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Postembryonic development of *Tisbe gracilis* (T. Scott) (Copepoda, Harpacticoida)

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All six naupliar and five copepodite stages of *Tisbe gracilis* (T. Scott, 1895) are described. A key for the identification of the nauplius stages is given. The oral appendages of all copepodite stages are described. Sexual dimorphism is visible from the copepodite IV stage on.

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Introduction

There are few harpacticoid genera that have been investigated as thoroughly as the genus *Tisbe*. In particular, life cycle studies have become numerous (review in Bergmans 1981). Despite this, the stages of the post-embryonic development of only a few species are known in any detail. Such descriptions are needed for many types of research that require clear distinction of the naupliar and copepodite stages. Studies of post-embryonic character differentiation are also apt to throw some light on phylogenetic relationships (Nicholls 1935; Itô 1984). Conclusions in this respect, however, can only be drawn when the developmental stages of a sufficient number of species are well enough known to allow meaningful comparison.

A case in point is provided by the differences reported by Lopez (1980) between his own *Tisbe cucumariae* and '*T. gracilis*' as described by Battaglia (1957). In fact the latter paper also refers to *T. cucumariae* (*fide* Volkmann 1979) and the discrepancies may for the most part be due to the incompleteness of the earlier description.

Tisbe gracilis was originally described by T. Scott (1895). Since then several authors have mentioned this species, some with misidentifications (see Volkmann 1979). The species, which seems to prefer low temperatures (Volkmann 1979), is regularly found associated with living and dead molluscs and ascidians. Like other species of the *gracilis* group, it appears to be a scavenger (e.g. Lang 1948).

The present study is the first description of the external morphology of all postembryonic stages of *T. gracilis*.

Material and methods

Tisbe gracilis was collected in 1976 and 1977 in the sluice dock of Ostend harbour (Bergmans 1979). In this habitat the species occurs irregularly throughout the year, both on *Ulva* thalli and artificial substrates (Bergmans 1983). A stock culture was maintained in two 2.5 l bowls, each receiving 75 ml of *Dunaliella* suspension twice a week. No other copepods were present in the culture, but no attempt was made to eradicate small contaminants (mainly *Euplotes, Oxyrrhis* and Rotifera) or to prevent the development of macroalgae. Temperature was 18°C, salinity 29–33 ppm and the rate of water renewal 1 l per 50 days.

Specimens were fixed in 5% buffered formaldehyde, dehydrated in 70% ethanol and suspended in W 15 (embedding medium of C. Zeiss Company). Microscopical preparations were achieved by a method similar to that of Sieg (1973). Nauplii are shown from the ventral, male copepodites from the dorsal and lateral side, female copepodites only from the dorsal side. Several specimens of each copepodite stage were used for description of the mouth parts.

Since in this study no asymmetry of segmentation (cf. Lopez 1980) or setation was ever observed between two appendages of the same pair, only one (of each type of appendage) has been pictured.

Body lengths were measured from the anterior to the posterior end of the naupliar body and from the base of the rostrum to the posterior edge of the caudal rami in copepodites. Body width is given as the broadest part of the copepodite cephalosome. Only the specimens described were measured, except for adults, where length and width of 10 specimens of each sex were measured and standard deviations of the mean calculated.

Descriptions

Naupliar stages of *Tisbe gracilis* (Figs. 1–3)

Throughout all 6 naupliar stages the larvae are flat and unpigmented but for the red eye.

Nauplius I (Fig. 2A)

Body form circular in outline. Body length 73 μm. Labrum a circular flap, crest without ornamentation. 3 appendages present: A1, A2, Md.

First antenna 3-segmented. First segment naked, 2nd with 1 large and 2 small setae, 3rd with an anterior seta and terminal aesthetasc and seta with common base.

Second antenna with coxa, basis, 4-segmented exopod and 1-segmented endopod. Coxa provided with setule row and naupliar process (short pro-gnathobasal projection) and 1 seta on its base. Basis proximally with 1 spine and 3 setae. First, 2nd and 3rd exopod segments with 1

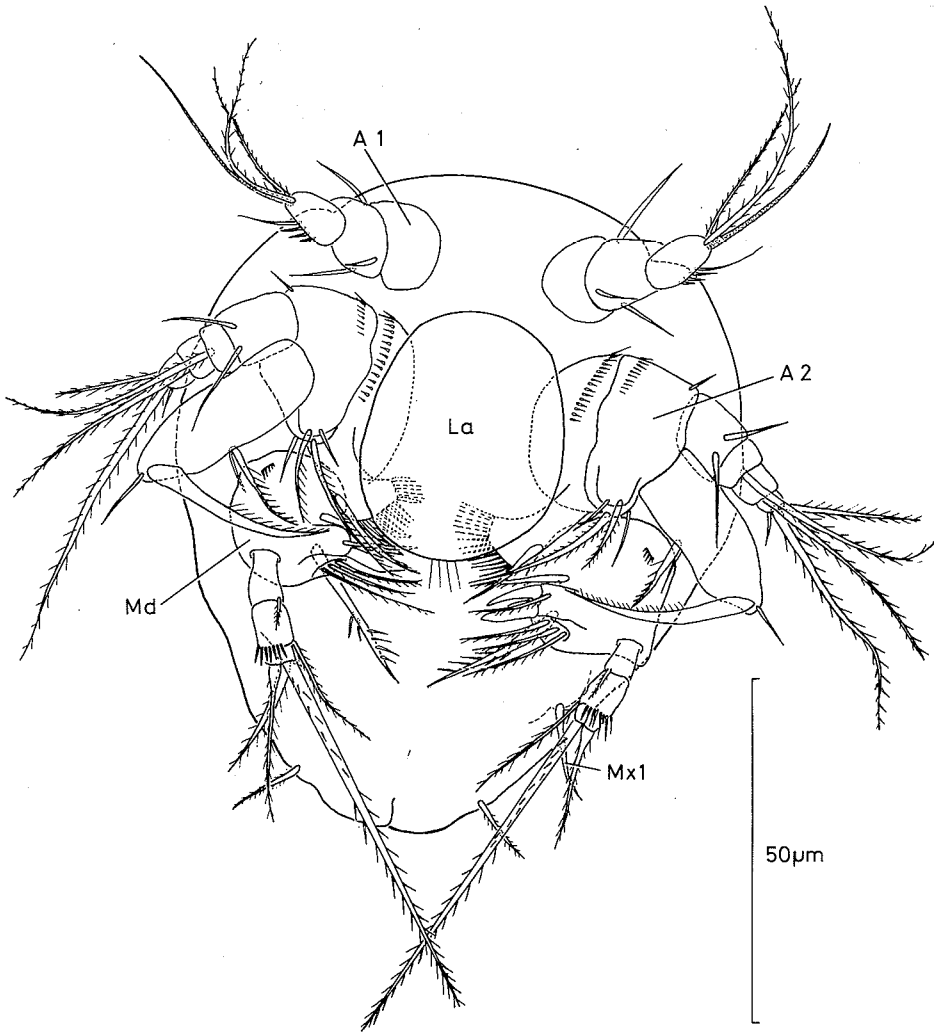

Fig. 1. Tisbe gracilis. Nauplius II, ventral view (*A1* first antenna; *A2* second antenna; *La* labrum; *Md* mandible; *Mx1* first maxilla).

terminal seta, 4th segment with 1 long and 2 shorter setae. Endopod with 2 small medial setae half-way along length, terminally with a claw and a small seta at base of claw.

Mandible with protopod (coxa–basis boundary not visible), 3-segmented exopod and 1-segmented endopod. Protopod with 1 spine. Endopod of one article bearing a sub-terminal setule row and 2 strong terminal spines (anterior one with hairs on labral side) and a dorso-lateral hillock with 3 setae. First and 2nd segment of exopod with 1 terminal seta each, 3rd segment with 1 long plumose seta and 1 shorter seta.

Single seta on both sides of anal area.

Nauplius II (Figs. 1, 2B)

Body length 92 µm. Differing from nauplius I as follows.

Body form ovoid (elongation begins and finds its climax in N VI).

First antenna with 3rd segment with a setule row on inner side.

Second antenna with coxa with 2 setae, 1 arising on tip of naupliar process; exopod with 2 setae on 1st segment.

Mandible with setule field on lateral side; endopod with 1 surface seta instead of sub-terminal setule row, dorso-lateral hillock with 4 setae; exopod with terminal setule row on 2nd segment.

First maxilla appears as a strong plumose seta posterior to mandible.

Nauplius III (Fig. 2C)

Body length 111 µm. Differing from nauplius II as follows.

First antenna with 3 setae and a setule row caudo-laterally on 2nd segment and with 6 'setae', including one aesthetasc (6 setae/aesthetasc), on 3rd segment.

Second antenna with coxa with 3 setae; endopod with 3 sub-terminal setules; exopod with 2 long and 1 smaller setae on its 1st segment.

Mandible with endopod with another sub-terminal seta and a row of fine hairs at ventral side, dorso-lateral hillock with 5 setae; coxa–basis boundary of mandible clearly visible. The aforementioned seta of protopod belongs to basis.

Anal area with 1 long and 1 shorter seta.

Nauplius IV (Fig. 2D)

Body length 132 µm. Differing from nauplius III as follows.

First antenna with 7 setae/aesthetasc on 3rd segment.

Second antenna with basis with a lateral setule row proximally; endopod with 3 setae medially.

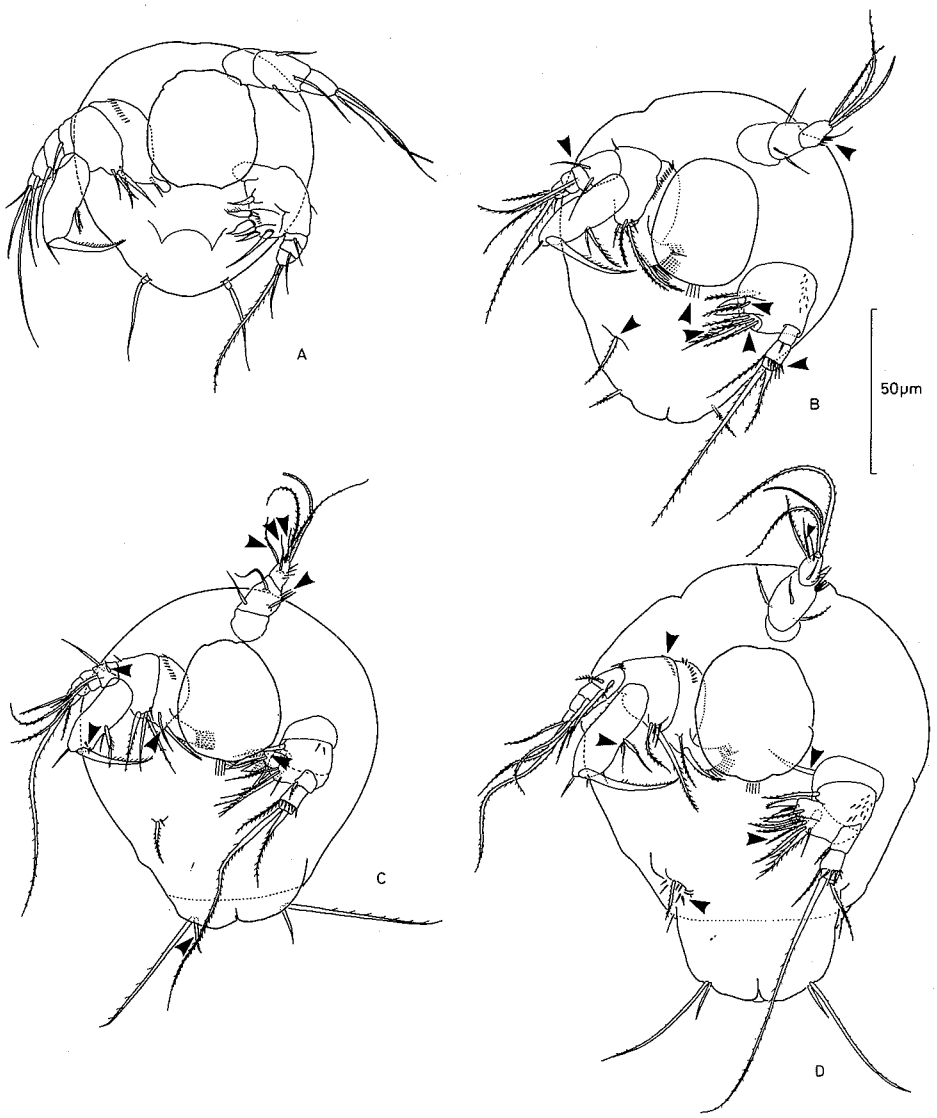

Fig. 2. Tisbe gracilis. Naupliar stages I–IV.—*A.* N I.—*B.* N II.—*C.* N III.—*D.* N IV. Only one appendage of each segment is shown. Arrows indicate differences between each instar and the preceding one.

Mandible with dorso-lateral hillock with 6 setae; mandibular coxa with 1 seta.

First maxilla bearing 1 seta and several setules.

Nauplius V (Fig. 3A)

Body length 146 μm. Differing from nauplius IV as follows.

First antenna with a lateral anterior row of hairs on 2nd segment and 8 setae/aesthetasc on terminal segment.

Second antenna with endopod with 4 dorso-lateral setules proximal to medial setae and 4 setules terminally; exopod with 4 setae on terminal segment.

Mandible with basis with 4 setules proximal to endopod.

First maxilla with 1 segment bearing 3 setae and 2 setule rows.

Anal area with 1 long, 2 medium and 1 small setae on each side.

Nauplius VI (Fig. 3B)

Body length 207 μm. Differing from nauplius V as follows.

First antenna with 1st segment with a few hairs; terminal segment with 10 setae/aesthetasc.

First maxilla with 4 setae.

Second maxilla appears as a limb bud with 5–7 setules.

Innermost caudal seta of anal area significantly elongated. Additional dorsal seta brings number of caudal setae to 5.

Key to the nauplius stages of *Tisbe gracilis*

1. Almost circular in shape; labrum naked; terminal segment of first antenna with 3 setae/aesthetasc only . . . . . N I
   Not so; first maxilla visible as 1 seta at least 2
2. 1 caudal seta on each side . . . . . N II
   More than 1 caudal seta on each side 3
3. Terminal segment of first antenna with 6 setae/aesthetasc; first maxilla present as 1 seta and 1 setule; coxa of mandible unarmed . . . . . N III
   Not so 4
4. First maxilla with 1 seta and several setules . . . . . N IV
   More than 2 caudal setae on each side 5
5. 4 caudal setae present; segment of first maxilla with 3 setae . . . . . N V
   Anal area with 4 terminal plus 1 dorsocaudal seta; segment of first maxilla with 4 setae; second maxilla visible as 5–7 setules . . . . . N VI

Fig. 3. Tisbe gracilis. Naupliar stages V–VI.—*A.* N V.—*B.* N VI. Only one appendage of each segment is shown. Arrows indicate differences between each instar and the preceding one.

Copepodite stages of *Tisbe gracilis*

Throughout all 5 copepodite stages the copepodids are unpigmented, except for the red eye and occasional orange droplets in the prosome. Their elongated, slightly dorso-ventrally flattened body is composed of a cephalothorax and at least 4 free trunk segments plus caudal rami. Anal operculum without dentation.

Copepodid I (Fig. 4A)

Body length 322 µm, width 148 µm. Body composed of cephalic shield, 4 trunk segments and caudal rami. Appendages include first and second antennae, mandible, maxillule, maxilla, maxilliped and pereiopods 1–3. Caudal rami with 5 setae each (Fig. 12A). The innermost long seta branches out into 2 terminal plumose setae, outermost 0.5× as long as innermost.

First antenna (Fig. 6A) consists of 4 segments. First segment with 3 setae, 2nd with 3 setae/aesthetasc. One of these setae and the aesthetasc with a common base, as always in subsequent stages. Third segment with 5 setae; 4th with 8 setae/aesthetasc; 1 terminal seta and the aesthetasc with a common base.

Second antenna (Fig. 7A) with basis, 2-segmented endopod and 4-segmented exopod. Basis with inner terminal seta, 1st segment endopod naked, 2nd with 10 setae. Exopod with 1 long and 1 medium seta on 1st, 1 on 2nd and 3rd, and 3 setae on 4th segment, one of which is very tiny. Distal segment also with a latero-terminal setule row. Gone are the gnathobase and the endopodal spines of the nauplius. Endopod has become much larger,

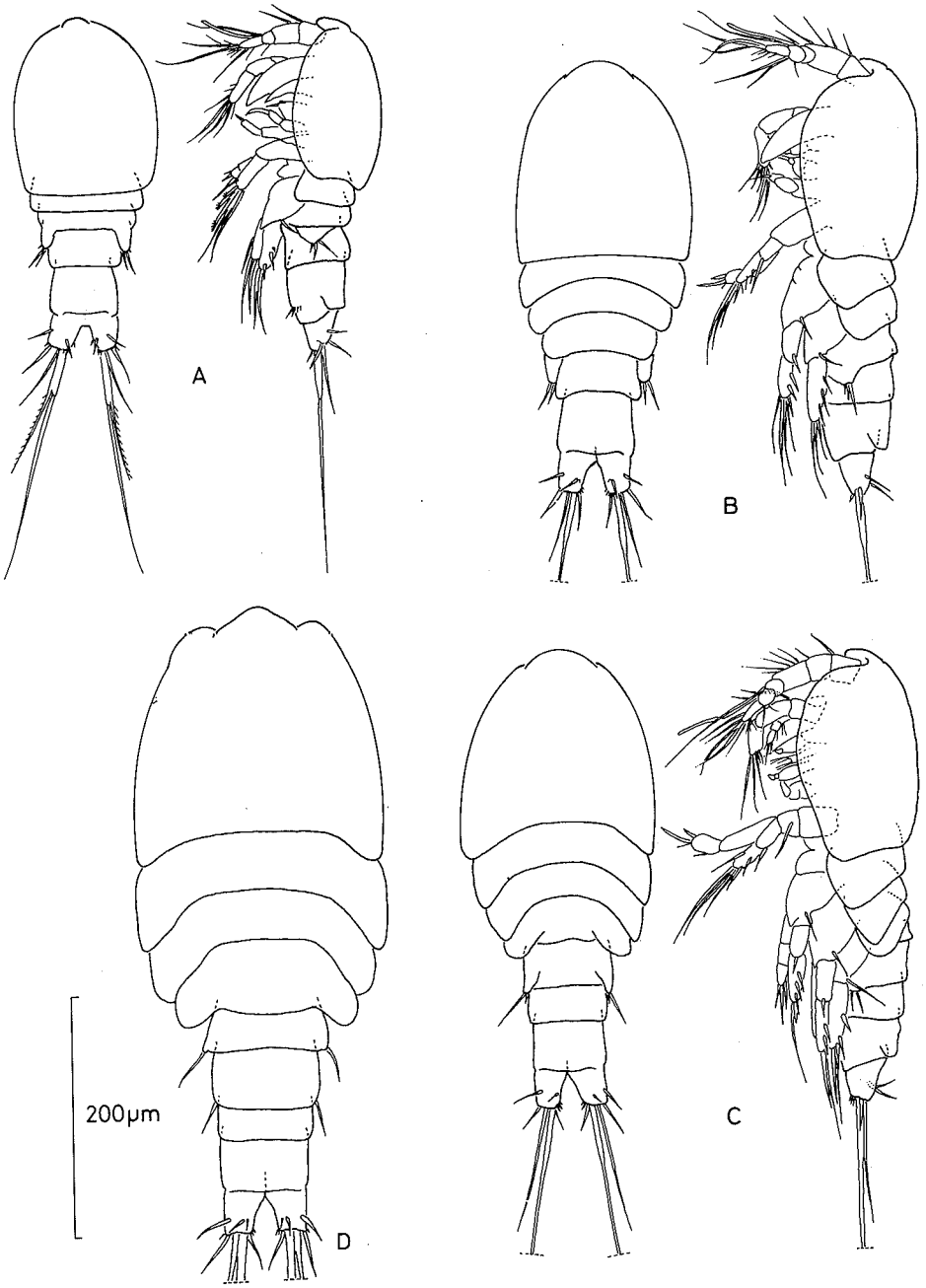

Fig. 4. Tisbe gracilis. Copepodite stages I–IV, dorsal and left-lateral views.—*A.* C I.—*B.* C II.—*C.* C III.—*D.* Female C IV.

its general structure resembling that of adult except for size and spinule setation.

Labrum (Fig. 8A) triangular and ornamented on its tip. It does not undergo marked metamorphic changes in the copepodite phase except for size.

Mandible (Fig. 8B) with *corpus mandibulae* with cutting edge, a spinule row at base of edge, 1 ventro-terminal plumose seta and a distinctly cuticularized medio-internal protrusion. Palp with 1 ventral seta. Endopod 1-segmented with 3 medial and 4 terminal setae; exopod with 3 terminal setae and 1 subterminal setule row.

First maxilla (Fig. 8G) with details not observed since the structure with its many setae and spines is difficult to interpret correctly (cf. Volkmann 1979).

Second maxilla (Fig. 8L) with syncoxa well developed with setules on outer margin and 1 endite bearing 1 seta. Basis small, bearing 1 spine on its strong claw. Claw with inner lateral row of short setules. Exo- and endopod absent.

Maxilliped (Fig. 9A) with coxa and basis well developed (not figured). Endopod 2-segmented; 1st segment with a subterminal dorsal setule row; 2nd segment with 1 surface setule, 2 sub-terminal setules and an apical claw with inner row of short setules.

P1 (Fig. 10) with coxa, basis and 2 rami, each consisting of 1 segment.

P2 (Fig. 10) with coxa, basis and 2 rami, each of 1 segment.

P3 (Fig. 10) appears as a limb bud with 3 setae.

Copepodid II (Fig. 4B)

Body length 414 µm, width 174 µm. Differing from C I as follows.

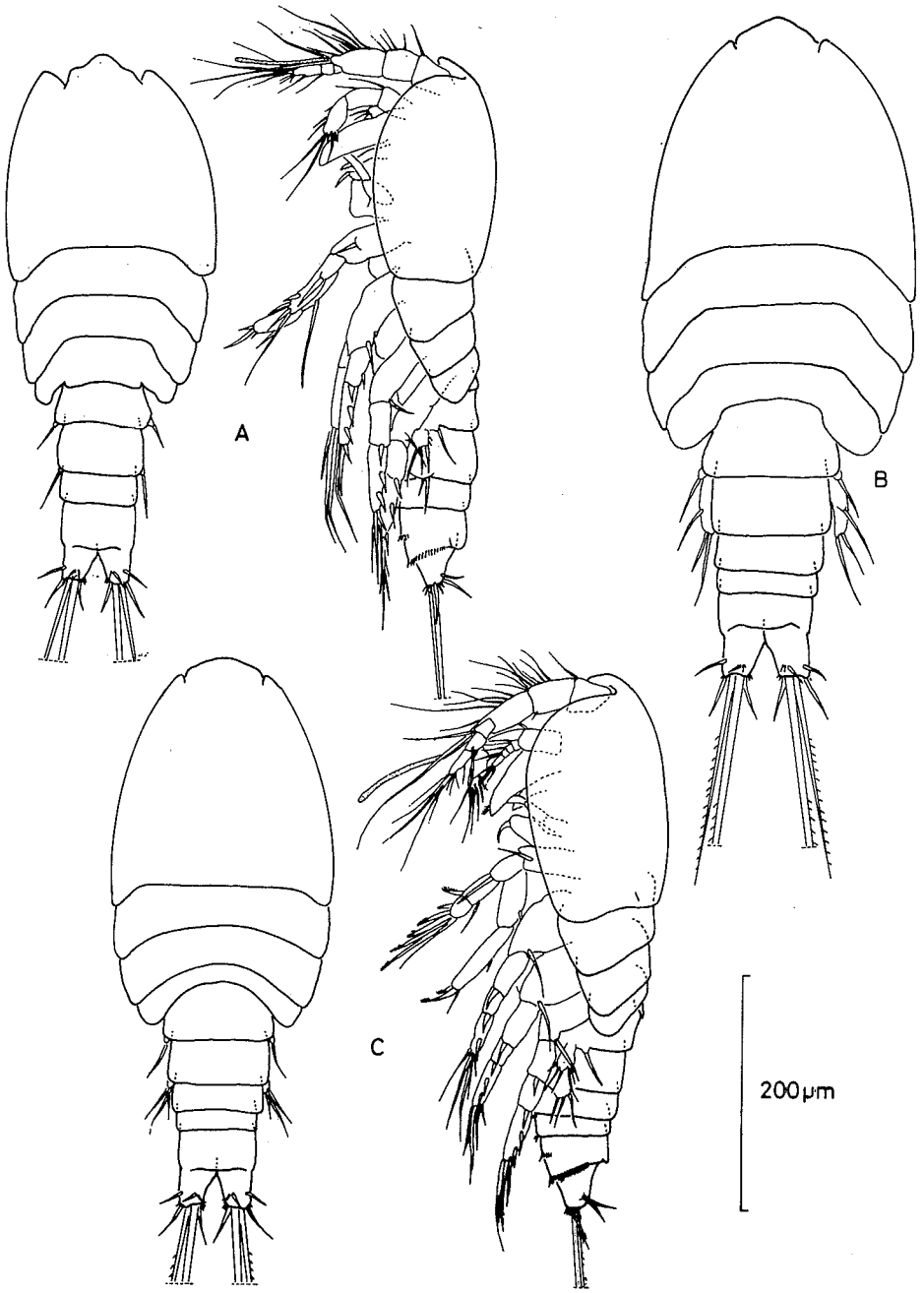

Fig. 5. Tisbe gracilis. Copepodite stages IV–V.—*A*. Male C IV.—*B*. Female C V.—*C*. Male C V.

Table I. Tisbe gracilis. *Setation and segmentation of pereiopods* (P) *of copepodite stages* (C). *Formulae are according to Lang (1948). Setation of basis is given in parentheses* (End *endopod*; Exp *exopod*; Lb *limb bud*; F *female*; M *male*; — *not present at this developmental stage*)

	P1		P2		P3		P4		P5		P6	
	(Basis) End	Exp	(Basis) End	Exp	(Basis) End	Exp	(Basis) End	Exp	(Basend.) End	Exp	End	Exp
CI	(1)		(1)		(—)		(—)		(—)			
	4	7	6	6	3 Lb		—		—		—	
CII	(2)		(1)		(1)		(—)		(—)			
	1.030	0.151	1,221	0.222	6	7	3 Lb		—		—	
CIII	(2)		(1)		(1)		(1)		(—)			
	1.130	0.151	1,321	1.323	1.321	7	6	7	2 Lb		—	
CIV	(2)		(1)		(1)		(1)		(3) M	(3) F		
	1.130	0.151	1.421	1.323	1.421	1.423	1.321	0.423	4 M	5 F	2 M	1 F
CV	(2)		(1)		(1)		(1)		(3) M	(3) F		
	1.1.030	0.1.051	1.2.221	1.1.223	1.2.321	1.1.323	1.2.221	1.1.323	5 M	5 F	3 MLb	2 FLb

Fig. 6. Tisbe gracilis. Development of copepodite first antenna.—*A*. C I.—*B*. C II.—*C*. C III.—*D*. Male C IV.—*E*. Male C V.—*E'*. Female C V.

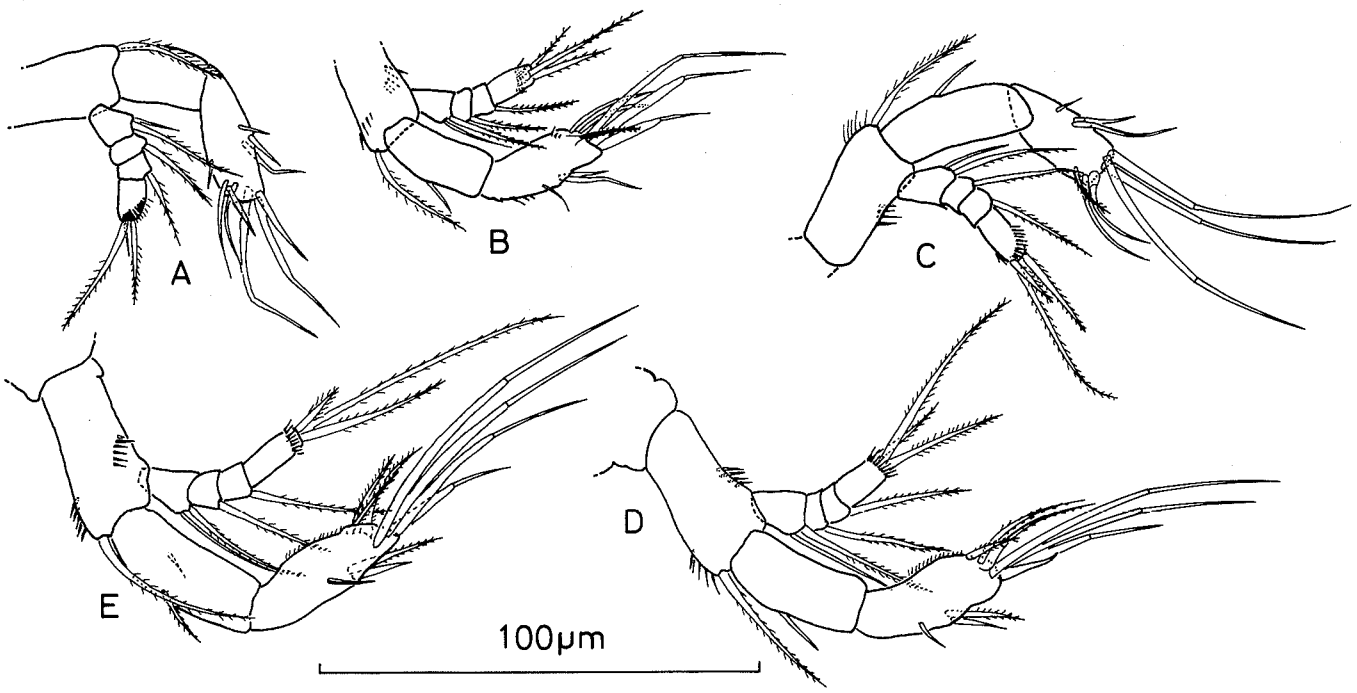

Fig. 7. Tisbe gracilis. Development of copepodite second antenna.—*A*. C I.—*B*. C II.—*C*. C III.—*D*. Male C IV.—*E*. Male C V.

Five free trunk segments. P4 present. Caudal rami with 6 setae (Fig. 12B), the 2 separate terminal setae representing the long furcal setae of adults therefore already present, outermost 0.3× as long as innermost. Caudal telsonic margin with spinule row ventrally.

First antenna (Fig. 6B) with 6 segments. First with 1 outer seta and setule row, 2nd with 6 setae/aesthetasc, 3rd with 1, 4th with 4, 5th with 2 setae and 6th with 8 setae/aesthetasc.

Second antenna (Fig. 7B) with 2 setule rows on basis and 1 seta on first segment of endopod.

Mandible (Fig. 8C) with 2 setule rows on exopod.

First maxilla as in Fig. 8H.

Second maxilla as in Fig. 8M.

Maxilliped (Fig. 9B) with an inner setule row and an additional dorsal, proximal setule row.

P1 and P2 (Fig. 10) with rami of 2 segments (for setation see Table I).

P3 (Fig. 10) with rami of 1 segment.

P4 (Fig. 11) appears as a limb bud with 3 setae.

Copepodid III (Fig. 4C)

Body length 432 µm, width 198 µm. Differing from C II as follows.

Six free trunk segments. P5 present.

First antenna (Fig. 6C) with 2nd segment with 8 setae/aesthetasc. Fourth segment with 5 setae, 5th with 1 seta.

Mandible (Fig. 8D) with endopod with several terminal setules. Exopod with 3 setule rows. Palp with some setules on ventral side forming the anlage of the setule row in subsequent stages.

First maxilla as in Fig. 8I.

Maxilliped (Fig. 9C) with a long sub-terminal seta on 2nd segment of endopod.

P1–P3 (Fig. 10) with rami of 2 segments.

P4 (Fig. 11) with rami of 1 segment.

P5 (Fig. 11) appears as a limb bud with 2 setae.

Copepodid IV (Figs. 4D, 5A)

Female body length 621 µm, width 266 µm. Male body length 523 µm, width 225 µm. Sexual dimorphism visible by size, maxilliped and morphology of P5 and P6 only. C IV differing from C III as follows.

Seven free trunk segments.

First antenna (Fig. 6D) with 7 segments. Second segment with 7 setae, 3rd segment with 10 setae/aesthetasc, 4th with 1, 5th with 5 and 6th with 2 setae.

Mandible (Fig. 8E) with *corpus mandibulae* with 1 surface setule row in the middle. Endopod with 6 terminal setae.

First maxilla as in Fig. 8J.

Maxilliped (Fig. 9D) becomes sexually dimorphic; endopod segment I somewhat shorter and broader in male, than in female.

P1–P4 (Figs. 10, 11) with rami of 2 segments.

P5 (Fig. 11) with exopod of female longer than that of male with 3 long and 1 small terminal setae and 1 seta in middle of outer margin of exopod. P5 exopod of male with 3 long and 1 small terminal setae only and some setules. Female P6 with 1 long seta and setule row; male P6 with 2 setae, innermost half as long as outermost.

Females are larger than males.

Copepodid V (Fig. 5B, C)

Female body length 709 µm, width 296 µm. Male body length 619 µm, width 245 µm. Sexual dimorphism visible by size and morphology of first antenna, maxilliped, P2 endopod, P5 and P6. C V differing from C IV as follows.

Eight free trunk segments.

First antenna (Fig. 6E, E′) consists of 8 segments. Second segment of male with 13, that of female with 14 setae. Third segment of female with 9 setae, that of male bearing 16 setae/aesthetasc. Fourth segment of female with 5 setae/aesthetasc. Male 4th segment bearing 2 setae.

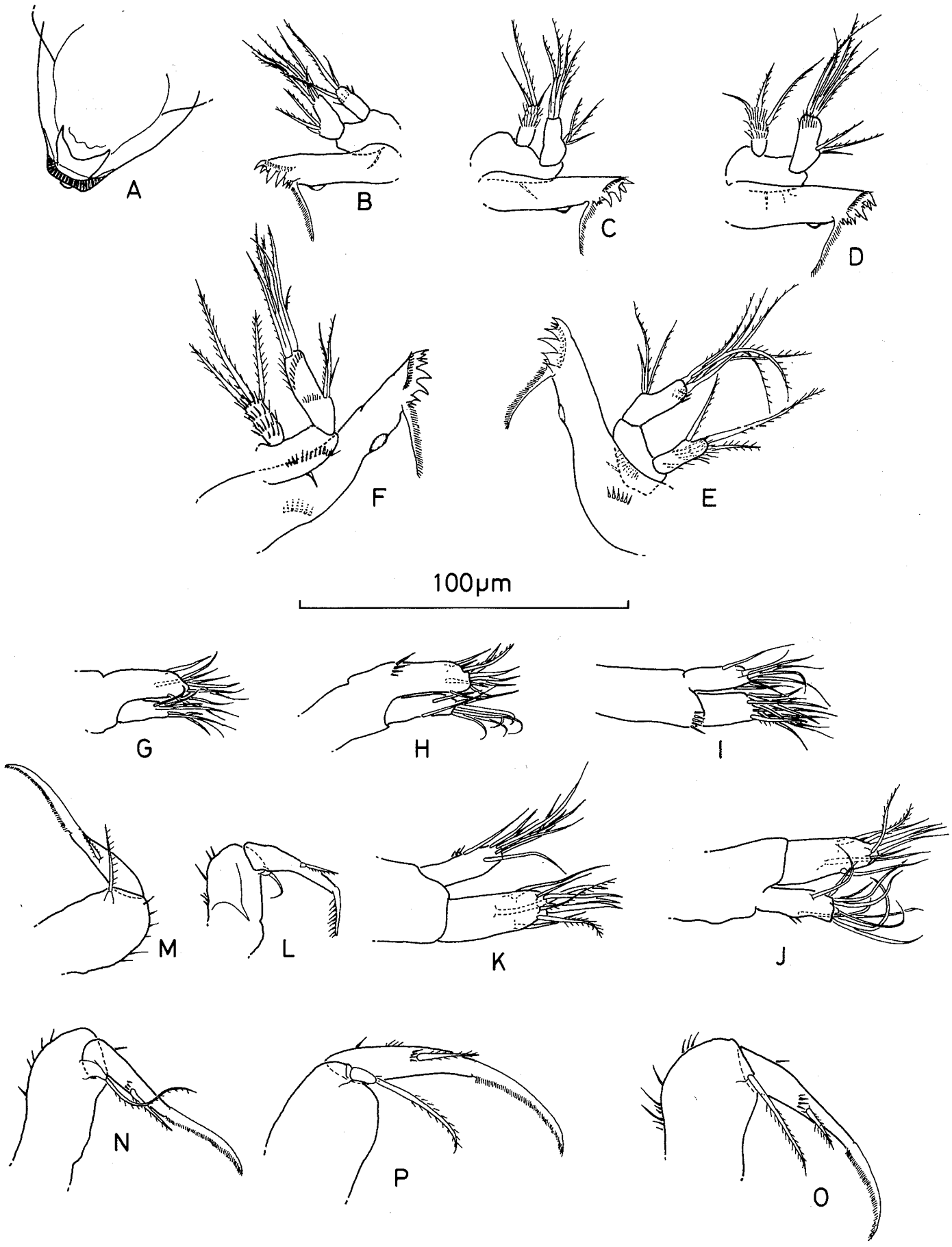

Fig. 8. Tisbe gracilis. Development of copepodite oral appendages.—*A*. Labrum of C I.—*B*. Mandible of C I.—*C*. Md of C II.—*D*. Md of C III.—*E*. Md of C IV.—*F*. Md of C V.—*G*. First maxilla of C I.—*H*. Mx1 of C II.—*I*. Mx1 of C III.—*J*. Mx1 of C IV.—*K*. Mx1 of C V.—*L*. Second maxilla of C I.—*M*. Mx2 of C II.—II.—*N*. Mx2 of C III.—*O*. Mx2 of C IV.—*P*. Mx2 of C V.

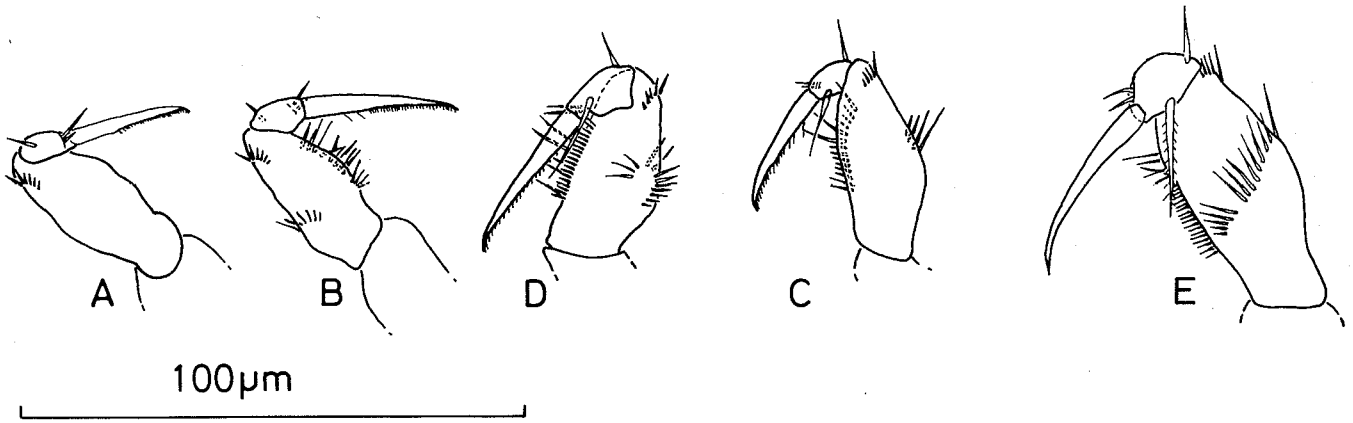

Fig. 9. Tisbe gracilis. Development of copepodite maxilliped.—*A.* C I.—*B.* C II.—*C.* C III.—*D.* Male C IV.—*E.* Male C V.

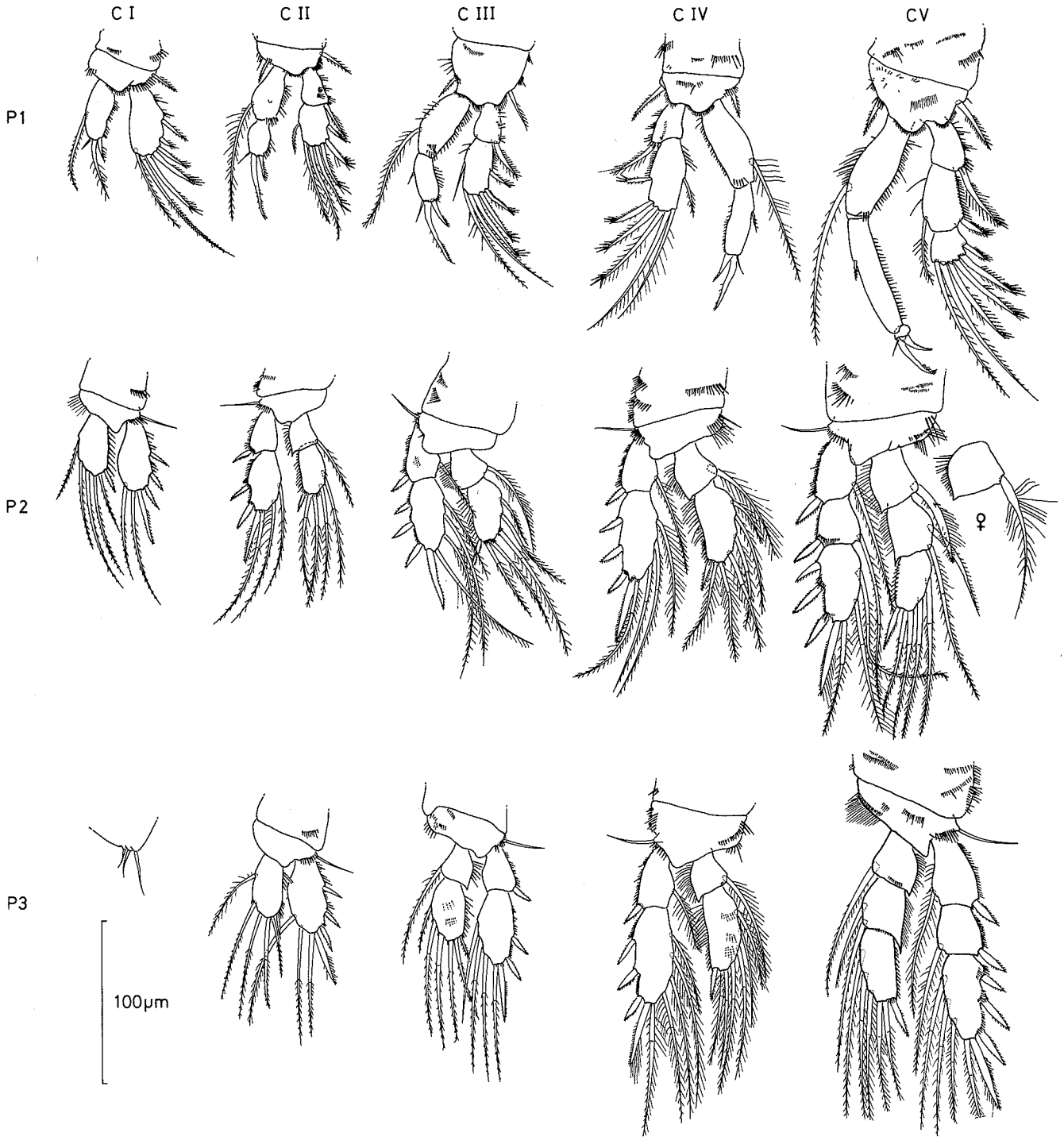

Fig. 10. Tisbe gracilis. Pereiopod 1–3 development of male copepodite stages. Each column illustrates appendages of one copepodite stage. Each row illustrates development of one pereiopod.

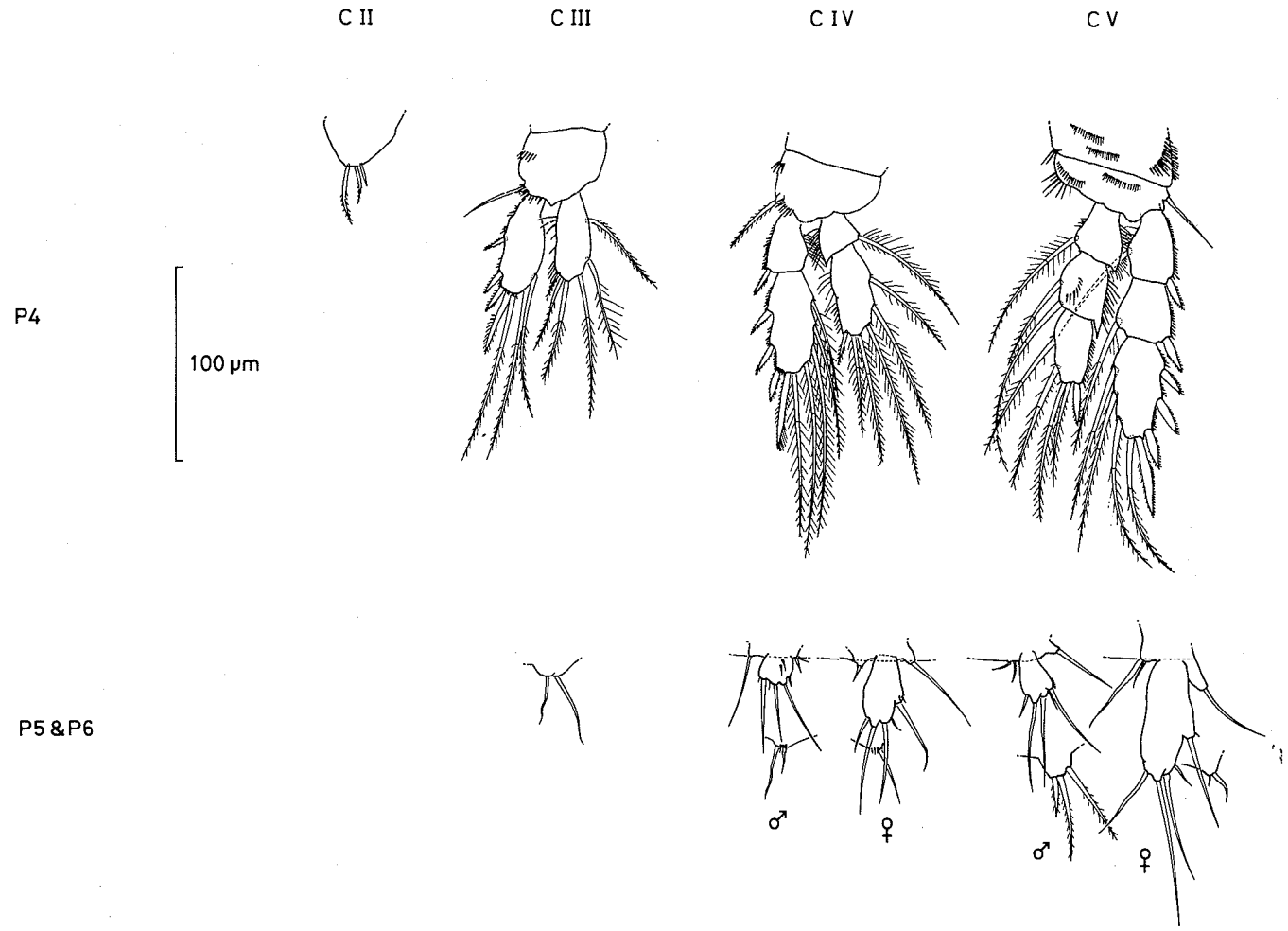

Fig. 11. Tisbe gracilis. Pereiopod 4–6 development of copepodite stages. Each column illustrates appendages of one copepodite stage. Each row illustrates development of one pereiopod.

Segments 5–8 of both sexes with identical setation: 5th segment with 2, 6th with 5, 7th with 2 and 8th with 8 setae/aesthetasc.

Second antenna (Fig. 7E) with 1st segment of endopod with 1 surface seta in middle.

Mandible (Fig. 8F) with a setule row on palp and 4 setule rows on exopod.

First maxilla as in Fig. 8K.

P1–P4 (Figs. 10, 11) with rami of 3 segments. First segment of P2 endopod showing sexual dimorphism: the inner seta shorter and stout in male, long and slender in female.

P5 (Fig. 11) with exopod of female 2.5× as long as male exopod; with 3 longer terminal, 1 small subterminal and 1 long seta in middle. Exopod of male with 3 long and 2 small terminal setae.

P6 (Fig. 11) female with 2 setae. A prominent lobe with 3 strong plumose setae in male.

Adult stage of *Tisbe gracilis*

Average body length of females 773 ± 67 µm, average body width 301 ± 60 µm (n = 10). Average body length of males 594 ± 33 µm, average body width 233 ± 22 µm (n = 10). The external morphology of adult male and female *Tisbe gracilis* has already been described by T. Scott (1895). The present material completely agrees with the description by Scott and especially with the more detailed one by Volkmann (1979), except for size (see below).

Discussion

Developmental instars of Tisbidae have been described by several authors. Branch (1974) showed the entire post-embryonic development of *Scutellidium patellarum*; Brian (1919) and Gurney (1933) reported on some post-embryonic features of *S. longicauda*. Ummerkutty (1960) described all the stages of *Tisbintra jonesi* and Humes (1960) the copepodite stages of *Sacodiscus ovalis*. Several species of *Tisbe* (sometimes erroneously identified: see Volkmann-Rocco 1971; Bergmans 1981) were studied by Johnson & Olson (1948), Battaglia & Talamini (1957), Griga (1960), Vilela (1969), Chua (1975), Park (1976) and Koga (1984). *Tisbe cucumariae*, a representative of the *T. gracilis* species group, was studied by Battaglia (1957) and Lopez (1980). At least some of the material described by Barnard & Reish (1960) is not *T. gracilis* as stated (Volkmann 1979).

The segment of the first antenna bearing the large aesthetasc in copepodid V is the third in the male and the fourth in the female. This must be related to the functional adaptation for grasping in the male. The articles proximal

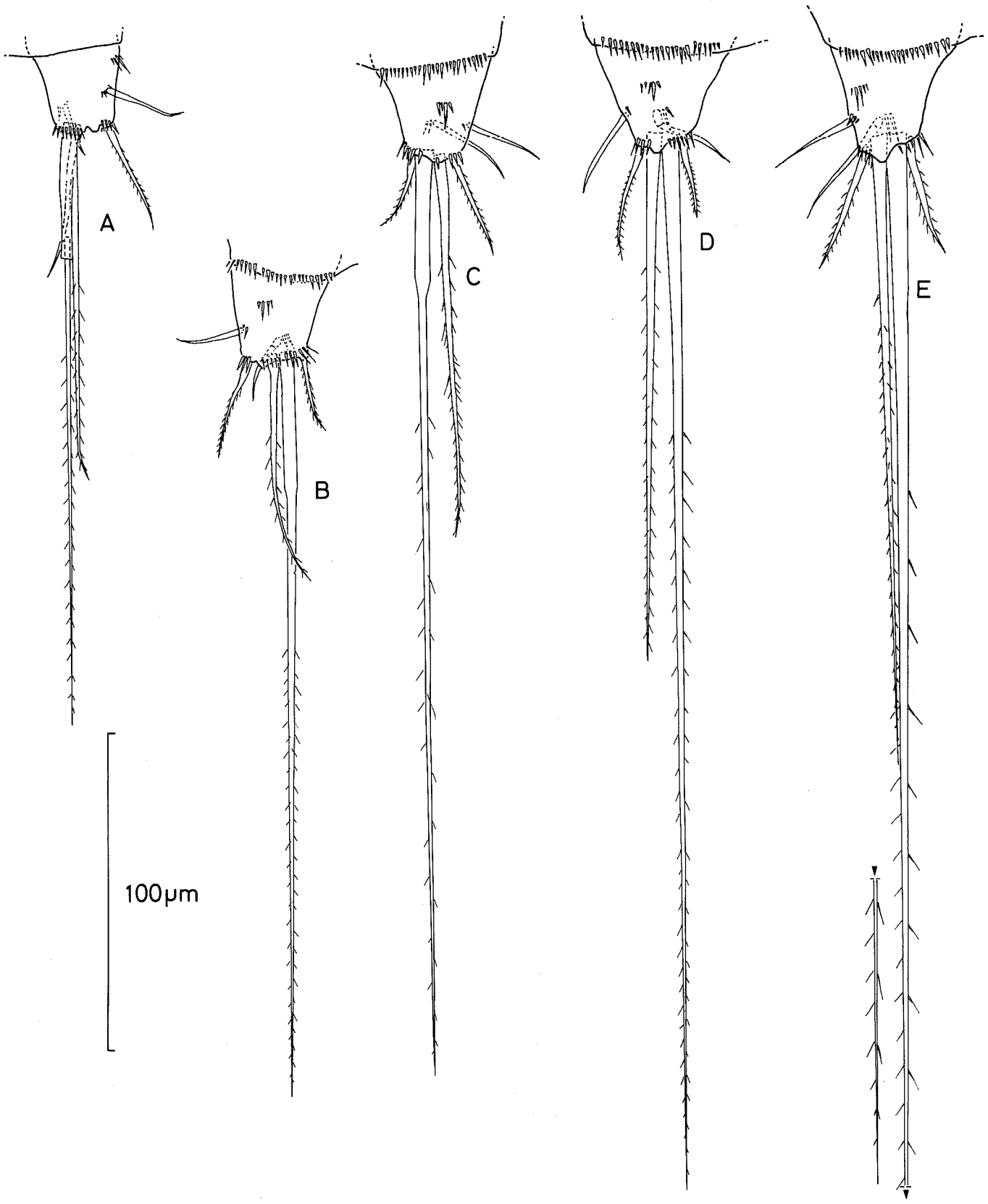

Fig. 12. Tisbe gracilis. Caudal ramus development of copepodite stages, ventral view.—*A.* C I.—*B.* C II.—*C.* C III.—*D.* Male C IV.—*E.* Male C V.

to the aesthetasc are much stouter than the subsequent ones (Dahms, in preparation). The number and grouping of setae provide good evidence that the third and fourth articles in the female correspond to the proximal and distal parts of the third article in the male, respectively.

Another interesting feature in the process of character differentiation is shown by the longest furcal seta of copepodid I. This seta bifurcates so as to terminate in two branches, the innermost of which is longer than the outermost. This peculiarity disappears in the second copepodite stage. An identical developmental sequence is mentioned for *Sacodiscus ovalis* by Humes (1960), for

Tisbe longisetosa by Chua (1975) and for *T. holothuriae* by Park (1976); Lopez's (1980) drawings of the copepodite stages of *T. cucumariae* suggest a similar course. Checking through our collection of copepodite stages of other *Tisbe* species we discovered that the seta in question also occurs in C I of *T. holothuriae* (confirming Park's statement), *T. battagliai, T. bulbisetosa* and *Drescheriella glacialis* (Dahms & Dieckmann 1987). The feature is not unique to the Tisbidae, however, as it is also reported for the C I of quite unrelated harpacticoid genera, e.g. *Macrosetella* (Björnberg 1965), *Platychelipus* (Barnett 1966) and *Phyllopodopsyllus* (Kitazima 1985).

According to Lang (1948) the length of adult *T. gracilis* females varies between 700 and 1300 μm, that of males between 720 and 870 μm. The specimens of Volkmann (1979) varied in length between 850 and 1050 μm for females and between 560 and 700 μm for males, and those of Bergmans (1979), working on the same laboratory population as studied here, averaged 870 μm for females and 650 μm for males. In the present study the average length for adult *T. gracilis* females was 770 μm, for adult males 590 μm. This somewhat smaller size is most likely due to a response (plastic, genetic or both) to crowding in the laboratory culture.

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References

Barnard, J. L. & Reish, D. J. 1960. Wood-browsing habits of the harpacticoid copepod *Tisbe gracilis* (T. Scott) in Southern California.—*Pacif. Nat. 1*(22): 9–12.

Barnett, P. R. O. 1966. The comparative development of two species of *Platychelipus* Brady (Harpacticoida). In *Some contemporary studies in marine science* (ed. H. Barnes): 113–127. George Allen & Unwin, London.

Battaglia, B. 1957. Ricerche sul ciclo biologico di *Tisbe gracilis* (T. Scott), (Copepoda, Harpacticoida), studiato in condizioni di laboratorio.—*Archo Oceanogr. Limnol. 11:* 29–46.

Battaglia, B. & Talamini, P. 1957. Osservazioni sullo sviluppo larvale di *Tisbe reticulata* Bocquet (Copepoda, Harpacticoida).—*Archo Oceanogr. Limnol. 11:* 63–68.

Bergmans, M. 1979. Taxonomic notes on species of *Tisbe* (Copepoda, Harpacticoida) from a Belgian sluice dock.—*Zool. Scr. 8:* 211–220.

Bergmans, M. 1981. A demographic study of the life cycle of *Tisbe furcata* (Baird, 1837) (Copepoda: Harpacticoida).—*J. mar. biol. Ass. U.K. 61:* 691–705.

Bergmans, M. 1983. Population biology of the harpacticoid copepod *Tisbe furcata* (Baird, 1837). Ph.D. thesis, Vrije Universiteit, Brussel.

Björnberg, T. K. S. 1965. Observations on the development and the biology of the Miracidae Dana (Copepoda: Crustacea).—*Bull. mar. Sci. 15:* 512–520.

Branch, G. M. 1974. *Scutellidium patellarum* n.sp., a harpacticoid copepod associated with *Patella* spp. in South Africa, and a description of its larval development.—*Crustaceana 26:* 179–200.

Brian, A. 1919. Sviluppo larvale della *Psamathe longicauda* Ph. e dell' *Harpacticus uniremis* Kröy. (Copepodi Harpacticoidi) (Descrizione della serie Copepodiforme).—*Atti Soc. ital. Sci. nat. 58:* 29–58.

Chua, T.-E. 1975. The developmental stages of *Tisbe longisetosa* Gurney, 1927 (Copepoda, Harpacticoida).—*Crustaceana 28:* 158–167.

Dahms, H.-U. & Dieckmann, G. 1987. *Drescheriella glacialis* gen. nov., sp. nov. (Copepoda, Harpacticoida) from Antarctic sea ice.—*Polar Biol. 7:* 329–337.

Griga, R. E. 1960. Development of some Harpacticoida of the Black-Sea.—*Trudy sevastopol'. biol. Sta. 13:* 68–77.

Gurney, R. 1933. Notes on some Copepoda from Plymouth.—*J. mar. biol. Ass. U.K. 19:* 299–304.

Humes, A. G. 1960. The harpacticoid copepod *Sacodiscus* (= *Unicalteutha*) *ovalis* (C. B. Wilson, 1944) and its copepodid stages.—*Crustaceana 1:* 279–294.

Itô, T. 1984. A phylogenetic study of the family Harpacticidae (Harpacticoida): Some problems in character differentiation processes through the copepodid stages.—*Crustaceana* Suppl. 7: 267–278.

Johnson, M. W. & Olson, J. B. 1948. The life history and biology of a marine harpacticoid copepod, *Tisbe furcata* (Baird).—*Biol. Bull. mar. biol. Lab., Woods Hole 95:* 320–332.

Kitazima, Y. 1985. Notes of larval stages of three closely-related harpacticoid species (Crustacea, Copepoda).—*J. Sci. Hiroshima Univ.* Ser. B, Zool. *31:* 223–234.

Koga, F. 1984. Morphology, ecology, classification and specialization of copepod nauplii.—*Bull. Nansei Reg. Fish. Res. Lab. 16:* 95–229. (In Japanese.)

Lang, K. 1948. *Monographie der Harpacticiden.* Reprint 1975. O. Koeltz Science Publishers, Koenigstein, F.R.G.

Lopez, G. W. 1980. Description of the larval stages of *Tisbe cucumariae* (Copepoda: Harpacticoida) and comparative development within the genus *Tisbe.*—*Mar. Biol. 57:* 61–71.

Nicholls, A. G. 1935. The larval stages of *Longipedia coronata* Claus, *L. scotti* G. O. Sars, and *L. minor* T. and A. Scott, with a description of the male of *L. scotti.*—*J. mar. biol. Ass. U.K. 20:* 29–45.

Park, C. W. 1976. The larval development of *Tisbe holothuriae* Humes (Copepoda, Harpacticoida) under the laboratory conditions.—*Publs Inst. mar. Sci. natn. Fish. Univ. Busan 9:* 33–48.

Scott, T. 1895. Additions to the fauna of the Firth of Forth. Part VII.—*Rep. Fishery Bd Scotl. 13:* 165–173.

Sieg, J. 1973. Zum Problem der Herstellung von Dauerpräparaten von Klein-Crustaceen, insbesondere von Typusexemplaren.—*Crustaceana 25:* 222–224.

Ummerkutty, A. N. P. 1960. Studies on Indian copepods 2. An account of the morphology and life history of a harpacticoid copepod, *Tisbintra jonesi*, sp. nov. from the Gulf of Mannar.—*J. mar. biol. Ass. India 2:* 149–164.

Vilela, M. H. 1969. The life cycle of *Tisbe* sp. (Copepoda, Harpacticoida) under laboratory conditions.—*Notas Estud. Inst. Biol. mar., Lisb. 36:* 1–16 (Plates I–V).

Volkmann-Rocco, B. 1971. Some critical remarks on the taxonomy of *Tisbe* (Copepoda, Harpacticoida).—*Crustaceana 21:* 127–132.

Volkmann, B. 1979. A revision of the genus *Tisbe* (Copepoda, Harpacticoida). Part 1.—*Archo Oceanogr. Limnol. 19* Suppl.: 121–284.