THE NAUPLIUS II, METANAUPLIUS, AND CALYPTOPIS STAGES OF *THYSANOPODA TRICUSPIDATA* MILNE-EDWARDS (EUPHAUSIACEA)

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ABSTRACT

A large, spinose metanauplius, a nauplius II, and calyptopis I, found in the Indian Ocean and Equatorial Pacific, are referred to *Thysanopoda tricuspidata*. The identifications are based on the distinctive morphological features shared by these larval stages and by the calyptopes II and III of *T. tricuspidata* identified by Sars (1885), and on the observed distribution of *T. tricuspidata* and the metanauplius in the Indian Ocean. Calyptopes II and III are redescribed to present the complete calyptopis phase of larval development in one account.

During a survey of euphausiids in the Indian Ocean (Brinton and Gopalakrishnan, in press), many specimens of a relatively large and very ornate metanauplius were found. There was conjecture that the curious, apparently undescribed form might be the larva of a species of the genus *Thysanopoda*, and it was sought for next in plankton from the Equatorial Pacific.

The metanauplius was found in these waters as were specimens of a seemingly related nauplius II and calyptopis I together with the calyptopis II, calyptopis III, furcilia, and juvenile stages of *Thysanopoda tricuspidata* identified by Sars (1885). When individuals of each of the larval stages were placed together, they appeared to form a natural developmental series; their relative size, the distinctive shape of developing eyes, telson, and carapace all suggested that the larvae were progressive stages of the same species. Evidence of their specific relationship was found in a detailed study of these features and of the morphology of larval appendages, and there seemed to be sufficient justification for referral of the three unidentified early stages to *T. tricuspidata*.

Redescriptions of the calyptopes II and III of *T. tricuspidata* are included in this paper with identification and description of the nauplius II, metanauplius, and calyptopis I, in order to present the complete calyptopis phase of the species in one account and to illustrate the setation of appendages more fully.

METHODS AND MATERIALS

Specimens of the metanauplius were observed in the standard collections, approximately 200-0 m depth, obtained during the International Indian Ocean Expedition (IIOE), 1962-65. About 100 metanauplii were removed for study. The distributions of *T. tricuspidata* and the metanauplius based on the data of Brinton and Gopalakrishnan are shown in Figure 9.

Selected samples taken during EQUAPAC Expedition by RV *Stranger* of the Scripps Institution of Oceanography in August-September 1956 between long 165°-175°W and lat 6°S-10°N by oblique tow in the top 200 m (Snyder and Fleminger, 1965) were sorted for the metanauplius and calyptopes. Positions of the samples yielding larvae and the developmental stages found in each sample are given in Table 1. The distribution of *T. tricuspidata* in the Pacific is described by Brinton (1962).

For measurement with an ocular micrometer, the larvae were straightened in a few drops of

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TABLE 1.—Location of samples collected by RV *Stranger* during EQUAPAC Expedition which contained larvae of *Thysanopoda tricuspidata* and the developmental stages found. Detailed station data for samples are given by Snyder and Fleminger (1965).

Station No.	Position		Sample (net)	Developmental stage				
	Lat	Long		Nauplius	Metanauplius	Calyptopis		
						I	II	III
15	5°59′N	166°40′W	45 cm	−	+	+	+	−
21	0°00′N	166°55′W	45 cm	−	+	−	−	−
25	4°00′S	167°03′W	45 cm	−	+	+	+	+
25	4°00′S	167°03′W	1 m	−	+	+	+	+
26	5°00′S	167°08′W	45 cm	+	+	+	+	+
26	5°00′S	167°08′W	1 m	+	+	−	+	+
28	5°58′S	175°02′W	45 cm	+	+	+	+	+
28	5°58′S	175°02′W	1 m	+	+	+	−	+
28	5°58′S	175°02′W	1 m	+	+	+	+	−
29	5°01′S	174°59′W	45 cm	−	+	−	+	+

2% formaldehyde in seawater on a slide. Total length (TL) was measured in dorsal view between center of anterior margin of carapace (excluding spines in metanauplius) or rostrum and distal point on posterior margin of telson excluding spines. Other measurements are explained by stage: nauplius II, width (W) at widest point in dorsal view; metanauplius, carapace length (CL) between midpoints of anterior and posterior margins excluding spines, carapace width (CW) at widest point between anterolateral margins excluding spines, both measured in dorsal view; calyptopes I and II, carapace length (CL) between midpoints of anterior and posterior margins measured in lateral view; calyptopis III, carapace length (CL) from rostrum to distal point on posterior margin measured in lateral view. The range (r) and mean (m) of each measurement and number (n) of specimens measured are given by stage.

Approximately equal numbers of the metanauplius stage from the Indian and Pacific Oceans were measured. The measurements given for nauplius II and calyptopes I-III, however, are based only on larvae from the Equatorial Pacific and, as calyptopis larvae of a single species have been shown to vary in size in different areas of the oceans (Mauchline and Fisher, 1969), it should be emphasized that the larvae measured for this study were collected during one season in one area of the Pacific. Measurements of some nauplius II and calyptopis stages sorted from Indian Ocean samples did fall well within the size ranges of Pacific larvae in equivalent developmental stages. Specimens of a nauplius I definitely referable to *T. tricuspidata* were not found.

For detailed study and dissection of appendages, larvae were placed in glycerine. Some were stained with Chlorazol Black E to clarify appendage setation. Fourteen nauplii and at least 20 individuals of each of the metanauplius and calyptopis stages I-III were examined in detail. At least 10 specimens of each stage were dissected for study of appendages. In a study of the larval development of *Nematoscelis difficilis* based on both larvae reared in the laboratory and larvae from the plankton, Gopalakrishnan (in press) found no variability in form or setation of appendages among individuals at the same stage of development. This also appears to be true of *T. tricuspidata* larvae, in the stages described, with respect to the mouthparts where setation is usually intact in preserved specimens. On antennules, however, the terminal setae, spines, and aesthetascs (sensory setae) were frequently broken; in calyptopis II, for instance, only 1 of 26 antennules examined had the third seta intact on the inner and outer flagella. An estimate of variability in the fragile setation in this species will require a detailed study of larvae either reared in the laboratory or collected specifically for the purpose.

Drawings of both whole larvae and appendages were prepared with the Wild M20[3] com-

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

pound microscope equipped with drawing attachment.

Nomenclature for description of appendages is based on that of Gurney (1942). For a review of the literature on larval development of the Euphausiacea and the nomenclature of their larval phases, the reader is referred to the papers by Gopalakrishnan (in press) and by Mauchline and Fisher (1969).

RESULTS

DESCRIPTION OF DEVELOPMENTAL STAGES

Nauplius II (Figure 1a, b)

Measurements: TL, r = 1.00-1.12 mm, m = 1.06 mm; W, r = 0.48-0.56 mm, m = 0.53 mm; n = 43.

Body oval, about 2 times as long as wide, anterior pointed, posterior truncate; posterior margin armed with 10 spines—3 pairs of posterolateral spines and 2 pairs of small to rudimentary medial terminal spines, posterolateral spine 1 (outer) is small, spines 2 and 3 are relatively large, only spine 3 (inner) bears spinules.

Antennule (Figure 4a) uniramous; with 2 terminal setae, 1 subterminal seta situated medioventrally, and small spiny prominences at base of each seta—that below largest terminal seta is like small lobe; spinules are distributed on surface as figured.

Antenna (Figure 5a) biramous; protopod may be constricted near middle and appear weakly segmented; endopod unsegmented with 3 terminal plumose setae, a rudiment of 4th terminal seta, 1 subterminal seta on inner margin, and rows of spinules at bases of setae; exopod with outer margin divided into about 10-11 segments (the segmentation was often indistinct in most distal and proximal parts of exopod), the 5 distal segments bear plumose setae—the terminal segment has 2 setae with a few spinules and the remaining 4 segments bear 1 seta each.

Mandible (Figure 6a) biramous and unsegmented; both rami bear 3 plumose setae with spinules at base of setae.

In well-developed nauplii nearing molt to metanauplius, the carapace of the metanauplius with its distinctive ornamentation could be seen inside the cuticle of the nauplius (Figure 1a), both the large long spines around the anterior margin which fold up and back around the body and the 4 large medial and smaller posterolateral spines on posterior margin may be visible and may be partially dissected out.

Metanauplius (Figure 1c, d)

Measurements: Equatorial Pacific larvae - TL, r = 1.36-1.50 mm, m = 1.43 mm; CL, r = 1.02-1.10 mm, m = 1.05 mm; CW, r = 0.60-0.70 mm, m = 0.64 mm; n = 39. Indian Ocean larvae - TL, r = 1.36-1.52 mm, m = 1.45; CL, r = 0.98-1.10 mm, m = 1.05 mm; CW, r = 0.61-0.68 mm, m = 0.65, n = 43.

Carapace with rounded frontal and anterolateral margins produced into long spines (the number of spines, counted in 25 individuals, ranged from 21 to 23 with 23 larvae having 22 spines), there may be tiny spines or "hairs" posterior to the posteriorly directed last large spine; posterolaterally deep winglike extensions of carapace curve ventrolaterally with margins produced into strong posteriorly directed spines which diminish in size around posterior margin where they are separated by small spines; the 4 large medial spines on posterior margin are usually relatively long and they project up dorsally away from body of larva. A faint outline of developing eyes is visible. Tail long and tapering with rounded posterolateral margins and median indentation, there is now a pair of lateral spines in addition to 3 pairs of posterolateral spines and 2 pairs of medial terminal spines, a small rudiment of one or both of inner (third) pair of terminal spines may be present.

In one well-developed metanauplius near molt, the telson of calyptopis I with invaginated terminal and lateral spines was visible beneath the cuticle (Figure 1e). As can be seen, posterolateral spine 3, although shorter than spine 2 in the metanauplius, is more deeply invaginated and longer than spine 2 in the developing calyptopis, and when extruded, it will have the greater relative length observed in the calyptopis stages of *T. tricuspidata.*

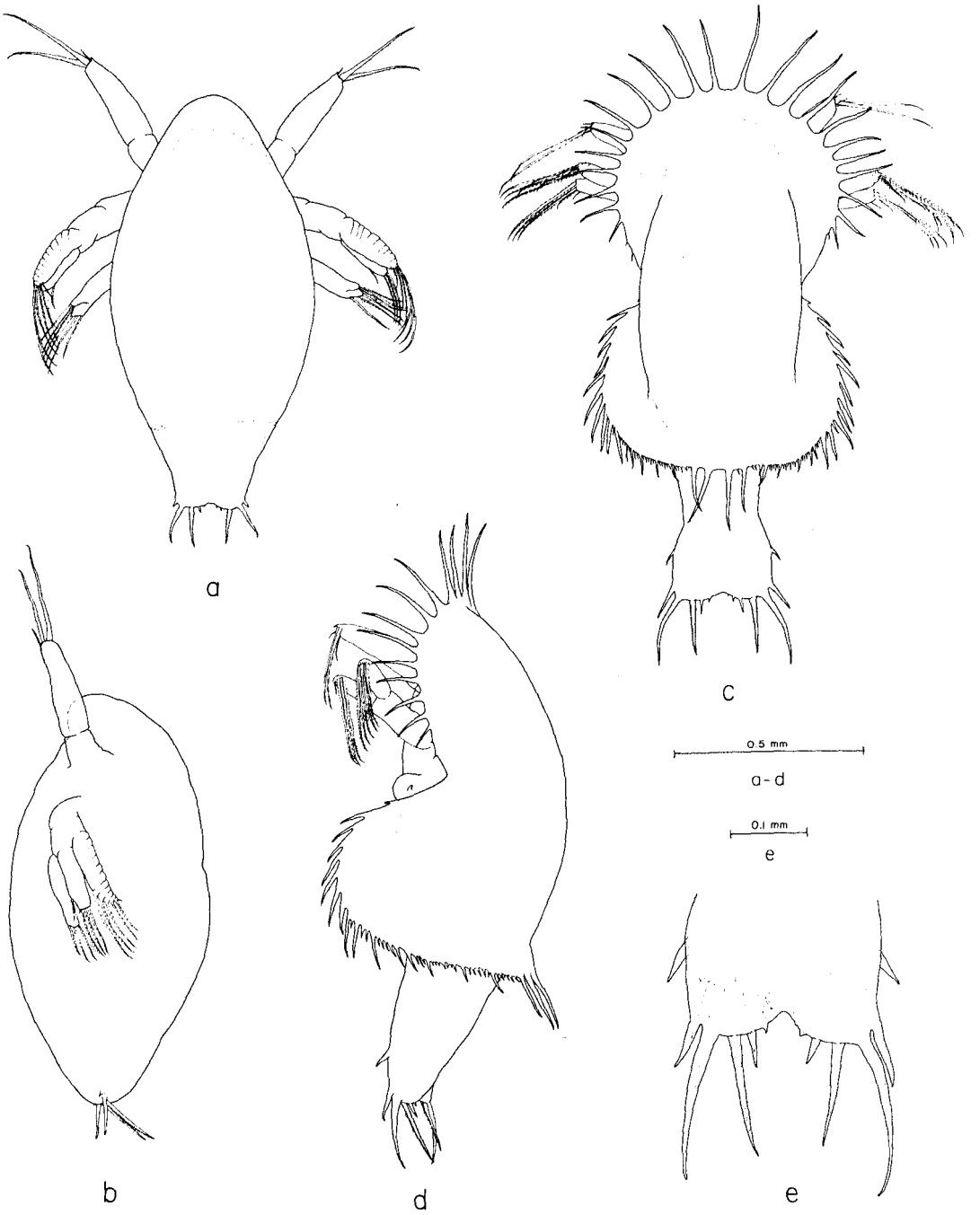
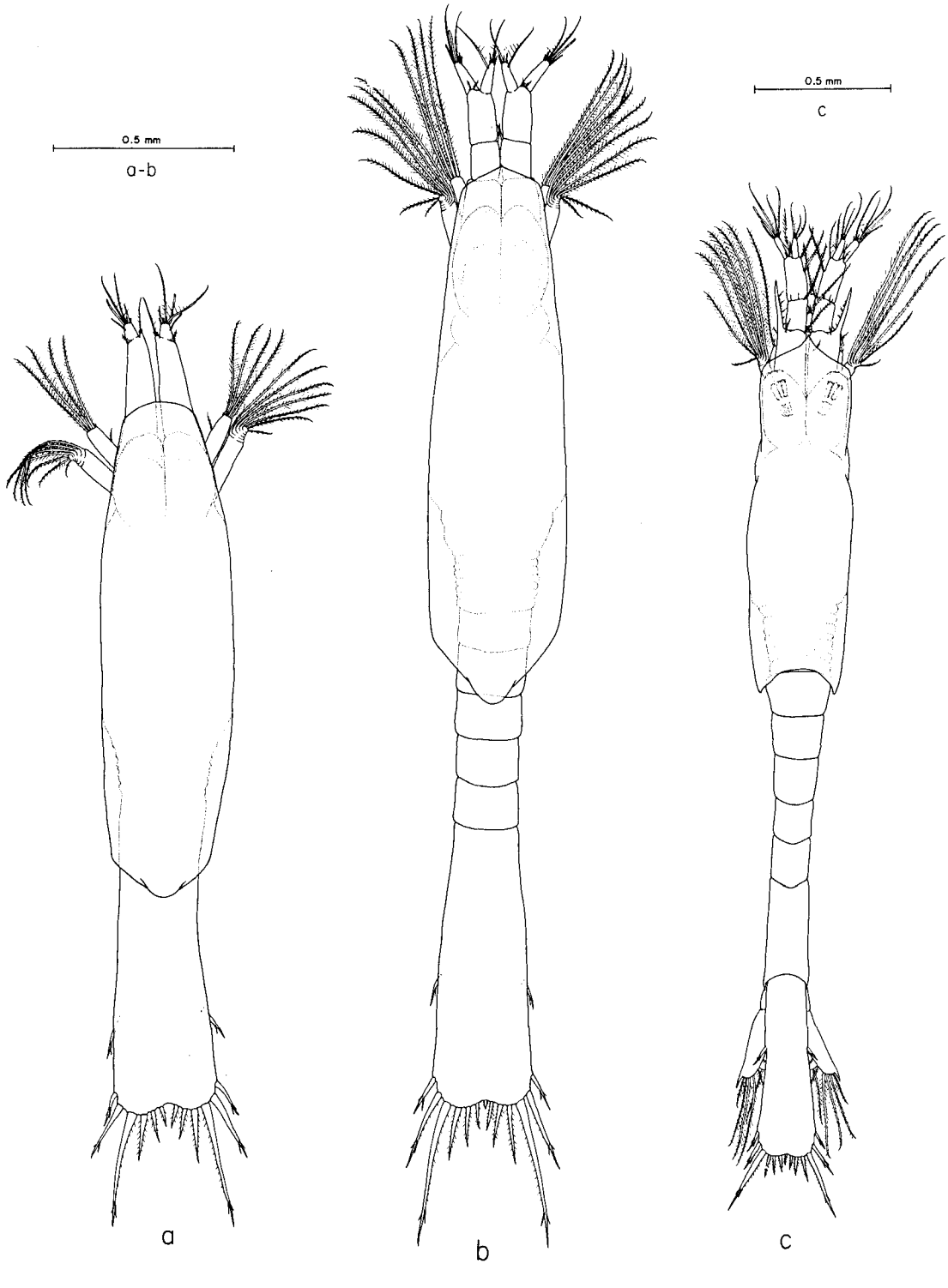


FIGURE 1.—Nauplius: a-b, dorsal and lateral views. Metanauplius: c-d, dorsal and lateral views; e, posterior enlarged showing invaginated spines of calyptopis I beneath cuticle.

FIGURE 2.—Calyptopis: a-c, stages I-III, dorsal views.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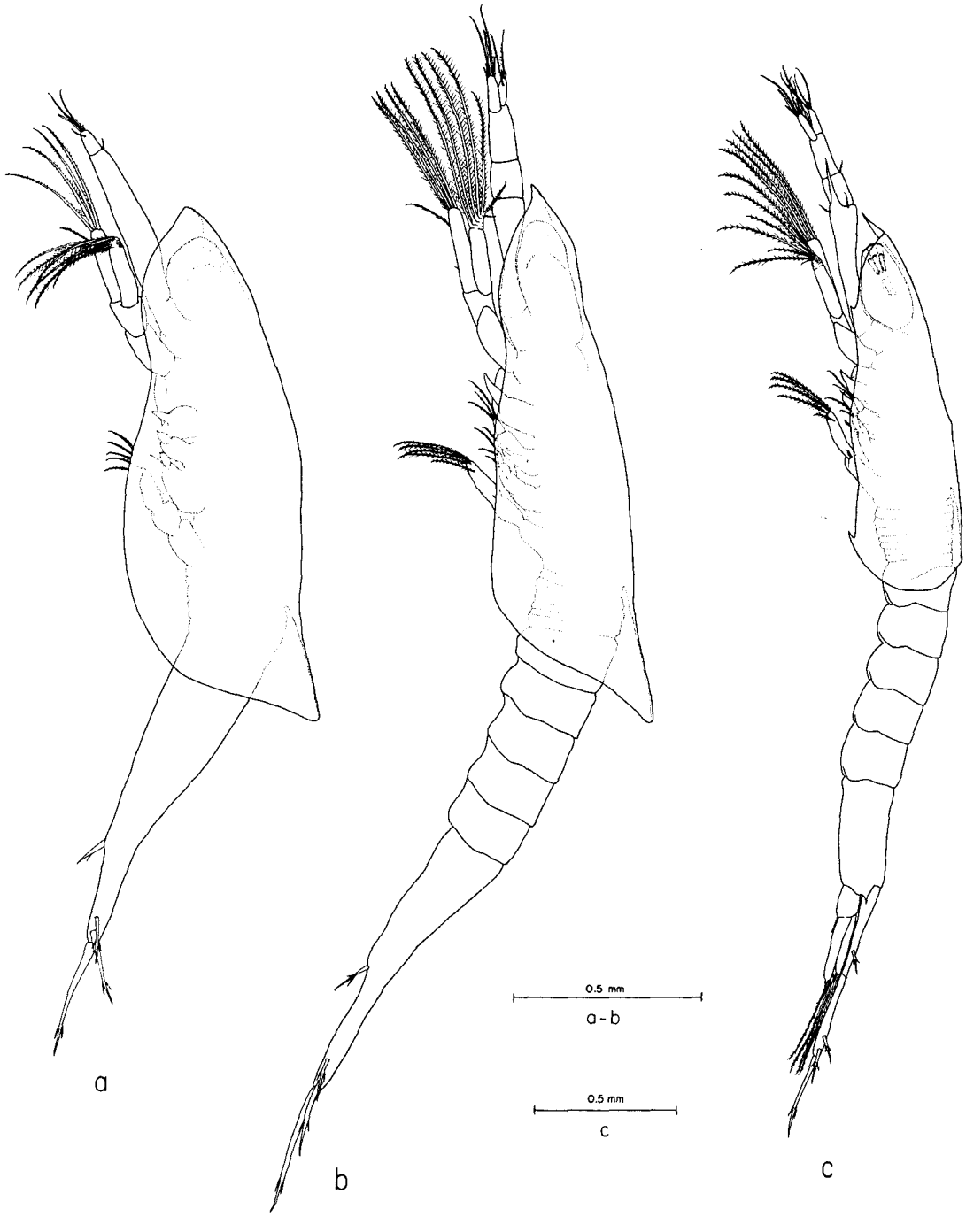

FIGURE 3.—Calyptopis: a-c, stages I-III, lateral views.

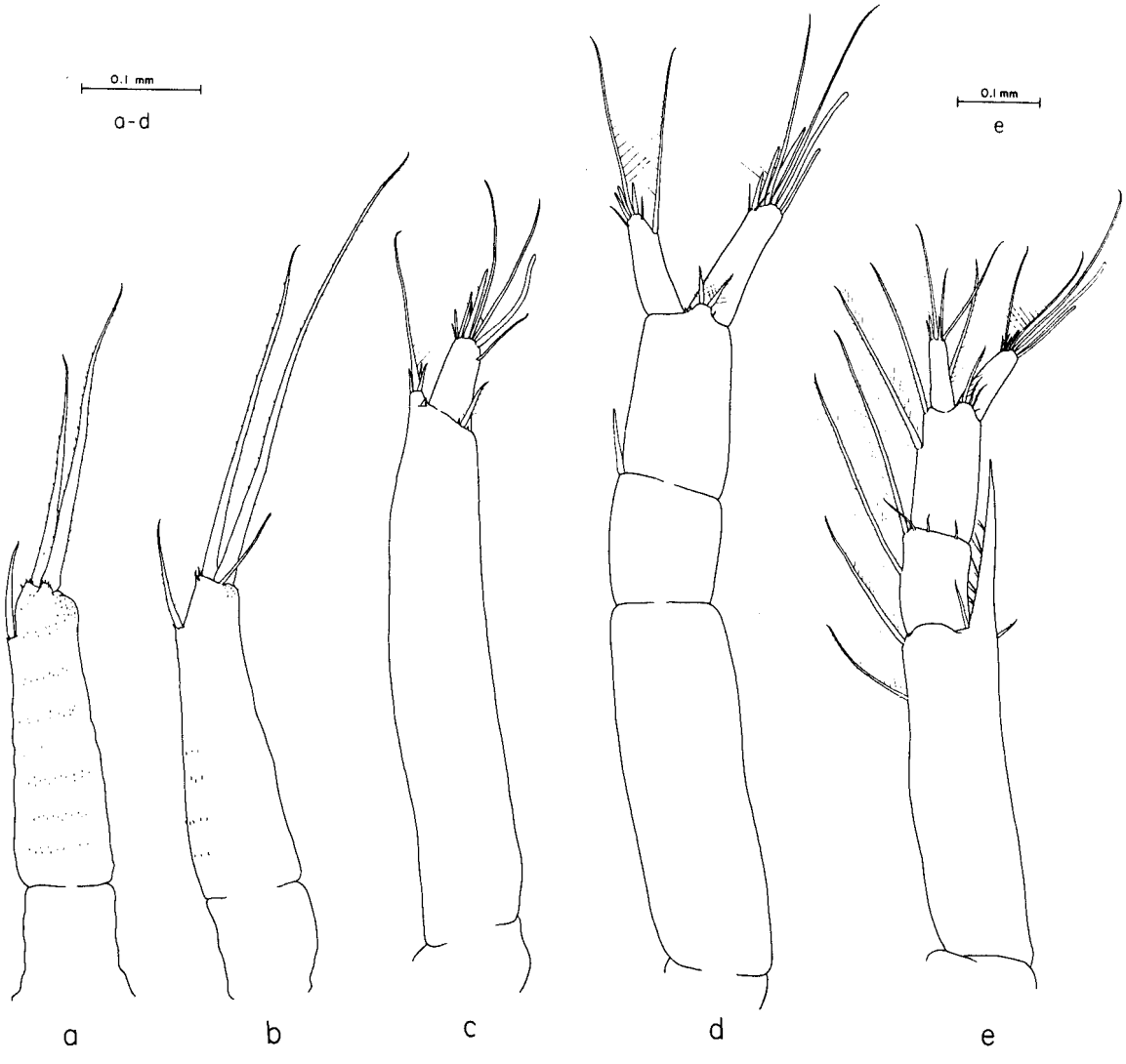

FIGURE 4.—Antennule, right, dorsal view: a, nauplius; b, metanauplius; c-e, calyptopes I-III.

Antennule (Figure 4b) now with 3 terminal processes, there is a small seta or sensory filament in place of spiny lobe; surface spinules appear to be organized into fewer simpler rows.

Antenna (Figure 5b) with protopod segmented into coxa and basis, there are a few spinules on inner distal margin of each; endopod with 4 terminal setae—1 seta is relatively short, and 2 setae on inner margin—the proximal seta is short to rudimentary; exopod with 5 short terminal segments but without proximal segmentation of outer margin seen in nauplius, the setation is unchanged although there may be a spinous rudiment of third seta on terminal segment.

Mandible (Figure 6b) reduced to rounded lobe bearing pointed lateral process.

Maxillule, maxilla, and maxilliped are represented only be rounded prominences. In specimens nearing molt, the rudimentary spines on endopod and endites of developing maxillules and

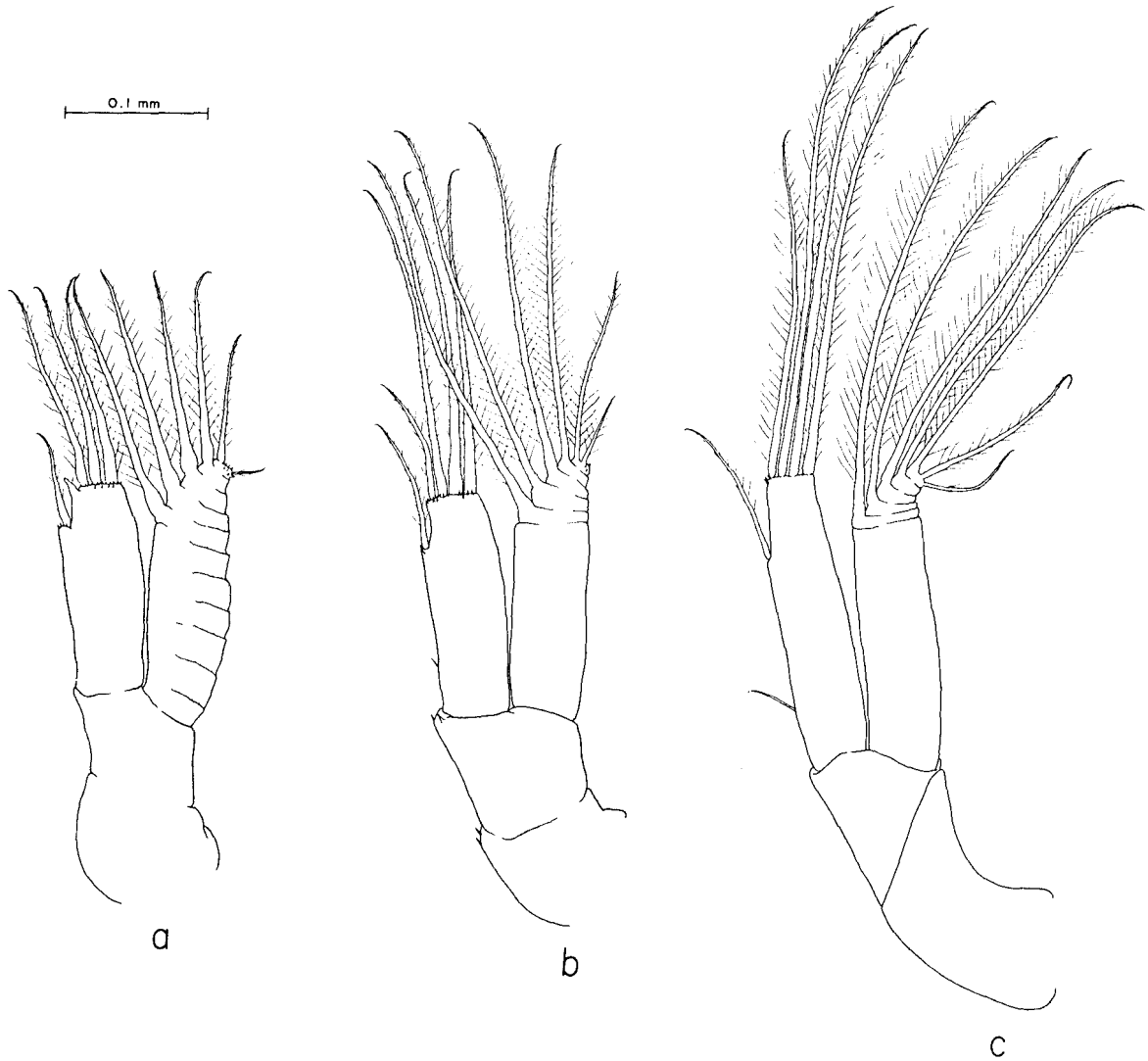

FIGURE 5.—Antenna, right, anterior view: a, nauplius; b, metanauplius; c, calyptopis I.

maxillae and setae of biramous maxilliped of calyptopis I may be seen through the cuticle. Figure 7a and d show such a maxillule and maxilla dissected from a metanauplius providing evidence of its relationship with the calyptopis I described.

Calyptopis I (Figures 2a, 3a)

Measurements: TL, r = 1.90-2.16 mm, m = 2.07 mm; CL, r = 1.38-1.48 mm, m = 1.44 mm; n = 34.

Carapace long and slender, without spines, anterior margin forming narrow hood over developing eyes, posterior margin pointed and curving dorsally. Abdomen unsegmented, telson with a pair of lateral spines, 3 pairs of posterolateral spines, and 3 pairs of medial terminal spines, posterolateral spine 3 is now longest; posterior margin curves in medially.

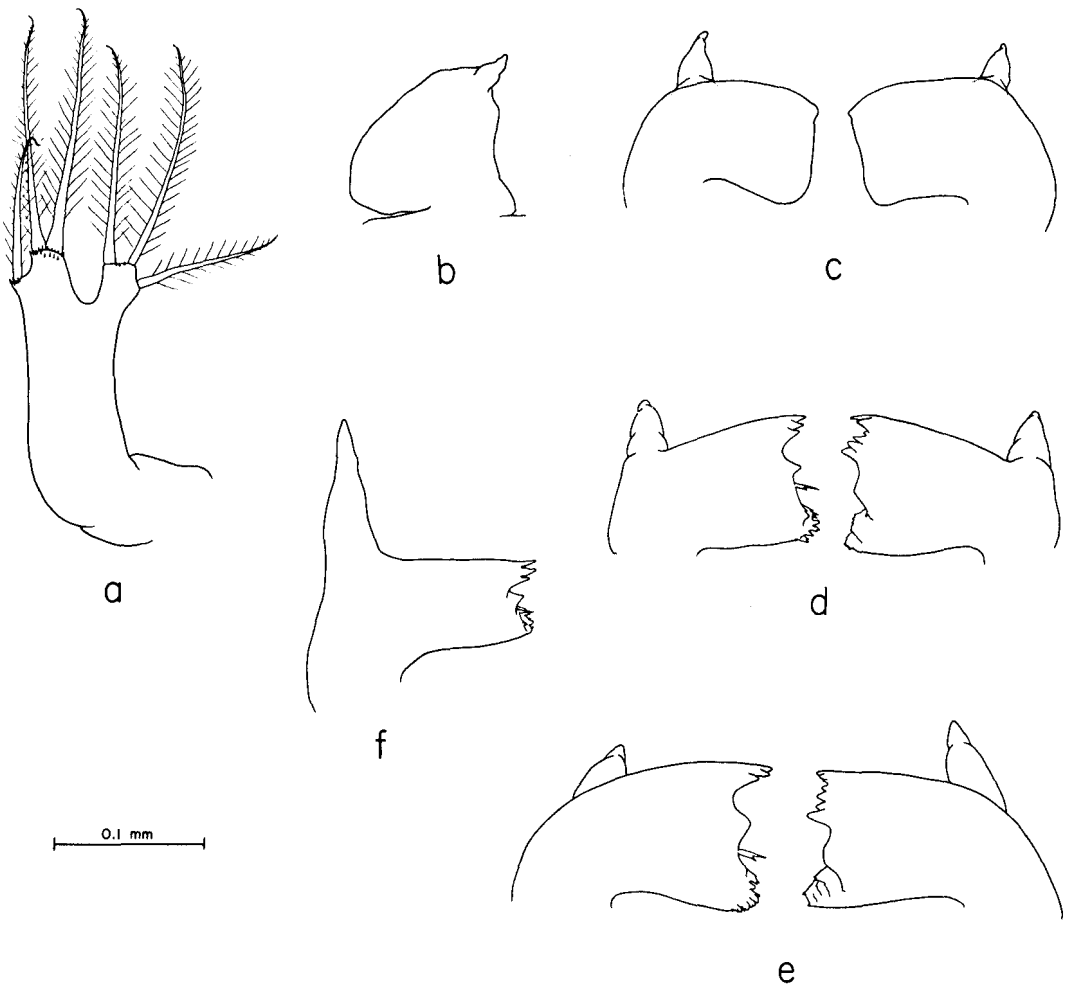

FIGURE 6.—Mandible: a, nauplius, right, anterior view; b, metanauplius, left, posterior view. Mandibles, posterior view: c-e, calyptopes I-III; f, right mandible of calyptopis II rotated to show relative length of triangular lateral process.

Antennule (Figure 4c) 2-segmented; protopod long and slender with small terminal segment forming outer flagellum which bears about 9 terminal processes including 2 long setae, 2 aesthetascs (one of these is situated slightly subterminally on outer margin), and about 5 spinous processes of varying sizes; there is rudiment of inner flagellum bearing 1 long seta and 3 spinous processes; a small spine is situated at base of inner ramus, and there is 1 seta and 1 or 2 small spines dorsally on distal margin of protopod at base of outer flagellum.

Antenna (Figure 5c) now with form found in calyptopis stages I-III; endopod with 4 long terminal setae and 2 setae on inner margin, proximal seta still relatively short; exopod with 7 plumose setae, the terminal segment now bears 3 setae; coxa and basis without spinules.

Mandibles (Figure 6c) rudimentary, with large lateral process, medial margins smooth except for 1 small incisor tooth on each mandible.

Maxillule (Figure 7b) armed only with rudimentary small spines; endopod of 1 segment with 3 spines; exopod a very small lobe bearing

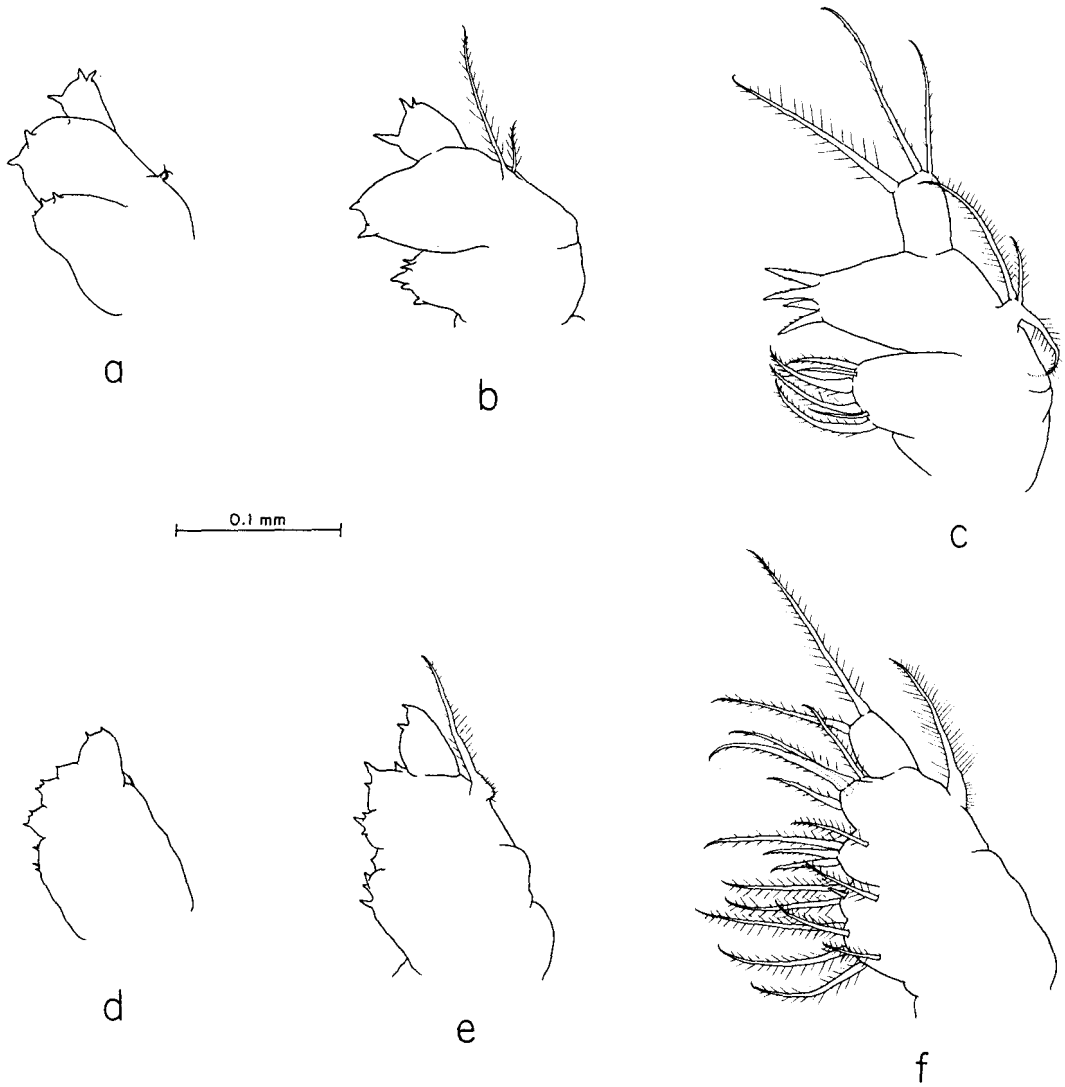

FIGURE 7.—Maxillule, left, posterior view: a, developing appendage of calyptopis I dissected from metanauplius; b-c, calyptopes I and II. Maxilla, left, posterior view: d, developing appendage of calyptopis I dissected from metanauplius; e-f, calyptopes I and II.

2 plumose setae; basal endite with 2 spines, there may be a tiny third spine between large spines; coxal endite with about 5 spines.

Maxilla (Figure 7e) with rudimentary setation except for 1 plumose seta arising from small finely setose lobe on lateral margin and representing exopod; endopod of 1 segment with 2 spines; medial lobes of endites discernible with small spines on medial margin.

Maxilliped (Figure 8a) biramous; exopod with 4 terminal plumose setae and 1 subterminal seta on outer margin, also a small stout seta at base of exopod near articulation with basis; endopod of 2 segments, terminal segment with 4 setae distally, 3 terminal and 1 subterminal; there are a few weak setae and rudiments of setae on medial margins of both coxa and basis and of proximal segment of endopod.

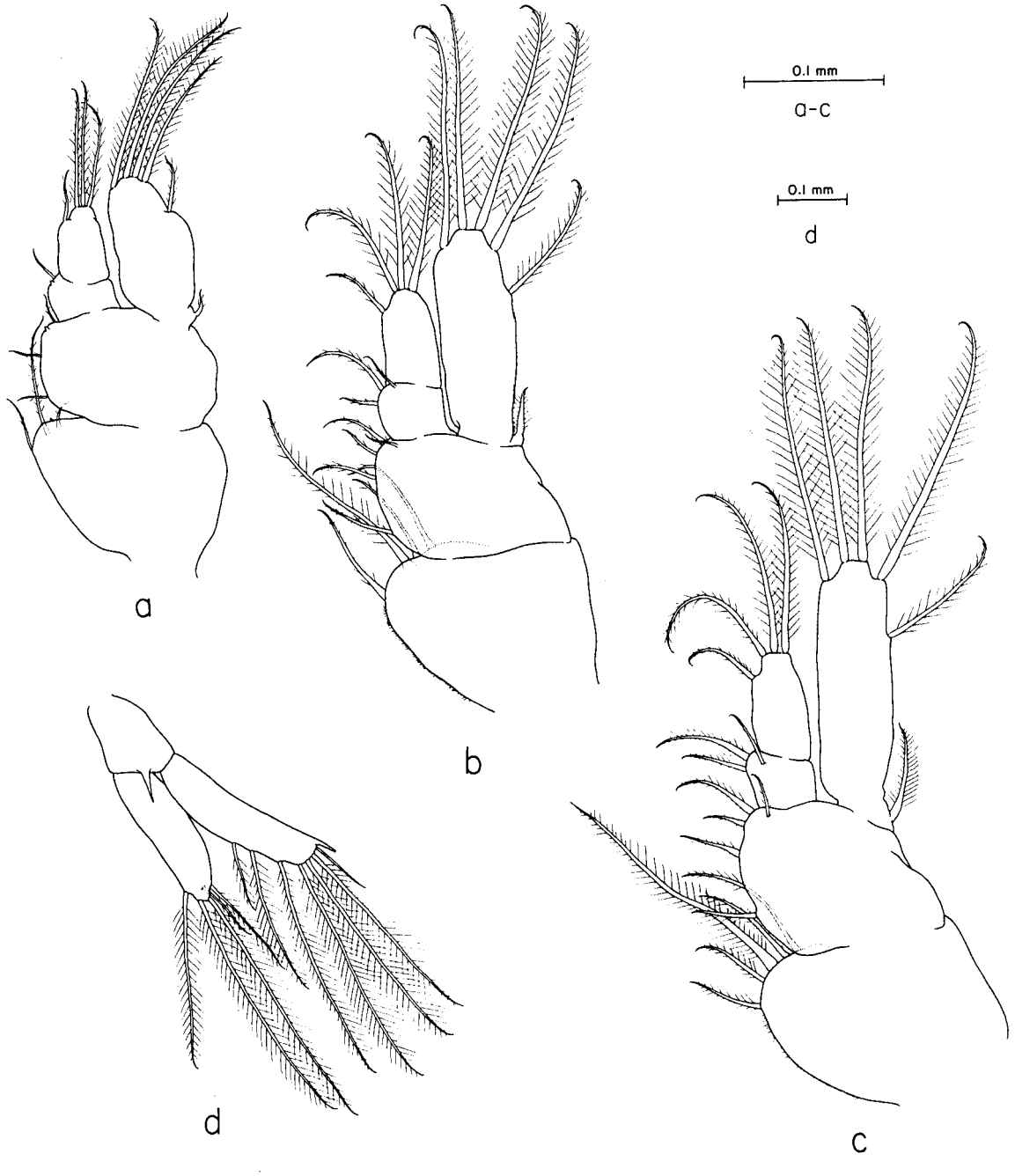

FIGURE 8.—Maxilliped, left, posterior view: a-c, calyptopes I-III. Uropod, left, ventral view: d, calyptopis III.

Calyptopis II (Figures 2b, 3b)

Measurements: TL, r = 2.50-2.74 mm, m = 2.63 mm; CL, r = 1.42-1.54 mm, m = 1.49 mm; n = 18.

Carapace with frontal margin produced into small triangular spine and posterior margin more pointed than in preceding stage; developing eyes may contain some pigment. Thoracic segments forming; abdomen segmented, sixth segment not separate from telson; posterior margin of telson with small median 7th terminal spine.

Antennule (Figure 4d) with protopod divided into 3 peduncular segments, there is stout seta distally on inner margin of second segment and a small dorsal lobe bearing 2 setae and a few small spines on distal margin of third segment at base of outer flagellum; outer flagellum with about 9 terminal processes including 2 setae, 2 aesthetascs, and about 4-6 spinous processes; inner ramus with about 6 terminal processes including 1 seta and usually 5 spines, there is 1 subterminal seta on inner margin.

Antenna as in calyptopis I.

Mandibles (Figure 6d) asymmetrical, now differentiated into incisor and molar areas, right mandible with slender articulated spine with spinule situated near molar area; right mandible rotated in Figure 6f to show relative length of lateral process.

Maxillule (Figure 7c) with setae and spines fully formed; endopod of 1 segment with 3 setae; exopod with 3 plumose setae; basal endite with 4 stout spines armed with spinules; coxal endite with 6 setae—2 are small smooth setae, 4 are setose and the largest bears strong spinules distally.

Maxilla (Figure 7f) with full setation; endopod of 1 segment with 2 setae; exopod represented by a single plumose seta on small setose lobe; basal endite with 3 medial lobes, coxal endite bilobed, lobes 1-5 with setation of 5-4-4-3-1 progressing distally, 1 seta on each of lobes 1-3 is situated on posterior face of maxilla, 1 marginal seta on lobe 2 is quite small.

Maxilliped (Figure 8b) now with full medial setation; coxa with 4 plumose setae, 1 seta is relatively long; basis with 5 setae; proximal segment of endopod with 3 setae; 1 distal seta on basis and 1 distal seta on first segment of endopod are situated slightly submarginally on posterior face, both are small and frequently difficult to locate; setation of exopod and terminal segment of endopod is unchanged.

Calyptopis III (Figures 2c, 3c)

Measurements: TL, r = 2.90-3.40 mm, m = 3.14 mm; CL, r = 1.30-1.42 mm, m = 1.35 mm; n = 34.

Larva now appears more slender for its length; carapace considerably altered, still forming narrow hood over eyes but in other respects more like carapace of furcilia, frontal margin produced into small triangular rostrum, lateral margins with small anterolateral spine below eye and large posterolateral denticle, posterior dorsal margin no longer tapering to point but indented medially. Eye with 7 well-developed facets arranged in a circle of 6 with seventh central facet, and ommatidia with pigment. Thoracic segmentation more distinct. Abdomen with 6 segments, there is dorsal ridge or fold around segment 1 and segment 6 carries biramous uropods. Setation of telson unchanged.

Antennule (Figure 4e) with distal lateral margin of basal peduncular segment produced into strong lateral spine which extends to or beyond midpoint of distal segment of peduncle; there are about 5 groups of 2 setae each along inner margin of this spine with spinules between 3 distal groups and a seta at base of spine on both outer and inner margins; basal segment of peduncle dorsoventrally flattened; the peduncular segments bear plumose setae along medial margins with 2-2-3 setae on segments 1-3 respectively, there are 3 small setae around distal margin of segment 2, and 3 setae and setules on dorsal lobe below outer ramus on distal margin of segment 3; outer flagellum with 2 aesthetascs, 3 setae, and about 4 small spines; inner flagellum with 3 terminal setae and about 3 spinous processes.

Antenna as in calyptopis I.

Mandibles (Figure 6e) similar to calyptopis II, medial teeth somewhat flattened.

Maxillule and maxilla as in calyptopis II.

Maxilliped (Figure 8c) with 5 setae on medial margin of coxa; there is no other change in setation.

No rudiment of the second thoracic appendage was observed.

Uropod (Figure 8d) biramous; protopod with stout ventral spine; exopod produced into posterolateral spine and bearing 7 plumose setae around posterior and medial margins, the seta near posterolateral spine is relatively small; endopod with 5 distal plumose setae, 1 seta is situated submarginally and projects dorsally.

IDENTIFICATION OF EARLY STAGES

The morphological evidence on which the identification of the larval series is based may be summarized as follows: 1) the nauplius II is linked to the metanauplius by dissection of the spinose carapace of the metanauplius from well-developed nauplii; 2) the metanauplius and calyptopes I-III are related by the setation of mouthparts, particularly the endopods of maxillule and maxilla; 3) the third calyptopis is identified with the larva described by Sars (1885) by the long and slender body, the distinctive 7-facetted eyes, and the setation of the exopod and 1-segmented endopod of the maxillule which bear 3 setae each.

There is additional evidence to support the identification of the metanauplius in the way in which the observed distribution of the larva corresponds with that of *T. tricuspidata* in the Indian Ocean as shown in Figure 9, and in the occurrence of the larvae within the range of *T. tricuspidata* in the Pacific.

DISCUSSION

The only description of *T. tricuspidata* larvae found which deals with the calyptopis stages is that of Sars (1885); other authors referring to larvae of the species (i.e., Tattersall, 1936; Gurney, 1947; Lebour, 1950; Pillai, 1957) discuss the furcilia stages only. Sars provides some details of setation with his general descriptions and figures the mandible, maxillule, maxilla, and maxilliped of the third calyptopis (1885, Plate 21, Figures 13-16). The mouthparts of the calyptopis III described in this study agree with those figured by Sars in the dentition of left mandible, in segmentation and setation of endopod and exopod of maxillule, in rudimentary exopod of maxilla, and in setation of exopod and terminal segment of endopod of maxilliped. The carapace of Sars' calyptopis III appears to be indented medially on the posterior margin rather than pointed as in calyptopis II, but it is not figured with a lateral denticle.

The descriptions of larvae of other species of the genus *Thysanopoda* are also almost entirely limited to the furcilia phase; only two exceptions were found. Einarsson (1945) described the calyptopes II and III of *T. acutifrons* and Lebour (1950) the calyptopis III of *T. cristata*, but figures of the appendages and the details of setation are not given.

The described larvae of *T. acutifrons* are larger than those of *T. tricuspidata* in equivalent stages; calyptopes II and III measure 3.4 and 3.8 mm in total length respectively while *T. tricuspidata* averages 2.6 and 3.1 mm (Sars' specimens measured 2.5 and 3.5 mm). The carapace of the third calyptopis of *T. acutifrons* is like that of the second calyptopis with "characteristic pointed end," and the lateral denticle is sometimes discernible although very small. Einarsson notes that the maxillule has a palp of 2 segments and an inner lobe with 7 bristles. Frost (1939) figures the appendages of the first furcilia of *T. acutifrons* showing the maxillule with 6 setae on the endopod and 4 setae on the exopod, and the endopod of the maxilla with 3 setae. This setation is probably also found on the calyptopis III of the species she describes. [Einarsson (1945) suggested that, based on the shape of the eye, Frost's larvae may instead belong to *T. microphthalma*; he notes, however, that the species are otherwise alike in development.]

Lebour (1950) describes and figures the carapace of the calyptopis III of *T. cristata* as long and "pointed behind," noting that the larva closely resembles the calyptopis III of *T. acutifrons* described by Einarsson. It is also very large, measuring 4.2 mm in length. Gurney (1947), in his description of the first furcilia

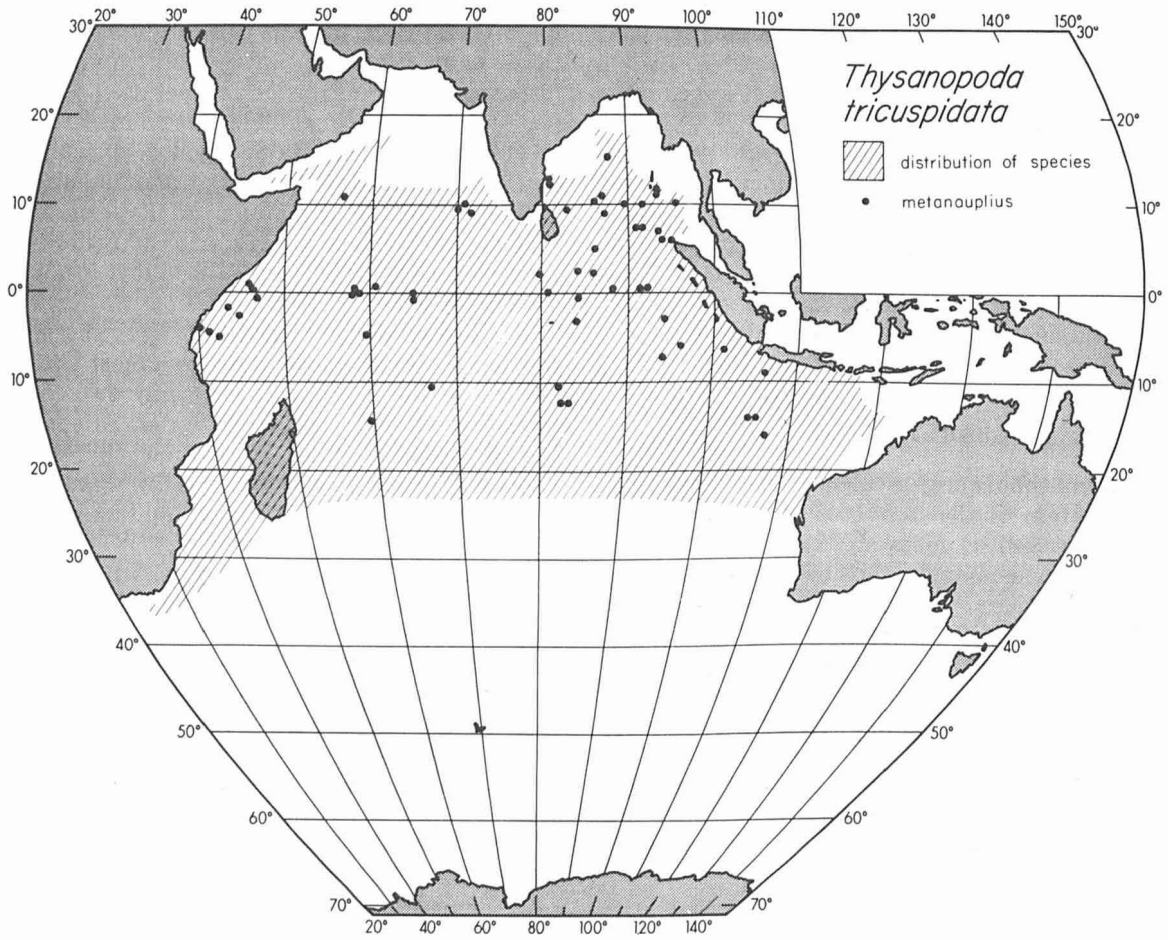

FIGURE 9.—The distribution of *Thysanopoda tricuspidata* and the metanauplius larva in the Indian Ocean based on the analyses of Brinton and Gopalakrishnan (in press).

of *T. cristata,* notes that the maxillule has an endopod of 2 segments, and again it seems likely that this is also found in the third calyptopis.

Both *T. acutifrons* and *T. cristata,* then, differ from *T. tricuspidata* in length of described stages, in shape of carapace in calyptopis III, and probably in details of segmentation and setation of maxillule and maxilla at least.

Calyptopes I and II of *T. monacantha* (identified by E. Brinton) were dissected to compare the endopods of the maxillule and maxilla with those of calyptopes I and II of *T. tricuspidata.* The calyptopis I had full setation of mouthparts and, in both stages, the maxillule, like that of Frost's furcilia, had an endopod of 2 segments with 6 setae and exopod with 4 setae, and there were 3 setae on the endopod of the maxilla. In fact, more setae were found on all of the mouthparts of the *T. monacantha* larvae with the exception of the endopod and exopod of the maxilliped which were like those of the *T. tricuspidata* calyptopes.

Information in these few accounts from the literature and from personal observation suggest that *T. tricuspidata* larvae may prove to differ from larvae of other species of the genus

in many respects. The partial segmentation of antennal exopod in the nauplius II and the form and armature of carapace and telson of the metanauplius may be distinctive, the rudimentary setation of mouthparts in calyptopis I appears to be unusual—indeed the larva seems ill-equipped to feed, there seems to be a reduction in dentition of mandibles and in numbers of setae on mouthparts in calyptopes II and III, and the carapace of calyptopis III is transitional between the usual calyptopis and furcilia forms. In addition, the larvae are known to deviate from trends within the genus in development of abdominal pleopods during the furcilia phase. According to Lebour (1950), *T. tricuspidata* is the most variable in pleopod succession of any *Thysanopoda* species, indeed of any euphausiid known and, as it has been demonstrated that there is a correlation between a more rigidly defined number of furciliar stages and a more oceanic distribution within the genus *Thysanopoda* (Mauchline and Fisher, 1969), such variability in the oceanic species *T. tricuspidata* is surprising.

Although there is too little information available at this time for speculation as to the significance of the unusual morphological features observed in this study, the details found in the literature did support the identification of the larvae in that the combination of setation of endopod and exopod of the maxillule and endopod of the maxilla of *T. tricuspidata* calyptopes was not noted or figured in descriptions of the larvae either of other species of *Thysanopoda* or of other genera of the family.

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