POST-EMBRYONIC DEVELOPMENT OF *TÁCHIDIUS DISCIPES* GIESBRECHT 1881 (COPEPODA, HARPACTICOIDA)

by

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Résumé

Le développement larvaire complet du Copépode Harpacticoïde *Tachidius discipes* Giesbrecht est décrit. Il comprend six stades naupliens et six stades copépodites (le sixième stade copépodite étant l'adulte). Le développement du corps et des appendices est étudié et comparé à celui d'autres Harpacticoïdes.

Introduction

Tachidius discipes is a euryhaline, cosmopolitan species largely confined to mesohaline localities (Muus, 1967), where it may be the dominant harpacticoid (Smidt, 1951; Noodt, 1957). It is epibenthic (Heip, 1973) though feeding only on the mud surface (Muus, 1967). According to Lang (1948), the species is distributed off Spitzbergen and the Norwegian coasts, in the Baltic, North and Irish Sea, and along the Channel and Atlantic coasts to Buzzards Bay. Gurney (1932) regarded *T. discipes* as the commonest and most abundant littoral species to be found around the British coast and also provided a description of the stage 1 nauplius with an incomplete description of the fifth copepodite. Muus (1967) stated that there are six naupliar and five copepodite stages in the post-embryonic development but he did not describe them.

The present paper provides descriptions of the developmental stages which have been made prior to an investigation of the life cycle of the animal in the field and laboratory studies on growth rates, respiration rates, etc., for which the identity of each instar must be known.

Materials and Methods

Gravid females of *T. discipes* from a mid-tide station on an estuarine mud flat in the River Lynher, Cornwall, U.K., were isolated into the cells of a leucocyte migration plate filled with 26 per mil filtered sea water (this being the mean annual salinity of the field site) to which was added one drop of *Tetraselmis* culture before being covered with a glass cover slip. Newly hatched nauplii

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were transferred daily to individual cells. Losses due to evaporation were replaced with deionised water to maintain salinity and algal food was kept in excess. Each exuvium was collected and transferred to a lactic acid mount. Additional material was collected from larger cultures; animals were removed from the cultures daily, preserved in 2 per cent formalin in 26 per mil sea water, and mounted in lactic acid on slides; measurements of length were taken from the rostrum to the caudal ramus, excluding the caudal setae.

DEVELOPMENTAL STAGES

Tachidius discipes develops through six naupliar stages, which have a circular body shape, and six copepodite stages — the sixth being the adult. The copepodite stages have the adult body shape and gain a further abdominal segment, in addition to an increase in number and complexity of the thoracic appendages, with each successive stage.

The morphology of the developmental stages is described in figures 1-6 and new developmental features occurring in each stage are arrowed.

Nauplius 1 (Fig. 1, A)

Length 78 µm, width 69 µm, circular in shape with one large red eye. *Antennule* of three segments bearing six setae. *Antenna* has well developed exopod which has four segments and bears four long setae with many spinules and one short spine. Basal segment with large prehensile branch. Single setae either side of anal region united by a ridge bearing 11 fine spines. Slightly anterior is another series of 13 much finer spines. *Mandible* with well developed exopod, three-segmented and bearing four spinulate setae. Lying beneath and slightly posterior to the mandible endopod is a complex of spines forming the posterior boundary of the mouth region.

Nauplius 2 (Fig. 1, B)

Length 87 µm, width 71 µm, body more elongated shape than NI. Two new setae develop on the terminal segment of the *antennule. Antenna* endopod develops one additional seta and spinules on the terminal spine. Coxopodite masticatory process increases in size. Spinules develop laterally to the anal setae while the anterior row of hairs has disappeared. *Anal setae* considerably thickened at base.

Nauplius 3 (Fig. 1, C)

Length 99 µm, width 88 µm. A new short seta appears on the first segment of the *antenna.* Characteristic forked appearance develops at the end of the inner spine on the *mandible endopod. Mandible exopod* increases in size and complexity. The outline of the developing rami is now apparent. Groups of spinules appear on the ventral hind body surface.

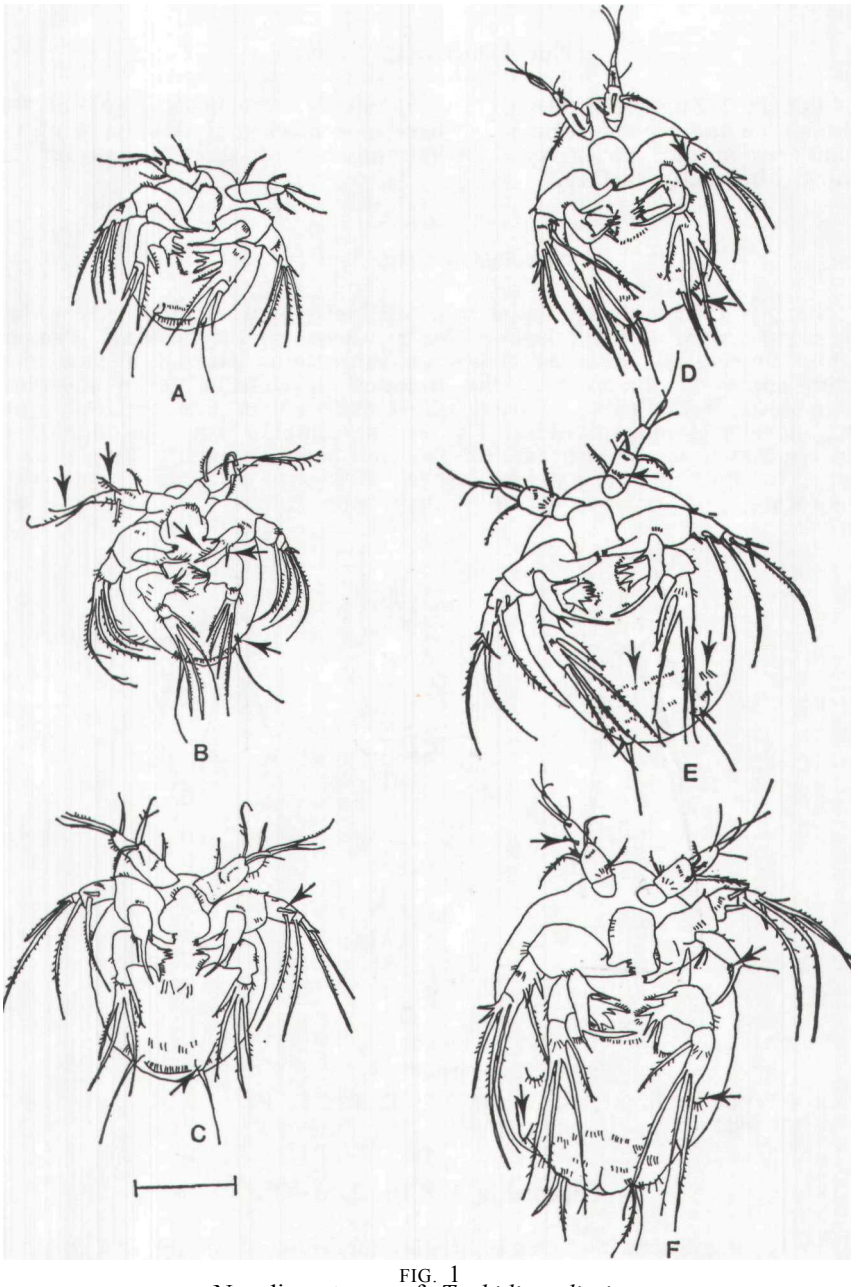

FIG. 1
Naupliar stages of *Tachidius discipes.*
A-F stages 1-6.
Scale line 50 μm.

Nauplius 4 (Fig. **1,** D)

Length 109 μm, width 87 μm, body shape less rounded becoming proportionally longer and thinner than preceding stages. Another new spine develops on the second segment of the antenna exopod and the spine on the basal segment becomes more prominent. One new spine appears laterally to each furcal spine.

Nauplius 5 (Fig. **1,** E)

Length 128 µ, width 99 µm. The *antennule* develops a group of five spinules on the second segment. There is a marked development of the *ramus region* and an increase in the number of short spines on the ventral hind body surface.

Nauplius 6 (Fig. **1, F)**

Length **120 µm,** body shape now distinctly longer and thinner than preceding stages. *Antennule* develops two setae on the terminal segment, both with setules. *Antenna* shows an increase in size of all the most recent spines of the exopod, the endopod develops **a** group of spines at the base of the claw. *Furcal spines* increase in size and the **inner** setae develop some spinules. The *second maxilla* and the *maxilliped* first appear as lobes with setules, the first maxilla having been present from N1. First *natatory swimming leg* is present as a small lobe with two spines, just anterior to the ventral body spines.

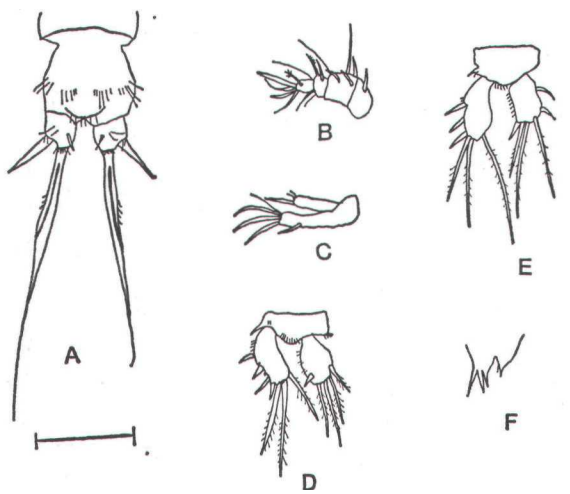

FIG. 2
Copepodite 1.
A, Caudal ramus: B, A1; C, A2; D, P1; E, P2; F, P3. Scale line 50µm.

Copepodite 1 (Fig. **2, A-F)**

Body now gains the characteristic harpacticoid shape and is composed of five segments, length 215 urn. *Anal* segment bears four groups of setae on the ventral surface and a semicircular ridge of spinules on the dorsal surface. *Furcal rami* are as long as they are broad, bearing one long inner caudal seta, a shorter outer spine, setae and a much shorter inner dorsal spine. Fine spines fringe the joint of the terminal seta with the ramus. *Antennule* is composed of four segments with only one spine on the basal segment. *P1.* Basis carries one naked spine and the internal distal edge is spinulate. Both rami are composed of one segment. Exopod has four naked outer setae and three much longer spinulose apical setae. Endopod has spinules on the external edge and one naked inner seta. There are three spinulose apical setae and one spinulose inner seta. *P2.* Both rami are composed of one segment. Basis bears one outer spine and the inner distal edge is spinulate.

Exopod bears three naked spines, two apical and one inner setae which are spinulose. Endopod bears spinules on the inner edge and one naked spine. There are three spinulose apical setae and two naked inner spines. *P3.* This is present as a small double lobe bearing three spines on the larger and two on the smaller lobe.

Copepodite 2 (Fig. 3, A-G)

Body is composed of six segments, length 251 µm. *Antennule* is composed of five segments and has three additional setae, one on the second segment and two on the third. Terminal setae of the *caudal rami* have now split to form a shorter outer seta and much longer inner one. A group of spinules develops on the inner edge of the rami and around the base of the large apical setae. *P1.* Both rami are composed of two segments. The basis develops an inner spine with spinules around the base; spinules also develop around the base of the

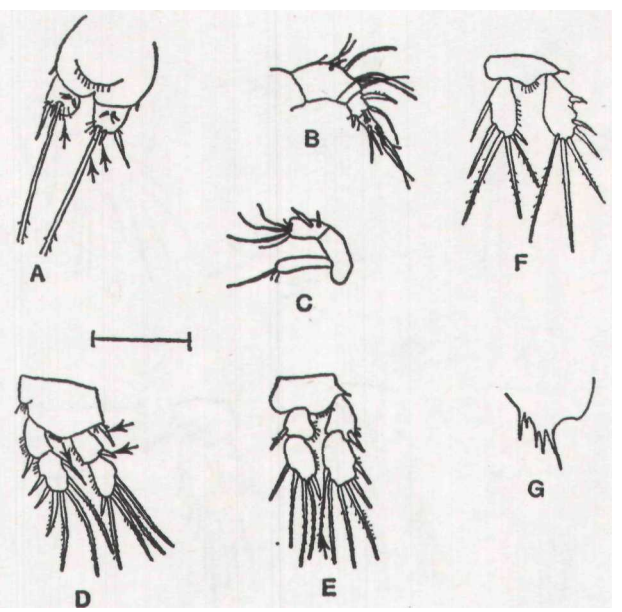

FIG. 3
Copepodite 2.
A, Caudal ramus; B, A1; C, A2; D, P1; E, P2; F, P3; G, P4.
Scale line **50µm.**

outer spine. Exopod and endopod each devlop an additional spinulose inner seta. *P2.* Both rami are composed of two segments. The exopod develops an additional spinulose inner seta while the endopod setation remains as in C1. *P3.* Both rami are composed of one segment. The basis bears one thin outer seta and the inner distal edge is spinulose. Exopod bears three naked outer spines and three longer spinulose apical setae. Endopod bears one naked spine and spinules on the outer edge, three spinulose apical setae and two naked inner setae. *P4.* This limb is present as a double lobe bearing three spines on the larger outer lobe and two on the inner lobe.

Copepodite 3 (Fig. 4, A-H)

The body is composed of seven segments, length 282 µm. *Antennule* is composed of six segments and has three additional setae, one on the

fifth and two on the fourth segments. The outer apical seta of each *caudal ramus* have now increased markedly in length and are about one quarter of the length of the inner seta, it is spinulose only on the outer edge. The two setae on the mid dorsal surface are also considerably larger than in C2. *Endopod* of the *antenna* develops a new spine midway along its length; exopod is now obviously made up of four segments. The setation has not changed markedly from C1 with the exception of the relative increase in size of the setae. *P1.* Endopod develops one new inner seta on the second segment. *P2.* Exopod develops one naked outer seta on the second segment. *P3.* Both rami are now composed of two segments. Short spinules develop on the outer edge of both exopod segments. *P4.* Both rami are composed of one segment. The basis has one outer spine and the internal distal edge bears spinules. Exopod has two naked outer spines and four apical spines. Endopod has three spinulose apical setae and an outer and inner seta, there is also a group of outer spinules below the outer seta. *P5.* This is composed of a small flap bearing three setae. The *anal segment* has two groups of short spines on the ventral surface.

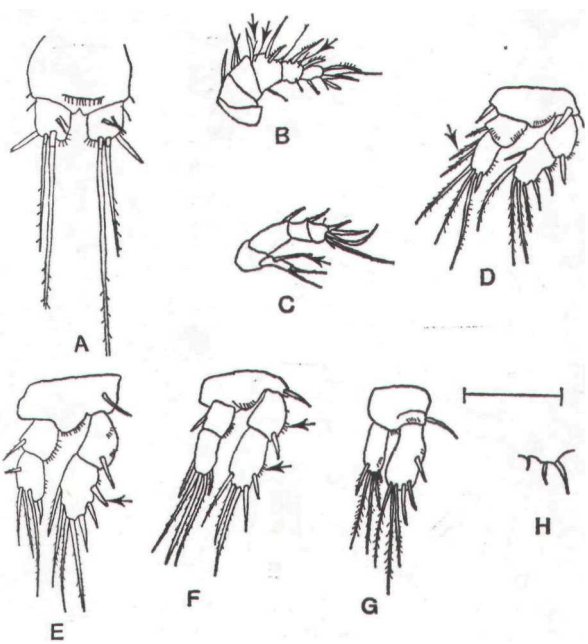

FIG. 4
Copepodite **3.**
A, Caudal ramus; **B, A1; C, A2; D, P1; E, P2; F, P3; G, P4; H, P5.**
Scale line **50 µm.**

Copepodite 4 (Fig. **5, A-L)**

The body is composed of eight segments, length 313µm. This is the first stage that the sex of the animal can be determined. *Antennule* of the male has a definite terminal claw which is not apparent on the female A1; there are also slight differences in setation. Antennules seven segmented. Each *caudal ramus* has an additional short inner spine and a new group of spinules on the inner dorsal surface. *P1.* No change from C3. *P2.* One spinulose inner seta develops on the first segment of the exopod and one spinulose inner seta develops on the second endopod segment. *P3.* Exopod has an additional naked outer spine and two spinulose inner setae. Endopod develops a new spinulose outer seta. The rami of the male P3 are slightly larger than those of the female. *P4.* Both rami composed of two segments. Exopod has an

additional naked outer spine and a spinulose inner seta. **The** outer edge of the endopod develops a group of setules. ***P5.*** **Limb has** now increased **in** size but the rami are not completely separated. **In** the **female** the exopodite portion **has** five setae while in the male there are **only** four. The inner portion **has** four **setae** in **the female** and three **in** the **male.** ***P6.*** Present only in the male **as small** lobe bearing two setae.

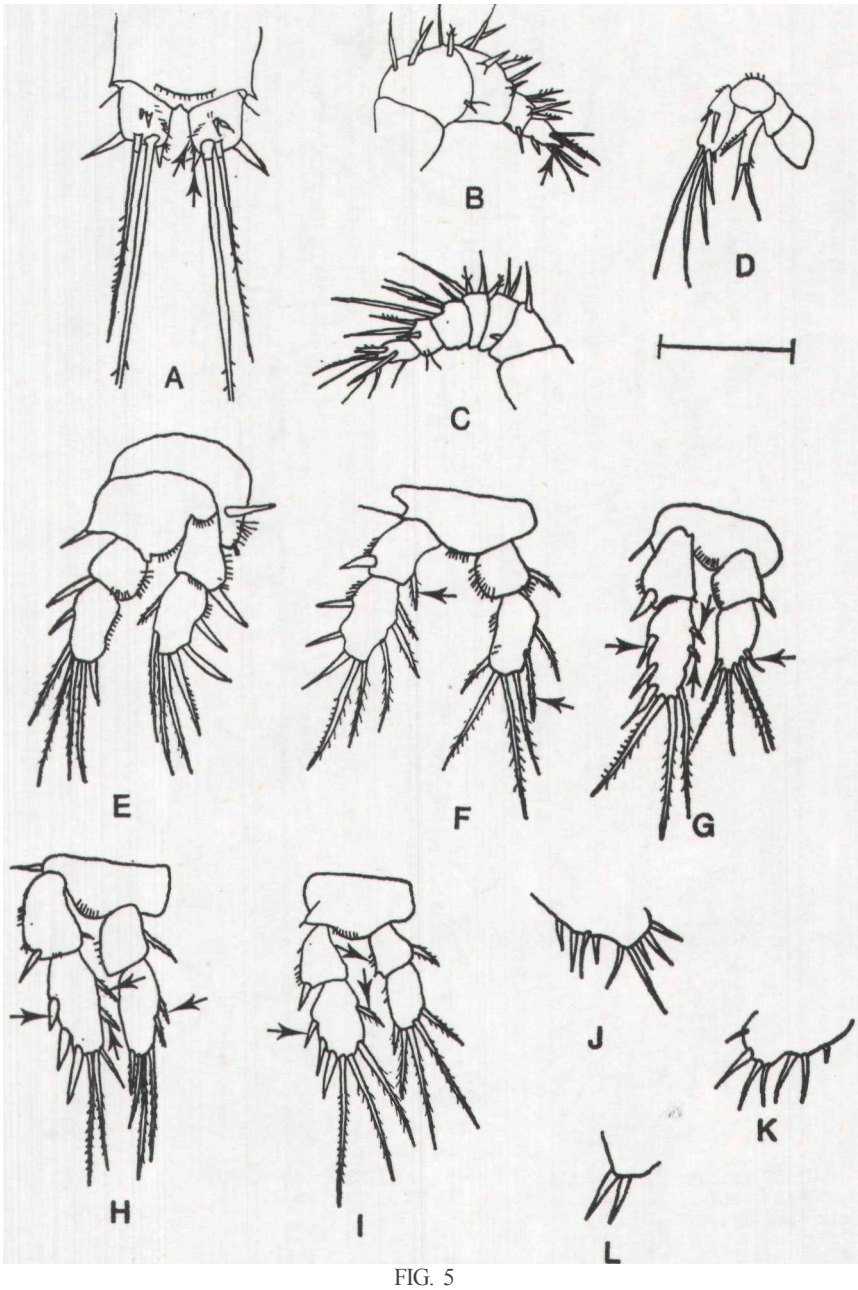

FIG. 5

Copepodite 4.

A, Caudal ramus; B, Al♂; C, Al♀; D, A2; E, P1; F, P2; G, P3♀; H, P3♂; I, P4; J, P5♀; K, P5♂; L, P6♂.
Scale line 50μm.

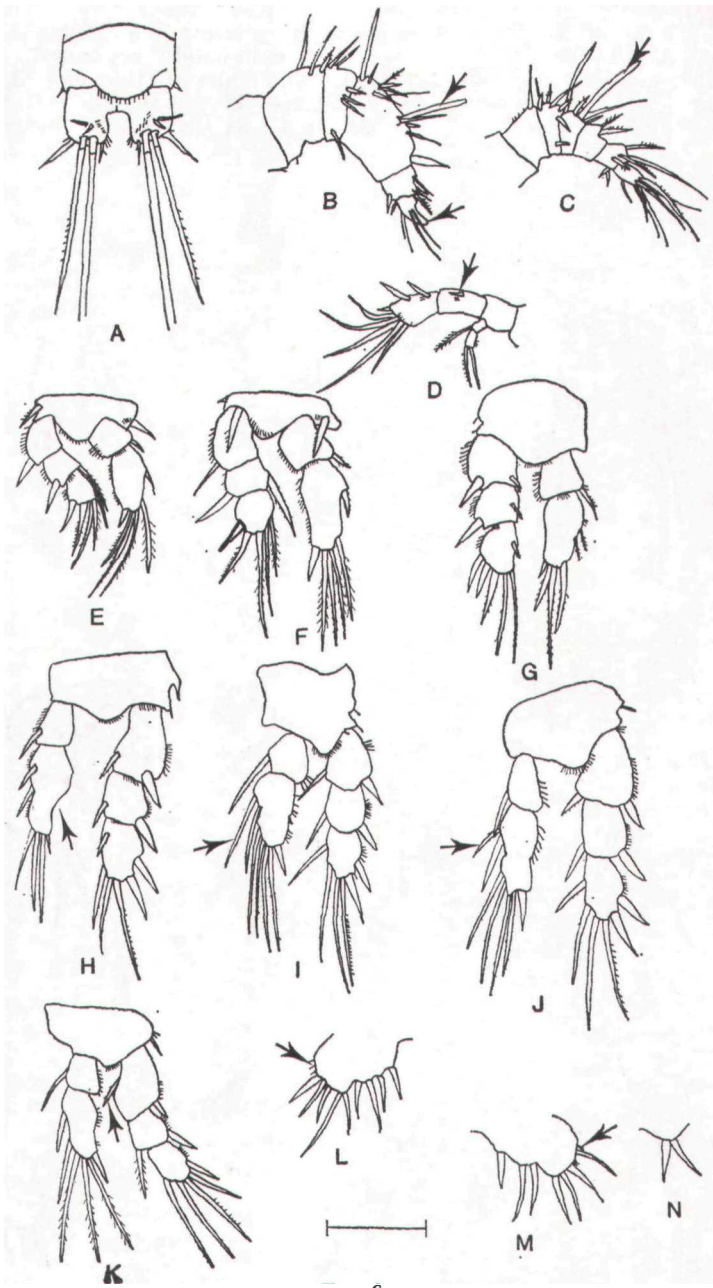

FIG. 6
Copepodite 5.
A, Caudal ramus: **B, A1♂; C, A1♀; D, A2; E, P1♀; F, P1♂; G, P2♀; H, P2♂; I, P3♀; J, P3♂; K, P4; L, P5♀; M, P5♂; N, P6♀.**
Scale line **50µm.**

Copepodite 5 (Fig. 6, A-N)

The body is composed of nine segments, 346 µm length. *Antennules* continue to show a marked sexual dimorphism with the terminal segment of the male being distinctly unguiform and the rest of the antennule

becoming swollen. One aesthete on the broad fourth segment. The female antennule is much thinner and is composed of seven segments which taper towards the tip; there is one aesthete on the fourth segment. The *antenna* carries one new short outer spine on the third segment of the exopod. *P1.* Endopod two-segmented, exopod three-segmented. Male and female the same except for size, both male rami being longer and more robust. *P2.* Endopod two-segmented, exopod three-segmented. Male differs from female in having larger more robust rami and in the shape of the second segment of the endopod which is longer and has an indentation on the outer edge. *P3.* Endopod two-segmented, exopod three-segmented. New spinulose inner seta on the second endopod segment. The exopod is longer than the female P2 and both rami of the male P3 are longer and stouter that those of the female. *P4.* Endopod two-segmented, exopod three-segmented with a new spinulose inner seta on the exopod first segment. The setation is now the same as the adult and there is no difference between male and female. *P5.* The setation is the same as in C4 except for new spinules around the base of the two outer setae in both sexes. *P6.* Present only in the male and not changed from C4.

Adult

The adults have already been adequately described by Sars (1910), Gurney (1932) and Lang (1948).

DISCUSSION

The post-embryonic development of *T. discipes* has many features in common with other harpacticoids.

There are six naupliar stages as in other species studied by a number of authors including: Johnson and Olson, 1948; Fahrenbach, 1962; Haq, 1965; Rao, 1967; Ito, 1970; Carter and Bradford, 1972; and Rosenfield and Coul, 1974. Carter and Bradford, 1972 suggest that where species with less than six naupliar stages have been described (eg. Gurney, 1932; Fraser, 1936 and Castel, 1976), there is a risk that the fourth or fifth nauplius has been overlooked, especially if it has not been possible to follow the development of individual nauplii.

The nauplii of *T. discipes* develop in a similar manner to those of *Euterpina acutifrons* (Dana), the only other member of the Tachididae in which development has been studied (Haq, 1965). However, the development of the ventral hind body spines is different, those in *T. discipes* not appearing until the third nauplius and then only two groups being present until the fifth nauplius. Haq identified both P1 and P2 in the sixth nauplius of *E. acutifrons,* but in *T. discipes* only P1 is present. The antenna exopod of *T. discipes* develops two additional spines, one in nauplius three and the other in nauplius four; this contrasts with *E. acutifrons* where the setation remains unchanged except for the addition of one small seta on the distal end of the last segment.

More important differences occur between the two species in the

development of the mouth parts. The masticatory process of the antenna (the coxopodite masticatory process) and associated spines are lost in the sixth nauplius of *E. acutifrons* as are the vertical and posterior ridges of stiff hairs in the oral region. Haq suggests that this is due to the pelagic life of this species and that these specialised feeding structures are more important for the benthic existence of species such as *T. discipes.* In *T. discipes,* an additional small spine develops on the mandible basipodite at nauplius 6 and there is no reduction of the endopod or evidence of the development of the gnathobase of the mandible as found in this stage of *E. acutifrons,* which seems to support Haq's theory.

The copepodid stages of *T. discipes* resemble miniature adults, one new abdominal segment being added at each moult. In copepodite I, the first two limbs are present, the rami being composed of one segment, and the third limb is present as a small lobe bearing setae. Successive moults to copepodite 4 are accompanied by the development of one new limb and limbs 1 to 4 all possess two segmented rami at this stage. The exopods of these limbs become three-segmented at copepodite 5 but the endopods only become three-segmented in the adult. This sequence of limb development is followed in *E. acutifrons* and the Laophontidae but the two species of *Platychelipus* studied by Barnett (1966) have greatly reduced endopods because of their adaptation to crawling locomotion. However, in *Tigriopus fulvus* (Fraser, 1936), *Tisbe furcata* (Johnson and Olson, 1948), *Sacodiscus ovalis* (Humes, 1960), *Harpacticus uniremus* (Ito, 1971), *Paramphiascella fulvofasciata* (Rosenfield and Coull, 1974), and *Harpacticus littoralis* (Castel, 1976), limb development follows the same pattern as calanoid copepods, both rami of limbs 1-4 becoming three-segmented in the fifth copepodite.

The sexes can be distinguished in *T. discipes* at copepodite 4, as in most other harpacticoids. There is a difference between sexes in limb size and setation of P5, and P6 is present only in the male; however, the most obvious dimorphism is in the structure of the antennule which, in the male, becomes powerful and broadened, bearing a terminal claw. The development of the antennule progresses by gaining an additional segment at each stage between C1 and C4 when it becomes seven-segmented, as in the adult. This is the same sequence as found in *E. acutifrons* but other harpacticoids have antennules composed of a greater number of segments and a different developmental sequence, e.g. Rosenfield and Coull, 1974; Castel, 1976.

Although the development of *T. discipes* is then similar to other harpacticoids, the family Tachididae does appear to have some unusual features, principally in the ventral hind body spines of the nauplius, in the sequence of development of the copepodite antennule and in the limb rami development. Comparison of the development of *E. acutifrons* and *T. discipes* indicates that the development of the feeding appendages differs between the two species. *T. discipes* retains the strong coxopodite masticatory process in the late nauplius stages and uses this in the selective grazing type of feeding it employs in the benthos.

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Summary

The complete post-embryonic development of the harpacticoid copepod *Tachidius discipes* Giesbrecht is described. There are six naupliar and six copepodite stages, the sixth copepodite being the adult. The development of the body and appendages is studied and compared with other harpacticoids.

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