

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/263348297>

16. Cephalocarida

Chapter · June 2014

CITATIONS

2

READS

5,156

5 authors, including:



[Jørgen Olesen](#)

University of Copenhagen

372 PUBLICATIONS 3,715 CITATIONS

[SEE PROFILE](#)



[Marcella Carcupino](#)

University of Sassari

56 PUBLICATIONS 849 CITATIONS

[SEE PROFILE](#)

JØRGEN OLESEN

SØREN VARBEK MARTINSEN

GEORGE HAMPSON

ALBERTO ADDIS

MARCELLA CARCUPINO

GENERAL: Cephalocarids are a species-poor group of small (less than 4 mm), marine, ancient-looking crustaceans (fig. 16.1A–C). They were first described by H. Sanders (1955), based on specimens from the muddy bottom of Long Island Sound, USA, but they have been found subsequently in the North and South Atlantic Ocean, the North and South Pacific Ocean, and (recently) in the Mediterranean Sea, at depths ranging from shallow subtidal to bathyal (Hessler and Elofsson 1992; J. W. Martin et al. 2002; Carcupino et al. 2006). To date, 12 species have been described, belonging to 5 genera, with *Lightiella* and *Sandersiella* being the most species rich (5 and 4 species, respectively) (Olesen et al. 2011). Adult cephalocarids are easily distinguished from other crustaceans by the number of body segments (20, including the telson) and their characteristic body tagmosis. The body (posterior to the cephalon) consists of nine limb-bearing thoracic segments (in *Lightiella* thoracic limb 8 is lacking), 10 limbless abdominal segments, and a telson. Because of their primitive appearance, cephalocarids have played an important role in discussions on crustacean phylogeny (e.g., H. Sanders 1957, 1963; Hessler 1992a; Walossek 1993). Cephalocarids are hermaphroditic. Their life cycle includes one to two large embryos borne on specialized egg-carrier limbs, and anamorphic development with at least 14 (*Hutchinsoniella macracantha*) or 15 (*Lightiella magdalenina*) metanaupliar stages, followed by a low number of juveniles.

LARVAL TYPES

Embryos: In *Hutchinsoniella macracantha*, the best-studied cephalocarid, the gonopores are at the posterior surface of thoracopod 6. When the large eggs emerge, they are directed to the posterior egg carriers (specialized ninth thoracopods), to which they are cemented and carried for a while (fig. 16.1A–D) (Hessler et al. 1995). *Hutchinsoniella* and *Lightiella* appear to be different with respect to the number of embryos being carried. In *Hutchinsoniella* two embryos are usually present, one on each egg carrier (fig. 16.1A–C), while 16 of 17 exam-

ined specimens of *Lightiella incisa* carried only a single embryo (H. Sanders and Hessler 1964), a tendency later confirmed in other samples of *Lightiella* (J. W. Martin et al. 2002; Addis et al. 2007; Olesen et al. 2011). In *H. macracantha* the bodies of the brooding embryos are tightly flexed within the eggs, so that the posterior part of the body is pressed under the cephalon, and they are always oriented the same way within the egg membrane (fig. 16.1D) (Hessler et al. 1995). Cephalocarids, and in particular their larvae, are extremely rare, so their development has been examined only in a few species; in some cases just a few stages are known. The 2 best-studied species are *Hutchinsoniella macracantha* and *Lightiella magdalenina* (H. Sanders 1963; Addis et al. 2007). In addition, several stages are known for *Lightiella incisa* (H. Sanders and Hessler 1964), while only a few stages have been reported for *L. serendipita* and *L. monniotae* (Jones 1961; Olesen et al. 2011).

Metanauplius: In the metanauplius, development appears to be rather gradual (anamorphic), with many instars separated only by small changes. H. Sanders (1963) described 18 post-embryonic stages for *Hutchinsoniella macracantha*, 13 of which carried an antennal naupliar process on the coxa (termed a masticatory spine in some other crustaceans), which are therefore, by definition, metanauplii. Recent (August 2011) sampling of *H. macracantha* by Jørgen Olesen, Søren Varbek Martinsen, and George Hampson yielded several larval stages (fig. 16.1E–H), at least one of which was not described by H. Sanders (1963). This undescribed stage has 12 trunk segments (fig. 16.1G) and falls between H. Sanders's stages 5 and 6. Hence the number of metanauplii of *H. macracantha* is higher than was reported by H. Sanders (1963), but a complete restudy of its larval development remains to be done. In *Lightiella magdalenina*, 15 metanaupliar larval stages and two juveniles have been described, but an earlier stage than this species' previously known stage 1 is described in this chapter (figs. 16.2A; 16.3A); the exact number of instars of *L. magdalenina* may still be unknown (Addis et al. 2007). The earliest-known stages of *H. macracantha* and *L. magdalenina* are already

metanauplii, as they have, in addition to the naupliar appendages (the antennules, antennae, and mandibles), relatively well-developed maxillules and early limb buds of the maxillae. The shortest stage 1 larva known for the Cephalocarida is that of *H. macracantha*, which has a trunk region composed of two incipiently jointed segments plus the telson; in the stage 1 specimen of *L. magdalenina* described by Addis et al. (2007), the trunk region is composed of five well-developed segments plus the telson. Additional sampling of the same species, however, has yielded an even earlier specimen, also with five trunk segments (plus the telson), but with trunk segments 4 and 5 being only weakly developed (figs. 16.2A; 16.3A). In the early part of the metanaupliar development, two body segments seem to be added for each molt (approximately stages 1–6), while only one segment is added per molt (with some variation) in the later part of development (Addis et al. 2007). In this respect the development of cephalocarids is less gradual than in *Artemia* and the Cambrian Orsten crustacean †*Rehbachella kinnekullensis* (Walossek 1993), for example. A striking characteristic of cephalocarid development—different from other gradually developing crustaceans—is that the body segments develop much faster than the trunk limbs. As remarked by Addis et al. (2007) and also treated by Olesen et al. (2011), the addition, development, and functionality of the trunk limbs are extremely delayed. When the formation of thoracic and abdominal segments is finished and their adult number has been achieved, only three trunk limbs are present in *L. magdalenina*.

MORPHOLOGY: Egg (embryo)-carrying adults of *Hutchinsoniella macracantha*, as well as four different larvae, are illustrated here (fig. 16.1), based on recent (August 2011) sampling. Three early stages of *Lightiella magdalenina*, two of which are described by Addis et al. (2007; their stages 2 and 4), are illustrated here (figs. 16.2; 16.3). An additional stage, which is apparently earlier than stage 1 of Addis et al. (2007), and therefore referred to as “stage 1,” is illustrated here as a supplement to their description (figs. 16.2A–E; 16.3A, B). In addition, a few illustrations of a late metanauplius of *L. monniotae* are included (figs. 16.2N–P; 16.3H–J), corresponding approximately to stage 10 of *L. magdalenina*, as well as an illustration of a late juvenile (fig. 16.2O). The general morphology of stage 1 of *Hutchinsoniella macracantha* and *Lightiella magdalenina* will be outlined first, followed by a summary of the development of the major morphological aspects (based on H. Sanders 1963; Addis et al. 2007; observations made when preparing this chapter).

Stage 1 of *Hutchinsoniella macracantha* is a metanauplius with a short, broad, flattened dorsal head shield; uniramous antennules; biramous antennae bearing naupliar processes (coxal masticatory spines in other crustaceans); biramous mandibles; weakly developed maxillules; two post-cephalic body segments; and a telson. Both stage 1 of *Lightiella magdalenina*, described by Addis et al. (2007), and the even earlier “stage 1” illustrated here (figs. 16.2A–E; 16.3A, B), are in general very similar to stage 1 of *H. macracantha*, but with

more post-cephalic body segments: five in stage 1 of Addis et al. (2007), while, in the “stage 1” illustrated here, the two posterior of these are incompletely developed (fig. 16.2A).

The uniramous antennules undergo only minor changes during their entire development. In the first stages of both *Hutchinsoniella macracantha* and *Lightiella magdalenina*, they are six-segmented and bear one seta on each of segments 2, 3, and 5, as well as a cluster of setae and a distinctly superficially segmented aesthetasc distally at the sixth segment. This same basic morphology is retained throughout development, with only some minor rearrangements of the setal distribution. Another minor change concerns the presence of a few clusters of small sausage-shaped sensillae on segments 5 and 6 in the “stage 1” of *L. magdalenina* (fig. 16.2B), which appear to be lacking in the later stages examined by SEM.

The antennae remain large and biramous during development and retain much of their original structure. One major change is that the naupliar processes are lost at the end of the metanaupliar phase. The antennal exopods are multiannulate in all known stages of the Cephalocarida (as in some other crustaceans, such as mystaccocarids and Orsten crustaceans). In both *Hutchinsoniella macracantha* and *Lightiella magdalenina*, the exopod is divided into 13 short segments in “stage 1” (fig. 16.2C), a number that is retained in *L. magdalenina* in stage 2 (fig. 16.3E) and, in both species, is increased during further development (15 segments in stage 4) (fig. 16.2J) to a total number of 19 in the adults. The endopod is two-segmented and rather short in all developmental stages. In *H. macracantha*, *L. magdalenina*, and *L. monniotae*, the antennal naupliar process is a finger-like coxal endite, with some distal setation (fig. 16.3B, D, H). In *L. magdalenina* there are three distal setae and one lateral seta, all pointing toward the mouth region. In *L. magdalenina* the naupliar process is lost after 15 stages, whereas in *H. macracantha* it is lost after 13 stages. This loss, by definition, marks the end of the metanaupliar phase.

The mandibles undergo significant changes during development, as the palp (basis and two rami) is gradually lost. In the earliest stages the mandible consists of the same components as the antennae: a protopod divided into a coxa and a basis. The coxa bears a broad endite with an already-formed gnathal endite; an endopod and an exopod are also present. For both *Hutchinsoniella macracantha* and *Lightiella magdalenina*, the gnathal edge of the mandibular coxal process is already well developed in stage 1 (fig. 16.3B) and basically is similar to that of the adult. In the earliest larval stages, the mandibular exopod has an annulate-like segmentation, as does the antennal exopod, but the mandibular exopod is by far the smaller of the two (only six to seven segments) (fig. 16.2P). The mandibular endopod in larval stages has often been described as bilobate, but it actually consists of two clear segments that are inserted on a rather large basis (fig. 16.3E, G, I). The bilobed appearance is caused by a large median protrusion of the proximal endopodal segment, making it almost as broad as the basis. In *H. macracantha* the palp (basis plus two rami) is reduced in stage 14 (the first juvenile stage), but atrophy of the exopod starts at least as early as stage 11 (still

a metanauplius; but note the uncertainty with respect to the true number of larval stages). In a late larva of *L. monniotae*, corresponding approximately to stage 10 of *L. magdalenina*, the palp is still present (endopod, fig. 16.3I; exopod, fig. 16.2P) (also see Olesen et al. 2011), and a rudiment of the palp is present long after the metanaupliar phase in *L. monniotae* (fig. 16.2O).

The maxillules undergo rather significant changes during development. In *Hutchinsoniella macracantha*, the maxillule starts as a relatively undifferentiated biramous limb. A short cone-shaped unsegmented median part constitutes the future endopod, and the exopod is a lateral broad flap-like structure, with some marginal setation. The early endopod segmentation appears to be clearer in the first stage of *Lightiella magdalenina* than in the first stage of *H. macracantha*. The endopod becomes significantly longer during development, and by stage 2 of *H. macracantha* it already has become four-segmented (also see fig. 16.3I, a late metanauplius of *L. monniotae*). In all adult cephalocarids the endopod is three-segmented, a condition that was shown to take place by a reduction of the fourth segment during ontogeny in *L. monniotae* (Olesen et al. 2011). During development, the exopod becomes larger and acquires more marginal setae, but its basic morphology is the same. The protopod undergoes much change during development. In the early part of development its median margin is loosely arranged into endites (fig. 16.3I, a late metanauplius of *L. monniotae*), but in stage 11 of *L. magdalenina* the proximal endite has started to enlarge into finger-like processes that are extended even farther in juveniles and adults, reaching into the atrium oris (fig. 16.2O, a late juvenile of *L. monniotae*).

The maxillae and thoracopods undergo much change during development. They are treated together here, because they have a very similar development and are almost identical in the adults. The maxillae are present as rudimentary lobed structures in stage 1 of both *Hutchinsoniella macracantha* and *Lightiella magdalenina*. Thoracopod 1 appears in stage 3 in *H. macracantha* and in stage 5 of *L. magdalenina*. Development from rudimentary lobes to adult morphology occurs in roughly three to four steps (H. Sanders 1963; Addis et al. 2007). All stages of limb development, because of serial displacement in the degree of development, are roughly exhibited in a single late-larval specimen of *Lightiella monniotae* (fig. 16.3J). Early in development the limb is a ventrally pointing bifurcate lobe, devoid of functional setae. The exopod and pseudopod (part of exopod) then become developed, but the endopod is a small unsegmented conical structure. Next, the endopod is segmented but still small. Finally, the limb is fully developed (e.g., see Olesen et al. 2011). The development of the thoracopods is much delayed, compared with the trunk limbs. Development of the left and right side limbs is asynchronous in the examined specimen of *L. monniotae* (fig. 16.3J).

A consistent correlation exists between the presence of tergopleura and trunk limbs. Tergopleura are broad lateral extensions of each tergite that cover the basal parts of limbs (fig. 16.2N). In the adult, only the thoracic segments have tergopleura, while the abdomen consists of ring-like segments,

most of which have lateral spines at the posterior margin. In the larvae, all trunk segments start as ring-like abdominal segments (but are more dorsoventrally flattened than in the adults). The anterior larval segments are transformed into thoracic segments with tergopleura, while the posterior segments are retained as ring-like abdominal segments. This transformation in morphology is displayed in a single late larval specimen of *Lightiella monniotae*, in which the anterior three to four segments bear tergopleura (fig. 16.2N) (Olesen et al. 2011).

MORPHOLOGICAL DIVERSITY: Larvae are known only from *Hutchinsoniella macracantha*, *Lightiella serendipita*, *L. incisa*, *L. magdalenina*, and *L. monniotae* (Jones 1961; H. Sanders 1963; H. Sanders and Hessler 1964; Addis et al. 2007; Olesen 2011), and they differ from each other only in minor aspects.

NATURAL HISTORY: Aspects of larval locomotion and feeding have been studied only for *Hutchinsoniella macracantha* (H. Sanders 1963). Larvae of *H. macracantha* are wholly benthonic (as are the adults), move over the substratum ventral side down, and feed on deposited detritus. In larvae (and adults), the antennules and antennae are responsible for locomotion, but in adults the leaf-like metachronally beating thoracopods play a major role in locomotion. When larvae of *H. macracantha* move around, the antennules are mostly beating constantly, while they are often held motionless in adults, indicating that they play a larger role for locomotion in larvae than they do in adults (observations by Jørgen Olesen in August 2011). Feeding in early larvae mainly involves the cephalic appendages and is therefore very different from that of the adults, where food is handled by the post-mandibular appendages and brought forward to the mouth region (atrium oris) (H. Sanders 1963). In larvae, food particles are swept inward by the exopods of the antennae and the mandibles and are then pushed to the posterior end of the labrum by means of spines and processes on the antennules, antennae, and mandibles. From here the food is passed to the molar process of the mandible by the endites of the first maxilla and the naupliar process of the antennae. H. Sanders (1963) called the larval method of feeding “cephalic feeding.” He noted that feeding is initiated in stage 2 in *H. macracantha*. In “stage 1” of *Lightiella magdalenina*, both the molar process of the mandible and the naupliar process of the antenna are well developed (fig. 16.3B), which suggests that the larva is feeding.

As thoracopods are added in the later larval stages, the adult (post-mandibular) method of feeding becomes predominant. Several structures important in larval cephalic feeding are gradually lost, such as the naupliar processes of the antennae and the palps of the mandibles. The maxillules play a central role in the cephalic (larval) and post-mandibular (adult) feeding systems, since food items from both the larval and the adult feeding systems are passed to these limbs before they are moved into the atrium oris.

PHYLOGENETIC SIGNIFICANCE: Cephalocarids have played a crucial role in debates over crustacean evolution and phylogeny since their discovery (H. Sanders 1957, 1963; Hessler 1992a; Walossek 1993). Very early, it was assumed that the primitive mode of development in the Crustacea probably was by a regular addition of segments and limbs at each molt (anamorphic development), somewhat similar to what is seen in annelids (e.g., Calman 1909). H. Sanders (1963) suggested that the Cephalocarida showed the closest approximation to such an assumed ancestral development. Cephalocarid development is indeed gradual (see H. Sanders 1963; Addis et al. 2007), but in some ways it seems modified, compared with that of certain branchiopods (anostracans) and the Orsten crustacean †*Rehbachella kinnekullensis* (Walossek 1993; Olesen et al. 2011). First, the development of the limbs is much delayed, compared with the development of the trunk segments. Second, there seem to be some jumps in the early phase of larval development, compared with some other gradually developing crustaceans. Based on what is known about cephalocarid development, two trunk segments appear to be added in one molt in the early part of their development, which is in contrast to some anostracans, where only one seg-

ment is added per molt, or to †*R. kinnekullensis*, which perhaps had an even more gradual development, with two molts per segment (Walossek 1993).

HISTORICAL STUDIES: The classic study of cephalocarid development is that of H. Sanders (1963), which is still the most important source for information about larval morphology and functional morphology.

Selected References

- Addis, A., F. Biagi, A. Floris, E. Puddu, and M. Carcupino. 2007. Larval development of *Lightiella magdalenina* (Crustacea, Cephalocarida). *Marine Biology* (Berlin) 152: 1432–1793.
- Olesen, J., J. T. Haug, A. Maas, and D. Waloszek. 2011. External morphology of *Lightiella monniotae* (Crustacea, Cephalocarida) in the light of Cambrian “Orsten” crustaceans. *Arthropod Structure and Development* 40: 449–478.
- Sanders, H. L. 1963. The Cephalocarida: Functional Morphology, Larval Development, Comparative External Anatomy. *Memiors of the Connecticut Academy of Arts and Sciences* No. 15. New Haven: Connecticut Academy of Arts and Sciences.
- Sanders, H. L., and R. R. Hessler. 1964. The larval development of *Lightiella incisa* Gooding (Cephalocarida). *Crustaceana* 7: 81–97.

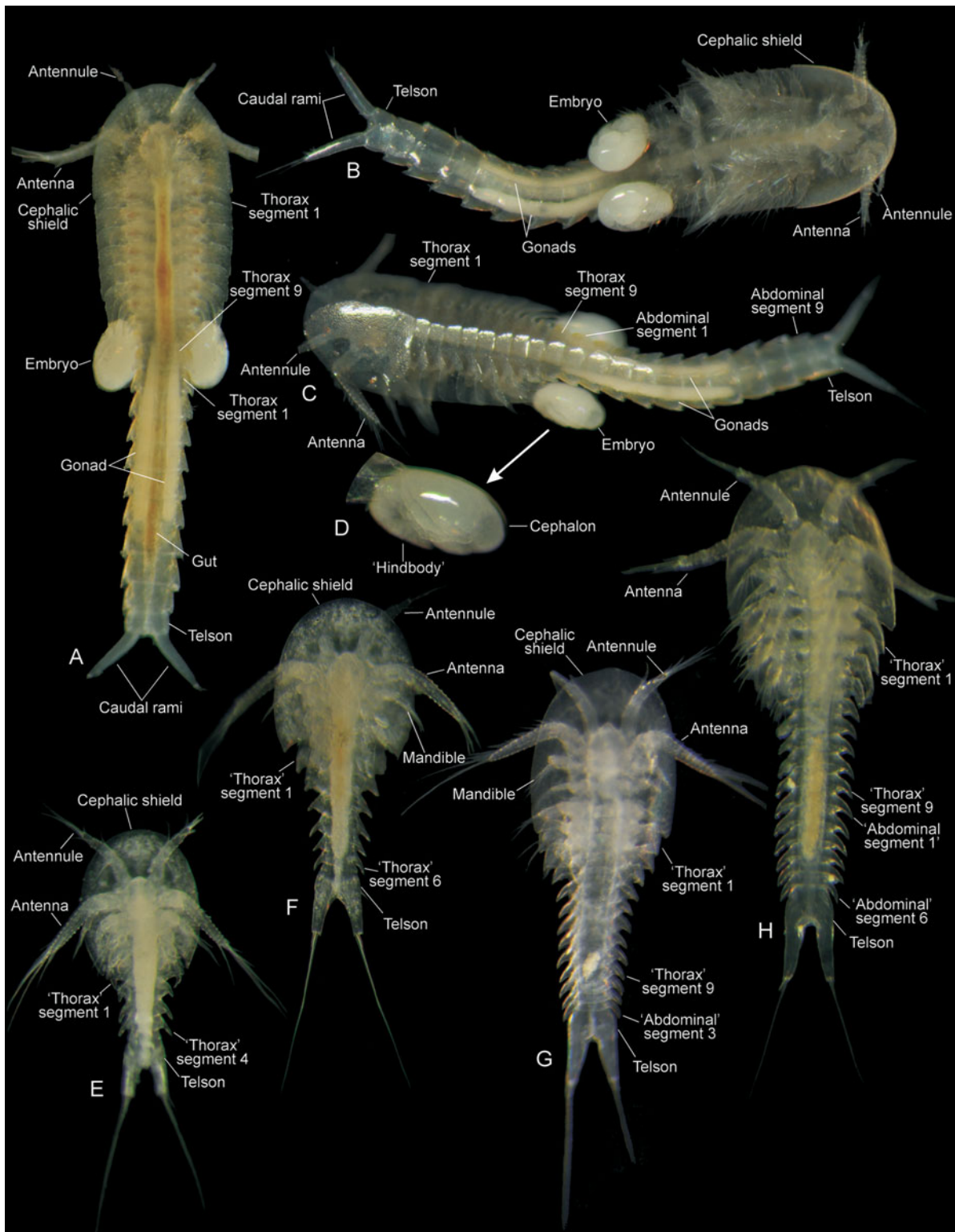


Fig. 16.1 *Hutchinsoniella macracantha* (Cephalocarida), live animals, light microscopy. A–D: egg (embryo)-carrying adults. A: adult, dorsal view. B: adult, ventral view. C: adult, laterodorsal view. D: closeup of the left-side egg (embryo). E–H: four different larval stages. E: stage with four trunk segments (plus telson), corresponding to stage 2 of H. Sanders (1963), ventral view. F: stage with six trunk segments (plus telson), corresponding to stage 3 of H. Sanders (1963), dorsal view. G: stage with 12 trunk segments (plus telson), between stages 5 and 6 of H. Sanders (1963) but not corresponding to either of these, ventral view. H: stage with 15 trunk segments (plus telson), corresponding to stage 8 of H. Sanders (1963). A–H original, of material collected in Buzzards Bay, Massachusetts, USA, in August 2011 by Jørgen Olesen, Søren Varbek Martinsen, and George Hampson.



Fig. 16.2 Metanauplii of the Cephalocarida, SEMs. A–M: stages “1,” 2, and 4 of *Lightiella magdalenina*. A: “stage 1” (earlier than the stage 1 described by Addis et al. 2007), with five trunk segments (plus telson), lateral view. B: antennule of “stage 1,” left side. C: antenna of “stage 1,” right side. D: closeup of the antennal exopod segments of “stage 1.” E: telson of “stage 1.” F: stage 2, with seven trunk segments (plus telson), lateral view. G: cephalic shield of stage 2. H: telson of stage 2. I: stage 4, with 11 trunk segments (plus telson), lateral view. J: antenna of stage 4, right side. K: stage 4, frontal view. L: trunk segments of stage 4. M: closeup of the lateral spine at the posterior margin of abdominal segment 2 of stage 4. N–P: late stages of *L. monniotae*. N: pleuroterga of a late metanauplius. O: closeup of the mandible, with rudimentary palp, and maxilla 1, with enlarged coxal endite, of a juvenile. P: closeup of the mandibular exopod of a late metanauplius. A–M original, of material from the Mediterranean Sea, collected at the same locality as the material used in Addis et al. (2007); N–P of material from New Caledonia, used in Olesen et al. (2011).



Fig. 16.3 Metanauplii of the Cephalocarida, SEMs. A–G: *Lightiella magdalenina*. A: “stage 1” (earlier than the stage 1 described by Addis et al. 2007), with five trunk segments (plus telson), ventral view. B: labrum and part of the feeding apparatus of “stage 1.” C: stage 2, with seven trunk segments (plus telson), ventral view. D: labrum and part of the feeding apparatus of stage 2. E: antenna and mandible of stage 2, right side. F: stage 4, with 11 trunk segments (plus telson), ventral view. G: labrum and part of the feeding apparatus of stage 4. H–J: late stage of *L. monniotae*. H: antennal naupliar process, left side. I: mandible and maxilla 1, right side. J: thoracopods 2 and 3 from the posterior of the metanauplius, in three different phases of development (indicated by the numbers 1–3 in parentheses); development of the left and right limbs is asynchronous. A–G original, of material from the Mediterranean Sea, collected at the same locality as the material used in Addis et al. (2007).