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Taxonomic Notes on Species of *Tisbe* (Copepoda, Harpacticoida) from a Belgian Sluice Dock

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Tisbe furcata, T. gracilis, T. bulbisetosa, T. holothuriae and *T. battagliai* are reported from the Sluice Dock near Ostend (Flemish Coast). The latter three species are new to the Belgian fauna. A cross-breeding experiment between strains of *T. holothuriae* from Ostend and Venice (Italy) confirms perfect interfertility and hybrid F_1 heterosis. *T. furcata,* the "stumbling block" of the genus, is redescribed and an account is presented of the characteristics and ontogeny of its colour pattern.

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1. Introduction

Identification of *Tisbe* species is notoriously difficult, and Volkmann-Rocco (1971) has stressed the necessity of extremely detailed observation, and sometimes even of cross-breeding experiments, to arrive at reliable identifications. Even the recent literature is teeming with misidentifications made by authors, some of them professional copepodologists, who were not thoroughly acquainted with the genus; and the number of times that different species have been lumped together under a single name can only be conjectured.

In the course of a three year sampling program (1975–1977), a survey has been made of the population dynamics of several sympatric species of *Tisbe* in an artificial lagunar habitat, the Sluice Dock ("Spuikom") of Ostend on the Flemish coast. In view of the taxonomic difficulties referred to above, and in view of the correspondingly poor biogeographical knowledge of the genus, it appears of interest to report on the species which have been found. A treatment of the population dynamics data will be deferred to a subsequent paper.

Fine descriptions are already available of *Tisbe holothuriae, T. battagliai, T. gracilis* and *T. bulbisetosa*. Of these, only *T. bulbisetosa* will here be examined from a purely morphological point of view, as some of its sibling species have yet to be described. Attention will mainly be focused on *T. furcata,* the "stumbling block" of the genus.

2. Methods

2.1. *Collecting*

The animals were obtained either by wringing out fragments of *Ulva* which had drifted to the border, or by scraping earthenware tiles after a fortnightly submersion in the center of the Dock. The *Tisbe* were sorted live in order to take advantage of differing colour patterns, and monospecific laboratory cultures were set up.

2.2. *Cross-breeding technique*

The procedure adopted was essentially the same as the one described by Battaglia & Volkmann-Rocco (1973).

In the *holothuriae* crosses, five synchronous ovigerous females were individually isolated from both the Venice and Ostend mass-cultures until they had released their nauplii. When these had grown up, experimental and control pairs were set up between an adult male and a subadult, and therefore virgin, female (4th or 5th copepodite) of a different "family". After fertilization the male was discarded and the female transferred to a new vial for each successive egg batch produced. The nauplii from the first egg batch of each female were subdivided in groups of five per dish to determine their survival under minimal crowding. All the offspring produced within the female's lifetime were counted and sexed upon reaching adulthood.

In the case of the *holothuriae*×*battagliai* crosses, mass culture males were used to fertilize the experimental and control females; reproductive success was evaluated qualitatively only (after 6 and 11 days). Further details were as in the *T. holothuriae*-experiment.

Throughout both experiments plastic petri-dishes (∅ 5.5 cm) containing 10 ml of seawater were used. Temperature and salinity were approximately constant at 18°C and 35 ppm. Each dish received 1 ml of full-grown *Dunaliella* culture every 5th day (every 3rd day for the most numerous F_1 batches).

3. Abbreviations in the text and figures

A_1	antennule
A_2	antenna
Md	mandible
Mxl	maxillula
Mx	maxilla
Mxp	maxilliped
P_1–P_6	legs 1–6
enp	endopod
exp	exopod

4. The species

4.1. Tisbe holothuriae *Humes, 1957*

This is one of a group of sibling species (Volkmann-Rocco 1972*b*, 1975) the females of which are qualitatively indistinguishable (but for *T. remanei*). The males however can be discriminated fairly easily by combined observation of their A_1, P_2 and P_5. The proximal endopod segment of the male P_2 bears a characteristically modified seta which is species-specific in the case of *T. holothuriae*. Fig. 1 is a *camera*

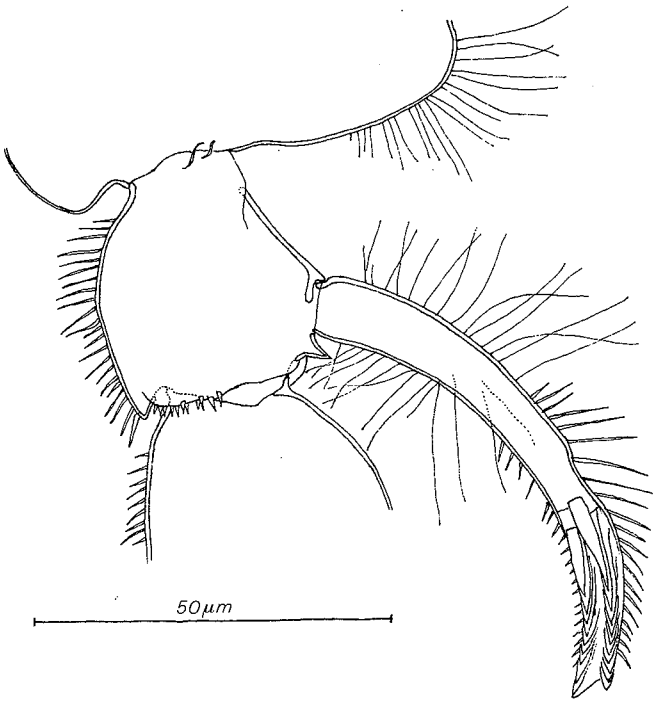


Fig. 1. Tisbe holothuriae Humes, ♂. Transformed spine on P_2 enp segment 1.

lucida drawing of this spine, featuring the biserial lamellar system and the point of attachment suggesting a mobile joint.

The identification on morphological grounds was checked by a cross-breeding experiment using a Venetian laboratory strain of *T. holothuriae* kindly put at my disposal by Dr Volkmann. (In view of the small number of crosses, the results presented must be considered indicative rather than quantitative.)

The proportion of unsuccessful crosses, though rather high (cf. Table I), is similar for experimental and control matings and, in fact, similar to the figure of 35% reported by Battaglia (1957) for intrapopulation controls in *T. reticulata*.

From the parameter values obtained in this experiment (Table I), two clear trends are apparent. First, for R_0 and F_1 sex ratio there is a definite influence of the female's geographic origin on the parameter value. Battaglia & Volkmann-Rocco (1973) have observed a strong correlation between the female's geographic origin and the number of nauplii of its first egg sac. The same effect is also substantiated in my data (♀V × ♂O: 36.4, ♀V × ♂V: 37.3, ♀O × ♂V: 41.4, ♀O × ♂O: 41.0).

Second and more important, the experimental crosses are consistently superior to the controls in all parameters considered. In spite of the low number of replicas, the net reproduction rate R_0, i.e. the number of F_1 females produced per P female, is significantly higher in "hybrid" crosses (cf. Table II). Also, it is interesting to note the heterotic effect of crossing distant populations on F_1 viability; it closely parallels the findings of Battaglia & Volkmann-Rocco (1973) even from a quantitative point of view (cf. Table III).

From the foregoing it is concluded that the Sluice Dock population under consideration freely interbreeds with Venetian *T. holothuriae* and, moreover, that it shows the characteristic behaviour of this species in crosses between widely spaced populations.

T. holothuriae has often been confused with *T. furcata* (Volkmann-Rocco 1971); it has also been described under at least one, and probably three, junior synonyms (Volkmann-Rocco 1971, 1972*b*). Its known geographical distribution is summarized in the last-mentioned paper.

The species is new for the Belgian fauna but its presence is hardly surprising, as it has been recorded from Wimereux (France) and Helgoland (Germany).

4.2. Tisbe battagliai *Volkmann-Rocco, 1972*

This is a sibling species of the former. The modified spine of the males is nearly indistinguishable from that of *T. remanei*, but their A_1 and P_5 both allow easy identification (Volkmann 1975).

The reproductive distinctness of the *holothuriae* and *battagliai* populations from the Sluice Dock was confirmed by a cross-breeding experiment involving both strains. The results (Table IV) are clearly conclusive.

T. battagliai is new for the Belgian fauna. Other localities where it is known to occur are given by Volkmann-Rocco (1972*b*). To these must be added the brackish ditches in the salt-marsh "Zwin" (Knokke, Flemish coast). A casual sample of superficial detritic mud taken there on 14-11-1976 yielded 6 adult *Tisbe* and 2 copepodites, all of which proved to be *T. battagliai*.

4.3. Tisbe gracilis *(T. Scott, 1895)*

This species belongs to another group with a sexually dimorphic P_2 which is, in this case, sufficient for unequivocal identification of the male. The females can be discriminated on the basis of the genital field (Volkmann-Rocco 1973*b*). The Sluice Dock specimens show a general agreement in morphology with Scott's (1895) and Volkmann-Rocco's (1973*b*) descriptions.

The suggestion made by Volkmann, that the whole animal length of 1.4 mm quoted by Scott includes the caudal setae, is not borne out by the latter's original paper (cf. the magnification mentioned in Scott 1895, p. 173). It has been found, though, that his size indications do not always agree with his material (Volkmann, pers. comm.). My own culture specimens average about 0.87 mm (5♀♀) resp. 0.65 mm (5♂♂)

Table I. *Summary of a cross-breeding experiment between* T. holothuriae *from Ostend and Venice*
The values in column 4–7 are averages over all fertile crosses

Type of cross	Number of crosses attempted	Number of sterile crosses	F_1 percentage survival (minimal crowding)	Total F_1 reaching adulthood per female	Percentage of females in F_1	R_0 (number of daughters per mother)
♀V × ♂O	11	4	95.2	410	51.3	212
♀O × ♂V	9	2	93.2	400	42.0	191
♀V × ♂V	9	3	87.3	296	39.9	129
♀O × ♂O	8	2	87.6	332	25.8	82

Table II. *Anovar of R_0 values for pooled experimental ($\bar{R}_0$=202, s.d.=121) and pooled control crosses ($\bar{R}_0$=106, s.d.=79) of* T. holothuriae

Source of variation	Sum of squares	Degrees of freedom	Mean square	F
Between levels	59 905	1	59 905	5.535
Residual	259 719	24	10 822	$P<0.05$
Total	319 624	25		

Table III. *Survival to adulthood of "hybrid" F_1 relative to intrapopulation controls in* T. holothuriae

V=Venice, O=Ostend, H=Helgoland, B=Beaufort, USA

Crosses considered	Relative viability of "hybrids"	Source
♀V × ♂O/ ♀V × ♂V	1.09	Present work
♀O × ♂V/ ♀O × ♂O	1.06	Present work
♀H × ♂B/ ♀H × ♂H	1.03	Battaglia & Volkmann-Rocco (1973)
♀B × ♂H/ ♀B × ♂B	1.10	Battaglia & Volkmann-Rocco (1973)

from the tip of the rostrum to the end of the furcal rami. These figures are in close agreement with those of Volkmann (0.85–1.05 mm resp. 0.56–0.70 mm). It must of course be remembered that size in copepods is strongly influenced by environmental factors, and also that an animal's length varies with its degree of contraction.

Living adults of both sexes as well as the later copepodid stages contain red droplets. These are distributed symmetrically on the ventral side of the body, a small group of them being situated in front of the attachment of swimming legs P_2–P_4. At least in my culture animals there appears to be a sexual dimorphism, the droplets of the females occurring in front of the P_1 as well and being rather more orange and definitely less opaque. In addition to the droplets and the bright red eye, there may also be a faint pinkish tinge in the cuticula of adult animals, especially in the abdomen.

T. gracilis does not seem to be a common inhabitant of the Sluice Dock; it has however been recorded (Persoone 1967) from artificial substrates in the harbour of Ostend to which the Dock is connected by a sluice. The species appears to be limited to the North Atlantic (Volkmann-Rocco 1973*b*).

4.4. Tisbe bulbisetosa *Volkmann-Rocco, 1972*

4.4.1. *Introductory remarks.* The species under consideration belongs to a group two members of which have been described by Klie (1949) and Volkmann-Rocco (1972*a*) respectively. A third sibling species has been named but not described (Fava & Volkmann 1975). In the Mediterranean, several populations of unclear taxonomic status have been subsumed under the name of *T. dilatata* (e.g. Marcus, quoted in Volkmann-Rocco 1972*a*; Renzoni 1974).

4.4.2. *Comparison with* T. dilatata *Klie, 1949.* My Sluice Dock specimens (3♀♀ and 4♂♂ dissected) differ from Klie's (1949) description in a number of ways, the two most important of these concerning (1) the female genital field, which bears three setae on each side, and (2) the Mxp, which is strongly sexually dimorphic. Both observations are in contrast with explicit statements by Klie. In addition, there are a number of minor differences involving the two lateral accessory furcal setae (of about equal length, 1/10 of the longest terminal seta); the spinulosity of all six furcal setae (not sparse as stated by Klie); the 2nd and 3rd A_1 segment of the female (length ratio 1.2 instead of 1); the 2nd enp segment of P_1 (length/width ratio 0.25 instead of 0.36); the P_5 of the female (the single seta on the basipodite and the marginal one on the exp not swollen at their base, as loosely stated, but not drawn, by Klie); the relative lengths of the marginal exopod seta and the adjacent subterminal one (reversed with respect to Klie's values). Instead of describing the female's mouthparts Klie refers to Sars's (1911) drawings of *T. furcata*, which are acceptable as to general shape but obscure as to details of the setation. It is clear however that small differences of setation do exist between species, and in particular between *T. furcata* and the population under consideration. Finally, quantitative differences between Klie's description and my specimens which concern the proportions of abdominal and P_1 segments may at least in part be attributed to the difficulty of obtaining well defined and objective measurements of them.

4.4.3. *Comparison with published descriptions of* T. bulbisetosa *Volkmann-Rocco, 1972.* Vilela's (1969) description of a *Tisbe* sp. may now beyond doubt be referred to *T. bulbisetosa* (Volkmann, pers. comm.). If one assumes that the setation of her specimens is not rendered in all completeness in her drawings, and further that the spines on the P_5 exp surface of females are not distributed irregularly (text) but in rows (drawing!), there is a close agreement between her material and mine. (The statement that the male A_1 is 8-segmented obviously results from overlooking the very small 4th segment.)

There also exist some differences between Volkmann-Rocco's (1972*a*) description and my material. The second A_1 segment of females bears 15 setae instead of 14 as in her drawing, the difference involving a rather short seta in the middle of the segment and usually closely appressed to it. Two setae are found on A_1 segment 5, exactly as in the *reticulata* group (Volkmann-Rocco 1973*a*) and *T. furcata*

Table IV. *Summary of a cross-breeding experiment between* T. holothuriae *and* T. battagliai *from the Sluice Dock*

Type of cross	Number of crosses attempted	Females retaining the eggs in the oviducts	Females extruding a sterile egg-sac	Females producing nauplii and copepodites
♀*hol* × ♂*bat*	10	9	1	–
♀*hol* × ♂*hol*	10	–	–	10
♀*bat* × ♂*hol*	9	7	2	–
♀*bat* × ♂*bat*	7	–	–	7

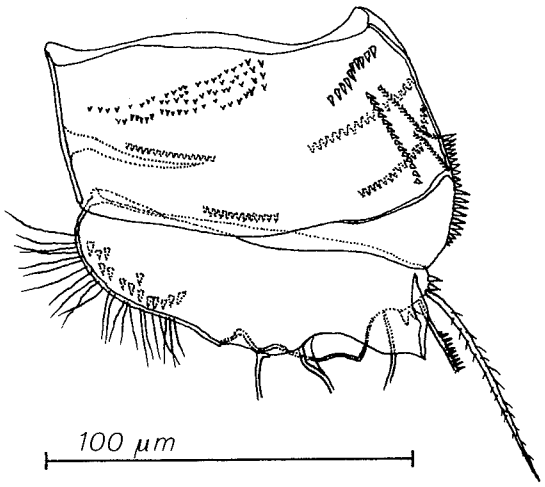


Fig. 2. Tisbe bulbisetosa Volkmann-Rocco, ♀. Coxa and basis of P_4, posterior view.

(this paper). The most external apical seta of Md exp is ciliated. The Mx endite bears a long *and a short* seta; the terminal (spiniform) Mx segment has a row of small hairs near its tip. The basis of P_1 has an anterior surface row. There exists a row of fine hairs along the upper part of the interior margin of P_1 enp segment 2, viz. above the insertion of the marginal seta. The row of hairs on the surface of P_1 exp segment 2 and the submarginal row of bristles on enp segment 1 occur on the *opposite* (posterior) side with respect to the rest of the surface adornment of the appendage drawn by Volkmann. In addition to this, exp segment 1 has a somewhat less conspicuous row of small hairs (oriented like that on exp segment 2) on its posterior surface. Similarly, the surface adornment of P_2–P_4 coxa and basis (as drawn by Volkmann) on one hand, and that of the rami on the other, occur *on different sides* of the appendages. As the ornamentation is nearly identical to that in *T. furcata,* the reader is referred to the relevant paragraph and to Figs. 8–10 for comparison. My material differs from *T. furcata* in the following P_2–P_4 details only:

- absence of the innermost surface comb of longer spinules on the coxa of P_2–P_4
- absence of the surface comb above the rami on the basis of P_2
- the posterior distal fringe of small hairs does not seem to be present on exp segment 1 of P_2–P_4
- spinules of the distal rim of the terminal enp segment apparently more numerous than in *T. furcata,* especially on P_2 where there are 6 or more of them
- posterior surface adornment of the P_4 coxa altogether different from that of *T. furcata;* it is shown in Fig. 2 and consists of a subhorizontal spinule field, a skew row and three subvertical ones, the external two staggered and made up of minute spinules.

Finally, as observed by Klie, the 2nd and 3rd abdominal segments carry *two* long hairs posteriorly on either side.

For morphological comparison, I dissected a female *T. bulbisetosa* which I had collected on October 7th, 1975 on the Arsenale canal wall, Venice (Station 5 of Fava & Volkmann 1975). This animal agrees with my Sluice Dock material in each of the details listed above, and hence I suspect the discrepancies between my material and Volkmann-Rocco's description to be due to slight inaccuracies of the latter. The only genuine difference which I observed concerns the posterior margin of the fourth abdominal segment. In the Venetian specimen the latter is ventrally provided with a central and two lateral rows of spinules separated by broad gaps, agreeing with Volkmann's statement. The Sluice Dock animals have a continuous row instead, but there is an abrupt transition to much finer spinules in the zones corresponding to the gaps referred to above.

There exist some slight differences concerning the male also. But for the sexually dimorphic A_1, Mxp, P_5 and P_6 its appendages agree with the female's in every detail. Segment 2 of A_1 bears 15 setae, though this is rather difficult to observe. Relative lengths of the second, third and fifth segment (posterior margin of sclerified parts) 2.50 : 1 : 2.05 (average of 4 specimens). P_5 exp surface with five rows of spinules, the additional one somewhat oblique and distal with respect to those drawn by Volkmann. The length of the terminal spine may be slightly shorter or slightly longer than the exp. Though I could not dissect a Venetian *bulbisetosa* male for reference, none of these differences appears to necessitate or warrant distinction at the species level.

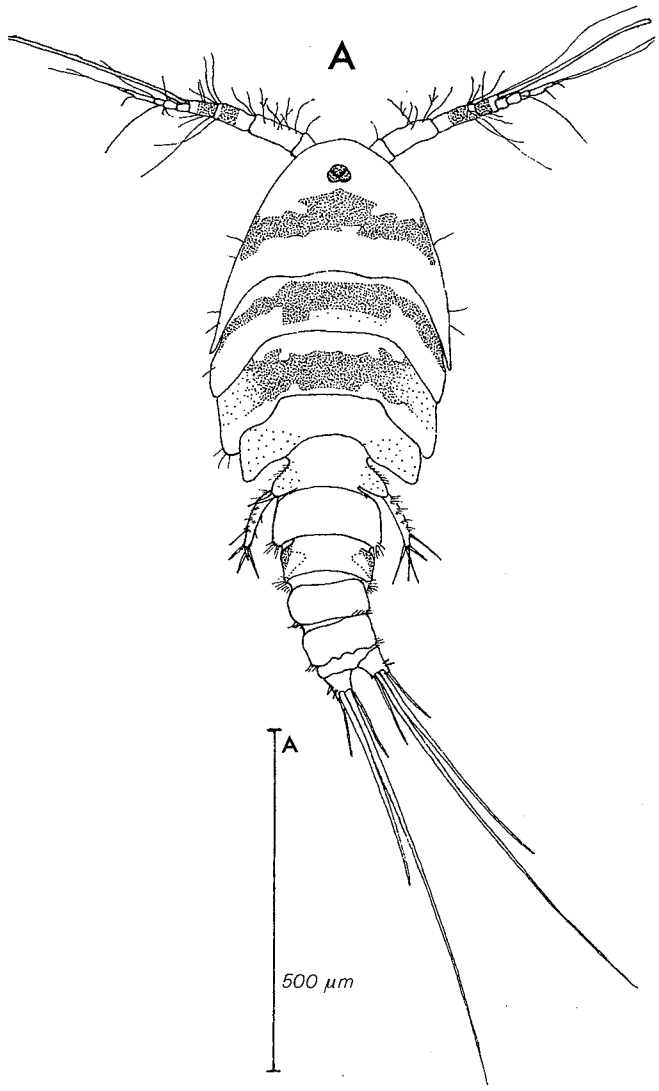
4.4.4. *Conclusions.* Taken together, this Sluice Dock population differs from *T. dilatata* on several points, one of which was considered by Klie to be diagnostic for the latter species. It does not differ significantly from either Vilela's or Volkmann-Rocco's specimens of *T. bulbisetosa.* The undescribed *T. inflatiseta* may only be distinguished from *T. bulbisetosa* on the basis of colour pattern (Volkmann-Rocco 1972*a*), as even the female genital field and P_5 are too variable to allow a reliable identification (Volkmann, pers. comm.). My material closely agrees with the *T. bulbisetosa* description even in these respects. It may therefore safely be assigned to *T. bulbisetosa,* even if more cross-breeding experiments must be awaited before the taxonomy of the *dilatata* group of sibling species will definitively be settled.

T. bulbisetosa is new for the Belgian fauna. Like *T. gracilis,* it may not be a regular inhabitant of the Sluice Dock. Its presence outside the Mediterranean region and relatively close to the type locality of *T. dilatata* may at first seem somewhat surprising. It has however also been reported from Beaufort, North Carolina (Volkmann-Rocco 1972*a*) and from Concarneau and Roscoff, France (Volkmann, in press).

4.5. Tisbe furcata (*Baird, 1837*)

4.5.1. *Introductory remarks.* Principally owing to the fact that many *Tisbe* species conform to a common "*furcata*" habitus, this species has given rise to considerable confusion in the literature (Volkmann-Rocco 1971). In fact, it may be asked to what extent its being recorded as cosmopolitic, eurythermic, nearly euryhaline, perennial and eurytopic (Lang 1948) is, at least in part, due to the lumping together of superficially similar but ecologically differentiated species. Sars's (1911) redescription of Baird's species does not adequately bring out the details characterizing it. My identification is based on a comparison with Venetian culture specimens, which have themselves been determined by Dr Volkmann on the basis of close comparative examination of Sars's material. The present record confirms the observation by Polk (1963) who first found *T. furcata* in the Sluice Dock.

The insufficiency of the accounts published so far calls for a redescription of this species. Measurements in this section



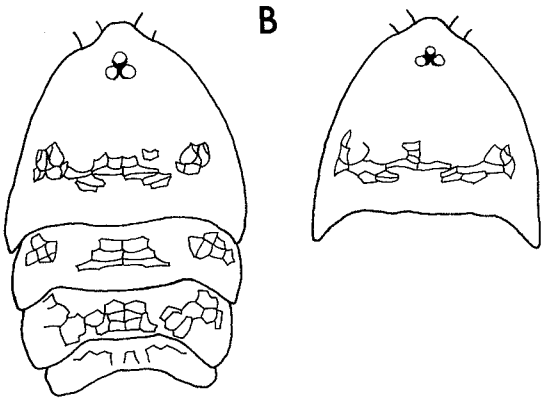


Fig. 3. Tisbe furcata (Baird), ♀. — *A*, habitus. — *B*, aspect of parts of the hypodermal cellular reticulum, as seen in two partly discoloured individuals.

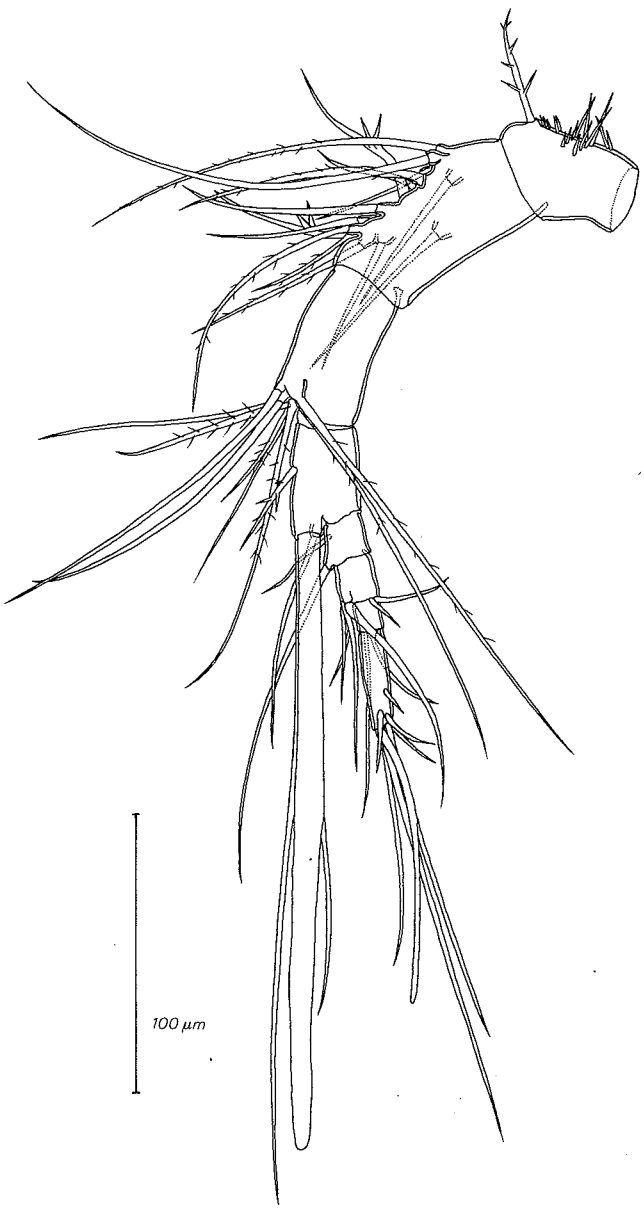


Fig. 4. Tisbe furcata (Baird), ♀. A_1.

are based upon wild-caught specimens unless stated otherwise.

4.5.2. *Description of the female.* Habitus (Fig. 3*A*) cyclopoid, as is the rule in the genus. The bright red eye consists of 3 ocelli. The total length, from tip of rostrum to end of furca, amounts to 0.99 mm (1.06–0.92 mm, 10 specimens); this value is given with the same reserve as mentioned for *T. gracilis*. Maximum width of the cephalothorax 0.40 mm (0.38–0.44 mm, 10 specimens). Genital double segment (Fig. 5*A*) dorsally and laterally with a suture, which contains some prominent spinules laterally only. Ventrally are two interlocking chitinous ridges surrounding the aperture of the oviducts, and a seminal receptacle of a characteristic though somewhat variable shape (Fig. 5*B*). Lang's (1948) drawing of the genital area of *T. furcata*, in my opinion, certainly refers to this very species. Second and third abdominal segment with a long and isolated seta inserted posteriorly on either side. Posterior rim of the genital double segment and the next two abdominal segments ventrally and laterally with spinules. The ventral ones are flat and triangular and much coarser than in *T. bulbisetosa* or, a fortiori, the *holothuriae* group; on the last-named (=4th) segment, such coarse spinules occur only laterally and centrally, being abruptly replaced by much finer ones in between.

Furca. Rami wider than long, with four long setae measuring 140 µm, 600 µm, 400 µm and 135 µm beginning with the most interior one. The longest two are often "telescoped" (independently of each other). The interior seta is often though not always bent. But for the proximal portion of the

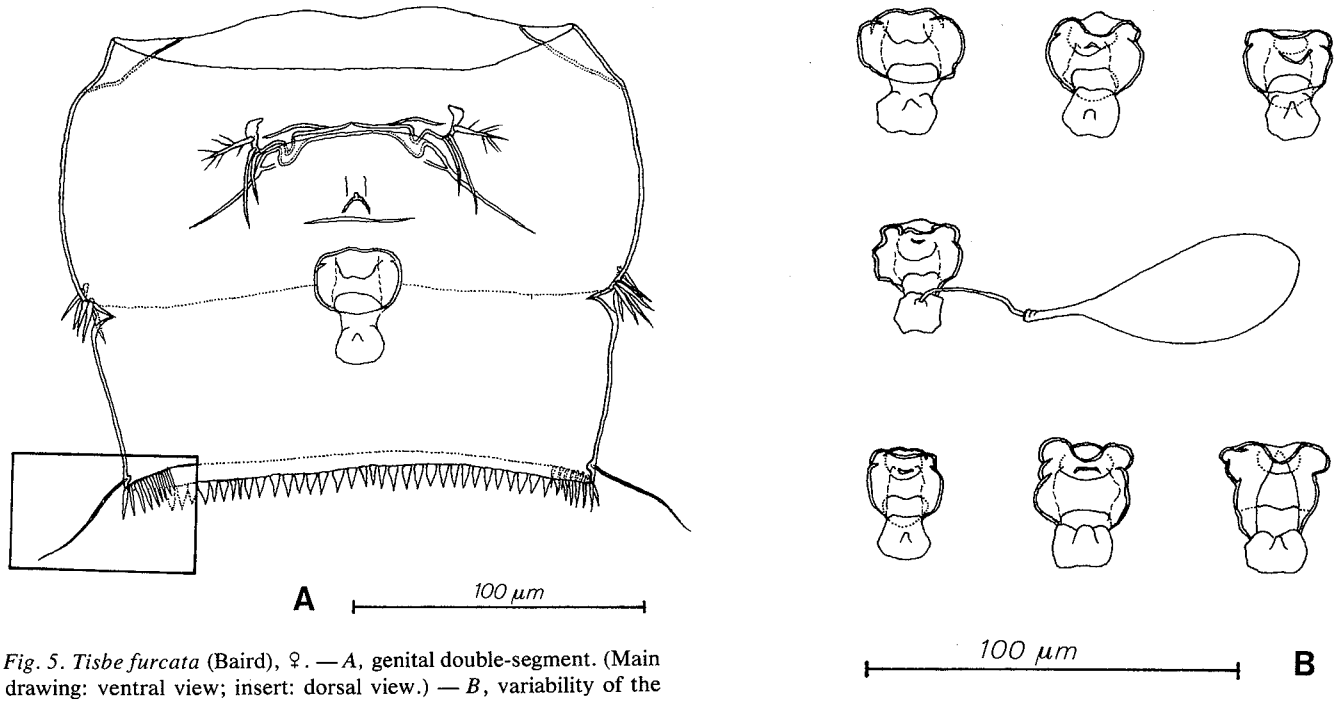


Fig. 5. Tisbe furcata (Baird), ♀. —*A*, genital double-segment. (Main drawing: ventral view; insert: dorsal view.) — *B*, variability of the seminal receptacle (laboratory culture specimens).

longest two, all four are provided throughout with spinules of gradually decreasing size. In addition to the four large ones, three shorter setae of about equal size occur; one is inserted dorsally between the two longest apical ones, another at about the same level as these on the exterior side of the ramus, and the third one ventral and more rostrad. The latter two have a comb of spinules above their point of attachment.

Antennule (A_1) eight-segmented, stouter than drawn by Sars (1911). E.g., the length–width ratio of segment 2 is usually much closer to 1.5 than to 2.0. Form and setation otherwise as in Fig. 4. Relative lengths of the sclerified parts of segments 2, 3 and 4 measured along the posterior (unarmed) margin 1.79 : 1.59 : 1 (1.71 : 1.62 : 1–1.89 : 1.57 : 1, 5 specimens). Number of setae on the successive segments 1/15/9/4+aesthetask/2/6/2/7+aesthetask. On the second segment, two of these setae are more robust and provided with 2 to 4 lateral tips giving them a characteristic "forked" appearance (which can be observed even on living animals at low magnification). These two setae are implanted somewhat "against the grain", a character shared with *T. bulbisetosa* and the *T. reticulata*-species group (cf. the drawings in Volkmann-Rocco 1973*a*). The central seta on segment 4 and the single one on segment 1 are intermediate in appearance between these two peculiar setae and the normal plumose type.

Antenna (A_2). The basis of the A_2 has a surface comb of about seven hairs near the implantation of the internal large seta. Enp segment 1 with one seta on the internal margin. The terminal enp segment has an external row of long thin hairs; it bears 9 large setae (5 of them bent and naked, 1 spiniform with a row of short hairs, 3 curved and plumose) and an additional internal one, which is smaller and thinner and has 2 to 3 short spinules of unlike length implanted near its base. In addition to the large distal seta of exp segment 1, there is a very short one in the middle of the interior margin. Subsequent exp segments with 1, 1 and 3 setae. All A_2 setae except those on the terminal enp segment are ciliated, although both Sars (1911, plate LI) and Lang (1948, figs. 12 and 164) picture one of the apical setae on exp segment 4 naked (which is true in the *holothuriae* group).

Mandible (Md) setation as follows. Inside of masticatory part with a strong regularly plumose seta, basal lobe with a much shorter, irregularly plumose one. Enp surface with two parallel oblique (sublongitudinal) rows of hairs (along with an apical one and one along each margin), exp surface with long bristles more or less distinctly organized into four transverse rows, including the apical one. Exp with 3 and enp with 3+6 setae, as usual; the most external exp seta is ciliated.

Maxillula (Mxl). I have been unable to observe the precise setation of Mxl.

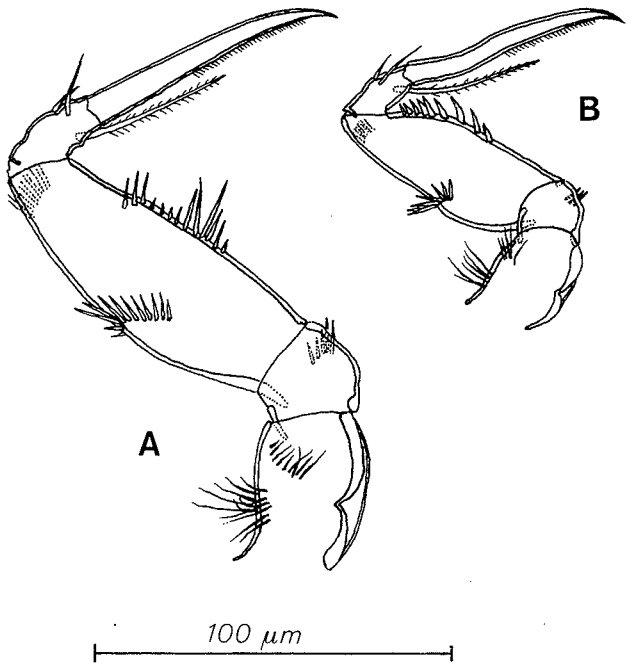


Fig. 6. Tisbe furcata (Baird). —*A*, Mxp of ♀. —*B*, Mxp of ♂.

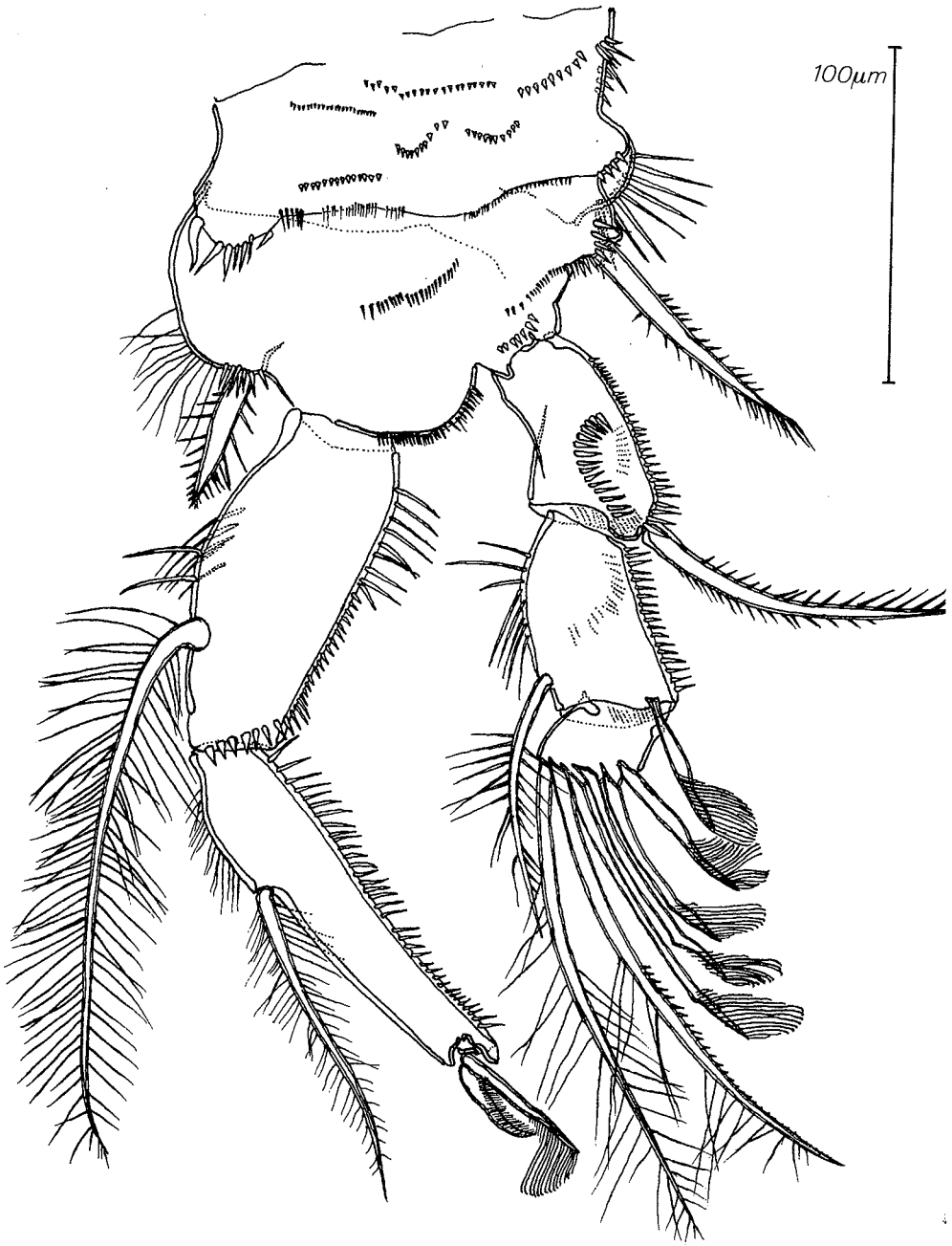


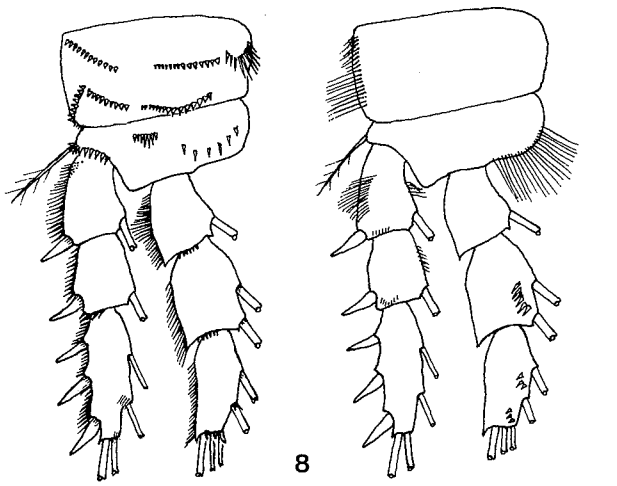
Fig. 7. Tisbe furcata (Baird), ♀. P_1, anterior view.

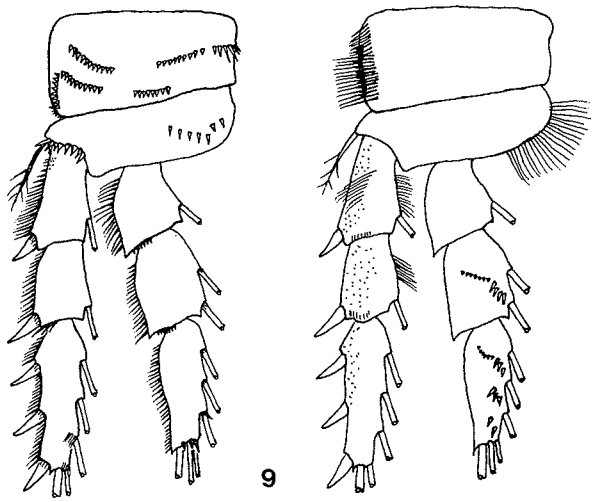
Maxilla (*Mx*). External rim of the Mx basal segment provided with a central row and a distal tuft of hairs, the latter being more dense than the former. The single endite bears a long and a short seta; claw-like enp with short hairs, its spiniform seta with long hairs. (The appendage under consideration is consistently, but erroneously, termed "first maxilla" by Volkmann-Rocco (1972*a, b*, 1973*a, b*). Though "maxilla" seems to be its most appropriate denomination, it has also been called "second maxilla" or "first maxilliped" by various authors: cf. Lang 1948, pp. 56–57.)

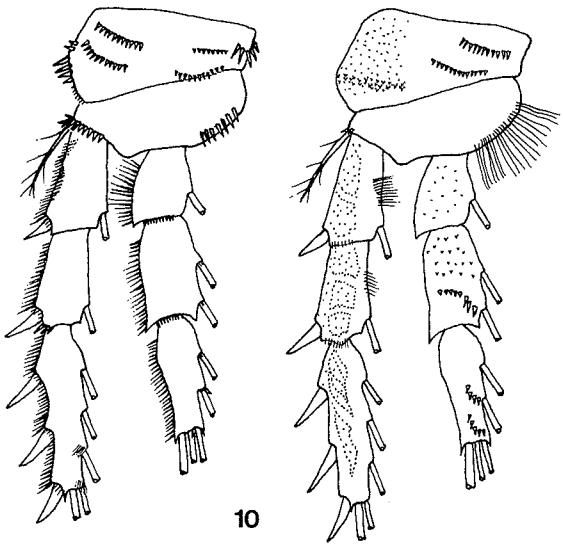
Maxilliped (*Mxp*) as shown in Fig. 6*A*.

First leg (P_1) (Fig. 7) with spines and setae distributed as typical for *Tisbe*. The external seta of exp segment 2, the four proximal ones of exp segment 3 and the longest of the two claws on enp segment 3 have a terminal tuft of hairs. Second claw with a row of short hairs on its concave side. (Again, it is drawn naked by Sars and Lang, as it should have been in the *holothuriae* group.) Setation of lateral segment margins as shown in Fig. 7. The coxa has an exterior-posterior flap bearing a row of long bristles. Surface adornment anterior on coxa and basis. Exp segment 1 with an anterior comb of spinules and a posterior row of short hairs. Surface adornment of exp segment 2 and enp segment 1 posterior. There is a fringe of hairs near the posterior distal borders of exp segments 1 and 2 (difference with *T. bulbisetosa,* which has no such fringe on exp segment 1 and an anterior one on exp segment 2!). There is a row of spinules near the anterior distal border of enp segment 1. Length–width ratio of enp segment 1 2.40 (2.21–2.71, 5 specimens); of enp segment 2 4.80 (4.38–5.24, 5 specimens). Enp segment 2 about 1.15 times as long as segment 1 (1.10–1.22, 5 specimens) and with its internal seta inserted proximally at 1/3 of the segment length.

Second to fourth leg (P_2–P_4) (Figs. 8–10) of the chaetotaxy typical for the genus (Lang 1948). Anterior surface adornment of the coxa in each case consisting of two subhorizontal sets of spinule rows and a subvertical one, the latter more marginal and prominent on P_4. On P_2 and P_3 there occurs a







Figs. 8–10. Tisbe furcata (Baird), ♀. Diagrams of P_2–P_4, respectively. (Left: external marginal and anterior adornment; right: internal marginal and posterior adornment.)

posterior row of hairs near to the external coxa rim; it consists of two series of hairs of dissimilar length and inclination. On P_3 only, this row is parallelled by one situated external (anterior) to it and consisting of short stiff hairs. P_4 posterior coxa adornment as indicated in Fig. 10. The bases of P_2–P_4 adorned as shown in the Figs. and bearing an external plumose seta; their distal rim with an anterior row of spinules along the seta implantation and exp attachment. Basis of P_2 only with an additional surface comb above the rami. Large bristle-like hairs are present along the external side of all exp and enp segments, whereas tiny spinules surround the base of the spiniform setae of the exps. Spinules of progressively smaller size can be found anteriorly on P_2 through P_4:

- on the distal rim of exp segment 2 (external part)
- dispersed among the apical setae and spines of the terminal enp segments (2–3, rarely more)
- on the distal rim of enp segments 1 and 2 (second quarter starting from the outside on P_2 and P_3, somewhat more extensive on P_4).

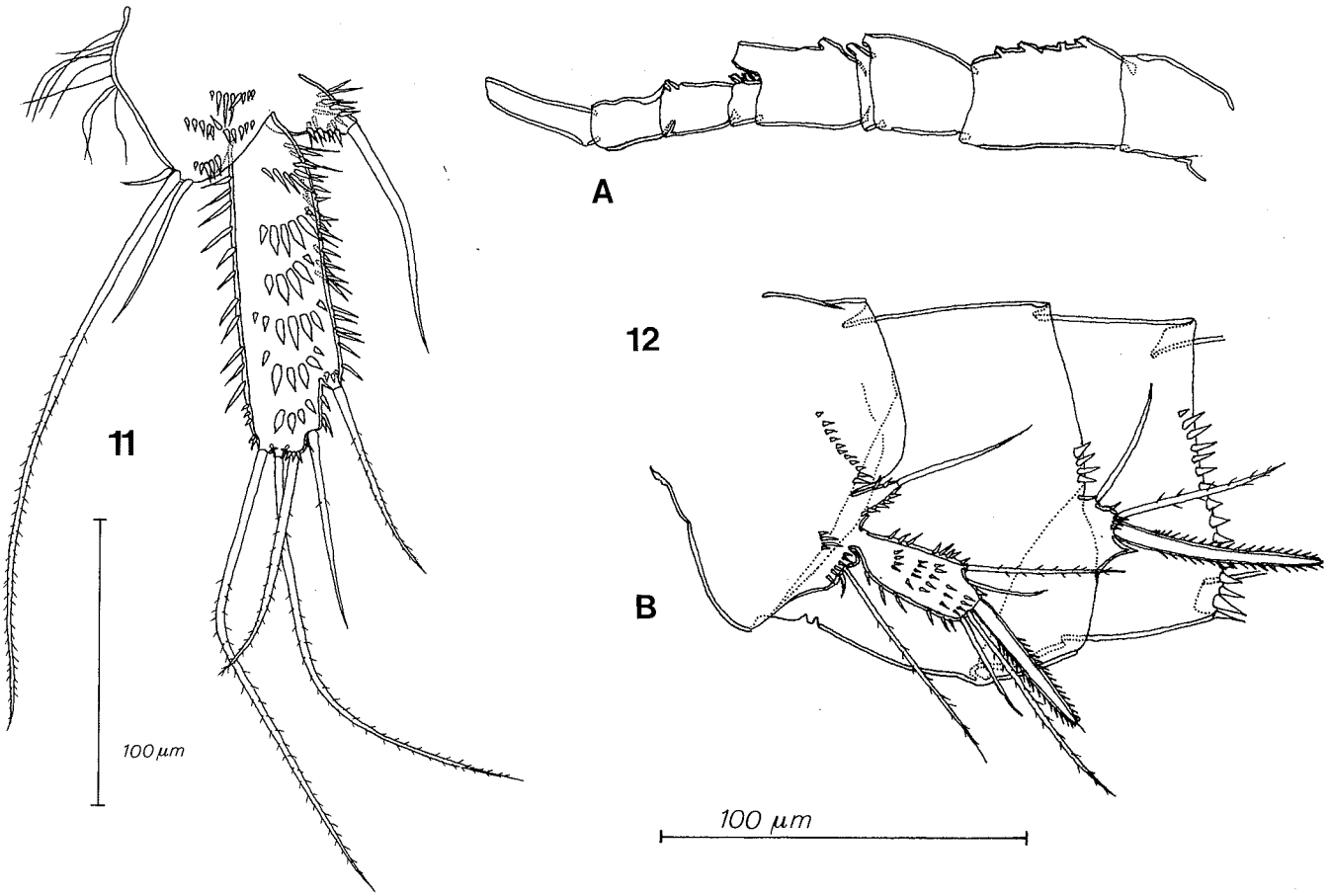
The attachment of the marginal setae of P_2–P_4 enp segments 2 and 3 is anteriorly surrounded by a few tiny spinules, which are especially prominent at the most distal seta. An anterior comb of fine hairs occurs above the insertion of the ultimate and penultimate interior setae of each exp segment 3 (the one above the ultimate seta of P_2 being inconspicuous).

Posterior surface adornment of the rami as follows. Exp segment 1 with a row of fine rather long hairs on its surface (P_2 and P_3) and on its internal margin (P_2–P_4); exp segment 2 also with a marginal row (P_2–P_4); both segments with a fringe of short hairs extending near their distal border (P_2–P_4). Enp segment 2 of P_2–P_4 with one oblique row of spinules; enp segment 3 with 2, 3 and 2 such rows on the successive pereiopods, respectively. P_4 enp segments 1 and 2 with scattered spinules; likewise, all P_3 and P_4 exp segments with numerous minute hairs. On P_4 exp segment 3 these occur in somewhat oblique, anastomosing rows. On segment 2, they are organized into three distinct, more or less square fields with well-marked limits; on segment 1 and 3 they are indistinctly divided into two groups. As I have observed the same striking P_4 pattern in my four other species, and as moreover it is pictured in the description of *T. bocqueti* (Volkmann-Rocco 1972*a*), one can be certain that it is much more widespread—perhaps even general—in the genus than is apparent from published descriptions.

Fifth leg (P_5) as pictured in Fig. 11. Baseoendopodite with three rows of spines on its surface. Its inner lobe bears three setae of widely different length. Length–width ratio of the exopodite 3.71 (3.52–4.00, 5 specimens). Its surface bears well-defined rows of rather flat and triangular spines. Six rows appear on intact specimens, though often a worn-like patch was found instead of the distal ones.

4.5.3. *Description of the male.* Habitus cyclopoid but more slender than the female (as usual in *Tisbe*). Total length averaging 0.66 mm (0.62–0.74 mm, 5 specimens); width of cephalothorax 0.27 mm (0.25–0.29 mm, 5 specimens). Distal border of the 2nd, 3rd and 4th abdominal segments ventrally and laterally fringed with spinules, exactly as in the female. On the first abdominal segment such spinules are present only laterally, above the P_6.

Appendages, but for their size, as in the female unless stated otherwise. The A_1 (Fig. 12*A*) is prehensile, 9-segmented, the 5th and 9th bearing an aesthetask. The peculiar forked setae are present here as well, with those on segment 2 especially prominent. The Mxp (Fig. 6*B*) exhibits a clear sex-dimorphism: the terminal hook is sinuous, the internal margin of the basal segment more arched distally and its bristles stronger, more procumbent and more regularly in-



Figs. 11, 12. Tisbe furcata (Baird). — *11.* ♀, P_5. — *12.* ♂. *A*, A_1 (setation omitted). *B*, P_5 and P_6.

serted than in the female. The dimorphism is however less pronounced than, e.g., in *T. bulbisetosa* (Volkmann-Rocco 1972*a*) and the *gracilis* species group (Volkmann-Rocco 1973*b*).

Male P_5 and P_6 as in Fig. 12*B* (size indications on these appendages refer to laboratory-raised individuals). Baseoendopodite of P_5 with an external spinulose projection carrying a seta of 42 µm (38–49 µm, 4 specimens); internal lobe, corresponding to the endopodite, with a seta of 66 µm (58–83 µm, 5 specimens) flanked by a very short internal one (6 µm; 4–7 µm, 6 specimens) and a few spinules more or less exterior to it. P_5 exp with five short transverse rows of spinules; it is 37 µm long (35–40 µm, 8 specimens) and 16 µm wide (14–18 µm, 7 specimens), with ratio 2.34 (2.16–2.50, 7 specimens). The rim of this segment bears (from inside to outside) a subterminal seta (30 µm; 25–38 µm, 5 specimens), a terminal seta (56 µm; 52–60 µm, 5 specimens), a stout terminal spine (43 µm; 36–48 µm, 9 specimens) carrying a short apical setule (4 µm; 2–5 µm, 7 specimens), a subterminal seta (22 µm; 18–28 µm, 4 specimens) and a final lateral one (44 µm; 41–46 µm, 4 specimens). P_6 represented by a lobe bearing a stout ciliated spine (59 µm; 55–67 µm, 6 specimens) and two setae, one of 48 µm (44–54 µm, 4 specimens) inserted near the base of the spine and one of 36 µm (29–41 µm, 3 specimens) at some distance anterior to it.

4.5.4. *Description and ontogeny of the colour pattern.* Living *Tisbe furcata* exhibit a distinctive colour pattern. Adult females (Fig. 3*A*) have a pigmented band of varying width across the cephalothorax and each of the three free thoracic segments, the last one however being extremely faint and indistinct. These thorax bands may be interrupted by unpigmented gaps between the lateral and central parts (sometimes one one side only). Central or lateral parts may be missing altogether. The first and third free thoracic segment also have some pigment concentrated ventrally along their exterior margin. The distal half of the 3rd and the proximal half of the 4th A_1 segment are also coloured; so are the margins of the labrum. The swimming legs appear increasingly pigmented towards their distal ends, but mainly at the joints and the external exopod spines. The P_5 (baseoendopodite+exp) and the large furcal setae may be slightly tinged pinkish. Finally, there is a streak of colour running along the lateral sutures of the genital double-segment and bending rostrad on the ventral side.

The pattern is somewhat different in adult males. They do have a band across the cephalothorax, but instead of those in the middle of each thorax tergite there is a thin stripe bordering its posterior margin (as in the *holothuriae* group). The margins of the abdominal segments are likewise coloured (hardly so in the female). There is an intense spot of pigment, ventrally on either side, in the turned-over edge of the cephalothorax—about on a level with the mouth. There are no streaks of colour in the genital area. A_1 pigmentation is present in the distal half of segment 3, segment 4 and the proximal half of segment 5.

As will be evident from the foregoing description, the localisation of pigment in this species is extremely similar to

that in *T. bulbisetosa* (Volkmann-Rocco 1972*a*), in *T. pentataenia* (Volkmann-Rocco 1973*a*) and in the *trifasciata* morph of *T. reticulata* (Bocquet 1951; Volkmann-Rocco 1973*a*).

The shade of the pigment may appear anything from brick-red in intensely coloured individuals, to pink, sometimes even with a faint orange tinge, in animals containing hardly any pigment at all. The intensity of the colouration is influenced by the molting cycle (cf. infra) but there remains considerable variation even when it is finally stabilized in adults. Also the relative intensities of different parts of the body may vary, the genital area of the female usually being stained more intensely than the cephalosome though it may hardly be marked on some occasions. The dorsal banding pattern often exhibits an antero-posterior gradient of intensity (and shade), just as can be observed in the *trifasciata* morph of *T. reticulata* (Bocquet 1951).

Serial observations on isolated individuals have shown that each newly molted copepodite stage is initially colourless. As pointed out by Bocquet (1951) on *T. reticulata,* stage III seems to be the first to show traces of the banding pattern. The latter is gradually acquired anew after each subsequent molt, the pigmentation of metasome and appendages being limited to the adult. Exuviae are normally colourless (cf. also Bocquet 1951). This is probably not due to a rapid loss of pigment, as exceptional banded exuviae remain so very long. It seems therefore that pigment is rapidly resorbed before each ecdysis and slowly reconcentrated afterwards. Mobilisation of carotenoids (dissolved in lipo-protein droplets) into the hemolymph has actually been observed by Lwoff (1927) in adult female *Tisbe* transferring pigment to the eggs during ovogenesis. (He was probably dealing with a species of the *holothuriae*-group rather than with *T. furcata.*)

Sexual dimorphism of the pigment distribution is expressed in the adults only. Casual observations on another species, *T. clodiensis,* revealed that in this species copepodites are banded while adults are not. Bocquet (1951) remarks how in *T. reticulata* the last molt is accompanied by "une véritable métamorphose pigmentaire" from the single copepodite pattern to the various colour morphs of that species.

In partly discoloured specimens of *T. furcata,* two of which have been drawn in Fig. 3*B*, the pattern of relict pigmentation points to the existence of a cellular reticulum which is very similar, though not identical, to that found in two species of the *reticulata*-group, viz. *T. reticulata* (Bocquet 1951) and *T. aragoi* (Volkmann-Rocco 1973*a*). The diversity of band contours which I have observed also suggests that the pigmentation of single cells may be controlled by a "minor polychromatism" as in *T. reticulata* (Bocquet 1951), though the bilateral symmetry of pigment presence is often imperfect in *T. furcata.* To someone acquainted with the papers quoted, the beautiful drawings by Itô (1976) of several species and colour morphs of *Scutellidium* (a genus closely allied to *Tisbe*) are also clear evidence of the presence of a reticulum. It may be assumed that both the general banding pattern and its expression on a cellular reticulum are widespread and presumably monophyletic characteristics shared by *Scutellidium* spp., *T. furcata* and many if not all members of the *reticulata, clodiensis* and *dilatata* groups.

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