathi Maran et al. 2013).

Pupal Stages: In the Nicothoidae there are three basic types of post-larval development (Hansen 1897; Heron and Damkaer 1986): (1) direct metamorphosis from copepodids to adults in both sexes; (2) indirect metamorphosis from copepodids via 1–3 intermediate pupal stage(s) to both sexes of adults; and (3) direct metamorphosis in one sex, but indirect in the other. Females of *Hansenulus trebax* appear to pass through two pupal stages of post-larval development before transformation to a small adult (fig. 27.9C) (Heron and Damkaer 1986). In the first pupal stage, the body is divided into a prosome and a hirsute trunk; the antennules bear a few vestigial setae; the antennae, maxillules, and maxillae are rudimentary; and the maxillipeds are one-segmented. The emerging second pupal stage has fully developed oral appendages and two pairs of swimming legs, similar in details and size to those of the adult female. Both pupal stages are attached to the marsupium of the mysid host by paired dorsal filaments extruding from a middorsal vent. Ohtsuka et al. (2007) inferred from the presence of a thin membranous structure within the copepodid exuvium of *Neomysidion rahotsu* that only one transient pupal stage may be passed through (as a double molt) as the copepodid enters the host (fig. 27.5D). In some Lernaeopodidae (e.g., *Nectobrachia indivisa*), the infective copepod becomes attached to its fish host by the frontal filament and molts into a stage that Heegaard (1947) referred to as the "pupa" and Kabata (1981) equated with the pre-adult, since no subsequent molting takes place. Pupal stages also feature in the life cycle of *Alella macrotrachelus* (Lernaeopodidae), where they are followed by either four (female pathway) or two (male pathway) chalimus stages (fig. 27.9B) (Raibaut 1985). The homologies between these pupae and traditional copepodid stages are as yet unknown.

Onychopodid: The life cycle and bizarre sexual biology of *Gonophysema gullmarensis* was elucidated by Bresciani and Lützen (1961) (fig. 27.5A). This species has a single nauplius stage, which is lecithotrophic and molts into a free infective copepodid stage. After settlement on the ascidian host, the copepodid undergoes a metamorphosis to the onychopodid larva, a simple elongate sac-like stage provided with paired grasping antennae that are used to attach the larva to the skin of the host. The conical head end of the onychopodid larva penetrates the

host epithelium and enters the underlying tissues, leaving the shed copepodid exuvium behind. The onychopodid migrates within the vascular tissues of the host before finally settling just below the epithelium of the peribranchial cavity, where the transformation into the adult female form takes place. These parasites lack any trace of a mouth, digestive tract, and anus in the adult, feeding instead by the uptake of nutrients across the specialized body integument (Bresciani 1986). The young stage in the transformation of the adult female is penetrated by one or more onychopodids. These male onychopodids enter the female via the atrial pore and atrium and pass into the testicular vesicle of the female. This testicular vesicle is of ectodermal origin and represents an invagination of the external surface (fig. 27.5B). Once in position, the males undergo a metamorphic reduction so that little tissue except the gonads remain (fig. 27.5C). *Gonophysema gullmarensis* is not hermaphroditic, as originally described (Bresciani and Lützen 1960); instead it exhibits cryptogonochorism, where males are reduced to little more than germinal layers and are housed within specialized invaginated vesicles within the body of the female.

Post-Mating Metamorphosis: Once attached to, or embedded in, the host fish, mated females of many species belonging to the Pennellidae and Sphyriidae (both Siphonostomatoida) and Lernaeidae (Cyclopoida) undergo a profound metamorphosis (without molting) to produce the final body form (figs. 27.6B–D; 27.9A). The metamorphosis involves a considerable increase in volume, especially in the trunk region. This is achieved partly by expansion of the highly folded integument, and partly by production of a new integument (J. Smith and Whitfield 1988). In the pennellid *Lernaeocera branchialis* (fig. 27.6D), straightening out these folds generates an approximately 6-fold increase in length, but this mechanism provides only part of the overall 10- to 20-fold increase in length that takes place.

MORPHOLOGICAL DIVERSITY

Nauplii: Differences among the six stages of a typical naupliar phase include changes in the number of limb buds, in segments of limb rami (exopod, endopod), and in setation elements on limb segments and the caudal rami. Nauplii are typically oval in shape, but they can be elongate in species leading a pelagic lifestyle (fig. 27.2K) (e.g., *Macrosetella gracilis*, see Tokioka and Bieri 1966; *Microsetella norvegica*, see W. Diaz and Evans 1983) or interstitial mode of life (e.g., *Paraleptastacus brevicaudatus*, see Dahms 1990a). The nauplius stages of *Rhincalanus* spp. and several members of the Pontellidae are characterized by extreme elongation and by a slender body that tapers posteriorly to an acute point (fig. 27.2G, I) (Gurney 1934; Björnberg 1972). Harpacticoids belonging to the superfamily Thalestrioidea typically have nauplii with very wide bodies (fig. 27.2F, H. L). The nauplius dorsal shield is usually smooth, although in some harpacticoids it can be ornamented with tiny spinules (fig. 27.2J). All nauplius stages of *Longipedia* are characterized by the presence of a long median caudal process, which becomes progressively shorter during the planktonic naupliar phase (fig. 27.2B) (Onbé 1984). Caudal

spines have also been reported in the early instars (NI–NII) of planktonic *Microsetella* spp. (W. Diaz and Evans 1983), and in the lecithotrophic nauplii of some Lichomolgidae, Taeniacanthidae, and Bomolochidae (Kabata 1976; Izawa 1987). Caudal spines (in planktonic harpacticoids) and enlarged caudal setae (in calanoids, e.g., *Euchaeta*, *Rhincalanus*, etc.) (fig. 27.2O) are assumed to play a role in swimming or maintaining buoyancy in pelagic nauplii. Left-right asymmetry is often expressed in the caudal setae of calanoid nauplii, with either the left side (fig. 27.2I) (in the Acartiidae, Candaciidae, Centropagidae, Fosshageniidae, Pontellidae, and Pseudodiaptomidae) or the right side (fig. 27.2G) (in the Eucalanidae and Rhincalanidae) being better developed. The nauplius stages of the planktonic *Euterpina acutifrons* lack a caudal spine but exhibit a cluster of long caudal spinules (fig. 27.2N) (Haq 1965; Dahms 1990c).

Copepod nauplii typically have a centrally placed nauplius eye toward the front of the dorsal shield (fig. 27.2A), consisting of a median ventral and two dorsolateral cup-shaped ocelli, with a common backing of two shielding pigment cells. The nauplius eye is absent in *Misophria pallida* (Gurney 1933b), and in 2 families of highly transformed parasites of polychaetes, the Herpyllobiidae (Lützen 1968) and the Xenocoelomatidae (Bresciani and Lützen 1974). Naupliar stages of the tisbid genus *Scutellidium* typically display a midventral oral sucker, which is derived from the labrum and used for adhesion to the surface of algal fronds (Brian 1919; Gurney 1933a; Branch 1974), but see Dahms (1990c) for an exception.

Nauplii of most copepods are planktotrophic, but lecithotrophy has evolved repeatedly. Lecithotrophic nauplii are often characterized by a yolk-rich body (fig. 27.10F), the absence of a labrum, a weakly invaginated stomodeum and proctodeum, and the absence of the antennary masticatory process (fig. 27.2P) and mandibular gnathobase. In the Calanoida, the members of the family Euchaetidae have lecithotrophic nauplii (fig. 27.2O), whereas in closely related families they are planktotrophic. Nauplii in the calanoid families Aetidaeidae (*Chiridius armatus*, *Aetideus armatus*—both with only four naupliar instars) and Phaennidae (*Xanthocalanus fallax*) rely entirely on their yolk supply until they reach the first copepodid stage (Matthews 1964). In the Harpacticoida, species of the genera *Pseudotachidius* and *Leptocaris* have lecithotrophic nauplii (Gurney 1932; Dahms 1989), and within the orders Cyclopoida and Siphonostomatoida many parasitic groups possess them (fig. 27.10E, F) (Izawa 1987; Boxshall and Halsey 2004). The antennary arthrite may be absent in the early naupliar stages of copepods that display a mixotrophic naupliar phase and lack a functional mouth at NI (e.g., *Calanus finmarchicus*, see Ferrari and Dahms 2007; *Pseudodiaptomus marinus*, see Uye et al. 1983). The planktotrophic nauplii in the family Ergasilidae carry a characteristic spatulate element on the distal segment of the mandibular endopod (e.g., Huys and Boxshall 1991, their fig. 2.10.24C, D). Sexual dimorphism in naupliar stages has not been recorded thus far (but see, e.g., Hendler and Dojiri 2009; Hendler and Kim 2010 for metanauplii). Both thaumatopsyllids (fig. 27.7A) (Dojiri et al. 2008) and monstrillids (fig. 27.8) (Malaquin 1901) have a protelean life

cycle, combining an endoparasitic naupliar phase and free-living non-feeding adults. Monstrillid eggs hatch into nauplii that locate a host and burrow into its tissues. After undergoing a considerable metamorphosis in the host's blood system, the endoparasitic sac-like naupliar stages develop root-like absorptive processes and bear virtually no resemblance to other crustacean larvae. Once development is complete, the monstrillid leaves its host as a last copepodid stage and undertakes a single molt into the adult. The infective nauplius stage of *Monstrilla hamatapex* was described in detail by Grygier and Ohtsuka (1995); the antennary arthrite and piercing mandibles in this lecithotrophic stage presumably assist in the attachment to and/or penetration of the host.

Copepodids: Ferrari and Dahms (2007) described the fundamental differences in post-naupliar body architecture between the gymnoplean *Ridgewayia klausruetzleri*, the podoplean *Dioithona oculata*, and the thaumatopsyllid *Caribeopsyllus amphiodiae*. Their paper should be consulted for a further discussion on the remaining variation in the association of somites along the anteroposterior axis of the body. This variation results from one of two processes: the formation of somite complexes that result from the failure of an arthrodial membrane to form between two somites, or the suspension of the addition of somites to the body. Readers interested in the evolutionary reduction of body somites in poecilostome Cyclopoida are referred to Izawa (1991). The morphology of the infective copepodid shows little variation in symbiotic copepods. In some families it attaches itself to the host by a cephalic frontal filament prior to molting into a chalimus stage (figs. 27.4B, C; 27.9A) (e.g., the Pennellidae, and caligiform families) or a pupal stage (fig. 27.9C) (some Nicothoidae). Sexual dimorphism is usually expressed in later copepodid stages of harpacticoids, most free-living cyclopoids, and many calanoids, particularly in body size, antennule segmentation and armature, and legs 1–5. In many harpacticoid families, males form a spinous process (apophysis) on a swimming-leg segment, which may originate as a produced segmental margin, or may be derived by modification of a setal element present in females (Lang 1948; Huys 1990c). Most poecilostome cyclopoids exhibit sexual dimorphism in the maxillipeds, which is typically first expressed at the molt to CoV (e.g., Itoh and Nishida 1995). According to Izawa (1986), sexual dimorphism in *Acanthochondria* is apparent as early as CoII, and this is probably characteristic of the speciose fish-parasitic family Chondracanthidae, with its tiny males and giant females (Boxshall and Halsey 2004). Dimorphic males (with different functions/lifestyles) have been recognized in the notodelphyid genus *Pachypygus* (Dudley 1966; Hipeau-Jacquotte 1978, 1987), the planktonic harpacticoid *Euterpina acutifrons* (Haq 1965) and the myicolid *Pseudomyicola spinosus* (Do et al. 1984). In all of these cases the expression of male dimorphism during development commenced at CoIV. Several planktonic families (e.g., the Aegisthidae, Euchaetidae, Lubbockiidae, Mormonillidae, and Pontoeciellidae) and deepwater harpacticoid lineages have non-feeding adult males with atrophied mouthparts, and male copepodid stages with fully functional mouthparts. Little information is available on

the precise developmental onset of this transformation in the feeding mode.

NATURAL HISTORY: Egg sacs (fig. 27.10A–E) are a typical attribute for most major copepod orders (the Cyclopoida [including the Poecilostomatoida], Harpacticoida, and Siphonostomatoida), and their presence has been confirmed in the Mormonilloida (Huys et al. 1992c). In most calanoid families, eggs are freely released into the water column. Exceptions—where eggs are either contained in single or paired multiseriate (or uniseriate) sac(s)—are found in the Aetideidae, Arietellidae, Clausocalanidae, Diaptomidae, Pseudodiaptomidae, and Temoridae, although it is not always clear whether these are true egg sacs, with an enclosing sac membrane (Huys and Boxshall 1991; Mazzocchi and Paffenhöfer 1998). Eggs are retained in a mass on the ventral side of the urosome in the Centropagidae and Euchaetidae and in some members of the Clausocalanidae and Temoridae. Gurney's (1933b) observations on *Misophria pallida* showed that its eggs are loosely attached to the female urosome and not contained in sacs; it is unknown if this is the typical condition for all Misophrioida. No information is available for the Gelyelloida or Platycopioida. Monstrillid females lack egg sacs; instead, the eggs are attached to the paired ovigerous spines by means of a mucous substance secreted by the terminal part of the oviduct (fig. 27.12C). Huys and Boxshall (1991) showed that egg masses are produced iteratively, the ovigerous spines growing accordingly when a new batch is being spawned (fig. 27.12B). The complex of caligiform and dichelesthiiform families within the Siphonostomatoida are characterized by (sometimes coiled) linear egg strings containing a single column of closely packed disc-shaped eggs (figs. 27.4B; 27.10G). The presence of caudal balancers (fig. 27.3G–I) in the nauplii of the Caligidae, Dissonidae, Kroyeriidae, and Pandaridae appears to be correlated with the possession of uniseriate egg sacs (G. A. Boxshall, pers. comm.). In the highly modified Phyllodicolidae, eggs are extruded in elongate masses that break down, with the eggs attached separately to an axial filament originating at the genital aperture (fig. 27.12A) (Laubier 1961). Similarly, in some members of the Chitonophilidae, eggs are attached to the genital area by individual filaments (fig. 27.11I, J) (Huys et al. 2002). The number of eggs contained in a single sac can range from one—such as in the siphonostomatoid families Calverocheridae (Stock 1968), Micropontiidae (Gooding 1957), and Stellicomitidae (Humes and Cressey 1958)—to 2,000–3,000 in the Chordeumiidae (Bartsch 1996). Within the benthic Harpacticoida, members of the Darcythompsoniidae (Lang 1948) and Phyllognathopodidae (Chappuis 1916) reportedly lack egg sacs and release their eggs directly into the environment, while parastenocaridids carry them for a short period before attaching them to the substratum (Schminke 1982). In some symbiotic families associated with invertebrates, eggs are either laid free inside the host (the Lamippidae, see Bouligand 1960; the Sponginticolidae, see Silén 1963), deposited in masses inside a gall on the host (the Mesoglicolidae, see Taton 1934), attached to the inside of the

tunic of the host ascidian (the Intramolgidae, see Marchenkov and Boxshall 1995), or laid inside a capsule enclosing the adult female (the Codobidae, see Heegaard 1951).

Specialized brooding in (semi)enclosed chambers formed from body somites and/or appendages has evolved independently many times in podoplean copepods (Grygier and Ohtsuka 2008). In several harpacticoids (*Phyllopodopsyllus*, *Eudactylopus*, *Phyllothalestris*, *Paramenophia*, and the Tegastidae), the eggs are retained in a single ventral sac, enclosed in a brood pouch formed by the modified foliaceous fifth legs (fig. 27.11E, F) (Lang 1948; Gamô 1969a, 1969b; Huys et al. 1996). Similarly, the paired multiseriate egg sacs in the Ascidicolidae (Cyclopoida) are partly or completely covered by the expanded fifth legs (Illg and Dudley 1980). The monstrillid genus *Maemonstrilla* represents the only example of subthoracic brooding among planktonic copepods (Grygier and Ohtsuka 2008). An incubatory pouch that is formed dorsally or dorsolaterally within one or more pedigerous somites (fig. 27.11A, B) is present in the cyclopoid families Buproridae (Illg and Dudley 1980), Gastrodelphyidae (Dudley 1964), and Notodelphyidae (e.g., Sars 1921). Similar brooding has been recorded in the mytilicolid *Pectenophilus ornatus*, although the origin of the brood pouch in this highly modified cyclopoid remains unknown (fig. 27.12E–H) (Nagasawa et al. 1988; Huys et al. 2006). Some Chordeumiidae maintain their loose egg masses in a subthoracic cage that is formed from modified and ventrally downturned cephalic appendages and thoracic outgrowths (fig. 27.11G, H) (Stephensen 1935; Goudey-Perrière 1979). The vermiform female of *Nucellicola holmanae*, a chitonophilid endoparasite of gastropods, is enveloped in a membranous tube that is possibly of host origin; the tube becomes filled with eggs and developing nauplii (Lamb et al. 1996). In members of the Micrallectidae, the lecithotrophic nauplii develop within the eggs retained in the genital tract of the female; the naupliar maxillae develop early and are visible through the body wall of the female (Huys 2001).

In many copepod species, adult males clasp subadult females for an extended period before transferring spermatophores. Males clasping juvenile females (CoI–CoV, inclusive) is interpreted as mate guarding and is widespread among podoplean copepods. It differs from copulation, which takes place only between adults, and is often distinguishable from mate guarding by a difference in the clasping posture (Boxshall 1990). Studies reporting pre-copulatory mate guarding in harpacticoid copepods have been summarized by Kern et al. (1984). Males may grasp female copepodids around their caudal setae, caudal rami, anal somite, or fourth leg, or by the posterolateral margins of the dorsal cephalothoracic shield (Lang 1948). Within the family Harpacticidae, adult males typically clasp all juvenile stages from CoI to CoV (e.g., Itô 1970). Fiers (1998) suggested that the atypical development of leg 4 in female copepodids of many of the Laophontidae is a juvenile adaptation to pre-copulatory mating guarding. Observations of adult males attaching themselves to the dorsal surface of female CoV stages have been recorded in both free-living cyclopoids (the Cyclopidae, see Hill and

Coker 1930) and symbiotic cyclopoids (the Notodelphyidae, see Thorell 1859; Giesbrecht 1882). Do et al. (1984) recorded adult males of the poecilostome species *Pseudomyicola spinosus* clasping juvenile stages from the third copepodid onward. Pre-copulatory mate guarding is a common phenomenon in the fish-parasitic Pennellidae and Caligidae, where males frequently clasp attached chalimus stages around the frontal filament (Ho 1966; Boxshall 1974, 1990).

Many freshwater cyclopoids enter diapause in the later copepodid stages (typically CoIV–V), although some may enter a state of complete torpor or active diapause as early as CoII (e.g., *Cyclops scutifer*). Marine calanoids that have dormant stages either produce diapause eggs (the Acartiidae, Centropagidae, Pontellidae, Temoridae, and Tortanidae) or diapause during the copepodid phase (the Calanidae). Freshwater calanoids (the Diaptomidae) can produce resting eggs that can lie in the sediment and remain viable for up to 300 years (Hairston et al. 1995); fossil eggs of *Diaptomus* were reported from Late Quaternary lake sediments (Bennike 1998). Borutzky (1929) reported encysted nauplii in the freshwater harpacticoid *Bryocamptus arcticus*. The only known example of juvenile marine harpacticoids going into dormancy is that by Dahms et al. (1990), who recorded copepodids of *Drescheriella* sp. in a non-encysted dormant stage within the ice in the Antarctic. Delayed naupliar development has been reported for some marine harpacticoids (Coull and Dudley 1976) and calanoids (Uye 1980), but it is not clear whether such prolongation of the naupliar phase represents a genuine form of dormancy. Reports of diapause for parasitic copepods are unknown. For an excellent review of copepod dormancy, see Williams-Howze (1997).

The nauplii of polyarthran harpacticoids (the Longipediidae and Canuellidae) are planktonic suspension feeders with good swimming abilities, while the copepodids remain close to the substratum (in sediment or on an invertebrate host). Oligoarthran harpacticoids typically have benthic nauplii (except *Microsetella* spp., see W. Diaz and Evans 1983) and even those species that secondarily became holoplanktonic complete an essentially substratum-bound life cycle. Björnberg (1965) noted that all developmental stages of *Macrosetella gracilis* are usually found in association with cyanobacteria (*Trichodesmium*), and it seems likely that all planktonic miraciids exhibit a similar specialized lifestyle (Huys and Böttger-Schnack 1994; O'Neil and Roman 1994). Ovigerous females of the widespread pelagic thalestrid species *Parathalestris croni* use floating macroalgal clumps as nests for their non-swimming nauplii (Ingólfsson and Ólafsson 1997). Members of the genus *Balaenophilus* live attached to their cetacean hosts (Bannister and Grindley 1966) or chelonian (juvenile loggerhead turtles) hosts (Ogawa et al. 1997) throughout their life cycles.

Various species of the Thalestridae (*Amenophia*, *Parathalestris*, and *Thalestris*) and Dactylopusiidae (*Dactylopusioides* and *Diarthrodes*) are obligatorily endophagous in macroalgae during most of all of their lives (Brady 1894; Bocquet 1953; Harding 1954; J. Green 1958; Fahrenbach 1962; Ho and Hong 1988; Shimono et al. 2004, 2007). Nauplii and copepodids live

in excavated burrows and galleries or in newly formed capsules or galls (for a discussion on trends in reduction and specialization in frond-mining nauplii, see Dahms 1990b). Stenheliinid nauplii move in a sideways crab-like crawl (Bresciani 1961) and, like all other developmental stages, build mucoid tubes (almost immediately after hatching) that extend into the sediment (Lorenzen 1969; Chandler and Fleeger 1984; Williams-Howze and Fleeger 1987). Their sideways motility and strongly ellipsoid body shape may be adaptations to tube-dwelling.

Very little information is available on the diets of planktotrophic nauplii, but they are recorded as feeding on phytoplankton and naupliar fecal pellets (E. Green et al. 1992). The antennae and mandibular palps are used for swimming and creating a weak feeding current (Paffenhöfer and Lewis 1989). According to Sekiguchi (1974), most calanoids have mixotrophic nauplii, which survive on their yolk reserves during the early stages of development before becoming planktotrophic. The first nauplius stage to feed varies among species, but NIII or NIV appears to be the most common (Mauchline 1998).

Copepodid I (rarely CoII) acts as the infective stage in most symbiotic copepods. Exceptions include species with a protelean life cycle and members of the Ergasilidae, where only the adult females are parasitic (NI–NVI or NI–NIII) and CoI–CoV and adult males are free-living (fig. 27.6A). Several pennellids have an unusual life cycle, involving two different hosts and, hence, two infections (fig. 27.6A). After a brief planktonic phase, the infective copepodid stage locates the first host, either a fish, as in *Lernaeocera* (Scott and Scott 1913; Sproston 1942; Slinn 1970) or a pelagic gastropod mollusk, as in *Cardiodectes* (Ho 1966; P. Perkins 1983). Development from the attached chalimus stages through to sexually mature adults takes place on the gills of the first host. Mating also occurs on this host, after which the mated female leaves the first host and finds a second host, usually a fish, but occasionally a marine mammal, where it completes its metamorphosis (fig. 27.9A). The naupliar and infective copepodid stages of symbiotic copepods can be temporary members of the plankton. A few genera, such as *Saphirella*, were established to accommodate unusual forms that are now known to be the copepodid stages of symbiotic adults (e.g., the Clausidiidae, see Itoh and Nishida 1995). The nauplii and first copepodid larvae of sea-lice (the Caligidae) function as the dispersal and infective stages of the life cycle, respectively, and even adult caligids (e.g., *Caligus elongates*) are not infrequently taken in coastal plankton samples. Pre-metamorphic adult females of the Pennellidae can be found in plankton samples, since it is this stage that is responsible for locating and infecting the final host. The majority of copepods that are parasitic on fishes use more than one type of attachment during their life cycles. The sequence of attachment devices (antennae, cephalothoracic suction cup, holdfast, frontal filament, bulla) used during the post-naupliar phase was reviewed by Kabata (1981), who recognized eight different types of attachment succession. As in *Gonophysema*, members of the highly modified Xenocoelomatidae (endoparasitic in terebellid polychaetes) exhibit cryptogonochorism (Bocquet et al. 1970; Bresciani and Lützen

1974), but no onychopodid is involved. The male copepodid penetrates the atrium of the female, molts, and passes into a special receptacle (*receptaculum masculinum*) formed by a modification of the spermatic ducts of the female. It then develops into a functional testis, resulting in a pseudohermaphroditic condition.

Metridinid calanoids are strongly bioluminescent from the nauplius stage through to the adults of both sexes, while all species of *Lucicutia* (Lucicutiidae) are probably bioluminescent, even in the copepodid stage (Herring 1988).

PHYLOGENETIC SIGNIFICANCE

Ordinal Level: Björnberg (1972) inferred ancestor-descendant relationships of free-living cyclopoid, harpacticoid, and calanoid copepods, using naupliar characters of a large number of planktonic species. Her analysis challenged the widely accepted view that calanoids are close to the base of the Copepoda and placed the Cyclopoida at this position instead, leaving the Calanoida as the most derived order. The gymnoplean type of tagmosis (displayed in the Platycopioida and Calanoida), in which articulation between the prosome and urosome lies between the fifth pedigerous and genital somites, is generally regarded as the plesiomorphic condition (Huys and Boxshall 1991). Ferrari et al.'s (2010) phylogenetic analysis, however—using naupliar and post-naupliar characters, with the Mystacocarida as the sister-taxon of the Copepoda—supported the controversial hypothesis that the highly specialized thaumatopsylloid tagmosis is the most ancestral one, while the gymnoplean architecture is the youngest. Dahms (1990c, 2004a) compared naupliar characters between oligoarthran and polyarthran harpacticoids and, in a subsequent paper (Dahms 2004b), suggested removing the Polyarthra from the Harpacticoida and placing it as the sister-group of all remaining copepods, because neither a larval nor an adult synapomorphy uniting oligoarthrans and polyarthrans could be identified (Tiemann 1984). Dahms (2004a) also used post-embryonic characters to confirm the monophyly of the Copepoda and hypothesized a sister-group relationship based on naupliar characters for the Copepoda/ Thecostraca. A recent molecular analysis by Huys et al. (2007) suggested that the order Monstrilloida is nested within a fish-parasitic clade of the Siphonostomatoida, sharing a common ancestor with the stem species of the caligiform families (sea lice); this unforeseen relationship was shown to be congruent with both antennulary and caudal ramus ontogeny. Boxshall and Huys (1998) analyzed the development of antennulary segmentation and setation patterns across 6 orders of copepods and produced a hypothetical general model for antennulary development in the Copepoda as a whole.

Family Level: Dudley (1966) employed attributes of the development of naupliar appendages and concluded that the Notodelphyidae should be placed in the gnathostome cyclopoids, rather than the poecilostome cyclopoids. Based on naupliar morphology, Dahms and Hicks (1996) concluded that the Parastenheliidae are related to the Thalestridae, which is in agreement with a recent analysis using adult

characters (Willen 2000). Dahms (1990b) noted that several of the assumed derived naupliar states in the Thalestridae are shared with some species of the Harpacticidae, hinting at a relationship between both families; since then, however, a close alliance between harpacticids and thalestridimorphs has been rejected (Willen 2000). Dahms (1993b) investigated comparative copepodid development in the Tisbidae and related tisbidimorph families and suggested a close relationship between the Tegastidae and Peltidiidae. The presence of three aesthetascs derived from ancestral segments XXI, XXV, and XXVIII on the antennule of copepodid I (or II) provides a useful signature for the poecilostome Cyclopoida and has recently been used to place taxa exhibiting a highly modified adult morphology (e.g., the Chordeumiidae, Chitonophilidae, and Herpyllobiidae) in this order (López-González and Bresciani 2001; Huys et al. 2002; Boxshall and Halsey 2004).

Genus and Species Levels: Dahms et al. (1991) inferred phylogenetic relationships for 6 species of *Tisbe*, based on the morphology of NVI; their final analysis, however, in which adult characters were integrated with naupliar ones, resulted in significant discrepancies. Ferrari (1991) abstracted segmentation patterns from the development of legs 1–6 to group species of the calanoid genus *Labidocera* and genera within the Diaptomidae (Calanoida) and Cyclopidae (Cyclopoida). Dahms (1993a) provided a phylogeny for 3 genera in the Tisbidae, based on naupliar character states. Dahms and Bresciani (1993) described the naupliar development of the stenheliinid species *Delavalia palustris* and discovered several apomorphies, warranting the removal of this species from the Miraciidae. In a later paper, Dahms et al. (2005) discussed the naupliar morphology within the Stenheliinae and the evolutionary novelties displayed by the nauplii of *Stenhelia peniculata*. Schutze et al. (2000) placed 35 species from 29 genera of the Cyclopidae into groups that were based on ten developmental patterns of the female antennule, while Ferrari (1998) and Ferrari and Ivanenko (2005) used developmental data on the maxilliped and legs 1–7 to derive ancestor-descendant relationships among genera within this family. Groups defined by antennulary developmental patterns (Schutze et al. 2000) are not comparable with the lineages derived from the development of thoracopods (Ferrari 1998; Ferrari and Ivanenko 2005). Ferrari and Ueda (2005) examined the development of the female leg 5 and the genital complex in the Centropagoidea and used them as attributes to group species into this calanoid superfamily. Dahms et al. (2009) proposed a phylogeny of 8 *Tisbe* species, using exclusively naupliar characters.

HISTORICAL STUDIES: Post-embryonic development in the Copepoda has been studied for over 250 years and has produced an impressive body of literature. For entry into this literature, interested readers should consult the comprehensive bibliography compiled by Ferrari and Dahms (2007), who also provided an overview of the early history of copepod developmental studies and a chronology of the important descriptive observations and conceptual discoveries (also see Damkaer 2002). Only a few are repeated here. J. Lange (1756)

depicted both nauplii and copepodids of a freshwater cyclopid, and his illustrations are also the earliest for a crustacean nauplius. Ramdohr (1805) described the complete life history of a free-living cyclopid. Surriray (1819) illustrated a nauplius that hatched from the egg of a transformed parasitic copepod. Burmeister (1835) described a chalimus, which Krøyer (1838) later identified as an immature stage of a parasitic copepod. C. Wilson (1905) illustrated the complete development of a caligid, including the nauplius, copepodid, chalimus, and adult stages. Nordmann (1832) compared the nauplius and the first copepodid of highly modified parasites (Lernaeopodidae) to similar instars of free-living copepods and concluded that both categories belonged to the same group of Crustacea. Oberg (1906) determined homologies of antennulary setae between NVI and CoI of *Temora longicornis* by studying intermolt stages. Giesbrecht (1913) proposed that during copepodid development, one new somite is added immediately anterior to the anal somite during each molt. Significant conceptual studies on the timing of setal additions during development were added by Illg (1949) and Dudley (1966). Björnberg (1972) used naupliar morphology to present the first phylogeny of copepods based on developmental data. Izawa (1987) studied the development of several parasitic poecilostome Cyclopoida with an abbreviated naupliar phase.

Harding (1954) pointed out that the new harpacticoid genus *Fucitrogus* described by Brady (1894) was, in reality, based on a nauplius stage of a *Thalestris* species. Various authors have proposed generic names based on copepodid stages. Some have been confidently synonymized with existing generic names (*Aphelura* = *Pontella*; *Euchaetopsis* = *Euchaeta*; *Pseudolovenula* = *Megacalanus*; *Pseudocletopsyllus* = *Cletopsyllus*), while others remained genera inquirenda: *Specilligus*; *Hessia*; *Centromma*; *Microcryobius*; *Mawsonella*; *Plagiopus*; *Faurea*; and *Nogagella*. The genera *Paurocope*, *Saphirella*, and *Lanowia* represent juvenile copepodid stages of clausidiids. The early copepodid stages of clausidiids, particularly the first copepodid, are commonly found in coastal plankton. The genus *Saphirella* is still used in the literature as a collective name for clausidiid juveniles.

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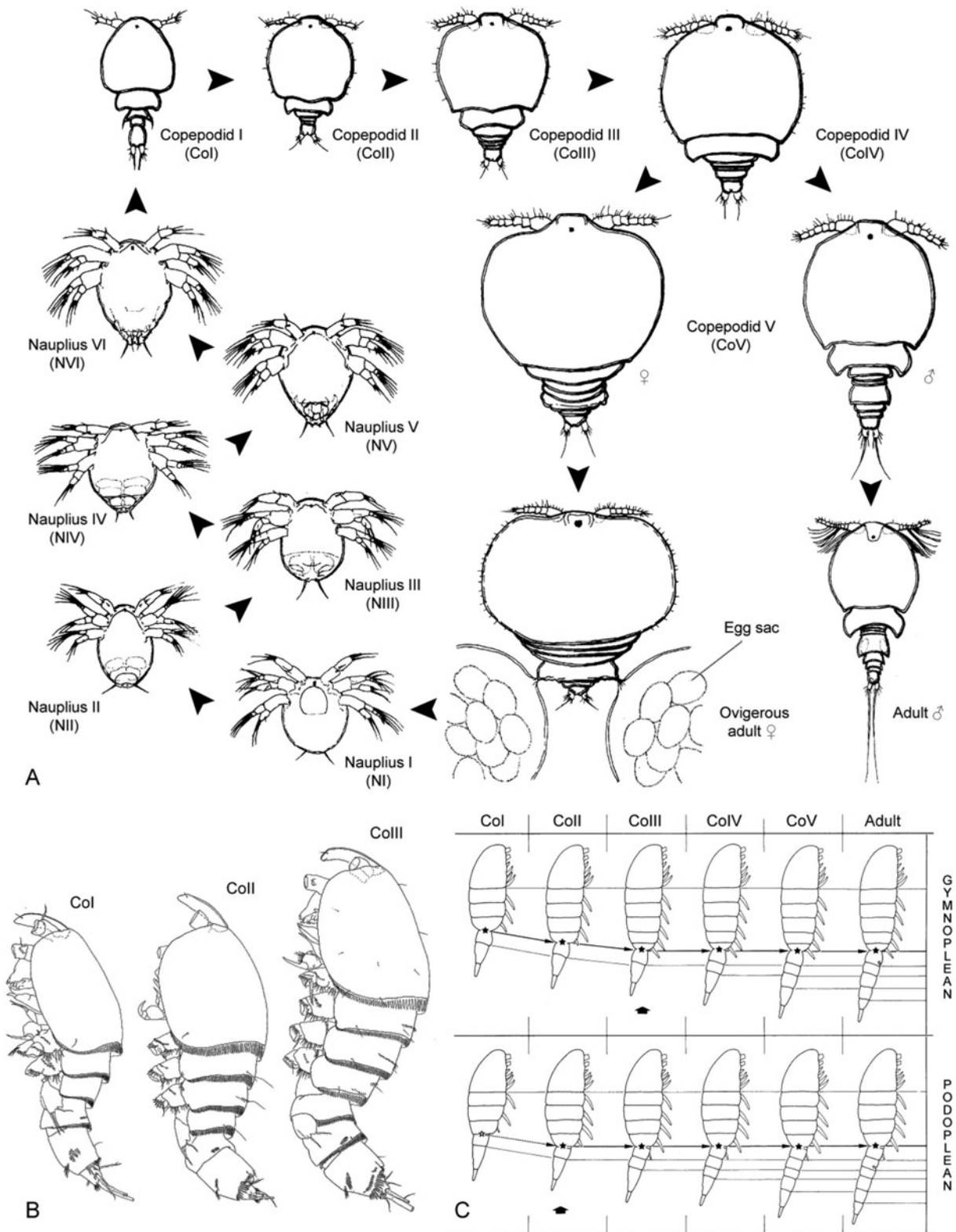
Fig. 27.1 A: drawing of the basic copepod life cycle, consisting of six naupliar and six copepodid stages, as exemplified by *Cancerilla tubulata* (Siphonostomatoida: Cancerillidae), dorsal view. B: drawing of copepodids I–III of *Parastenhelia megarostrum* (Harpacticoida: Parastenhe-liidae), lateral view. C: comparison of the developmental pattern in podoplean and gymnoplean copepods, lateral view; solid stars indicate the position of the major body articulation, a hollow star indicates the poorly defined flexure plane, and arrows indicate the stage at which definitive tagmosis is attained and specialization of the joint commences. A modified after Carton (1968); B modified after Dahms (1993c); C modified after Huys and Boxshall (1991).
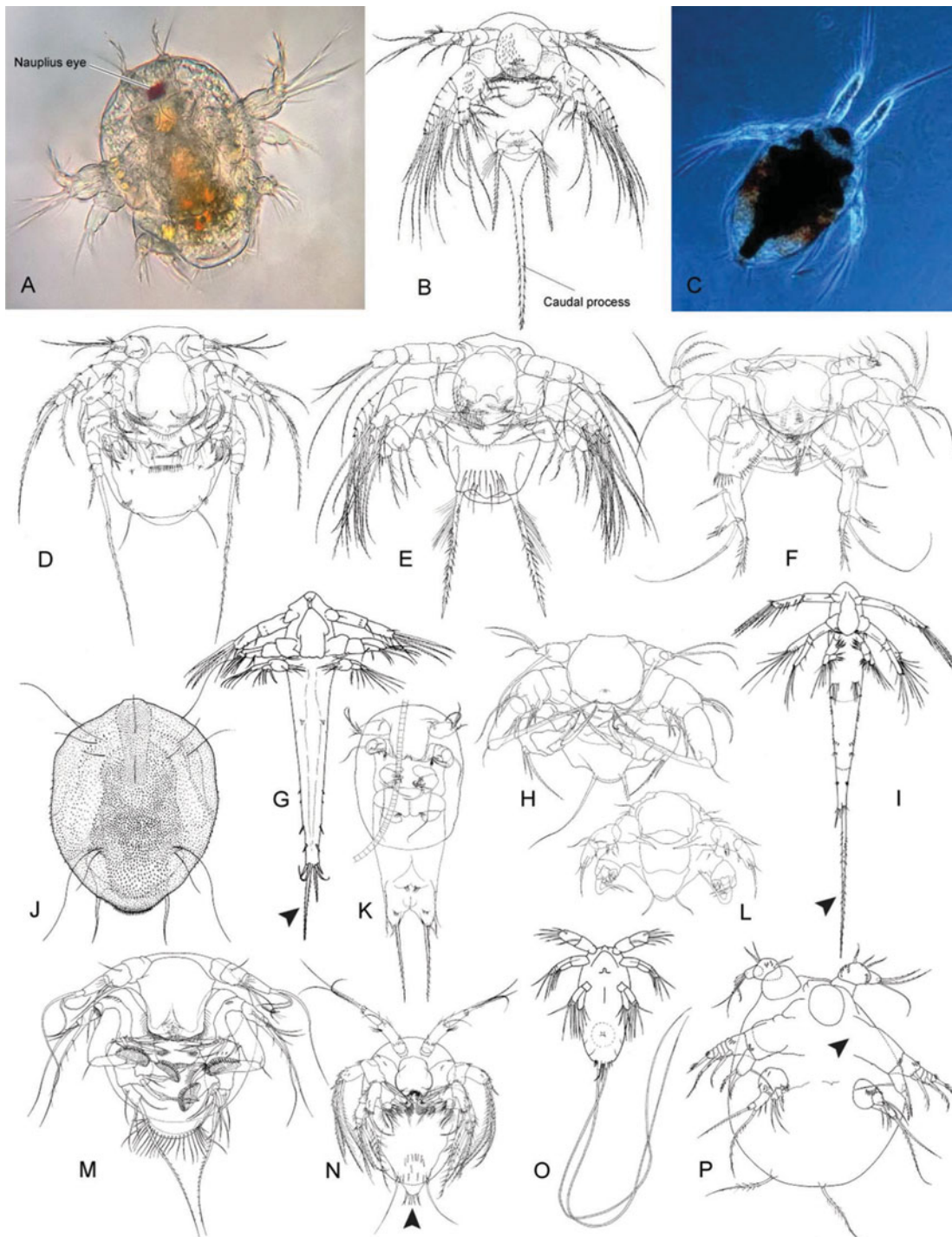
Fig. 27.2 Examples of naupliar diversity, drawings (unless otherwise indicated). A: unidentified *Cyclops* sp. (Cyclopoida: Cyclopidae), light microscopy, dorsal view. B: nauplius I of *Longipedia minor* (Longipediidae), ventral view. C: unidentified instar of *Ergasilus sieboldi* (Cyclopoida: Ergasilidae), light microscopy (note the cyan pigment inside), ventral view. D: nauplius II of *Phyllognathopus viguieri* (Phyllognathopodidae), ventral view. E: nauplius I of *Canuella perplexa* (Canuellidae), ventral view. F: nauplius II of *Delavalia palustris* (Miraciidae), ventral view. G: nauplius IV of *Rhincalanus cornutus* (Rhincalanidae), ventral view; the black arrow shows the asymmetry of the caudal setae. H: nauplius I of *Alteutha oblonga* (Peltidiidae), ventral view. I: nauplius IV of *Pontellopsis brevis* (Pontellidae), ventral view; the black arrow shows the asymmetry of the caudal setae. J: nauplius I of *Rhizothrix minuta* (Rhizothricidae), dorsal view. K: nauplius VI of *Macrosetella gracilis* (Miraciidae), holding a *Trichodesmium* filament, ventral view. L: nauplius I of *Parategastes sphaericus* (Tegastidae), ventral view. M: nauplius I of *Zaus spinatus* (Harpacticidae), ventral view. N: nauplius I of *Euterpina acutifrons* (Tachidiidae), ventral view; the black arrow indicates a cluster of enlarged spinules. O: lecithotrophic nauplius VI of *Euchaeta marina* (Euchaetidae), ventral view. P: lecithotrophic nauplius I of *Pseudotachidius* sp. (Pseudotachidiidae), ventral view; the black arrow indicates the absence of the antennary masticatory process. A courtesy of Sam Brutcher; B, D–F, H, J–N, and P (harpacticoid nauplii) modified after Dahms (1990c); C original; G, I, and O (calanoid nauplii) modified after Björnberg (1972).
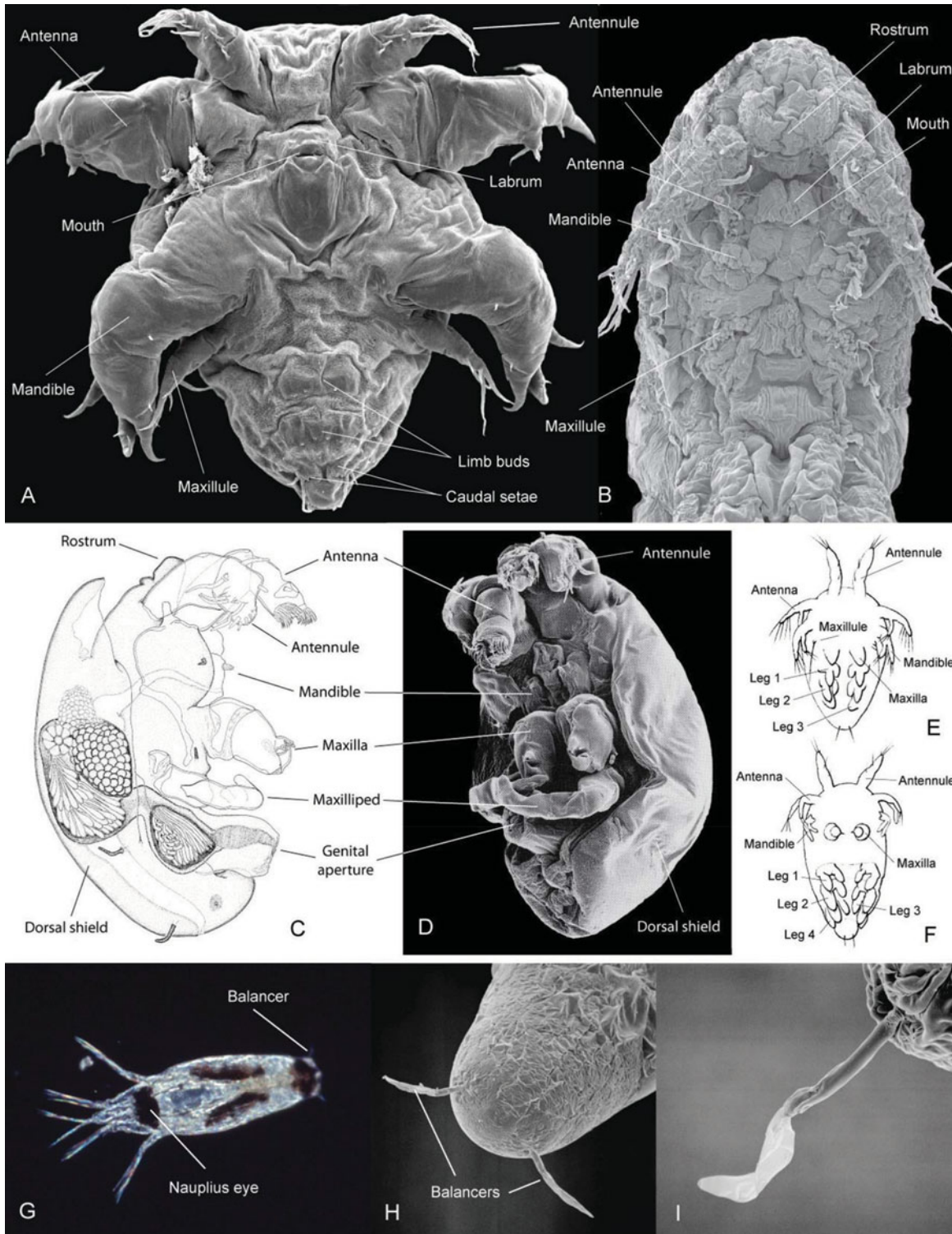
Fig. 27.3 Metanauplii and caligiform nauplii. A: intermediate-size metanauplius of *Caribeopsyllus amphiodiae* (Thaumatopsyllidae), with rudimentary limb buds, SEM, ventral view. B: recently molted copepodid I of *Thaumatopsyllus paradoxus* (Thaumatopsyllidae), showing the vestigial antennae, mandibles, and maxillules, SEM, ventral view. C and D: adult male of *Micrallecto fusii* (Micrallectidae), showing the metanaupliar organization C: drawing, lateral view. D: SEM, lateroventral view. E and F: drawings of *Chordeumium obesum* (Chordeumiidae). E: first metanauplius, showing leg buds 1–3, ventral view. F: second metanauplius, showing leg buds 1–4, ventral view. G: nauplius I of *Lepeophtheirus pectoralis* (Caligidae), light microscopy. H: hindbody of nauplius I of *Lepeophtheirus* sp., showing the balancers, SEM. I: closeup of the same. A courtesy of Masahiro Dojiri and Gordon Hendler; B original; C and D modified after Huys (2001); E and F modified after Jungersen (1914); G–I courtesy of Geoffrey Boxshall.
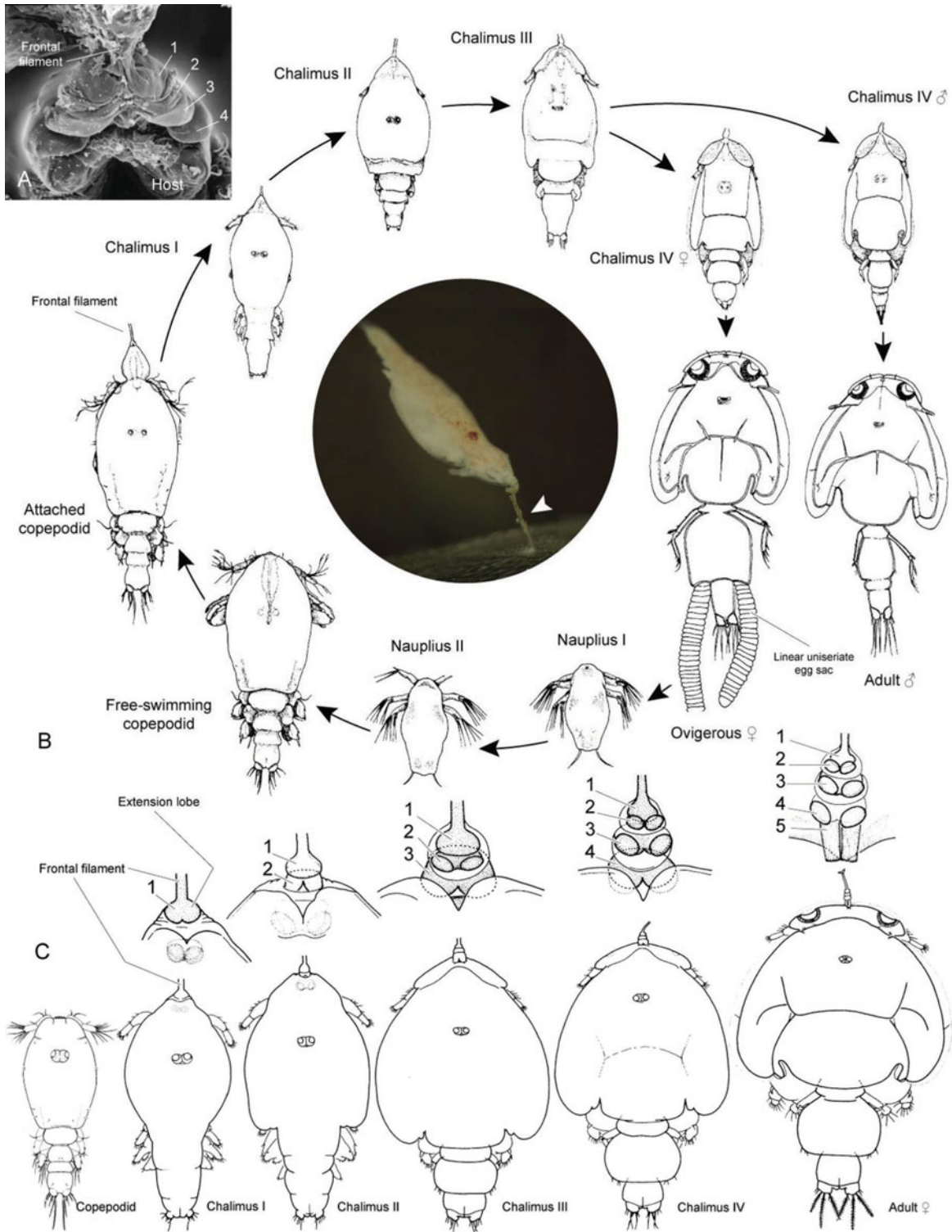
Fig. 27.4 Chalimus stages, showing the frontal filaments and extension lobes. A: frontal filament of chalimus IV of *Lernaeocera branchialis* (Pennellidae), with the numbers 1–4 representing the bulb-like extension lobes secreted around the base of the filament during each post-copepodid molt, SEM; adult males use their antennae to grasp early chalimus stages in the vicinity of their frontal attachment apparatus (which is not molted with the rest of the exoskeleton) when exhibiting mate guarding. B: drawing of the life cycle of *Caligus clemensi* (Caligidae); photograph (*center*) shows the attached chalimus of *C. elongatus*, with an arrow indicating the frontal filament. C: drawing of the post-naupliar development of *C. punctatus*; insets show the sequential addition of extension lobes at the origin of the filament during subsequent molts. A courtesy of Geoffrey Boxshall; B modified after Parker and Margolis (1964), Kabata (1972), and Raibaut (1985), with photograph courtesy of Øivind Øines; C modified after I.-H. Kim (1993).
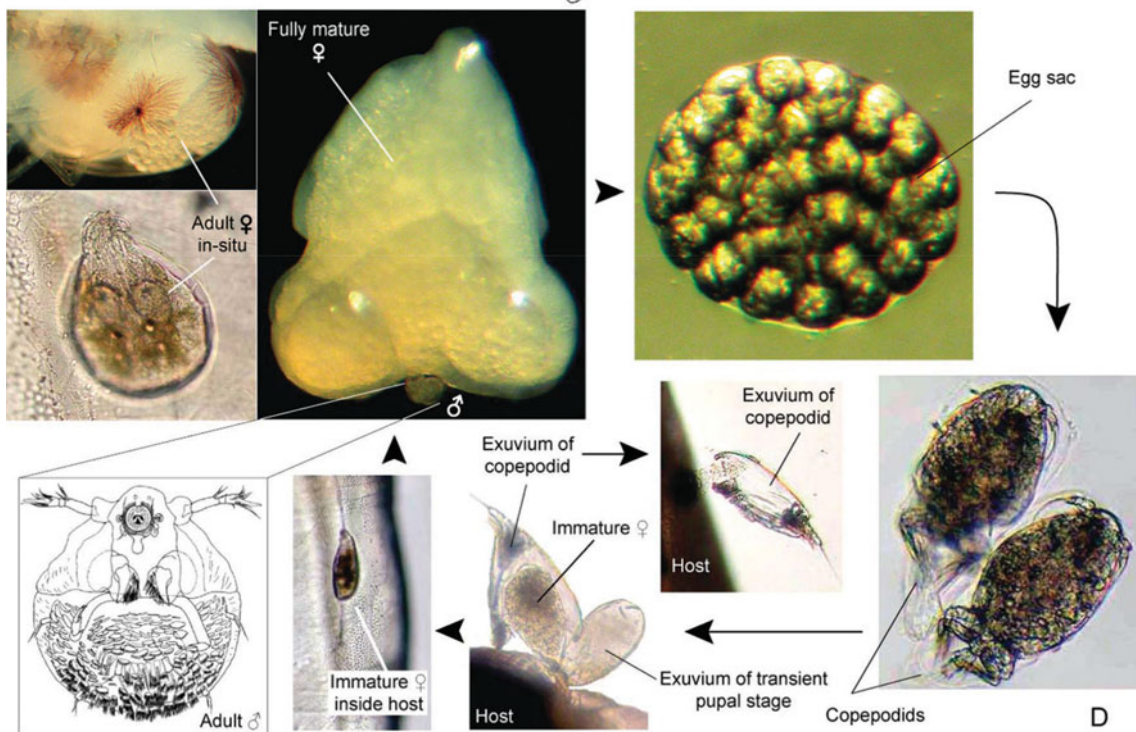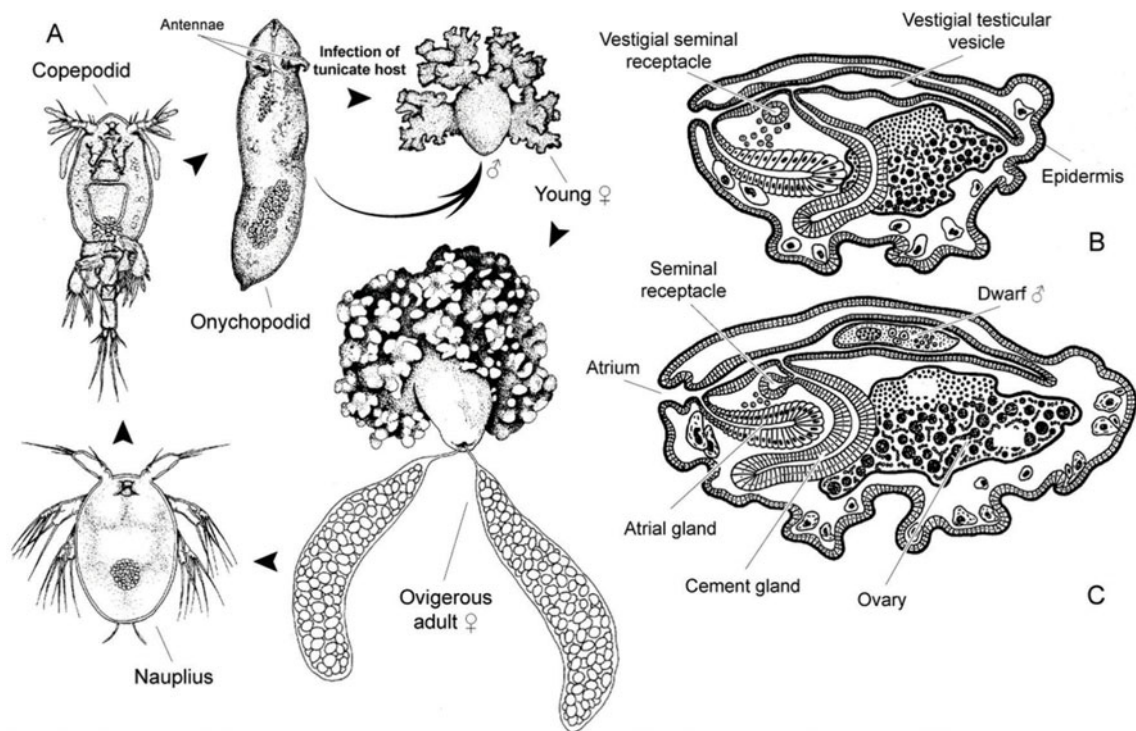
Fig. 27.5 Onychopodids and pupal stages. A: drawing of the life cycle of *Gonophysema gullmarensis* (Cyclopoida *incertae sedis*), dorsal view. B and C: schematic representations of the sagittal sections of *G. gullmarensis*, lateral view. B: young female. C: adult female; note the meta-morphosed male in the testicular vesicle. D: life cycle of *Neomysidion rahotsu* (Nicothoidae), light microscopy (except for the drawing in the lower left). A modified after Bresciani and Lützen (1960) and Raibaut (1985); B and C modified after Bresciani and Lützen (1961); D modified after Ohtsuka et al. (2005, 2007).

Fig. 27.6 (*opposite*) Life cycles and post-mating metamorphosis. A: chart of types of life cycles of free-living and parasitic Copepoda (PM ⚥ = post-metamorphic female); (a) Calanoida, Harpacticoida, free-living Cyclopoida; (b) Ergasilidae, in part (Urawa et al. 1980a, 1980b; Abdelhalim et al. 1991; Alston et al. 1996); (c) Notodelphyidae and Ascidicolidae (Dudley 1966); (d) Cancerillidae (Carton 1968), many poecilostome Cyclopoida associated with invertebrate hosts (e.g., Gibson and Grice 1978; Do et al. 1984; Costanzo and Calafiore 1985; Kuei and Björnberg 2002); (e) Philichthyidae (Izawa 1973); (f) Ergasilidae (in part) (Ben Hassine 1983); (*cont. on next page*)
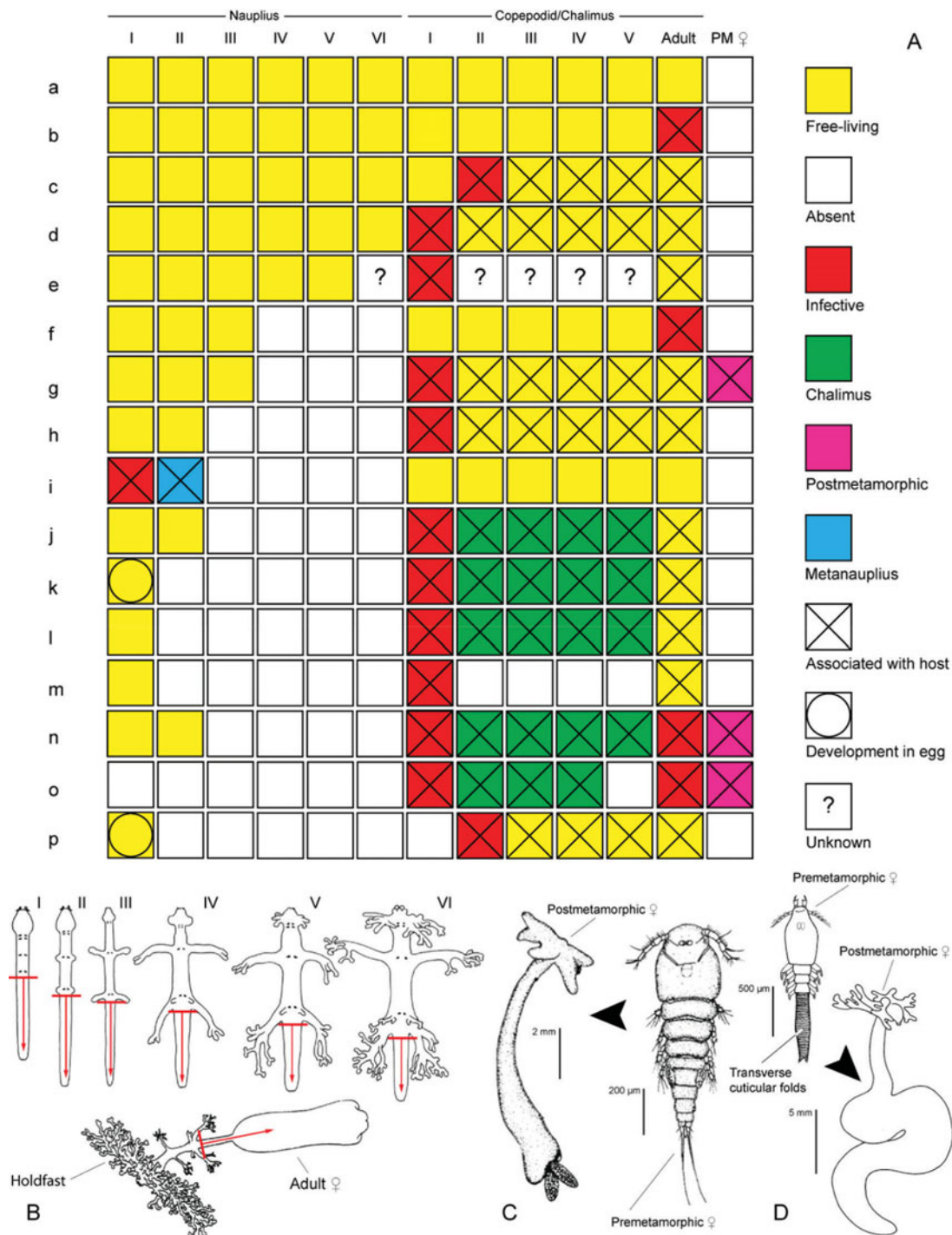
(g) Lernaeidae (Grabda 1963); (h) Lernanthropidae (Cabral et al. 1984); (i) Thaumatopsyllidae (Bresciani and Lützen 1962; Fosshagen 1970; Dojiri et al. 2008); (j) Caligidae (e.g., Kabata 1972; I.-H. Kim 1993; Ho and Lin 2004; Ohtsuka et al. 2009); (k) Lernaeopodidae, in part (e.g., *Salmincola californiensis*) (Kabata and Cousens 1973); (l) Lernaeopodidae, in part (e.g., *Alella macrotrachelus*) (Caillet 1979; Kawatow et al. 1980; Raibaut 1985); (m) Lernaeopodidae, in part (e.g., *Clavella adunca*) (Shotter 1971); (n) Pennellidae, in part (e.g., *Lernaeocera* spp., *Lernaeenicus sprattae*) (Scott and Scott 1913; Sproston 1942; Kabata 1958; Slinn 1970; T. Schram 1979); (o) Pennellidae, in part (e.g., *Cardiodectes medusaeus*) (P. Perkins 1983); (p) Chordeumiidae (*Parachordeumium amphiurae*) (Goudey-Perrière 1979). B: drawing of stages in the extensive metamorphosis of post-mated *Phrixocephalus cincinnatus* (Pennellidae), dorsal views; the first six stages are passed as the copepod traverses the eye of its flatfish host, and metamorphosis is completed when it penetrates the retina and becomes embedded in the choroid layer of the eye, where it develops an elaborate holdfast; the genital-abdominal region is marked off by a red transverse line and arrow. C: drawing of the metamorphosis of a post-mated female of *Lernaea cyprinacea* (Lernaeidae). D: drawing of the metamorphosis of a post-mated female of *Lernaeocera branchialis* (Pennellidae), dorsal views. A modified after Kabata (1981); B modified after Kabata (1969, 1979); C modified after Raibaut (1985); D modified after Boxshall (1992).
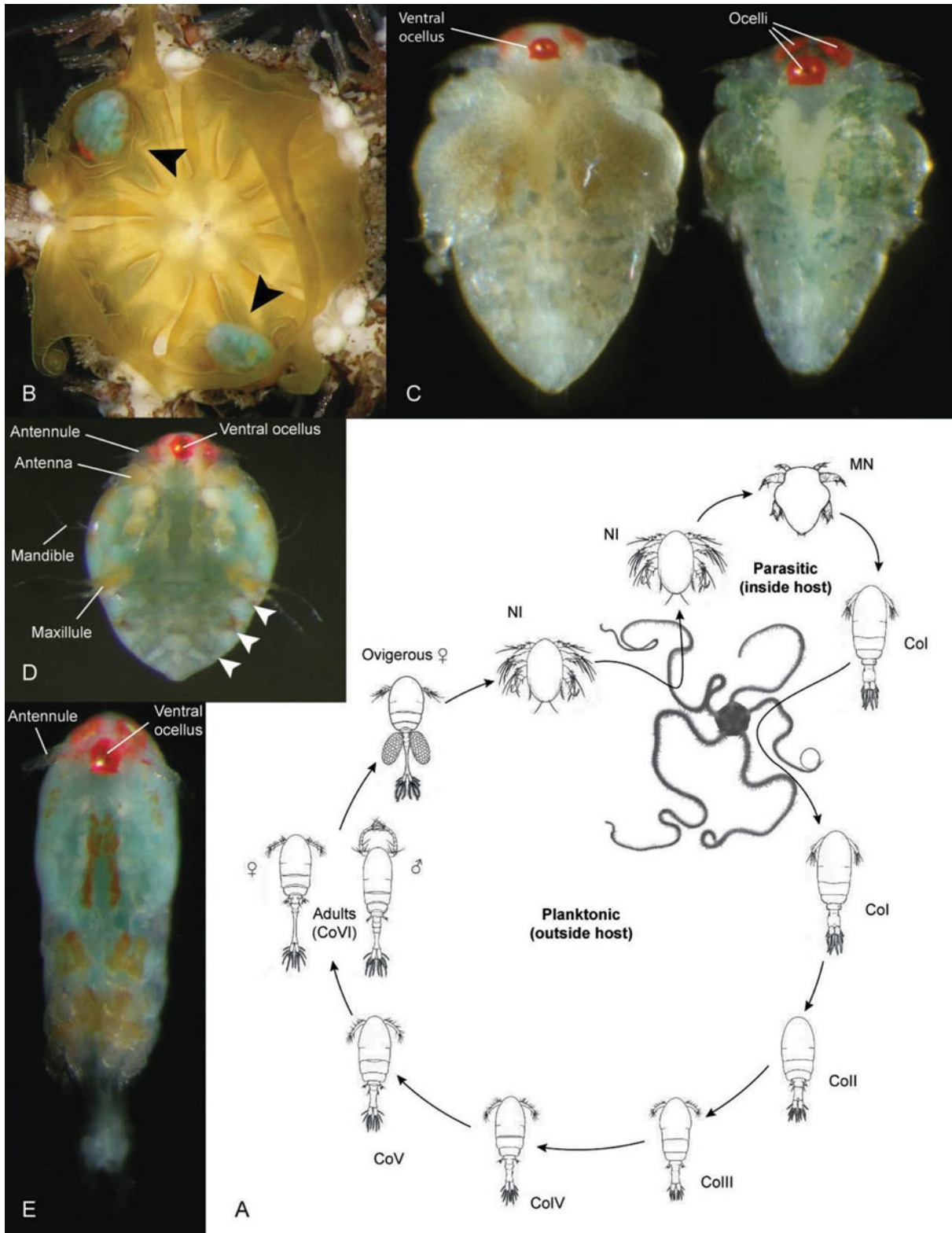
Fig. 27.7 Thaumatopsyllidae. A: drawing of the protelean life cycle of *Caribeopsyllus amphiodiae*. B: *Caribeopsyllus* sp. A (*sensu* Hendler and Kim 2010), with black arrows indicating two metanauplii in the stomach of *Ophiothrix angulata*, light microscopy, dorsal view. C: advanced metanauplii of *C. amphiodiae*, female (*left*) and male (*right*), showing the contrast between the sexes in the relative size of the nauplius eye's ventral ocellus, light microscopy, ventral view. D: metanauplius of *Caribeopsyllus* sp. A, with arrows showing the cephalic appendages and subcuticular primordia of the swimming legs, light microscopy, ventral view. E: copepodid I of *Caribeopsyllus* sp. A, light microscopy, ventral view. A modified after Dojiri et al. (2008); B, D, and E courtesy of Gordon Hendler; C courtesy of Gordon Hendler and Masahiro Dojiri.
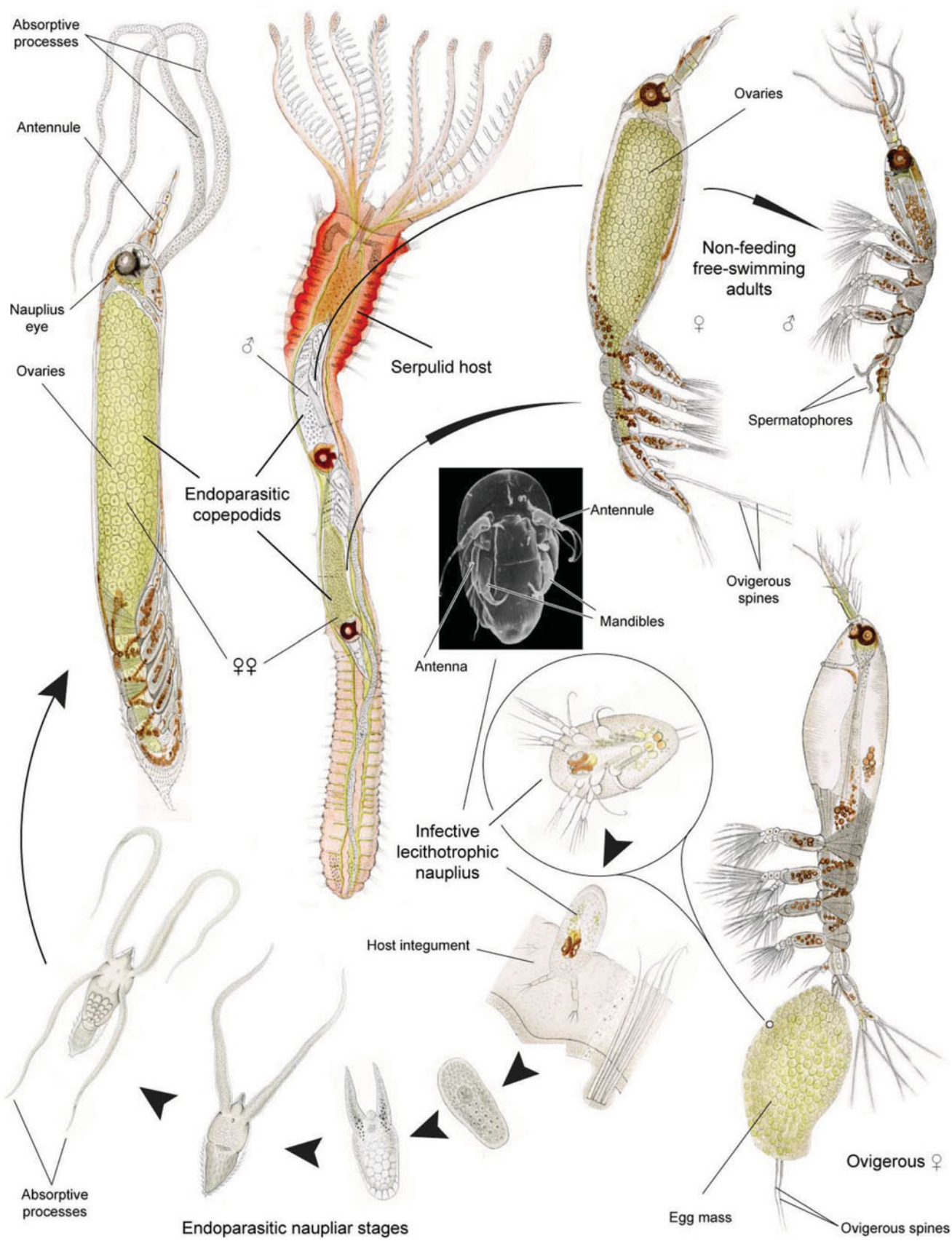
Absorptive processes

Antennule

Nauplius eye

Ovaries

Serpulid host

Endoparasitic copepodids

♂

♀♀

Ovaries

Non-feeding free-swimming adults

♀   ♂

Spermatophores

Ovigerous spines

Antennule

Mandibles

Antenna

Infective lecithotrophic nauplius

Host integument

Absorptive processes

Endoparasitic naupliar stages

Egg mass

Ovigerous ♀

Ovigerous spines

Fig. 27.8 Protelean life cycle of *Haemocera danae* (= ?*Cymbasoma rigidum*) (Monstrillidae), with the SEM (*center*) showing the infective nauplius of *Monstrilla hamatapex*. Drawing reconstructed from illustrations in Malaquin (1901); SEM modified after Grygier and Ohtsuka (1995).
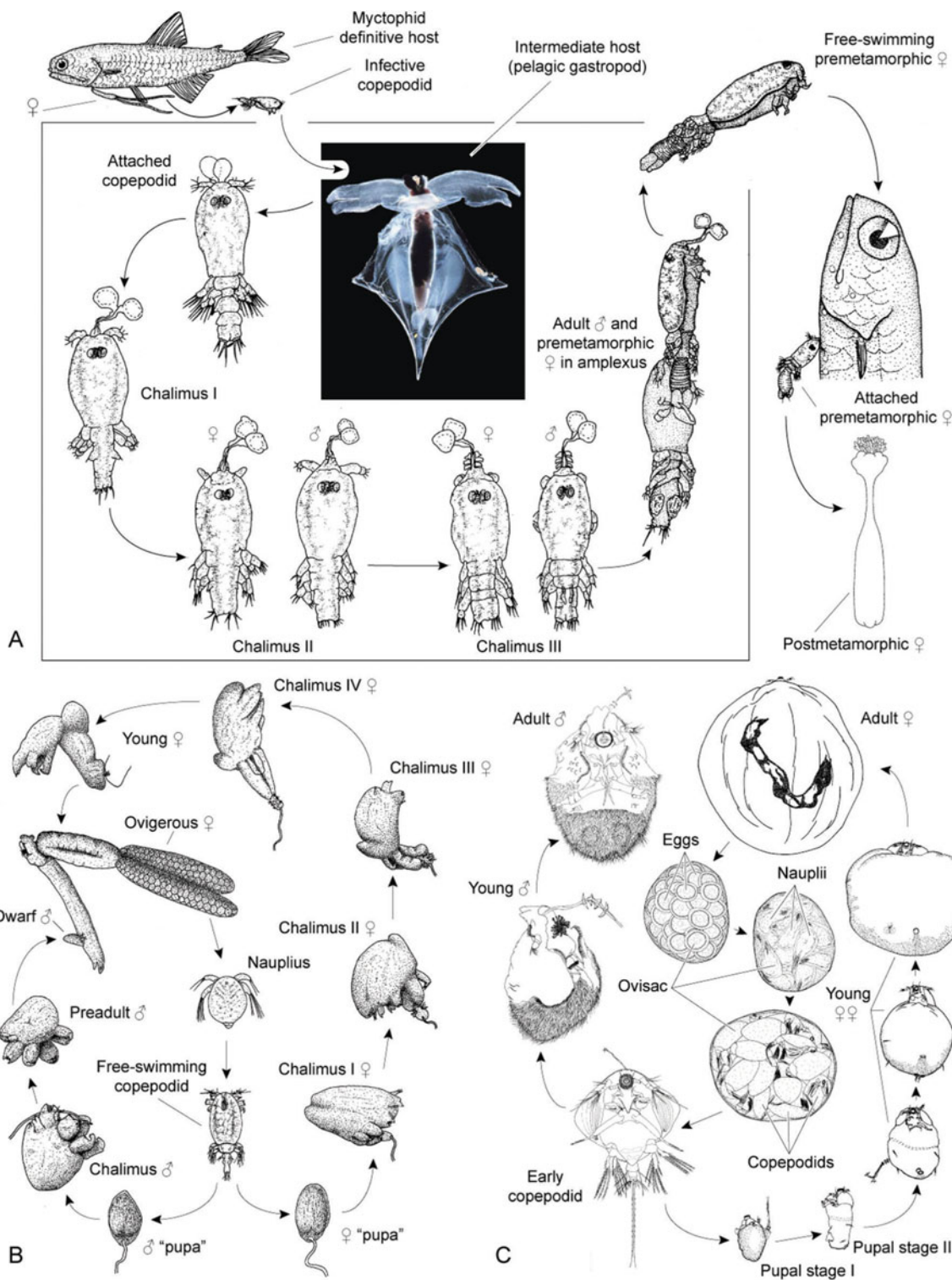
Fig. 27.9 Life cycles of parasitic copepods. A: drawing of the two-host life cycle of *Cardiodectes medusaeus* (Pennellidae), involving the thecosome gastropod intermediate host *Clio pyramidata* (photography, *center*) and the myctophid definitive host *Stenobrachius leucopsarus*. B: drawing of the life cycle of *Alella macrotrachelus* (Lernaeopodidae). C: drawing of the life cycle of *Hansenulus trebax* (Nicothoidae); a series of pupae and gradually advanced young females are illustrated at the same magnification as the adult female, showing the differences in body proportions caused by developing ovaries, which bring about the expansion of the trunk. A modified after P. Perkins (1983), with illustration of a post-metamorphic female modified after Boxshall and Halsey (2004) and photograph courtesy of Ron Gilmer and Richard Harbison; B modified after Caillet (1979), Kawatow et al. (1980), Raibaut (1985), and Benkirane (1987); C reconstructed from Heron and Damkaer (1986).
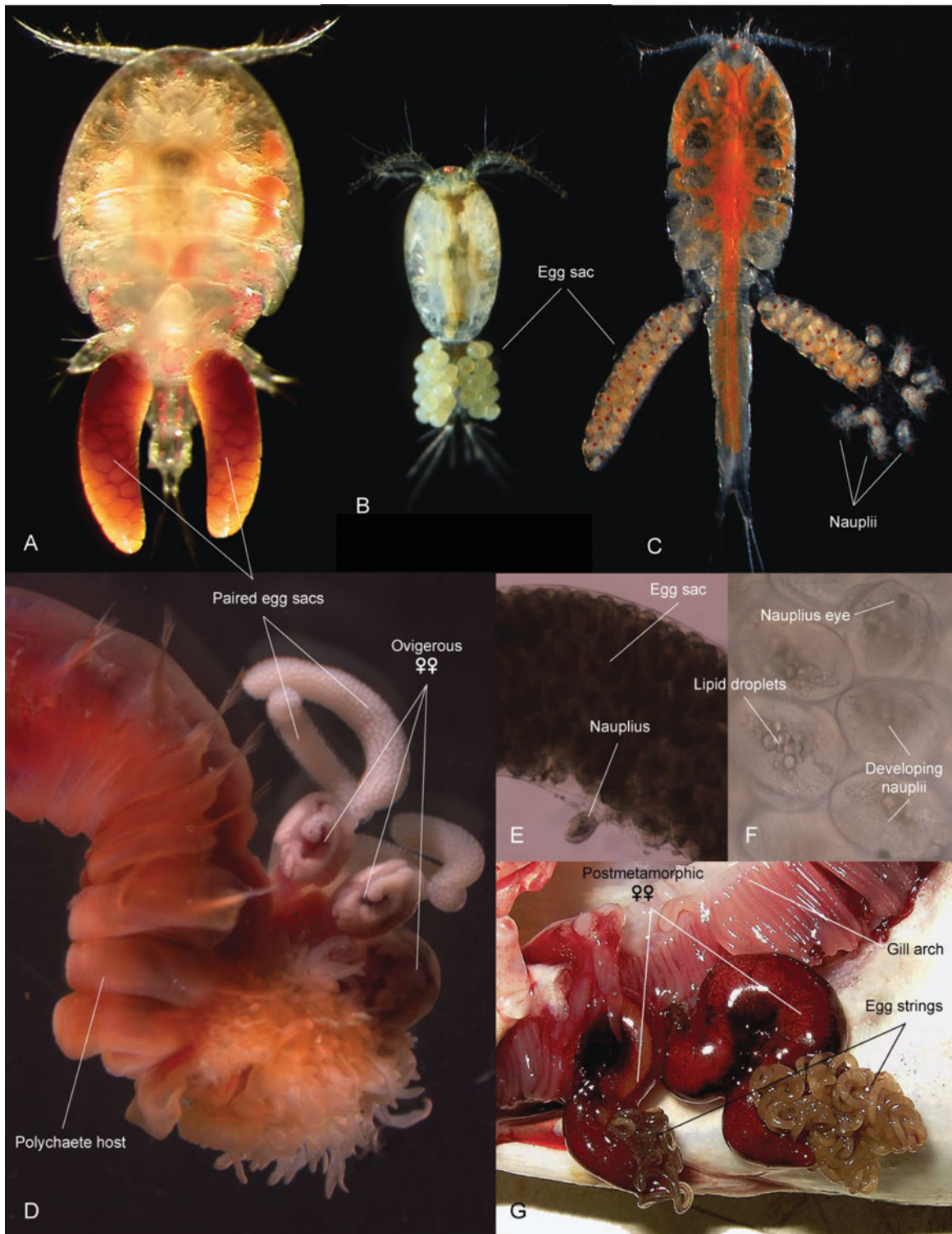
Fig. 27.10 Egg sacs and egg strings, light microscopy. A: ovigerous female of *Clausidium* sp. (Clausidiidae), with paired dorsolateral egg sacs, dorsal view. B: ovigerous female of *Cyclops* sp. (Cyclopidae), with paired laterodorsal egg sacs, dorsal view. C: ovigerous female of Lichomolgoidea sp., with paired lateral egg sacs, showing the eclosion of nauplii, dorsal view. D: three ovigerous females of *Melinnacheres steenstrupi* (Saccopsidae) attached to the gills of their terebellid host, *Terebellides stroemi*, lateral view. E: closeup of the egg sac of *M. steenstrupi*, showing the eclosion of the infective nauplius. F: closeup of eggs of *M. steenstrupi*, containing lecithotrophic nauplii at an advanced state of development. G: two post-metamorphic ovigerous females of *Lernaeocera branchialis* (Pennellidae), showing the spirally coiled uniseriate egg strings, attached to the gill arch of their gadid host, *Merlangius merlangus*, dorsal view. A and C courtesy of Arthur Anker; B courtesy of Jean-François Cart; D, E, and F original; G courtesy of Hans Hillewaert.
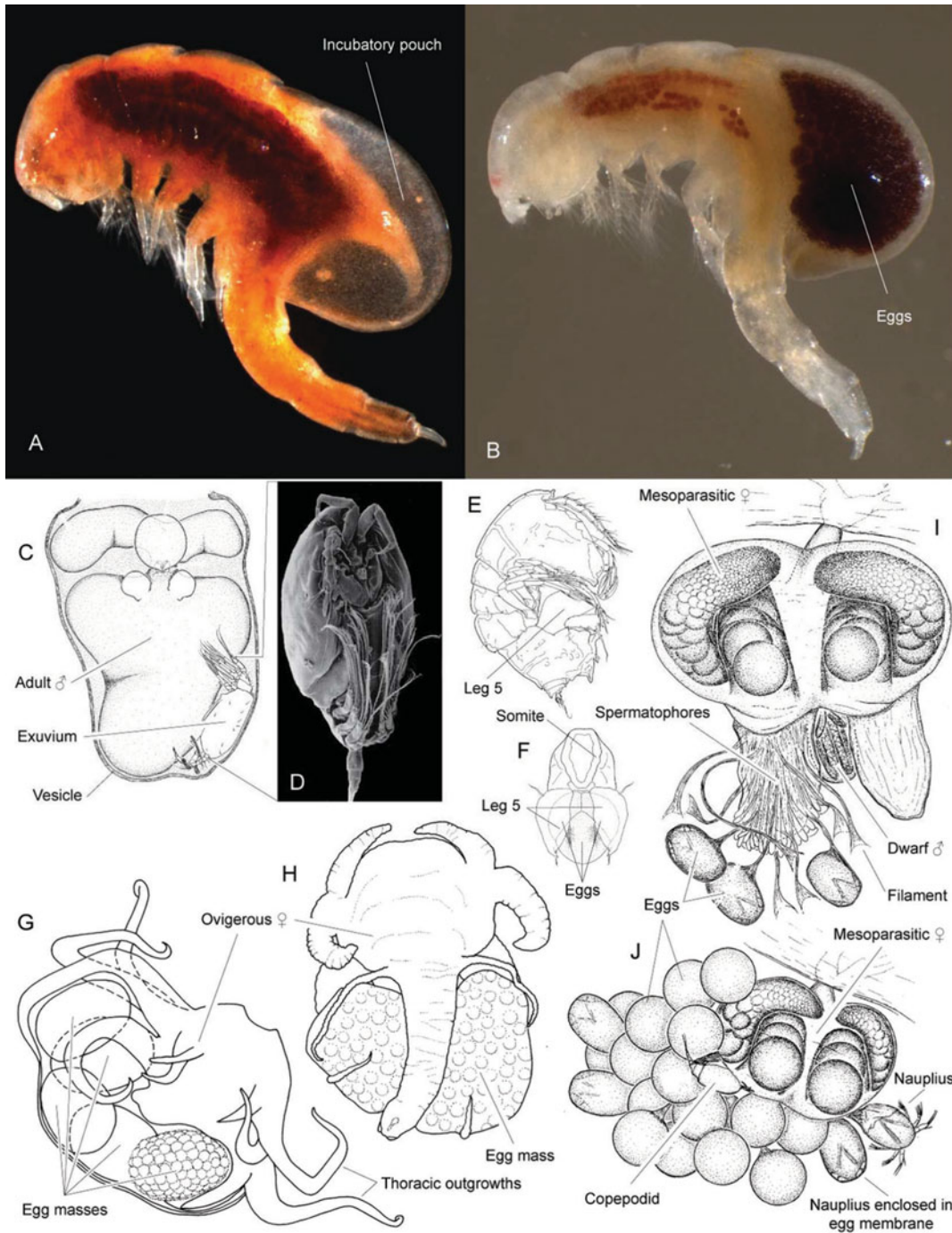
Fig. 27.11 A and B: *Pachypygus* sp. (Notodelphyidae), light microscopy. A: non-ovigerous female, with a fully developed incubatory pouch, lateral view. B: ovigerous female, with eggs retained inside the dorsal incubatory pouch, which is formed by the modification of the fourth pedigerous somite, lateral view. C: drawing of an adult male of *Nucellicola holmanae* (Chitonophilidae) enclosed in the membranous vesicle, together with the exuvium of the preceding copepodid, depicting a discrepancy in size as a result of hypermorphosis, ventral view. D: late copepodid (equivalent to CoIII) of *Lepetellicola brescianii* (Chitonophilidae), SEM, ventral view. E and F: drawings of *Parategastes sphaericus* (Tegastidae). E: adult female, lateral view. F: adult female, with foliaceous legs 5 forming a brood pouch shielding the eggs, ventral view. G: drawing of an ovigerous female of *Ophioika appendiculata* (Chordeumiidae), maintaining six egg masses in a subthoracic cage formed from the modified and ventrally downturned cephalic appendages and thoracic outgrowths, laterial view. H. drawing of an ovigerous female of *Parachordeumium amphiurae* (Chordeumiidae) holding a loose egg mass in the subthoracic brood cage, dorsal view. I: drawing of a mesoparasitic adult female of *L. brescianii* attached to a cocculiniform host (Mollusca), showing an attached dwarf male, spermatophores, and eggs attached to the genital area via individual filaments, ventral view. J: ovigerous female of *L. brescianii* attached to a host, with offspring at different stages of development: eggs, a young nauplius enclosed in an egg membrane, a fully developed nauplius in the process of eclosion, and a copepodid I, ventral view. A and B courtesy of Arthur Anker; C modified after Huys et al. (2002); D, I, and J modified after Huys et al. (2002); E and F modified after Huys et al. (1996); G and H modified after Boxshall and Halsey (2004).
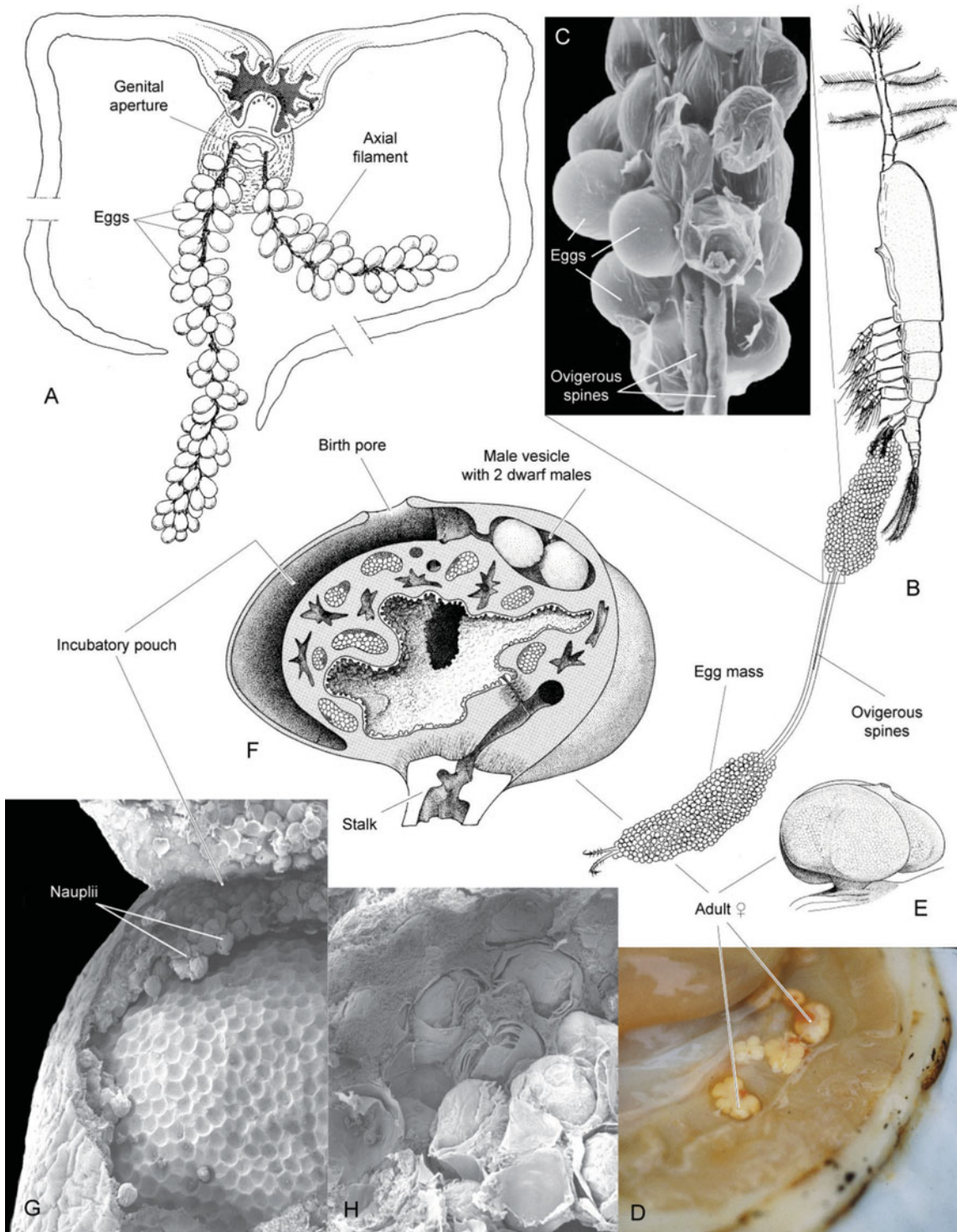
Fig. 27.12 A: drawing of an ovigerous female of *Phyllodicola petiti* (Phyllodicolidae) with eggs attached separately to the axial filament origi-
nating at the genital aperture, dorsal view. B: drawing of an ovigerous female of *Monstrilla longicornis* (Monstrillidae) with two egg masses,
lateral view. C: detail of an egg mass of *M. helgolandica* attached to ovigerous spines, SEM. D: females of *Pectenophilus ornatus* (Mytilico-
lidae) at various stages of development, attached to the gills of their bivalve host, *Patinopecten yessoensis*, light microscopy. E: drawing of
mature females of *Pectenophilus ornatus*, lateral view. F: drawing of the median section through an adult female *P. ornatus*, showing the
position of the incubatory pouch, birth pore, and dwarf males contained in the vesicle. G and H: *P. ornatus*, SEMs. G: adult female, with the
body wall partly removed to reveal the honeycomb-structured wall of the incubatory pouch. H: nauplii inside the brood pouch, at different
stages of eclosion. A modified after Laubier (1961); B and C modified after Huys and Boxshall (1991); D courtesy of Kazuya Nagasawa; E and
F modified after Nagasawa et al. (1988); G and H modified after Huys et al. (2006).