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EUPHAUSIACEA

LARVAE

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Nomenclature

The development of euphausiids has been reviewed by EINARSSON (1945), SHEARD (1953) and MAUCHLINE and FISHER (1969). Fifty seven of the eighty five known species shed their eggs freely into the sea; the remaining twenty eight species, comprising the genera *Nematobrachion*, *Nematoscelis*, *Nyctiphanes*, *Pseudeuphausia*, *Stylocheiron* and *Tessarabrachion*, protect the embryos until a nauplius emerges. The embryos are attached to the posterior pairs of thoracic legs. The nauplius moults to a second nauplius. The second nauplius produced in species that protect the embryos is more advanced and often refered to as a pseudometanauplius. The second nauplius and pseudometanauplius develop into metanauplii. The succeeding larval stages have been given peculiar names, first ascribed to them by G. O. SARS (1885). CLAUS (1863) was the first person to examine euphausiid larvae but, failing to recognize them as such, he gave them generic and specific names. SARS simply applied these names to distinguish the various phases of development, defining the phases as follows.

a. Nauplius stage. Body oval, unsegmented. No compound eyes. Only three pairs of limbs present, the anterior (antennulae) simple, the two other (antennae and mandibular legs) biramous, natatory.

b. Metanauplius stage. Form of the body as in the nauplius stage. Only two pairs of limbs (antennulae and antennae) developed; mandibular legs lost. Mandibles, maxillae and maxillipeds present merely as bud-like prominences.

c. Calyptopis stage. Body divided into two principal divisions. Carapace distinct, forming anteriorly a hood-like expansion. Tail becoming segmented. Compound eyes still imperfectly developed, immobile, and covered by the carapace. Mandibles, maxillae and maxillipeds distinct, but no trace of legs and pleopoda. Uropoda becoming developed.

d. Furcilia stage. Compound eyes more fully developed, mobile and projecting beyond the sides of the carapace. Antennae still retaining their original structure, natatory. Anterior pairs of legs and pleopoda successively developing.

e. Cyrtopia stage. Antennular flagella becoming elongate and distinctly articulate. Antennae transformed, so as not to serve the purpose of locomotion. Posterior legs and gills successively appearing.

f. Post-larval stage. All the legs developed. Telson assuming its definite form and armature.

Stage e, the cyrtopia, is not used now and the later larvae originally ascribed to this stage are referred to as late furciliae.

North Atlantic species

EINARSSON (1945) and GLOVER (1952) have carried out extensive surveys in the North Atlantic and recorded larvae of the following species:

Thysanopoda acutifrons HOLT & TATTERSALL
Nyctiphanes couchii (BELL)
Meganyctiphanes norvegica (M. SARS)
Euphausia krohnii (BRANDT)
Thysanoëssa inermis (KRØYER)
Thysanoëssa longicaudata (KRØYER)
Thysanoëssa raschii (M. SARS)
Nematoscelis megalops G. O. SARS
Stylocheiron longicorne G. O. SARS

Larvae of a further seven species may also be found on occasion, especially in southern regions and at sub-surface depths. These are:

Bentheuphausia amblyops G. O. SARS
Thysanopoda microphthalma G. O. SARS
Thysanoëssa gregaria G. O. SARS
Stylocheiron elongatum G. O. SARS
Stylocheiron maximum HANSEN
Stylocheiron abbreviatum G. O. SARS
Nematobrachion boöpis (CALMAN)

Identification of Species

Descriptions of all the larvae of all the species are not available. The larvae that are so far undescribed are shown in Table 1. Thus the entire larval development has only been fully described in *Meganyctiphanes norvegica*, *Thysanoëssa inermis* and *T. raschii*. Consequently, the following remarks and provisional keys can only act as guides to identifying individual larvae. In many sea areas only one or two species would be expected to breed to any great degree so that, in practice, knowing the adults present the larvae can be identified relatively easily from the figures and descriptions given here. It is also much easier to identify larvae when successive stages are present in the samples. Eggs, nauplii and metanauplii of many species are, where known, closely similar and difficult to identify. Some specific differences are evident among calyptopis larvae and hence those of more species have been identified and described. Differences tend to become enhanced in the furciliae and they are much more easily identified. The pleopods develop in the early furciliae. They appear on more anterior segments first and as bud-like prominences with no setae. These rudimentary pleopods become setose at the next moult. Thus a calyptopis III can moult to a larvae with 3 pairs of rudimentary (non-setose) pleopods (3′), one pair on each of the first three abdominal segments (Fig. 2f). This larva then moults to a Furcilia II larva with 3 pairs of setose pleopods and two pairs of non-setose pleopods (3″2′) as in Fig. 2g. At the following moult all pleopods become setose. Different species develop these pleopods in different manners.

Larvae of *Thysanoëssa* species frequently follow the following pathway of development: Calyptopis III $\rightarrow 0' \rightarrow 5' \rightarrow 5''$.

Meganyctiphanes norvegica often follows the pathway: Calyptopis III $\rightarrow 3' \rightarrow 3''2' \rightarrow 5''$.

Most larvae of a species in a sea area may follow one or two dominant pathways, e.g. $3' \rightarrow 3''2' \rightarrow 5''$ and $4' \rightarrow 4''1' \rightarrow 5''$.

A few larvae, however, may follow other pathways:

$$1' \rightarrow 1''4' \rightarrow 5''$$
$$2' \rightarrow 2''3' \rightarrow 5''$$
$$5' \rightarrow 5''$$
$$\text{or} \quad 0' \rightarrow x' \rightarrow x''y' \rightarrow 5''$$

A furcilia larva with no pleopods normally moults to one with non-setose pleopods and so on. Thus this type of larva usually represents an extra moult, through which larvae pass. It has been placed under the heading of Furcilia Ia, Furcilia Ib referring to larvae with non-setose pleopods. The details of development for any one species undoubtedly vary geographically and seasonally. This is illustrated by the two studies on *Thysanoëssa raschii*, one in the Iceland/Greenland area by EINARSSON (1945), the other in the Clyde sea area by MAUCHLINE (1965). The results are given under the specific descriptions of larvae of *T. raschii*. Consequently, complete agreement with the descriptions of the different larval stages of the different species given here must not necessarily be expected. Further, body sizes of comparable larvae of the same species from different sea areas also vary; for example the later furciliae of *T. raschii* from Iceland and the Clyde.

Eggs

The following species, of those listed above, carry their eggs attached to the posterior pairs of thoracic legs: *Nyctiphanes couchii*, *Nematoscelis megalops*, *Nematobrachion boöpis*, *Stylocheiron* species. Eggs of the other species are laid freely in the sea. The embryo is enclosed in egg membranes and a space, the perivitelline space, usually exists between the inner or vitelline membrane and the outer membranes. The size of this space varies but is frequently fairly constant in any one species in a given sea area. For example, eggs of *Thysanoëssa raschii* (Fig. 9 a, b) usually have a much smaller space than those of *Meganyctiphanes norvegica* (Fig. 5a) or *T. inermis* (Fig. 7a). Eggs of *M. norvegica*, in a fresh condition, are pinkish in colour while the closely similar eggs of *T. inermis* are colourless.

Nauplii

Many of these are undescribed (Table 1). Fresh nauplii of *Meganyctiphanes norvegica* can often be distinguished from those of *Thysanoëssa raschii* and probably also from other *Thysanoëssa* species by a pinkish colouration. Other possible features of distinction between other species are mentioned under the descriptions of individual species.

Metanauplii

A few metanauplii have what are probably specific peculiarities although the metanauplii of many species are undescribed (Table 1).

1. Heavy build. Carapace has gibbous prominence and has irregular spines round anterior end. *Meganyctiphanes norvegica* (Fig. 5e).
2. Slender build. Carapace has regular spines round anterior end. *Thysanoëssa inermis* and *T. raschii* (Figs. 7c, d).
3. Carapace has anterior fringe and two spines on dorsal posterior edge. *Euphausia krohnii* (Fig. 6a).

Calyptopes

Several calyptopes have not been described (Table 1) but the following provisional key might be helpful. It is modified from EINARSSON (1945). It is not a key in the strict sense because the characters used to compare one pair of species have not been used to compare another pair of species. For example, 4a states that there are large chromatophores on the tail of *N. couchii* and 4b states that they are not present on the tail of *M. norvegica*. MAUCHLINE has not examined larvae of *N. megalops* (4c) nor larvae of *N. couchii*; other authors have not described the pigmentation of calyptopes and have used other characteristics to distinguish between pairs of species. The chromatophores are very frequently destroyed in preservation. Consequently, this "key" will only act as a guide until further information is available on chromatophores and other characteristics.

1 a. Heavily built larvae 2
1 b. Slenderly built larvae 5
2 a. Carapace conspicuously produced posteriorly 3
2 b. Carapace not produced posteriorly 4
3 a. Rostrum plain ..... *Thysanopoda acutifrons* (Figs. 2b–e)
3 b. Rostrum fringed ..... *Euphausia krohnii* (Figs. 6b–d)
4 a. Two large orange-red chromatophores on tail ..... *Nyctiphanes couchii* (Figs. 4h–j)
4 b. No large orange-red chromatophores on tail ..... *Meganyctiphanes norvegica* (Figs. 5f–h)
4 c. Posterior margin of carapace of Calyptopes II and III has smooth rounded projection ..... *Nematoscelis megalops* (Figs. 11f–h)
5 a. Carapace produced posteriorly ..... *Thysanoëssa longicaudata* (Figs. 8a–c)
5 b. Carapace not produced posteriorly 6
5 c. Possibly undescribed larvae of *Thysanoëssa gregaria*.
5 d. Carapace tends to be elongated oval. *Stylocheiron* species.
6 a. Two pairs of orange-red chromatophores on the tail ..... *Thysanoëssa raschii* (Fig. 9d)
6 b. In Calyptopis I chromatophores in one patch on the telson. In Calyptopes II and III chromatophores in two patches ..... *Thysanoëssa inermis* (Figs. 7e–g)

Furciliae

Descriptions of furciliae larvae are available for all species except *Bentheuphausia amblyops*, *Thysanopoda microphthalma*, and *Nematobrachion boöpis*. Consequently, the following key, modified from that of EINARSSON (1945) should prove helpful.

1 a. With lateral denticles on the carapace 2
1 b. No lateral denticles on the carapace 5
2 a. Eyes divided into three portions (Fig. 2a). Dominants are $3' \rightarrow 3''2' \rightarrow 5''$ ..... *Thysanopoda acutifrons* (Figs. 2a–o)
2 b. Eyes not divided, circular or sub-circular 3

3 a. Larvae of heavy build with broad rostrum with no fringe. Where mixed populations occur larvae of *M. norvegica* have a pinkish colour whereas those of *N. couchii* are reported to be colourless. Larvae of *N. couchii* are reported to have two chromatophores on telson when material freshly preserved but confirmation is required; these chromatophores have consequently not been figured in Figs. 4k–n..... 4

3 b. Larvae of heavy build with broad rostrum with fringe. Rostrum becomes narrower in later furciliae..... *Euphasia krohnii* (Figs. 6e–j)

3 c. Larvae of heavy build with narrow rostrum. Eyes become divided in later furciliae..... *Nematoscelis megalops* (Figs. 11j–m)

3 d. Larvae slenderly built..... *Thysanoëssa raschii* (Figs. 9e–i)

3 e. Possibly also slender larvae of *Thysanoëssa gregaria* (Figs. 10a, b).

4 a. Two orange-red chromatophores on telson..... *Nyctiphanes couchii* (Figs. 4k–n)

4 b. No large chromatophores on telson; larvae pinkish all over. Dominants $3' \rightarrow 3''2' \rightarrow 5''$ ..... *Meganyctiphanes norvegica* (Figs. 5i–l)

5 a. Rostrum broad, leaf-like. Dominants $0' \rightarrow 5' \rightarrow 5''$. Legs of later furciliae slender, the second pair only slightly elongated and thickened *Thysanoëssa longicaudata* (Figs. 8d–i)

5 b. Rostrum narrower, often truncate. Developmental paths are variable. Legs of later stages strong, the second often conspicuously long and thickened..... *Thysanoëssa inermis* (Figs. 7h–k)

5 c. Eyes usually on short or long stalks. Dominants are probably: $0' \rightarrow 1' \rightarrow 1''2' \rightarrow 3''2' \rightarrow 5''$ ..... *Stylocheiron species* (Figs. 12–14)

Development in the species

1. *Bentheuphausia amblyops*

None of the larval stages are known.

2. *Thysanopoda acutifrons*

Einarsson (1945) describes the calyptopes and furciliae of this species and suggests that the larvae described by Frost (1939) belong to both *T. acutifrons* and *T. microphthalma*.

Nauplius, Metanauplius, Calyptopis I

No descriptions available.

Calyptopes II and IIII (Figs. 2b–e)

Carapace without lateral denticles in Calyptopis II, occasionally a pair of small denticles in Calyptopis III (Fig. 2d). These larvae are larger than comparable larvae of other North Atlantic species; the body lengths of *Stylocheiron* larvae require confirmation (Table 2).

Furciliae (Figs. 2f–o)

Dominant forms of early furciliae: $3' \rightarrow 3''2' \rightarrow 5''$. Variant forms: Einarsson (1945) found no variant forms. Furciliae of this species are large (Table 3).

Furcilia I: has three pairs non-setose pleopods. Antennal endopodite is unsegmented. Carapace now in form retained throughout larval life, a lateral denticle being present posteriorly on the margin (Fig. 2f). Rostrum pointed and reaches about half-way up first antennular segment. Carapace has dorsal median crest (gibbous prominence). Eyes have characteristic three lobed form (Fig. 2a, f). No photophores present.

Furcilia II: has three pairs setose and two pairs non-setose pleopods. Antennal endopodite unsegmented. First three abdominal segments have photophores (Fig. 2g).

Furcilia III: (Figs. 2h, j) all pleopods are setose. Antennal endopodite shows signs of segmentation but exopodite is not in form of scale. Antennular flagellae beginning to be segmented. Photophores on first three abdominal segments now distinctly developed.

Furcilia IV: (Fig. 2k). Antennular flagellae segmented. Antennal endopodite has segmented flagellum and two peduncular segments, and exopodite is developed as scale. First four abdominal segments have photophores.

Furcilia V: Telson has lost the outermost pair of long lateral spines but retains 7 terminal spines (Fig. 2l).

Furcilia VI: Telson has 5 terminal spines (Fig. 2m).

Furcilia VII: Telson has 3 terminal spines (Fig. 2n).

Furcilia VIII: Terminal part of telson now attained the adult form (Fig. 2o). The lateral denticle on the carapace is still present but is very small and inconspicuous.

3. *Thysanopoda microphthalma*

No descriptions of the larvae of this species are available. Einarsson (1945) only remarks that the pleopods of the early furciliae develop in the same manner as in *T. acutifrons*, that is: $3' \rightarrow 3''2' \rightarrow 5''$.

4. *Nyctiphanes couchii*

Lebour (1924, 1925) describes the morphological characteristics of the larvae of this species, but the development of the furciliae is incompletely known.

Eggs

These are carried by the female.

Nauplii

Nauplii (Figs. 4a–c) develop inside the egg membranes while attached to female. A pseudometanauplius (Fig. 4d–e) emerges from the egg membranes and lives freely in the sea.

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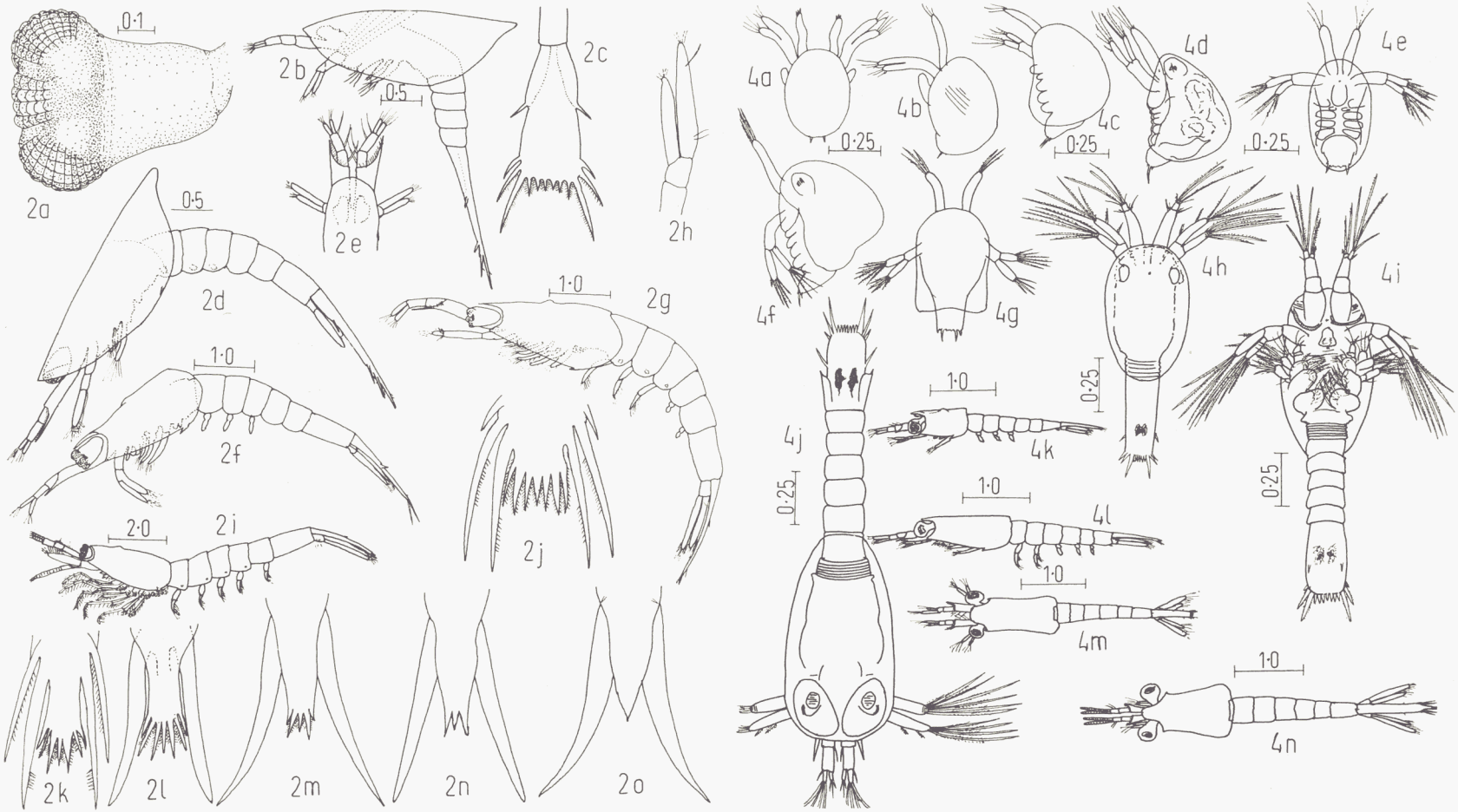


Plate I

2. *Thysanopoda acutifrons* 2a, eye of furcilia IV. 2b, calyptopis II, side view. 2c, calyptopis II, telson. 2d, calyptopis III, side view. 2e, calyptopis III, anterior end. 2f, furcilia I, side view. 2g, furcilia II, side view. 2h, furcilia III, antenna. 2i, furcilia V, side view. 2j, furcilia III, telson. 2k, furcilia IV, telson. 2l, furcilia V, telson. 2m, furcilia VI, telson. 2n, furcilia VII, telson. 2o, furcilia VIII, telson.

4. *Nyctiphanes couchii* 4a, nauplius removed from adult female. 4b, nauplius, side view. 4c, later nauplius removed from female. 4d, pseudometanauplius, side view. 4e, pseudometanauplius, ventral view. 4f, metanauplius, side view. 4g, metanauplius, dorsal view. 4h, calyptopis I, dorsal view. 4i, calyptopis II, ventral view. 4j, calyptopis III, dorsal view. 4k, furcilia I, side view. 4l, furcilia II, side view. 4m, furcilia II, dorsal view. 4n, dorsal view of late furcilia with 3 terminal spines on telson.

Figs. 2a–g, i–o after Einarsson (1945). Fig. 2h after Einarsson (1945) and Jones (1969). Figs. 4a–j after Lebour (1924). Figs. 4k–n after Lebour (1925). Larvae of species 1 and 3 are not figured.

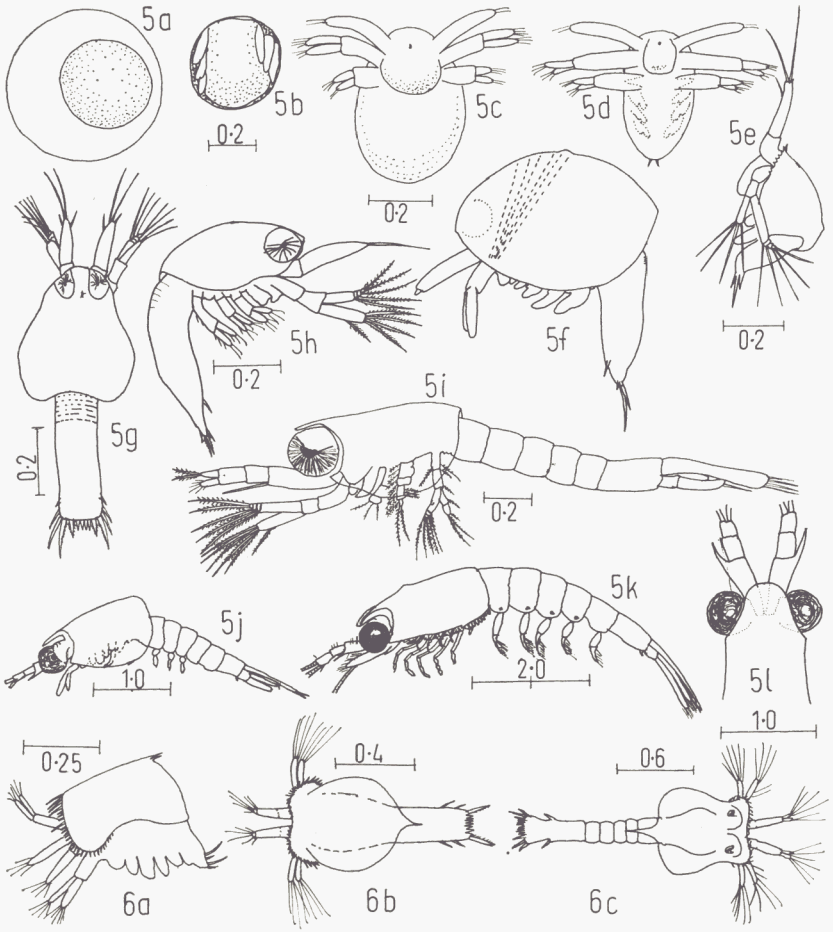
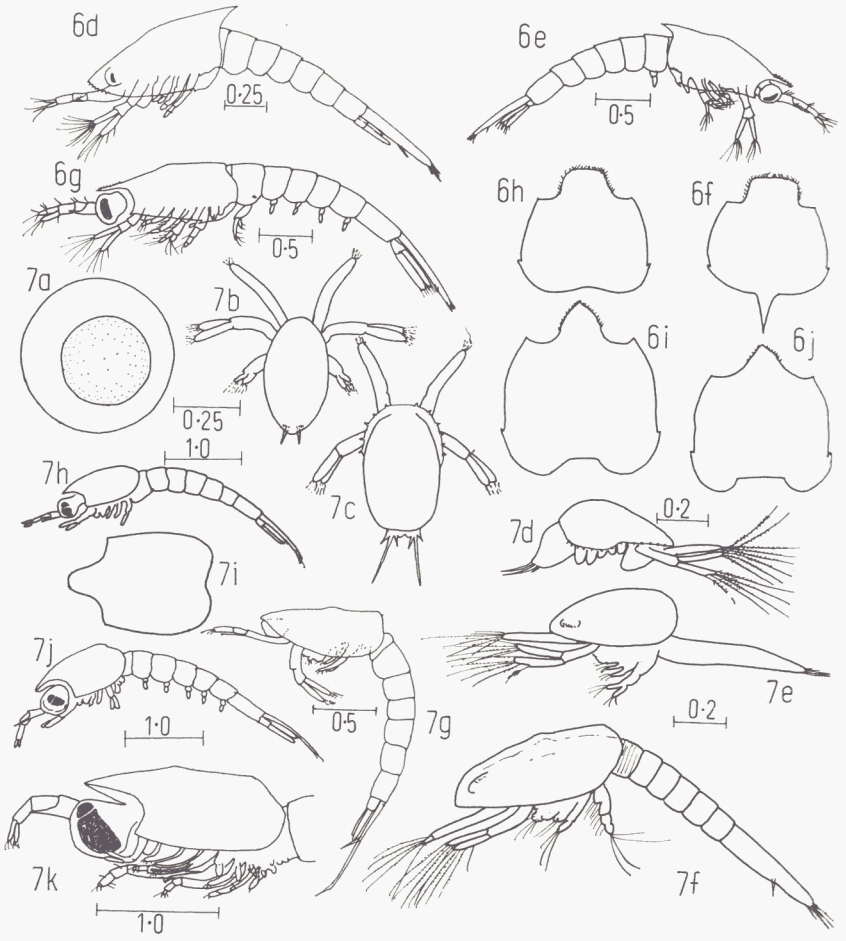


Plate II

5. *Meganyctiphanes norvegica* 5a, egg showing relatively large perivitelline space. 5b, nauplius developing within egg membranes. 5c, large nauplius. 5d, second nauplius, showing limbs of metanauplius developing. 5e, metanauplius, side view. 5f, calyptopis I, side view. 5g, calyptopis I, dorsal view. 5h, calyptopis II, side view. 5i, furcilia I with no pleopods, from Gullmarfjord. 5j, more common form of furcilia I. 5k, furcilia V, side view. 5l, dorsal anterior end of furcilia V.

6. *Euphausia krohnii* 6a, metanauplius, side view. 6b, calyptopis I, dorsal view. 6c, calyptopis II, dorsal view. 6d, calyptopis III, side view. 6e, furcilia I, side view. 6f, furcilia I, carapace. 6g, furcilia II, side view. 6h, furcilia II, carapace. 6i, furcilia III, carapace. 6j, furcilia IV, carapace.



7. *Thysanoëssa inermis* 7a, egg showing relatively large perivitelline space. 7b, nauplius II, dorsal view. 7c, metanauplius, dorsal view. 7d, metanauplius, side view. 7e, calyptopis I, side view. 7f, calyptopis II, side view. 7g, calyptopis III, side view. 7h, furcilia Ia with no pleopods. 7i, furcilia I, carapace. 7j, furcilia Ib, with 5 non-setose pleopods. 7k, furcilia IV, anterior end.

Figs. 5a–e, g–i after Heegaard (1948). Figs. 5f, j–l, 7a–c, g–k after Einarsson (1945). Figs. 6a, c, f, h–j after Frost (1934). Figs. 6b after Lebour (1926c). Figs. 6d, e, g after Sars (1885). Figs. 7d–f after Lebour (1926a).

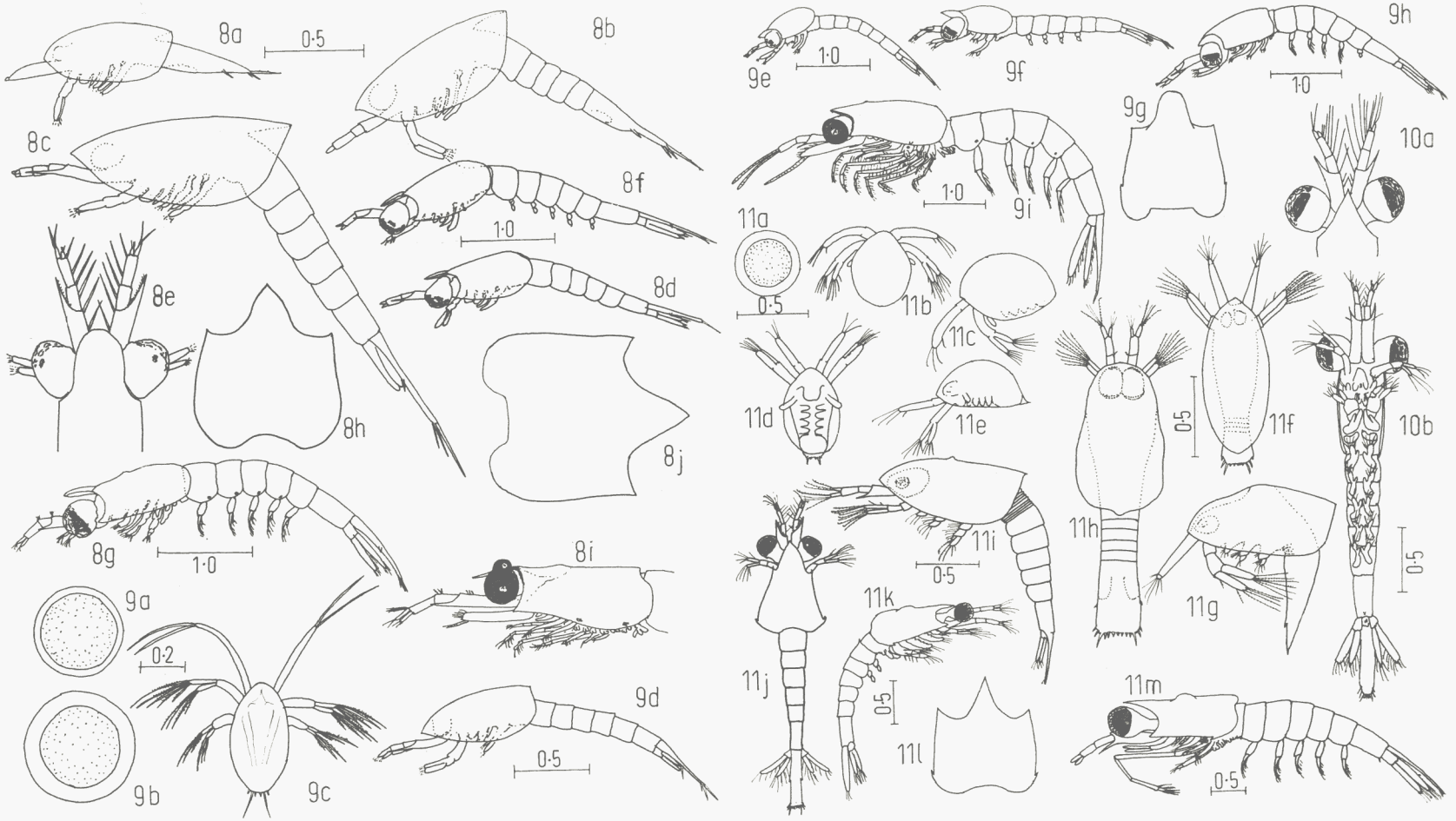


Plate III

8. *Thysanoëssa longicaudata* 8a, calyptopis I. 8b, calyptopis II. 8c, calyptopis III. 8d, furcilia Ia, side view. 8e, furcilia I, anterior end. 8f, furcilia Ib. 8g, furcilia III. 8h, furcilia IV, carapace. 8i, furcilia V, anterior end. 8j, furcilia VI, carapace.

9. *T. raschii* 9a, egg with small perivitelline space. 9b, egg with larger perivitelline space. 9c, nauplius II, as illustrated by MACDONALD. 9d, calyptopis III. 9e, furcilia Ia. 9f, furcilia Ib, with 4 pairs of non-setose pleopods. 9g, furcilia I, carapace. 9h, furcilia II. 9i, furcilia VIII.

10. *T. gregaria* 10a, furcilia II, anterior end. 10b, furcilia III, ventral view.

11. *Nematoscelis megalops* 11a, egg removed from female. 11b, nauplius. 11c, nauplius, side view. 11d, pseudometanauplius, ventral view. 11e, pseudometanauplius, side view. 11f, calyptopis I, dorsal view. 11g, calyptopis I, side view. 11h, calyptopis II, dorsal view. 11i, calyptopis III, side view. 11j, furcilia I, dorsal view. 11k, furcilia I, side view. 11l, furcilia II, carapace. 11m, late furcilia.

Figs. 8a–j, 9d–i after EINARSSON (1945). Figs. 9a–c after MACDONALD (1928). Figs. 10a–b after GURNEY (1947). Figs. 11a–i after BODEN (1955). Figs. 11j–m after FROST (1935).

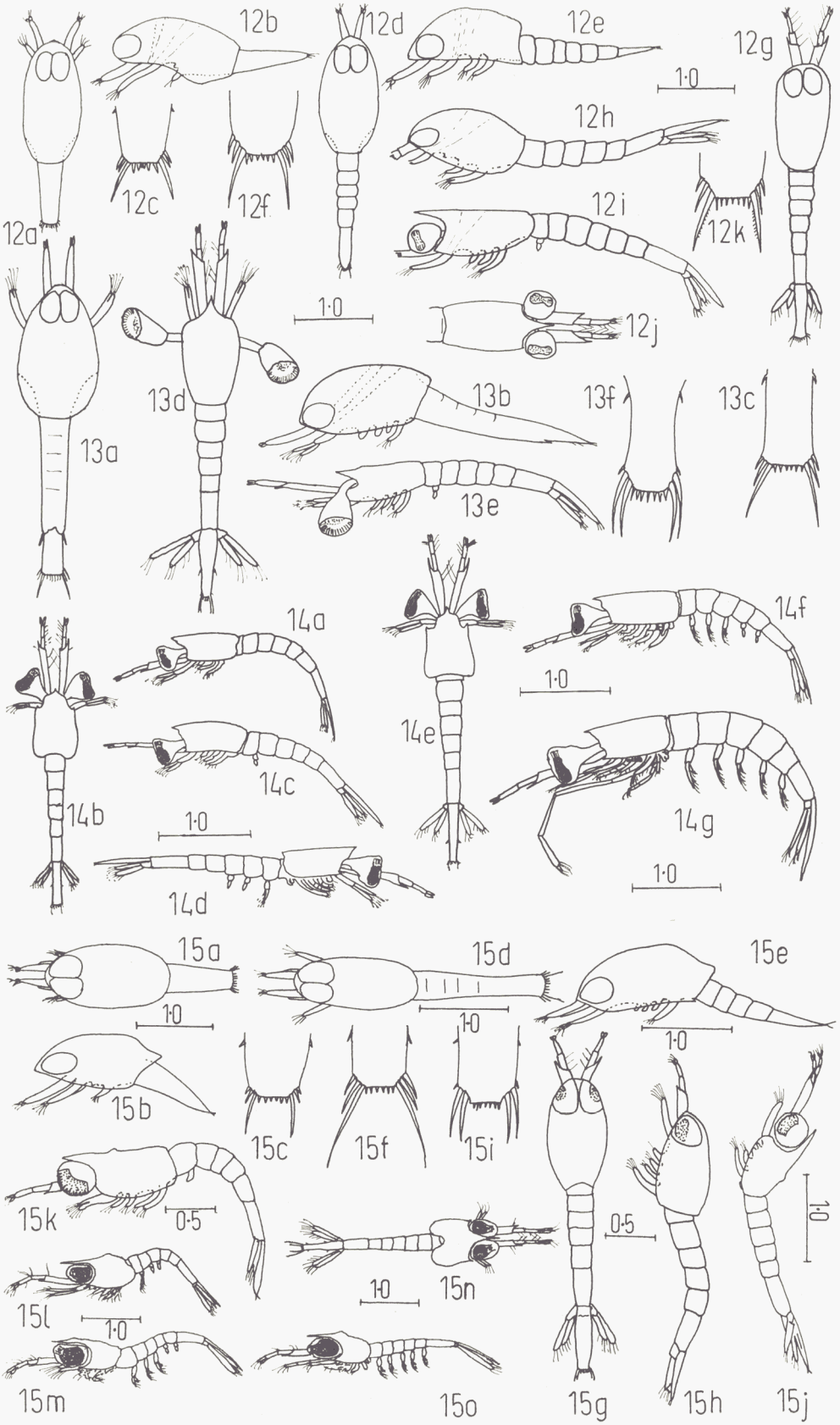


Plate IV

12. *Stylocheiron elongatum.*

12a, calyptopis I, dorsal view.
12b, calyptopis I, side view.
12c, calyptopis I, telson.
12d, calyptopis II, dorsal view.
12e, calyptopis II, side view.
12f, calyptopis II, telson.
12g, calyptopis III, dorsal view.
12h, calyptopis III, side view.
12i, furcilia Ib, side view.
12j, furcilia I, anterior end.
12k, furcilia I, telson.

13. *S. maximum.*

13a, calyptopis II, dorsal view.
13b, calyptopis II, side view.
13c, calyptopis II, telson.
13d, furcilia I, dorsal view.
13e, furcilia Ib, side view.
13f, furcilia I, telson.

14. *S. longicorne.*

14a, furcilia Ia, side view.
14b, furcilia Ia, dorsal view.
14c, furcilia Ib with one pair of non-setose pleopods.
14d, furcilia IIa, side view.
14e, furcilia IIa, dorsal view.
14f, furcilia IIb.
14g, last furcilia.

15. *Stylocheiron abbreviatum.*

15a, calyptopis I, dorsal view.
15b, calyptopis I, side view.
15c, calyptopis I, telson.
15d, calyptopis II, dorsal view.
15e, calyptopis II, side view.
15f, calyptopis II, telson.
15g, calyptopis III, dorsal view.
15h, calyptopis III, side view.
15i, calyptopis III, telson.
15j, furcilia Ia, side view.
15k, furcilia Ib, side view.
15l, furcilia IIa, side view.
15m, furcilia IIb, side view.
15n, furcilia IIb, dorsal view.
15o, furcilia IV or V, side view.

Figs. 12a–k, 13a–f, 15a–k after Lewis (1955).
Figs. 14a–g after Frost (1935).
Fig. 15l–o after Lebour (1926d).

Metanauplius (Figs. 4f–g).
This larva is heavily built and similar to that of *Meganyctiphanes norvegica* except that there are no spines round the anterior margin of the carapace.
Calyptopes I–III (Figs. 4h–j).
These larvae are similar to those of *M. norvegica* except that there are large chromatophores present in the tail.
Furciliae (Figs. 4k–n)
The dominant pathways of development of the pleopods in the early furciliae are unknown. According to Lebour (1926b) early furciliae with 5′ and with 1″4′ did not occur in her samples. Consequently, the most likely paths of development, deduced from the various types of larvae that she found, are:
$0' \rightarrow x' \rightarrow y''z' \rightarrow 5''$, $2' \rightarrow 2''3' \rightarrow 5''$, $2' \rightarrow 2''2' \rightarrow 4''1' \rightarrow 5''$, $3' \rightarrow 3''2' \rightarrow 5''$ or $4' \rightarrow 4''1' \rightarrow 5''$.
Other variant forms recorded are: 1′, 1″3′.
It is probable that there are no dominant forms in this species and that a variety of forms will be found in any one area as in other species of this genus (Mauchline & Fisher, 1969).
Later development probably follows the following path:
Furcilia III: Five pairs setose pleopods. Antennal endopodite unsegmented. 7 terminal spines on telson.
Furcilia IV: Antennal endopodite segmented. 5 terminal spines on telson.
Furcilia V: 3 terminal spines on telson.
Furcilia VI: 1 terminal spine on telson; two pairs of long lateral spines still persist.
Furcilia VII: Outermost pair of long lateral spines on telson lost.

5. *Meganyctiphanes norvegica*

Larvae of this species have been described by Lebour (1924, 1925), Macdonald (1927), Einarsson (1945), Heegaard (1948), Mauchline (1959, 1967) and Soulier (1965). These larvae are similar to those of *Nyctiphanes couchii* but they are larger in body size (Table 3).
Eggs (Figs. 5a–b)
They generally, although not always, have a large perivitelline space which distinguishes them from those of *Thysanoëssa raschii*. Their pinkish colour in a fresh state distinguishes them from the colourless eggs of *T. inermis* (Fig. 7a).
Nauplii (Figs. 5c–d)
Heegaard (1948) described the pigmentation of these larvae. Live nauplii of *M. norvegica* can be distinguished by their pink colour from those of *T. raschii* and *T. inermis*. Nauplius I has no conspicuous spines at posterior end.
Metanauplius (Fig. 5e)
The regular anterior dentition on the carapace and the gibbous prominence of the carapace make this larva recognizable from those of other species.
Calyptopes (Figs. 5f–h)
These larvae are heavily built and similar to those of *Nyctiphanes couchii* from which they can be distinguished by the absence of large orange-red chromatophores on the telson.
Furciliae (Figs. 5i–l)
Dominant forms of early furciliae: $3' \rightarrow 3''2' \rightarrow 5''$. Variant forms: 0′, 1′, 2′, 4′, 1″3′, 1″4′, 2″2′, 2″3′, 4″1′.
Furcilia I: Normally has 3 pairs non-setose pleopods (Fig. 5j).
Furcilia II: Normally has 3 pairs setose, 2 pairs non-setose pleopods.
Furcilia III: has 5 pairs setose pleopods. Antennal endopodite not segmented. Photophores present on first four abdominal segments. 7 terminal spines on telson.
Furcilia IV: antennal endopodite has two segments and exopodite is scale-shaped. 7 terminal spines on telson.
Furcilia V: telson has 5 terminal spines (Fig. 5k–l).
Furcilia VI: telson has 3 terminal spines.
Furcilia VII: telson has 1 terminal spine. There are one or two pairs of long lateral spines.
Furcilia VIII: has one pair of long lateral spines.

6. *Euphausia krohnii*

Claus (1863), Sars (1885) as *E. pellucida*, Lebour (1926c) and Frost (1934) have desdribed the larvae of this species.
Eggs and nauplii
Not described.
Metanauplius (Fig. 6a)
This larva has a characteristic fringed anterior end, described as a fringed rostrum, and two setae projecting from the dorsal posterior end of the carapace.
Calyptopes I–III (Figs. 6b–d)
These larvae have the characteristic fringed rostrum. A lateral denticle develops on the carapace in Calyptopis III and is present in all succeeding stages.

Furciliae (Figs. 6e–j)
These larvae have the characteristic fringed rostrum and a lateral denticle on the carapace.
Dominant forms of early furciliae: $1' \rightarrow 1'4'' \rightarrow 5''$. Variant forms: none recorded.
Furcilia I: has 1 pair of non-setose pleopods (Fig. 6e–f).
Furcilia II: has 1 pair of setose, 4 pairs of non-setose pleopods. A photophore is present on the first abdominal segment (Fig. 6g–h).
Furcilia III: has 5 pairs of setose pleopods and photophores present on first four abdominal segments. Telson has 7 terminal spines (Fig. 6i).
Furcilia IV: telson has 5 terminal spines. Rostrum still fringed (Fig. 6j).
Furcilia V: telson has 3 terminal spines.
Furcilia VI: telson has 1 terminal spine and two pairs of long lateral spines.
Furcilia VII: telson has one pair of long lateral spines.

7. *Thysanoëssa inermis*

The larvae of this species have been described by Lebour (1926a) and Einarsson (1945).
Egg (Fig. 7a)
Closely similar to that of *Meganyctiphanes norvegica* except that, in the live state, it is colourless.
Nauplii (Fig. 7b)
Nauplius I has no spines on posterior end. Nauplius II has 3 pairs of posterior spines, two pairs being relatively inconspicuous (Fig. 7b).
Metanauplius (Fig. 7c–d)
Carapace is regularly toothed along anterior margin.
Calyptopes I–III (Figs. 7e–g)
These larvae are slenderly built. They may be distinguished from those of *T. longicaudata* by the general shape of the carapace and in Calyptopis III by the total coverage of the eyes by the carapace in *T. longicaudata* and only partial coverage in *T. inermis* (Figs. 7g, 8c). No lateral denticle on carapace.
Furciliae (Figs. 7h–k)
Dominant forms of early furciliae: $0' \rightarrow 5' \rightarrow 5''$. Variant forms: $1'$, $2'$, $3'$, $4'$, $1''2'$, $1''4'$, $2''3'$, $3''2'$, $4''1'$.
No lateral denticle present on carapace of furciliae.
Furcilia Ia: (Fig. 7h–i) has no pleopods.
Furcilia Ib: (Fig. 7j) generally has 5 pairs of non-setose pleopods.
Furcilia II: generally has 5 pairs of setose pleopods.
Furcilia III: has 5 pairs of setose pleopods. Antennal endopodite not segmented. 7 terminal spines on telson. Photophores on first two abdominal segments.
Furcilia IV: (Fig. 7k) antennal endopodite not segmented. Telson has 7 terminal spines. These larvae are larger (Table 3) than Furciliae III and although Einarsson (1945) does not say so, there may now be photophores present on first 3 abdominal segments.
Furcilia V: antennal endopodite is segmented and exopodite beginning to look like a scale. Telson has 7 terminal spines.
Furcilia VI: telson has 5 terminal spines.
Furcilia VII: telson has 3 terminal spines.
Furcilia VIII: telson has 1 terminal spine but still retains the two pairs of long lateral spines.
Furcilia IX: telson has 1 pair of long lateral spines.

8. *Thysanoëssa longicaudata*

Larvae of this species have been described by Einarsson (1945) and Jones (1969).
Eggs, Nauplii, Metanauplius
These have not been described.
Calyptopes I–III (Figs. 8a–c)
The carapace is pointed posteriorly and normally covers the eyes in Calyptopis III.
Furciliae (Figs. 8d–i)
Dominant forms of early furciliae: $0' \rightarrow 5' \rightarrow 5''$. Variant forms: $1'$, $3'$, $4'$, $1''4'$, $2''3'$, $3''2'$, $4''1'$.
Rostrum of the furciliae I and II is much broader than in comparable larvae of *T. raschii* or *T. inermis*. No lateral denticle on carapace.
Furcilia Ia: (Fig. 8d) normally has no pleopods.
Furcilia Ib: (Fig. 8f) normally has 5 pairs of non-setose pleopods.
Furcilia II: normally has 5 pairs of setose pleopods. Photophores on first four abdominal segments only slightly pigmented.
Furcilia III: (Fig. 8g) antennal endopodite unsegmented. Telson has 7 terminal spines. Photophore present on second thoracic leg.
Furcilia IV: (Fig. 8h) antennal endopodite of two segments. Telson has 5 terminal spines.
Furcilia V: (Fig. 8i) telson has 3 terminal spines.
Furcilia VI: (Fig. 8j) telson has 1 terminal spine but still retains two pairs of long lateral spines.
Furcilia VII: telson has one pair of long lateral spines.
Jones (1969), quoting unpublished work of Rees, criticizes Einarsson's description of the development. The samples examined by Jones were very small and his results may be misleading. A furcilia stage is an intermoult and Jones has undoubtedly grouped several stages together.

9. *Thysanoëssa raschii*

Larvae of this species have been described by MACDONALD (1928), EINARSSON (1945) and MAUCHLINE (1965, 1967).

Eggs (Figs. 9a–b)

The pervitelline space is normally much smaller than that of eggs of *T. inermis* (Fig. 7a) and *Meganyctiphanes norvegica* (Fig. 5a). MACDONALD (1928) noted that the live egg has a bright red pigment spot on its surface and this is indeed true of eggs found in the Clyde sea area; no confirmation of this observation from other sea areas has been obtained.

Nauplii (Fig. 9c)

There are two nauplii which closely resemble those of *T. inermis*. From EINARSSON's figure of the Nauplius II of *T. inermis* (Fig. 7b) and MACDONALD's of the Nauplius II of *T. raschii* (Fig. 9c) it appears that the posterior pairs of small spines are more prominent in *T. raschii* but this requires confirmation.

Metanauplius

This larva is very similar to that of *T. inermis* (Figs. 7c–d) and probably indistinguishable from it.

Calyptopes I–III (Fig. 9d)

These larvae can not, at present, be distinguished from those of *T. inermis*. Live calyptopes of *T. raschii* in the Clyde sea area have two red pigment spots on the telson, as MACDONALD pointed out, but these disappear on preservation, as EINARSSON remarks.

Furciliae (Figs. 9e–i)

Dominant forms of early furciliae: $0' \rightarrow 4' \rightarrow 4''1' \rightarrow 5''$, $0' \rightarrow 3' \rightarrow 3''2' \rightarrow 5''$, $0' \rightarrow 5' \rightarrow 5''$. Variant forms: 1′, 2′, 2″2′, 3″1′. The furciliae with no non-setose pleopods has no lateral denticle on the carapace (Fig. 9e).

All other furciliae of *T. raschii* are distinguished from those of *T. inermis* and *T. longicaudata* by the presence of a lateral denticle on the carapace. The development of this species has been examined in detail by EINARSSON (1945) in Iceland and by MAUCHLINE (1965) in the Clyde sea area. The detailed development was found to be different.

	Iceland	Clyde
Furcilia Ia:	No pleopods. Length about 3 mm.	No pleopods. Length 2.1–3.3 mm.
Furcilia Ib:	Dominant forms: 3′, 4′, 5′. Variant forms: 2′. Length, about 3.5 mm.	Dominant forms: 3′, 4′, 5′. Variant forms: 1′, 2′. Length, 2.7–4.1 mm.
Furcilia II:	Dominant forms: 4″1′, 5″. Variant forms: 3″2′. Length, about 4.0 mm.	Dominant forms: 3″2′, 4″1′, 5″. Variant forms: 2″2′, 2″3′, 3″2′. Length, 3.0–4.8 mm.
Furcilia III:	Antennal endopodite unsegmented. Photophores on first 2 abdominal segments. Length, about 4.5 mm.	Antennal endopodite unsegmented. Photophore on first abdominal segment. Length, 3.5–4.9 mm.
Furcilia IV:	Antennal endopodite unsegmented or shows signs of segmentation. Photophores on first 3 abdominal segments. Length, 4.5–5.0 mm.	Antennal endopodite unsegmented. Photophores on first 2 abdominal segments. Length, 4.2–5.3 mm.
Furcilia V:	Antennal endopodite of 3 segments. Photophores on first 4 abdominal segments. Telson has 7 terminal spines. Length, 4.5–5.5 mm.	Antennal endopodite unsegmented. Photophore on first 3 abdominal segments. Telson has 7 terminal spines. Length, 4.9–5.8 mm.
Furcilia VI:	Antennal endopodite and exopodite shaped like flagellum and scale respectively; flagellum unsegmented. Telson has 7 terminal spines. Length, 5–6 mm.	Antennal endopodite unsegmented. Photophores on first 4 abdominal segments. Telson has 7 terminal spines. Length, 5.2–6.2 mm.
Furcilia VII:	Telson has 5 terminal spines. Length, 5.0–6.5 mm.	Antennal endopodite segmented. Telson has 7 terminal spines. Length, 5.8–6.7 mm.
Furcilia VIII:	Telson has 3 terminal spines; two pairs of long lateral spines present. Length, 5.5–7.0 mm.	Telson has 5 terminal spines. Length, 6.2–8.6 mm.
Furcilia IX:	Telson has 1 terminal spine; two pairs of long lateral spines still persist. Length, 6.0–7.5 mm.	Telson has 3 terminal spines. Length, 8.0–9.1 mm.
Furcilia X:	Telson has one pair of long lateral spines. Length, 6.5–9.0 mm.	Telson has 1 terminal spine. Length, 8.8–10 mm.

10. *Thysanoëssa gregaria*

The furciliae of this species have been described by EINARSSON (1945), GURNEY (1947) and BARY (1956).

Eggs, nauplii, metanauplius, calyptopes

No descriptions of these larvae are available.

Furciliae (Figs. 10a–b)

The development of the furciliae has not been studied thoroughly but the probable path of development may be deduced from the descriptions of larvae given by GURNEY (1947). This developmental series is only tentative and requires confirmation. The rostrum of these furciliae is pointed (Fig. 10a) and is unlike that of furciliae of other *Thysanoëssa* species (Figs. 7i; 8e, h, j; 9g).

Probable dominant forms of early furciliae. $0' \rightarrow 5' \rightarrow 5''$. Variant forms: $1'$, $3'$, $1''4'$, $2''3'$, $4''$.

Furcilia Ia: no pleopods. No lateral denticle on carapace.

Furcilia Ib: 5 pairs of non-setose pleopods. Lateral denticle on carapace.

Furcilia II: 5 pairs of setose pleopods. No abdominal photophores.

Furcilia III: 5 terminal spines on telson. Photophore on first abdominal segment.

Furcilia IV: 3 terminal spines on telson. Photophore on first abdominal segment.

Furcilia V: 1 terminal spine on telson. Photophores on first four abdominal segments. Antennal endopodite becoming segmented.

Furcilia VI: antennal exopodite in form of scale, endopodite consisting of 3 segments.

Furcilia VII: telson has lost outermost pair of long lateral spines.

11. *Nematoscelis megalops*

Larvae of this species have been described by FROST (1935), LEBOUR (1950) and BODEN (1955). The development, however, of this species is still incompletely known in the furciliae.

Eggs (Fig. 11a)

These are carried by the female.

Nauplius (Figs. 11b–c)

Has no appendages or processes at posterior end.

Pseudometanauplius (Figs. 11d–e)

The body is more elongated that that of the nauplius and the developing telson with spines protrudes from the posterior end.

Metanauplius

This larva has not been described.

Calyptopes I–III (Figs. 11f–i)

The carapace of calyptopis I is long, high and with a very narrow dome which covers the entire anterior part of the body. The carapace of calyptopis II is similar except that there is a smooth round projection from the posterior margin. That of Calyptopis III is also similar except for the addition of a dorsal protuberance (gibbous process).

Furciliae (Figs. 11j–m)

Probable dominant forms of early furciliae: $2' \rightarrow 2''3' \rightarrow 5''$. Variant forms: $1'$, $3''2'$.

There is a lateral denticle on the carapace and the rostrum is pointed.

Furcilia I: probably has two pairs of non-setose pleopods (Figs. 11j, k).

Furcilia II: (Fig. 11,l) probably has 2 pairs setose and 3 pairs non-setose pleopods.

Furcilia III: has 5 pairs setose pleopods and 7 terminal spines on telson.

Furcilia IV: has 5 terminal spines on telson.

Furcilia V: has 3 terminal spines on the telson.

Furcilia VI: antennal endopodite is segmented. Telson has 1 terminal spine.

12. *Stylocheiron elongatum*

Larvae of this species have been described by LEWIS (1955) but the whole developmental sequence has not been examined. These larvae are similar to those of *S. longicorne*.

Eggs

These are carried by the female.

Nauplius, metanauplius

Not described.

Calyptopes I–III (Figs. 12a–h)

Carapace is oval and completely covers the eyes in all three stages. These larvae are similar to those of *S. maximum* and *S. abbreviation*.

Furciliae

A stage with no pleopods is probably present and the dominant forms of early furciliae are probably: $0' \rightarrow 1' \rightarrow 1''2' \rightarrow 3''2' \rightarrow 5''$.

Furcilia Ia: has an elongated central portion of the eye which is darker in colour and distinct from the rest of the eye.

Furcilia Ib: Eyes are on a short stalk (Fig. 12j) and very like those of the adult in form.

None of the later furciliae have been described.

13. *Stylocheiron maximum*

Larvae of this species have been described by LEWIS (1955). A stalk-eyed larva described by GURNEY (1947) and LEBOUR (1950) has been tentatively assigned to this species. It is probable that the larvae figured by LEWIS and illustrated here (Figs. 13a–f) are those of *S. maximum* but confirmation is required.

Eggs

These are carried by female.

Nauplius, metanauplius, Calyptopes I and III

These larvae have not been described.

Calyptopis II (Figs. 13a–c)

This is the only calyptopis described and it is similar to those of *S. elongatum* and *S. abbreviatum.*

Furciliae (Figs. 13d–f)

The only early furcilia so far described is one with 1 pair of non-setose pleopods. The eyestalks are very long as are the antennular peduncles. LEWIS found this larva to measure about 4 mm while LEBOUR describes a later larval stage with 3 pairs setose, two pairs non-setose pleopods that only measures 2.2 mm (see Table 3).

No other furciliae have been described.

14. *Stylocheiron longicorne*

Furciliae of this species have been described by FROST (1935).

Eggs

These are carried by the female.

Nauplius, metanauplius, Calyptopes I–III

These have not been described.

Furciliae (Figs. 14a–g)

Dominant forms of early furciliae: $0' \rightarrow 1' \rightarrow 1''2' \rightarrow 3''2' \rightarrow 5''$. Variant forms: none reported.

Furcilia Ia: no pleopods.

Furcilia Ib: one pair non-setose pleopods.

Furcilia IIa: one pair setose, two pairs non-setose pleopods.

Furcilia III: 5 pairs setose pleopods and 7 terminal spines on telson. Second pair of thoracic legs are becoming obviously elongated.

The later furciliae are inadequately described but are probably recognizable by a sequential reduction of the number of terminal spines on the telson.

15. *Stylocheiron abbreviatum*

Larvae of this species have been described by GURNEY (1947), LEBOUR (1926d, 1950) and LEWIS (1955).

Eggs

These are carried by the female.

Nauplius, metanauplius

These larvae have not been described.

Calyptopes I–III (Figs. 15a–i)

Carapace is oval and completely covers the eyes in all stages. These larvae are similar to those of *S. elongatum* and *S. maximum.*

Furciliae (Figs. 15j–o)

Dominant forms of early furciliae: $0' \rightarrow 1' \rightarrow 1''2' \rightarrow 3''2' \rightarrow 5''$. Variant forms: $2'$, $3'$, $2''3'$.

The furciliae of *S. abbreviatum* seem to be similar in shape to those of *S. maximum* except that the eyes are not on pronounced stalks and the carapace has a mid-dorsal protuberance. No detailed descriptions of the later furciliae are available.

16. *Nematobrachion boöpis*

No larvae of this species have been described.

TABLE 1.

Unknown larval stages, designated as "NO", of the various species.

	Nauplius	Metanauplius	Calyptopes I–III	Furciliae
1. *Bentheuphausia amblyops*	NO	NO	NO	NO
2. *Thysanopoda acutifrons*	NO	NO	Calyptopis I	–
3. *Thysanopoda microphthalma*	NO	NO	NO	NO
4. *Nyctiphanes couchii*	–	–	–	incomplete
5. *Meganyctiphanes norvegica*	–	–	–	–
6. *Euphausia krohnii*	NO	–	–	–
7. *Thysanoëssa inermis*	–	–	–	–
8. *Thysanoëssa longicaudata*	NO	NO	–	–
9. *Thysanoëssa raschii*	–	–	–	–
10. *Thysanoëssa gregaria*	NO	NO	NO	incomplete
11. *Nematoscelis megalops*	–	NO	–	incomplete
12. *Stylocheiron elongatum*	NO	NO	–	incomplete
13. *Stylocheiron maximum*	NO	NO	Calyptopes I & III	incomplete
14. *Stylocheiron longicorne*	NO	NO	NO	incomplete
15. *Stylocheiron abbreviatum*	NO	NO	–	incomplete
16. *Nematobrachion boöpis*	NO	NO	NO	NO

TABLE 2.

Approximate ranges in body lengths (mm) of early larval stages. Mean sizes shown in brackets, single measurements not in brackets are of doubtful accuracy.

Species	Nauplii		Metanauplius	Calyptopes		
	I	II		I	II	III
1	–	–	–	–	–	–
2	–	–	–	–	3.5–3.8	4.5–4.7
3	–	–	–	–	–	–
4	–	0.56	0.57	1.00	1.44	1.92
5	0.48	0.48	0.50–0.52	(1.03)	(1.59)	(2.4)
6	–	–	0.4–0.6	0.9–1.4	1.6–2.0	1.8–2.8
7	0.48–0.56	0.51–0.60	0.58–0.65	1.00–1.45	1.60–2.20	2.40–2.70
8	–	–	–	1.0–1.5	1.8–2.0	2.5
9	0.45–0.47	0.47–0.49	0.56	0.70–1.05	1.2–2.0	1.7–2.6
10	–	–	0.9–1.1	0.9–1.4	1.4–1.6	2.0–2.5
11	0.43–0.53	0.53–0.57	–	0.97–1.00	1.6–2.0	2.4–2.9
12	–	–	–	2.52	3.08	3.64
13	–	–	–	–	3.92	–
14	–	–	–	–	–	–
15	–	–	–	2.24	2.66	2.87
16	–	–	–	–	–	–

TABLE 3.

Approximate body lengths of different forms of furciliae; these are not necessarily sequential stages in the development (see detailed descriptions of development of each species) but are merely easily recognized furciliae. There is geographical and seasonal variation in each species of the forms of the same furcilia and so these measurements are only approximate. (– equals unknown).

	Pleopod development			Antennal endopodite unsegmented	Antennal endopodite segmented	Number of terminal spines on telson		
Species	0′	x′	y″y′			5	3	1
1	–	–	–	–	–	–	–	–
2	–	5.8–5.9	6.8–6.9	7.8	9.0–9,5	10.5–11.0	11.0	11.0–11.5
3	–	–	–	–	–	–	–	–
4	2.5	2.5–3.5	3.2–4.0	4.0–4.3	–	4.3	4.5	4.5–4.8
5	–	2.4–3.5	3.2–4.4	3.5–5.5	4.8–6.3	5.7–7.7	6.7–8.3	7.8–10.7
6	–	3.0–3.5	3.6–4.3	3.9–4.7	–	5.4	4.3–5.4	5.8–7.0
7	3.0	3.5	4.0	4.5	5.5	6.0	6.5	7.0
8	3.2	3.7	4.0	4.5	–	4.9	5.5	5.8
9	2.1–3.3	2.7–4.1	3.0–4.8	3.5–4.9	5.8–6.7	6.2–8.6	8.0–9.1	8.8–10.0
10	2.4	2.8–3.0	2.7–3.2	–	–	3.1–3.5	3.0–3.5	3.3–3.9
11	–	3.3	4.0	–	–	4.8	–	5.0–5.1
12	3.9	4.2	–	–	–	–	–	–
13	–	4.0	2.2*	–	–	–	–	–
14	2.6	2.7	3.0–3.3	3.4	–	3.6	–	3.8–4.0
15	2.5	ca. 3.0	3.0–3.2	–	–	ca. 3.0	–	–
16	–	–	–	–	–	–	–	–

* LEBOUR's small larva, see text.

TABLE 4.

Dominant (D) and variant (V) of early furciliae. (′) denotes pairs of non-setose, (″) pairs of setose pleopods.

Species	0′	1′	2′	3′	4′	5′	1″2′	1″3′	1″4′	2″2′	2″3′	3″1′	3″2′	4″	4″1′	5″
1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	–	–	–	D	–	–	–	–	–	–	–	–	D	–	–	–
3	–	–	–	D	–	–	–	–	–	–	–	–	D	–	–	–
4	V	V	V	V	V	–	–	V	–	V	V	–	V	–	V	V
5	V	V	V	D	V	–	–	V	V	V	V	–	D	–	V	–
6	–	D	–	–	–	–	–	–	D	–	–	–	–	–	–	–
7	D	V	V	V	V	D	V	–	V	–	V	–	V	–	V	D
8	D	V	–	V	V	D	–	–	V	–	V	–	V	–	V	D
9	D	V	V	D	D	D	–	–	–	V	V	V	D	–	D	D
10	D	V	–	V	–	D	–	–	V	–	V	–	–	V	–	D
11	–	V	D	–	–	–	–	–	–	–	D	–	V	–	–	–
12	D	D	–	–	–	–	D?	–	–	–	–	–	D?	–	–	–
13	D?	D	–	–	–	–	D?	–	–	–	–	–	D?	–	–	–
14	D	D	–	–	–	–	D	–	–	–	–	–	D	–	–	–
15	D	D	V	V	–	–	D	–	–	–	V	–	D	–	–	–
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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