

SEXUAL DIMORPHISM IN AEGISTHID CEPHALOSOMIC APPENDAGES (COPEPODA, HARPACTICOIDA): A REAPPRAISAL

by

RONY HUYS

Marine Biology Section, Institute of Zoology, State University of Gent,
K. L. Ledeganckstraat 35, B-9000 Gent, Belgium

ABSTRACT

The cephalosomic appendages, including the rostrum, are redescribed in the bathypelagic harpacticoid *Aegisthus mucronatus* Giesbrecht, 1891 (Aegisthidae). Profound sexual dimorphism was found in all cephalosomic appendages. For the first time reference is made to the presence of a mandible in the male and figures are given for the male maxillula. Distinct sexual differences are also observed in the structure of the labrum and the labium. The structure and ornamentation of the male antennula clearly shows that the Aegisthidae belong to the monophyletic group Cervinoidea, including also the Rotundiclipeidae and Cerviniidae. Brief comments are made on the nature of the first pedigerous somite, the structure of the anal somite and of the caudal rami. The occurrence of sexual dimorphism in postantennular cephalosomic appendages of harpacticoids is reviewed.

RÉSUMÉ

Les appendices céphalosomiques, rostrum y compris, sont redécrits pour le Harpacticoïde bathypélagique *Aegisthus mucronatus* Giesbrecht, 1891 (Aegisthidae). Un dimorphisme sexuel accusé est remarqué dans tous les appendices céphalosomiques. La présence d'une mandibule chez le mâle est signalé pour la première fois, et des figures sont données pour la maxillule du mâle. Les différences sexuelles sont marquées aussi dans la structure du labrum et du labium. Structure et ornementation de l'antennule du mâle montrent clairement que les Aegisthidae appartiennent au groupe monophylétique des Cervinoidea qui comprend aussi les Rotundiclipeidae et les Cerviniidae. De brefs commentaires sont faits sur la nature du premier somite pédigère, sur la structure du somite anal et des branches caudales. On passe en revue les cas de présence de dimorphisme sexuel dans les appendices céphalosomiques postantennulaires des Harpacticoïdes.

INTRODUCTION

The Aegisthidae Giesbrecht, 1892 is one of the three harpacticoid families currently assigned to the superfamily Cervinoidea (Huys, in press). In contrast to the marine cave-dwelling Rotundiclipeidae and the predominantly deep-sea

inhabiting Cerviniidae, the aegisthids are common members of the bathypelagic community in both the Atlantic (Jones, 1952; Grice, 1963; Owre & Foyo, 1964, 1967; Boxshall, 1979; references in Lang, 1948) and the Pacific Oceans (Gamô, 1893; references in Lang, 1948); fewer Indian Ocean records (Stebbing, 1910; Sewell, 1940) are known.

Though only three species are considered valid today (Boxshall, 1979), the taxonomic history of the genus *Aegisthus* is complex. In particular the common *A. mucronatus* seems to be the stumbling block of the genus as is clearly exemplified by the number of species considered synonymous with it. The pre-Langian literature on the subject bristles with glaring mistakes and even in more recent times misinterpretations have been made by various authors.

Despite not having inspected any type specimens, Lang (1948) succeeded in clearing up the enormous nomenclatural imbroglio created by such authors as Dahl, T. Scott, Wolfenden, Sars, and Farran.

The cause of the taxonomic difficulties within the genus is principally the astounding sexual dimorphism expressed, unlike other harpacticoids, in the structure of the rostrum and the cephalosomic appendages. As a result, females and their respective males were often classified as separate species, since intersexual variability within a species often exceeds the differences between females of distinct species.

The genus *Aegisthus* was established by Giesbrecht (1891) to include two species, *A. mucronatus* and *A. aculeatus*, collected in the Pacific Ocean near the Galápagos Islands. Later, Giesbrecht (1892) described and figured both species in detail on the basis of females. In

a footnote Giesbrecht (1892) assigned the genus to a separate family, the Aegisthidae, but this has been overlooked by most authors. T. Scott (1893) collected both sexes of a new species, *A. longirostris*, from the Gulf of Guinea. Of the male cephalosomal appendages Scott drew attention only to the antenna and the maxilla which was incorrectly regarded as the maxilliped. Disregarding *A. mucronatus* with which the new species agreed well, T. Scott (1893) briefly made comparison with *A. aculeatus*. On the basis of the diagnostic rostrum, Thompson (1903) was the first to suspect that both *A. longirostris* and *A. mucronatus* belong to the same species. Subsequently, A. Scott (1909), dealing with the copepods collected during the Siboga Expedition, listed his father's species among the synonyms of *A. mucronatus*.

Dahl (1895) contributed a great deal to the taxonomic confusion of the genus by splitting up T. Scott's *A. longirostris*. He regarded part of *A. longirostris* as synonymous with *A. mucronatus* but incorrectly assigned the remainder to a new genus and species *Hensenella mirabilis*. Furthermore, Dahl (1895), being unaware of Giesbrecht's (1892) account, grouped *Aegisthus*, *Hensenella* and *Pontostratiotes* in a new subfamily Hensenellinae. Monard (1927) lumped together the same genera (quoting incorrectly *Hensella*); however, he applied the family name Pontostratiotidae, originally proposed by A. Scott (1909) to include *Aegisthus* and *Pontostratiotes*. Lang (1948) rightly refuted these reassessments altogether in favour of Giesbrecht's family name Aegisthidae.

Wolfenden (1902) described a new species *A. atlanticus* on the basis of a single specimen of unknown sex and without presenting any drawings. Lang (1948), inspired by Johnson's (1937) work on the development of *A. mucronatus* and exaggerating the importance of the structure of the sixth leg, assumed Wolfenden's specimen to be the male of *A. mucronatus*. However, some of Wolfenden's (1902) statements give evidence that he was dealing with the female, not the male: (1) the antennula consists of 6 segments bearing a strong spine on the 2nd and aesthetascs ("peculiar process (sensory?)") on the

3rd and 6th segments, (2) the rostrum is long, stout and curved downwards, and (3) the maxillula and maxilliped agree closely with those of Giesbrecht's (female!) specimens of *A. mucronatus*. Hence, it can be safely concluded that *A. atlanticus* is synonymous with female *A. mucronatus*.

Sars' (1916) description of *A. dubius* from the Sargasso Sea was based on two males and, as Lang (1948) pointed out, apparently comprises a wrongly figured first pedigerous somite. According to Johnson (1937) Sars' species is standing alone only on the basis of the absence of serrations on the posterior margins of the body somites and the relatively small size. My own observations revealed that the former character is often less expressed in males and consequently can be easily overlooked; Boxshall (1979) found the body length in aegisthids to be extremely variable in both sexes. Sars (1916) mentioned the resemblance between his males and female *A. mucronatus*, though he regarded them as a separate species because of the absence of the rostrum (described for the first time in males), the antennular structure and the striking reduction of the mouthparts. It is clear that Sars (1916) did not compare *A. dubius* with the male of *A. longirostris* which shows exactly the same structure in the antennula and the maxilla. Farran (1926) also had strong suspicions that *A. dubius* was a synonym of *A. mucronatus* since he always found *A. mucronatus* females in every gathering in which *A. dubius* males occurred. The author, however, hesitated synonymizing both because of the presumed "arostrate" male of T. Scott's *A. longirostris* which had since been recognized as being synonymous with *A. mucronatus*.

Owre & Foyo (1967) were the first to describe the male of *A. aculeatus*. Their photographs of the "male" rostrum and antennula (figs. 748-749) are, however, taken from a female. The drawing of the male antennula of *A. mucronatus* is simply a copy of Sars' (1916) figure.

Farran (1905), reporting on the Copepoda of the Atlantic slope off Ireland, described *A. spinulosus*. Lang (1948) suspected that the species represents a last copepodite stage of *A.*

aculeatus. Boxshall (1979) regarded *A. spinulosus* as a valid species provided that Farran's drawings are accurate.

The presence of a maxillula in the male of the Aegisthidae was reported for the first time by Boxshall (1979) but unfortunately not figured. On the other hand he failed in tracing any structure which could be identified with certainty as representing the male mandible.

In conclusion, sexual dimorphism in post-antennular cephalosomic appendages has been demonstrated, but not always figured, for the antenna (Sars, 1916; Boxshall, 1979) the maxillula (Boxshall, 1979), the maxilla (T. Scott, 1893; Sars, 1916; Boxshall, 1979) and the maxilliped (Sars, 1916; Boxshall, 1979). A detailed redescription of *A. mucronatus* proved all cephalosomic appendages to be present in both sexes, but showing profound dimorphism.

MATERIAL AND METHODS

The redescription of the cephalosomic appendages is based on specimens of *Aegisthus mucronatus* collected at "Discovery" station 7089 in the region of the Cape Verde Islands (18°N 25°W) using the RMT 1+8 net system (Boxshall, 1979).

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel.

All drawings have been prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The terminology is adopted from Lang (1948, 1965) except for (1) the terms pars incisiva, pars molaris and lacinia mobilis which are omitted in the description of the mandibular gnathobasis (Mielke, 1984a), (2) the segmental composition of the mandible and maxilliped which are followed according to Boxshall (1985: 341-345). The terminology of Huys (1988) for the caudal ramus structure is used.

Both females and males of *A. mucronatus* were examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Specimens were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter coated with gold.

SYSTEMATICS

Family AEGISTHIDAE Giesbrecht, 1892

Hensenellinae (part.) Dahl, 1895.

Pontostratiotidae (part.) A. Scott, 1909; Monard, 1927.

Arpacticidae (part.) Stebbing, 1910.

Diagnosis (modified from Boxshall, 1979). — Cervinioidea. Distinct separation between prosome and urosome. P1-bearing somite free dorsally and laterally, about equal in size to the following somite, without sensillae. Genital double-somite with dorsal and lateral suture lines. Anal somite tapering posteriorly; anal operculum weakly developed. Caudal rami extremely long, at least twice as long as body; closely pressed together and fused in the female, partly free in the male; furnished with 3 setae (?II, ?III, VII). Sexual dimorphism in rostrum, antennula, antenna, mandible, maxillula, maxilla, maxilliped, fifth leg, caudal rami and in genital segmentation.

Rostrum fused with cephalosome; well developed in female, reduced in male. Antennula 6- or 7-segmented in female, with aesthetasc on 3rd and terminal segments; of the haplocer type and 7- or 8-segmented in male, penultimate segment extremely elongated, with aesthetascs on segments 2, 3, 4 and 7 or 8. Antenna slender; allobasis extremely long (spinulose and with seta in female, almost bare and without seta in male); exopodite 2-segmented (spinulose and with well-developed seta on segment 1 in female; smooth and with minute setule on segment 1 in male); endopodite 1-segmented (with 3 subdistal and 6 terminal setae in female; with 1 subdistal and 4 terminal setae in male). Labrum well developed and denticulate in female; unarmed in male. Mandible without palp, represented by coxa only; strikingly developed in female, obsolete in male. Female maxillula with well-developed praecoxal arthrite (with 10 marginal and 2 surface setae); coxa with 2 setae, epipodite absent; basis confluent with endo- and exopodite. Male maxillula reduced; represented by praecoxal arthrite and small coxa-basis. Labium with long hairs in female, not differentiated in male. Maxillar syncoxa with 4 (?) endites in female, none in male; basis forming a strong claw; endopodite 3-segmented, rudimentary in male. Maxilliped stenopodial; 3-segmented and well developed in female, rudimentary in male.

Swimming legs with 3-segmented rami; without sexual dimorphism; proximal exopodite

segment of P1 with inner seta. Leg 5 elongate; baseoendopodite without process on endopodite; exopodite 1-segmented (confluent or not with basis) with 1 plumose and 5 serrate setae in female, 2-segmented (segment 1 fused with basis) with 2 plumose and 5 serrate setae in male. Leg 6 in both sexes consisting of an elongate free segment with 2 setae.

Free-living, marine, bathypelagic. Bioluminescence (in females only?).

Type and sole genus: *Aegisthus* Giesbrecht, 1891.

Genus *Aegisthus* Giesbrecht, 1891

Hensenella Dahl, 1895.

Hensella Dahl (lapsus calami, Monard, 1927).

Diagnosis. — As for family.

Type species: *A. mucronatus* Giesbrecht, 1891 (by subsequent designation; Boxshall, 1979).

Other species: *A. aculeatus* Giesbrecht, 1891; *A. spinulosus* Farran, 1905.

Aegisthus mucronatus Giesbrecht, 1891

Redescription. — Various authors (e.g. Owre & Foyo, 1967; Boxshall, 1979; Gamô, 1983) have provided information on the habitus, structure of the swimming legs and urosome, but none of them gives a complete description of the cephalosomic appendages. Therefore the following redescription is principally focused on the morphology of these parts in both sexes.

Female (figs. 1B, D; 2A, a, b; 3A, C; 4A, C, D; 5-7; 8A, B, C).

Rostrum (figs. 6A; 7B, C) very long, round in transverse section and anteriorly directed, slightly curved downwards, sensillae absent.

Antennula (figs. 1B, D; 6A; 7B, C) slender, 6-segmented. First segment widening anteriorly and forming medially a strong hook-like process from which a slender seta arises. Second segment with several spinules along outer margin; furnished with 2 minute plumose, 1 strong bipinnate and 3 small smooth setae in proximal half; anterior part with 2 bare setae and a small tube pore. Third segment with 10

minute setae (7 plumose, 3 smooth) and 2 extremely long setae; distal part forming a distinct process with a long aesthetasc in addition to a minute bare seta and a longer bipinnate one. Fourth segment with 4 setae along the inner margin and 1 bi-articulated slender seta at the outer subdistal corner. Fifth segment smallest and bearing 2 setae (this segment is the equivalent of fused segments 4 and 5 in the 7-segmented antennula of *A. aculeatus* and *A. spinulosus*). Outer side of apical segment armed with 4 bi-articulated setae; distal part with slender seta and long aesthetasc fused at base with bipinnate seta.

Antenna (figs. 2A, a, b; 7D). Coxa well defined, with several spinules along the outer margin. Basis and proximal endopodite segment forming elongated allobasis; showing a distinct spinular pattern in proximal third and several longitudinal spinular rows distally; furnished with inner bipinnate seta near articulation with distal endopodite segment. Exopodite 2-segmented; segment 1 provided with several fine spinules and a bipinnate seta at the inner distal corner; segment 2 very small, wider than long, bare, with a long plumose seta. Endopodite with 4 groups of long spinules along the outer edge; with 3 setae at about middle of inner margin; with 6 pinnate setae (of which 2 fused at base) apically.

Labrum (figs. 8A, B) well developed, divided in two parts, each bearing numerous recurved denticles; deeper area furnished with long spinules.

Mandible (figs. 4C, D; 8A, B). Palp absent; represented by well-developed coxa only. Gnathobasis strong, with several stout teeth and a bipinnate seta at the dorsal side; ventral part with long hair-like setules.

Labium (figs. 7E, F; 8A) forming the posterior wall of the oral area; no trace of fused paragnaths; provided with long hairs arranged in a distinct pattern.

Maxillula (figs. 3A; 8A) well developed. Praecoxal arthrite with ten stout bipinnate spines at the margin and two strong plumose setae on the anterior surface; posterior surface with minute spinules. Coxa without epipodite;

with some diminutive spinules and a weakly defined endite bearing 1 bipinnate and 1 plumose seta. Basis rectangular, without endites or any trace of exo- or endopodite; furnished with 4 bipinnate setae apically.

Maxilla (figs. 3C; 6A; 8C) strongly developed, prehensile. Syncosa long, integument pitted in a distinct pattern; furnished with 4 (?) endites (it is difficult to decide whether the distalmost one is standing on the syncosa or the basis; see male); middle two rudimentary and with 2 setae, proximal and distal ones subcylindrical and with 4 and 3 setae, respectively. Basis forming a hollow, curved claw which is finely spinulated and opening at the tip; furnished with 2 bipinnate setae, 2 serrate spines and a distinct tube pore at the basis of the claw. Endopodite 3-segmented; proximal segment with 1 geniculate seta, middle segment with 2 geniculate setae, distal segment with 2 geniculate and 2 bipinnate setae.

Maxilliped (figs. 4A; 7E, F) stenopodial, strong; indistinctly 3-segmented. Praecoxa not entirely free, fused along the inner side with the coxa (forming a syncosa), armed with a few spinules. Coxal part with numerous spinules of different shape and length, most of them occurring at the anterior surface, armed with 3 enlarged spines (proximal one bipinnate, distal two serrate) in addition to a slender bipinnate seta. Distal segment rectangular and possibly derived from the fused basis and endopodite; outer margin with long spinules; furnished with 1 subapical plumose seta and 2 long bipinnate setae apically.

Male (figs. 1A, C, a-c; 2B, c-e; 3B, D, E; 4B, E; 8D, E, F; 9-10).

Rostrum (fig. 9B) not well defined, confluent with anterior margin of cephalosome; provided with 2 sets of 3 pores anteriorly and 2 big pores ventrally. Ventral wall of preantennular area of cephalosome exhibiting numerous minute perforations.

Antennula (figs. 1A, C, a-c; 9A, D) very long and slender; 8-segmented; haplocer, geniculation between segments 6 and 7. First segment with 1 small seta. Second segment fur-

nished with 10 minute setae along the inner margin and 1 long outer plumose seta; proximal half with a long aesthetasc covered at base by a small operculum. Segment 3 with 1 long and 5 minute setae; a long aesthetasc is arising from the inner edge. Fourth segment long; proximal half with 3 minute setae and a slender one standing on a small process; distal half with 1 bare and 2 characteristic pinnate spines in addition to a long aesthetasc which is fused with a minute seta at its basis. Segment 5 small, with 1 minute seta and 1 pinnate spine. Segment 6 with 2 minute setae and 1 pinnate spine and forming haplocer apparatus with following segment (in *A. aculeatus* segments 5 and 6 are fused). Segment 7 extremely elongated, thin-walled, armed with 4 setae. Distal segment bearing a slender seta and a very long aesthetasc at the top; inner margin with 4 bare setae; outer margin with 5 bi-articulated setae.

Antenna (figs. 2B, c-e; 9A; 10D). Coxa forming a swollen process armed with long spinules. Basis and first endopodite segment partially fused and forming an elongated allobasis, spinulated along the outer margin. Exopodite 2-segmented; proximal segment long and bare, having a small seta at the inner subdistal corner; distal segment indistinctly fused with the long apical seta. Distal endopodite segment furnished with 2 groups of long spinules along the outer side; with at about middle of inner edge an aesthetasc-like seta showing a small basal process (rudimentary seta?); terminal part having an articulating aesthetasc-like seta in addition to some minute spinules and fused with 1 bipinnate outer seta and 2 long aesthetasc-like setae.

Labrum (figs. 9A, C). Prelabral area wrinkled as well as lateral zones in which the mandibles are embedded. Oral aperture without any ornamentation.

Mandible (figs. 4E; 9C, E) small, rudimentary, without palp. Tegument of coxa wrinkled; gnathobasis with at least 8 spiny processes and a distinct seta which is fused at the basis.

Labium (fig. 9C) without hairs; tegument wrinkled; paragnaths not differentiated.

Maxillula (figs. 3B; 9C, F) embedded in



Fig. 1. *Aegisthus mucronatus* Giesbrecht, 1891. Male: A, antennula; C, detail of distal part of segment 8; a, b, c, characteristic spines of segment 4. Female: B, antennula (arrow indicating tube pore); D, detail of distal part of segment 6.

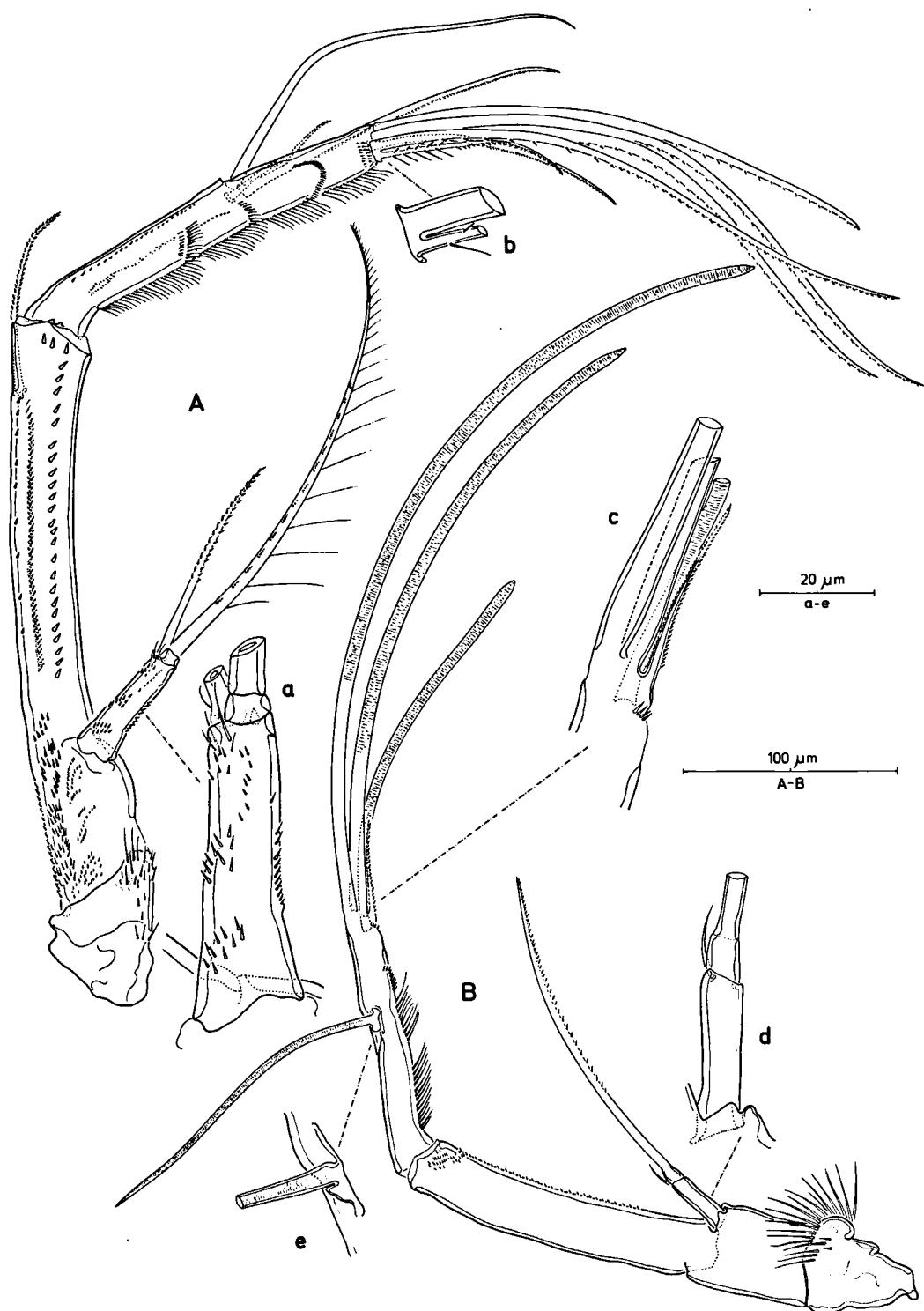


Fig. 2. *Aegisthus mucronatus* Giesbrecht, 1891. Female: A, antenna; a, detail of exopodite; b, detail of distal setae. Male: B, antenna; c, detail of distal part of endopodite; d, detail of exopodite; e, detail of inner seta of endopodite.

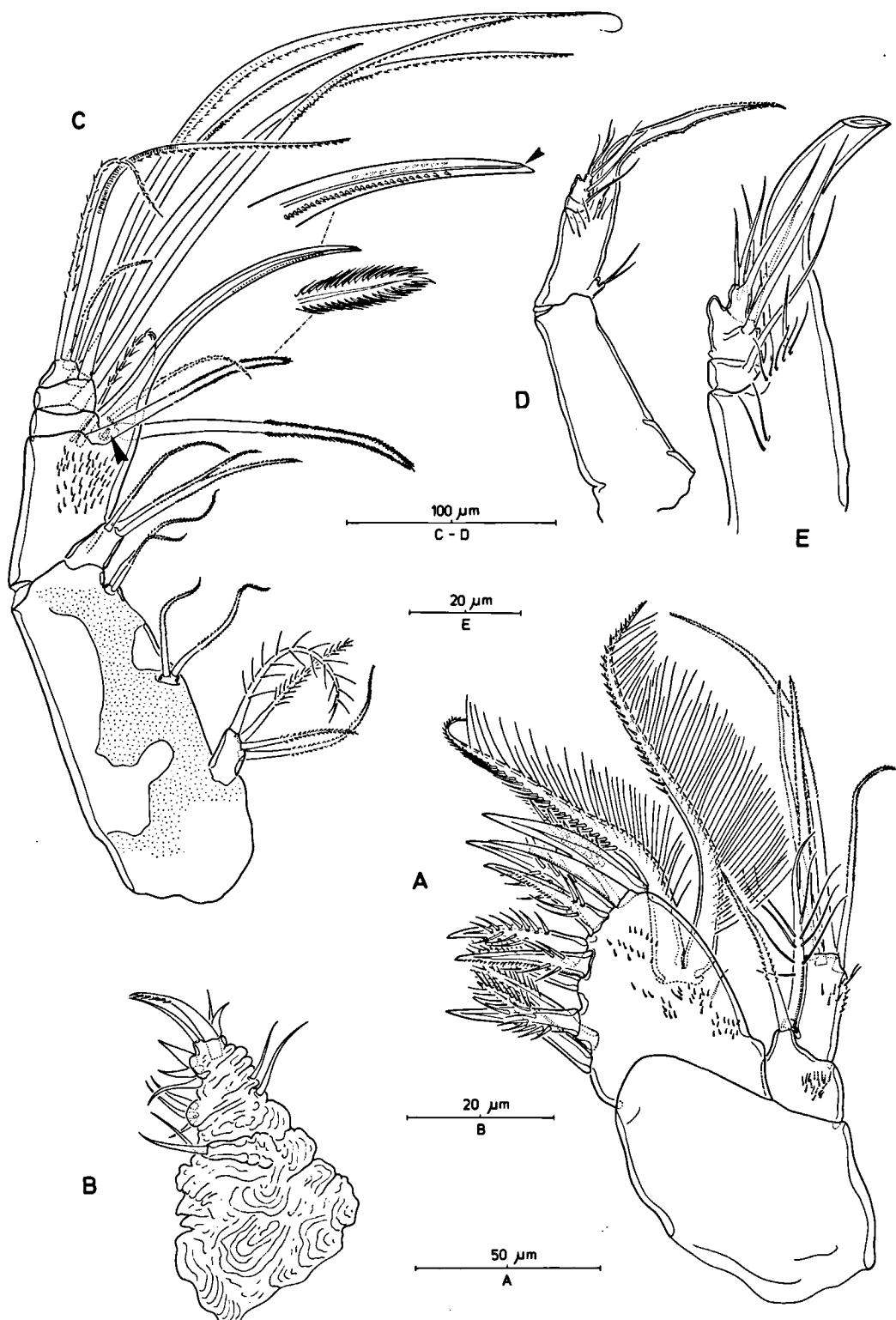


Fig. 3. *Aegisthus mucronatus* Giesbrecht, 1891. Female: A, maxillula; C, maxilla (arrows indicating tube pore and apical pore of claw). Male: B, maxillula; D, maxilla; E, detail of maxillar basis and endopodite.

wrinkled tegument of postlabial area; small, rudimentary, tegument wrinkled at the basal part. As in the female the praecoxal arthrite bears 10 marginal setae and 2 surface setae. Coxa and basis are fused and represented by a common elongate process (coxa-basis) having 2 apical setae.

Maxilla (figs. 3D, E; 9A; 10A, B, C). Syncoxa smooth, lacking endites. Basis forming a spinulated curved claw which is slightly swollen in the middle; furnished proximally with a small bilobed baso-endite with 2 setae, distally with some long spinules and 1 minute seta. Endopodite indistinctly 3-segmented, thin-walled; segment 1 with 1 seta; segment 2 with 2 setae and partially fused with segment 3 which is bearing 4 setae.

Maxilliped (figs. 4B; 9A; 10A) small, rudimentary, without any trace of segmentation (tegument wrinkled); distal part an elongate process, forming a minute lobe proximally, widening and armed with 2 setae distally. A long vestibulum is present between the maxillipeds and the first leg (see below).

ADDITIONAL MORPHOLOGICAL REMARKS

(1) The first pedigerous somite is not fused with the cephalosome both dorsally and laterally. Ventrally, however, no suture could be observed. A distinct chitinous plate running from the bases of the maxillipeds to the interpodal bar of the first pair of thoracic legs is present (figs. 7E; 9A). The first pedigerous somite is, unlike other thoracic and urosomal somites (except penultimate somite), devoid of sensillae or integumental pores (figs. 6A; 8D). This situation has been found in other harpacticoids with a free P1-bearing somite (Cerviniidae, Rotundiclipeidae, Phyllognathopodidae and Chappuisiidae; Huys, unpubl.).

(2) The ventral side of the anal somite is slightly notched in the middle and shows 2 distinct integumental pores in addition to 2 smaller ones on either side near the articulation with the caudal ramus. The lateral surface is also furnished with a distinct pore (fig. 8F). The anal aperture is triradiate and opening dorsally

as in all Cervinoidea. The anal operculum is weakly developed. The paired anal sensillae are situated anteriorly to the anal operculum instead of laterally as in most non-cervinioid families.

(3) Boxshall (1979) reviewed the homology of the appendages of the anal somite. In *A. mucronatus* the length of the caudal rami is averaging 5-7 times the body length. In females the caudal rami are fused along a considerable distance. Each ramus (fig. 5) is provided with 1 bare outer seta at about the middle third but the insertion place is not symmetrical in both rami (see also T. Scott, 1893); this seta is probably homologous with the anterolateral seta (II) in other families. The distal end is armed with 2 setae; the largest is tri-articulate at the base, furnished with long spinules, directed outward and undoubtedly the equivalent of the dorsal seta (VII); the second one is shorter, implanted subterminally and probably representing the posterolateral seta (III). The surface of each ramus exhibits a bilateral pattern of minute, flattened triangular spinules (fig. 6D). In males the same setal configuration is observed. The caudal rami are pressed closely together along the proximal fourth but not fused; from this point onwards the rami are divergent and often show (non-functional?) kinks in preserved specimens.

(4) Bioluminescence of *Aegisthus* has been reported by Herring (1985). The luminous sites occur on the head, swimming legs and the uosome, but have not yet been more precisely located (Herring, in press). Boxshall (pers. comm.) found only female *A. mucronatus* of luminous capability but probably males were not tested.

DISCUSSION

Because of the combination of sexually dimorphic features in the cephalosome which is only approximated by *Cervinia magna* (cf. Montagna, 1979, 1981) and some *Metahuntemannia* species (Becker et al., 1979), it is clear that the Aegisthidae occupy a unique place within the Harpacticoida in general and within the Cer-

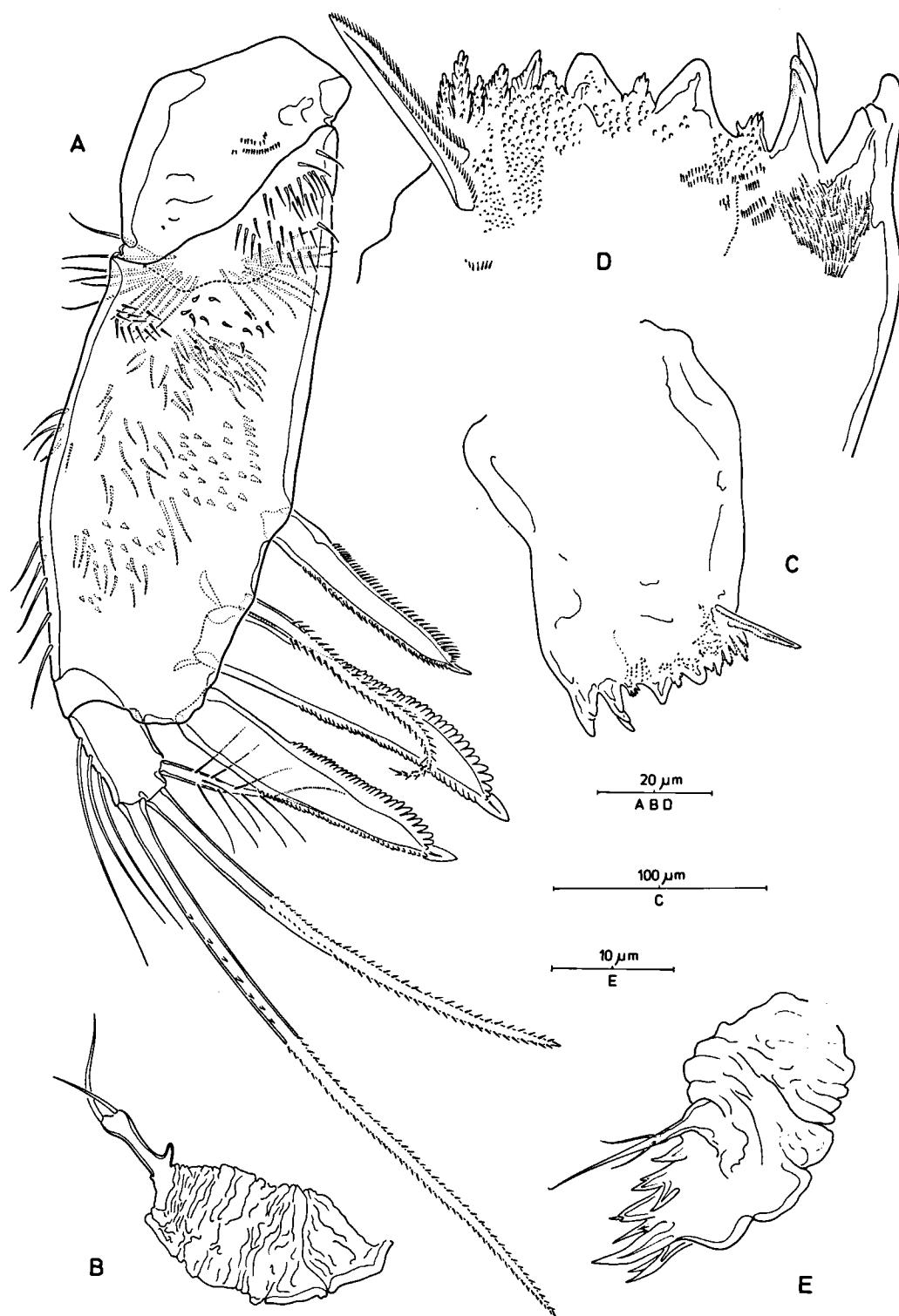


Fig. 4. *Aegisthus mucronatus* Giesbrecht, 1891. Female: A, maxilliped; C, mandible; D, mandibular gnathobasis. Male: B, maxilliped; E, mandible.

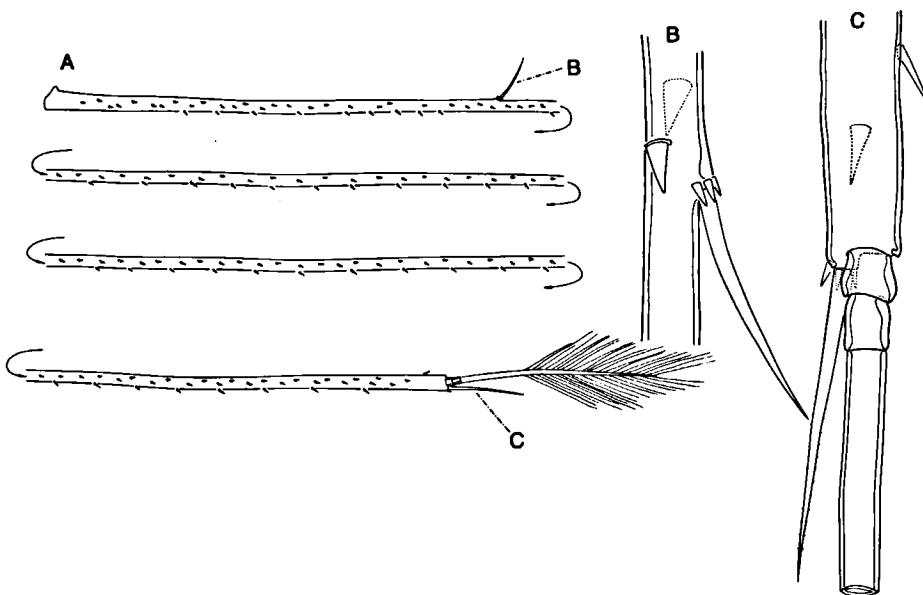


Fig. 5. *Aegisthus mucronatus* Giesbrecht, 1891. Caudal ramus of female.

vinoidea in particular. Huys (in press) reviewed the interfamilial phylogenetic relationships and concluded that the Aegisthidae represent the closest relatives of the chiefly deep-sea inhabiting Cerviniidae. Aegisthids can be assigned to the Cervinoidea on the basis of, amongst other synapomorphies, the aesthetasc arrangement of the male antennula. All members of this superfamily primitively have aesthetascs on segments 2, 3, 4 and on the distal segment (= segment 10 in Rotundiclipeidae; segment 6, 7 or 8 in Cerviniidae; segment 7 or 8 in Aegisthidae). Moreover, the aesthetasc on the 2nd segment arises medially, associated with a distinct integumental aperture and covered at the basis by a small smooth operculum.

The sexual dimorphism amongst the three known *Aegisthus* species is markedly constant. Apart from differences in the antennular segmentation in the male, Boxshall (1979) found that the maxilla and maxilliped are closer to the female condition in *A. aculeatus* males than in *A. mucronatus* males. In *A. aculeatus* males the maxilliped is 3-segmented, the middle segment bearing 2 setules and the distal one

being armed with 3 setae (Boxshall, 1979). With respect to Farran's (1905) figure of the female mandible of *A. spinulosus*, it is doubtful whether the bisetose process really represents the palp or is just simply part of the adjacent maxillula.

More than in any other copepod order, the Harpacticoida display an astounding variety of sexual dimorphism. In fact, one can hardly imagine an appendage or other part of either the prosome or urosome for which sexual dimorphism does not exist in the harpacticoid realm. The Tetragonicipitidae, Canthocampidae and Laophontidae have developed the greatest degree of sexual dimorphism in various body parts. Other families, such as the Ectinosomatidae, which are abundant in sandy habitats, show little sexual dimorphism. In this family, and in others, the only significant and consistent differences between sexes are in the structure of the P6-bearing (=genital) somite (cf. genital double-somite) and in the segmentation and ornamentation of the antennula; and to a lesser extent in body size (males nearly always being smaller than females). Usually the fifth leg can also aid in distinguishing females

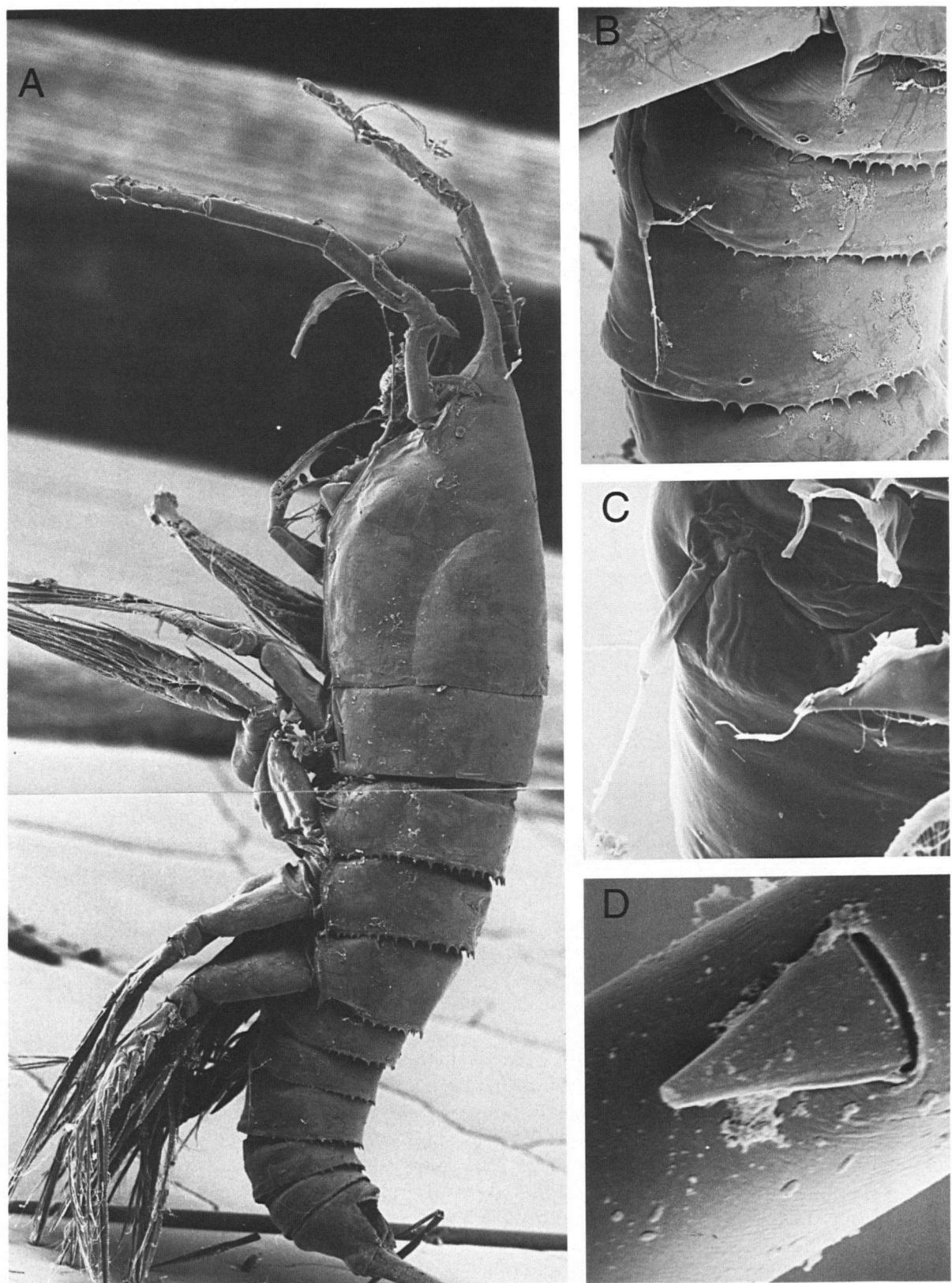


Fig. 6. *Aegisthus mucronatus* Giesbrecht, 1891 (SEM micrographs). Female: A, habitus, lateral view; B, genital double-somite, lateral view; C, genital complex and P6; D, spinule on caudal ramus.

from males; however, some exceptions (e.g. Rotundiclideidae; Huys, in press) exist.

Sexually dimorphic characters are usually important for taxonomic analysis, especially for species discrimination when other features are inconclusive (e.g. sibling species of the *Tisbe holothuriae*-group; Volkmann, 1974). Sexual dimorphism can also provide a good (or the only) criterion to distinguish between genera such as *Amonardia*, *Amphiascopsis* and *Metamphiascopsis* (Lang, 1965: 226). Dimorphism in swimming legs is amply illustrated throughout the literature and often proved to be diagnostic at the family level. Sexes also differ in abdominal ornamentation (e.g. freshwater Canthocamptidae), caudal rami (e.g. Tetragnicipitidae), dorsal fan-shaped organ between 2nd and 3rd urosomal somites (*Darcythompsonia*), epimera of P4-bearing somite (*Porcellidium*), opercular spines (*Darcythompsonia*), body shape (Paranannopidae), colour (*Tisbe reticulata*-group), etc.

Males and females frequently show morphological differences in the rostrum. Apart from the Aegisthidae where it is extremely pronounced, significant dimorphism in the shape of the rostrum is reported in Porcellidiidae and some members of Harpacticidae (*Zausodes*; Lang, 1965; Geddes, 1968) and Cholidyinae (*Cholidyella*; Avdeev, 1986). Profound sexual dimorphism is also shown in the rostrum of some *Metahuntemannia* (Becker et al., 1979) and in at least two species of Diosaccidae: *Pseudomesochra gemina* and *Stenelia (Delavalia) bifidia* (cf. Coull, 1973b, 1976).

The antennula is the only appendage showing sex-dependent differences in all harpacticoid families. Lang (1948) considered a geniculate antennula to be the rule in males, however he states (: 40): "Ausnahmen bilden nur gewisse Cerviniiden und die Aegisthiden, bei denen sie nur wenig von denen des Weibchens abweichen. Ob sie bei diesen als Greifwerkzeuge dienen, ist unwiss.". Due to recent studies (Boxshall, 1979; Itô, 1982, 1983; present account) it is now clear that Lang's claim cannot be supported and that males of the Cervinoidea exhibit a geniculate antennula of

the haplocer type, bearing 4 aesthetascs (Huys, in press).

In comparison, harpacticoids have apparently been less successful in developing sexual dimorphism in post-antennular cephalosomic appendages. Indeed, sexual modification in the structure of the mandible, maxillula and maxilla is a rare phenomenon. Sexual dimorphism in the antenna and maxilliped has been reported more frequently and obviously has evolved on several occasions during harpacticoid evolution.

In addition to the Aegisthidae sexually dimorphic antennae within the Cervinoidea have been reported only for the cerviniid *Pontostriatoties pacificus*, the male endopodite being less spinulose than in the female (Itô, 1982).

Modifications in the antenna of male Harpacticidae have been shown in at least four genera. Male *Tigriopus* specimens differ from females in the absence of the strong inner seta on the allobasis which is usually rather slimmer. In all probability this feature is diagnostic for the genus as it has been reported by Bradford (1967, *T. raki*), Itô (1969, *T. japonicus*; 1977, *T. igai*) and Soyer et al. (1987, *T. kerguelensis* and *T. crozettensis*); this modification was also quoted earlier by Božić (1960). Examining copepodite stages of *T. japonicus*, Itô (1970) clearly demonstrated that the male condition is not attained until the final moult. According to Itô (1969), *Paratigriopus hoshidei* displays the same sexual dimorphism. As in *Tigriopus*, sexual differences in the antenna cannot be detected in the fifth copepodite stage (Itô, 1976a). Slight differences in the spinulation of the allobasis between both sexes have been described for *Harpacticella paradoxa* (Itô & Kikuchi, 1977). Several authors (Frost, 1967; Itô, 1976b, 1979) mentioned sexual dimorphism in *Harpacticus* species; male *H. compressus*, *H. nipponicus*, *H. septentrionalis yamadai* and *H. purpureus* all have more slender antennae with fewer or no spinules. These features were not noted by Lang (1965) in the two new species described by him from the Californian Pacific coast.

Subtle but not significant differences are noted in the antenna of both sexes of the com-

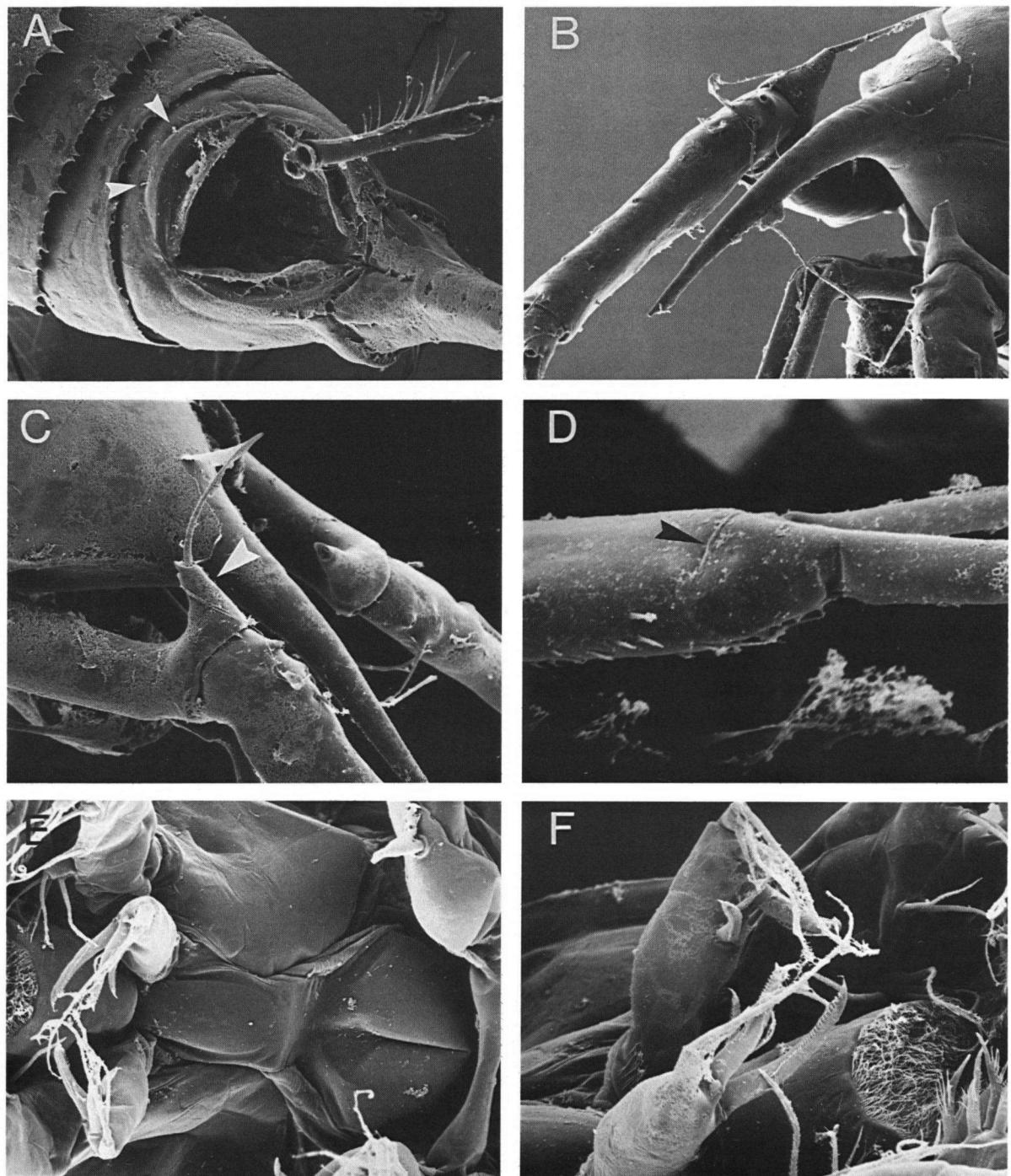


Fig. 7. *Aegisthus mucronatus* Giesbrecht, 1891 (SEM micrographs). Female: A, anal somite, dorsal view (arrows indicating sensillae); B, rostrum, anterolateral view; C, proximal segments of antennula (arrow indicating inner process); D, antennal exopodite (arrow indicating segmental boundary); E, vestibulum between maxilliped and first thoracic leg; F, maxilliped, lateral view.

mensal *Balaenophilus unisetosus* collected from the baleen plates of the Blue Whale (Vervoort & Tranter, 1961).

Stenelia (Delavalia) noordti is the sole member of the Diosaccidae for which antennal sexual dimorphism is reported (Schriever, 1982); however, I am inclined to believe that these differences as well as those shown in the mandible, maxilliped and exopodite of the second leg are due to deficiencies in the description.

Boxshall (1979) was the first to mention sexual dimorphism in the miracid *Macrosetella gracilis*; males apparently have a separate basis and a 2-segmented endopodite in contrast to the allobasis of the females.

A peculiar form of sexual dimorphism can be found in some Paramesochridae described from South America (Mielke, 1984b, 1985a). Females of both *Diarthrorella chilensis* and *Rosso-psyllus kerguelensis quellonensis* have a 2-segmented antennal exopodite with 2 setae on each segment; males possess a small 1-segmented exopodite bearing a minute seta and a peculiar transparent appendage. An analogous modification is reported in *D. galapagoensis*, the exopodite being, however, 2-segmented (Mielke, 1984b). In the same study Mielke mentions a second form of antennal sexual dimorphism: male *D. neotropica* can be easily recognized by the presence of a hyaline, setose and 3-articulate structure on the proximal endopodite segment.

Within the Langian "Cletodidae" a sexually modified antenna is found only in two typically deep-sea genera: *Metahuntemannia* and possibly *Mesocletodes*. Slight sexual differences have been noted in *Metahuntemannia* and *M. peruana* but unfortunately not figured (Becker et al., 1979). According to Schriever (1983) male *Metahuntemannia pseudomagniceps* have two inner setae on the allobasis whereas females have none. This difference is questionable as damage or loss of setae is a common problem in the study of deep-sea species. Schriever (1985b) found basis and proximal endopodite segment to be at least partially separated in *Mesocletodes faroerensis* males but at present it remains uncertain whether this really is sexual dimorphism or not.

In contrast to other features the general outline of the laophontid antenna is fairly constant throughout the family and even between both sexes. The only exception is *Heterolaophonte wellsi* which has two subdistal spines on the male endopodite instead of one in the female (Hamond, 1973). As two curved spines (and an additional hair-like seta) seem to be the rule in most laophontid genera it is likely that the author has overlooked the second spine in the female (Hamond, pers. comm.).

Thus far, *Cervinia magna* seems to be the only member of the Cerviniidae with sexual dimorphism in the mandible. Moreover, significant differences between the sexes could be observed for all postantennal cephalosomal appendages; only the antenna has the structure typical of the female. The male mandible differs in the outline of the coxal gnathobasis (Montagna, 1979, 1981).

A second example of mandibular sexual dimorphism is the family Porcellidiidae. The tetrasetose basis has the innermost seta shorter and more slender in the male. Various authors (Humes & Gelerman, 1962; Humes & Ho, 1969; Tiemann, 1977, 1978; Ho, 1986) have reported on this somewhat cryptic modification and the structure shows a remarkable constancy. This feature may be diagnostic for the genus *Porcellidium* and the family Porcellidiidae as a whole.

Sexual dimorphism in the mandible is not always confined to either the coxa or the basis. In the diosaccid genus *Pararobertsonia* the male endopodite is represented by a strikingly swollen segment. This feature is a well defined generic trait as it has been shown in both *P. abyssi* and *P. chesapeakensis* (Sars, 1906; Wilson, 1932). Schriever's (1982) claim of mandibular sexual dimorphism in *Stenelia (Delavalia) noordti* is doubtful (see above).

According to Schriever (1985a) males of *Cylindronanopus bispinosus* are distinguishable from females by the presence of a 1-segmented exopodite. It is possible that the latter structure was lost during the dissection of the female as Schriever's figure does not illustrate the entire mandible. In addition his drawing of the male

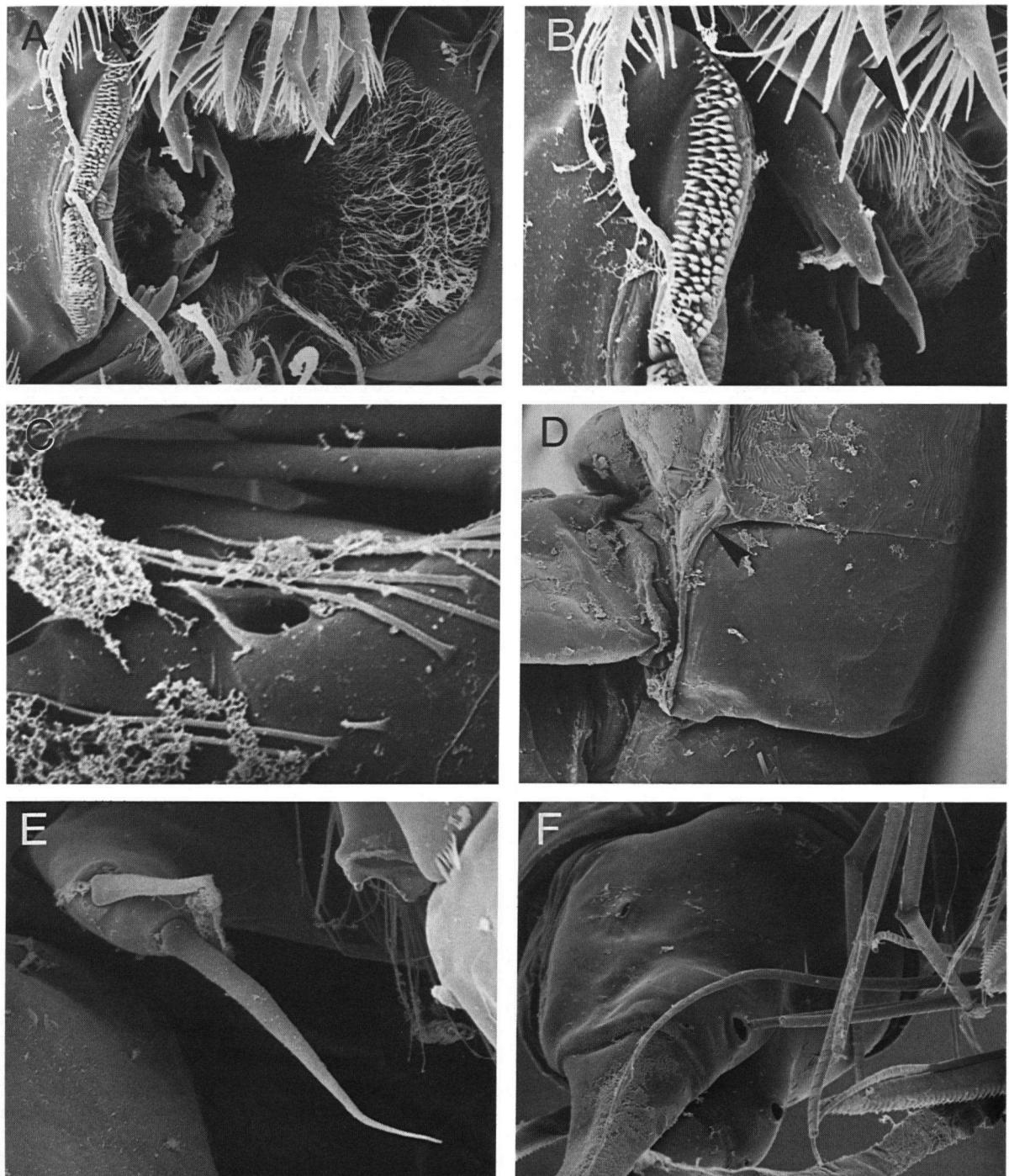


Fig. 8. *Aegisthus mucronatus* Giesbrecht, 1891 (SEM micrographs). Female: A, oral area with labrum, labium and mandibular gnathobases; B, mandibular gnathobasis (arrow indicating hair-like setules) and part of labrum; C, tube pore on maxillary basis. Male: D, first pedigerous somite, lateral view (arrow indicating ventral fusion with cephalosome); E, sixth leg; F, anal somite, lateroventral view.

mandible shows only 3 setae on the basis instead of 4 in the corresponding female and in both sexes of other species (Coull, 1973a; Becker et al., 1979).

Except for the Aegisthidae, intersexual differences in the structure of the maxillula are with certainty known only in *Cervinia magna*. Both sexes differ profoundly in the ornamentation of the arthrite, coxa and basis (Montagna, 1979, 1981). Becker (1972), in the description of the male of *Metahuntemannia talpa*, at first had some doubts about the real nature of an appendage found between the mandible and maxilliped and stated that he must "...vorläufig dahingestellt bleiben, ob es sich um ein Rudiment der Mx.1 oder der Mx.2 handelt.". The discovery of additional males, however, revealed that this structure is homologous with the maxilla whilst the maxillula is identical in both sexes. Consequently, the structure indicated as "Mx1 oder Mx2 ♂" by Becker et al. (1979: fig. 29) represents the maxilla. This aegisthid-like reduction of the maxillary endites is only found in the *talpa*-group of *Metahuntemannia*.

Males of *Cervinia magna* are exceptional in having a transformed claw ("bottle opener", cf. Montagna, 1981) on the basis of the maxilla in addition to small differences in setation.

Recently Dahms & Dieckmann (1987) noticed a slight intersexual difference in the maxilla of a newly described genus *Drescheriella* (Tisbidae). According to the authors, male *D. glacialis* can be discriminated from females by the length of one of the setae at the basis of the terminal claw. This subtle modification does not allow to distinguish both sexes in the copepodite V stage as the seta in question is not formed until the final moult (Dahms, 1987). Vervoort (1962) mentioned sexual dimorphism in the maxilla of another tisbid, *Tisbe acanthifera*, but this was refuted by Volkmann (1979).

The only maxillary intersexual variability within the Miraciidae is the number of endites of *Macrosetella gracilis* (2 in female, 1 in male) according to Boxshall (1979).

Although sexual dimorphism of the max-

illiped is reported in a wide range of families, the modifications are generally slight and not as profound as in the aegisthids. This is well illustrated in e.g. *Cervinia magna* (see Montagna, 1979, 1981) where differences exist only in the shape of the spines on the coxa (not basis as mentioned by the author).

Por (1983), in describing mangrove swamp-inhabiting Darcythompsoniidae, figured a 3-segmented maxilliped in the female of *Kristensenia pallida*; however, this appendage was not found in the male. Inspection of the holotype male revealed the maxilliped to be exactly the same as that of the female (Huys, unpubl.).

The only published record of maxilliped sexual dimorphism in the family Harpacticidae is that of *Tigriopus brevicornis* by Božić (1960). The males lack the plumose seta on the basis, a character not found in any other species of *Tigriopus* (Hamond, pers. comm.). Some *Perisscope* species have a similar modification (Hamond, pers. comm.). In addition to sex-specific differences in the antenna and the first leg, Brady (1910) illustrated sexual dimorphism in the maxilliped of *Harpacticus robustus*. From what little can be distinguished in the original inadequate drawings, it seems doubtful that Brady was dealing with females and males of the same species (see also Lang, 1948).

The sexually dimorphic maxilliped is an important character in the taxonomy of the genus *Tisbe* in particular and of the subfamily Tisbinae in general. The fact that the male maxilliped can display various types of modification but can also show no dimorphism (e.g. the *T. bermudensis*-, *T. tenella*-, and *T. angusta*-groups) supports the hypothesis that maxillipedal sexual dimorphism has originated independently several times within the genus *Tisbe*. Following Volkmann (1979) three main types of maxillipedal modification can be distinguished: (1) with different spinulation ("setation") on the basis ("endopod segment I") as in the *T. holothuriae*-group (e.g. Volkmann-Rocco, 1969, 1972a); (2) with different setation on the endopodite ("endopod segment II") as in *T. bulbisetosa* and *T. inflatiseta* (Volkmann-

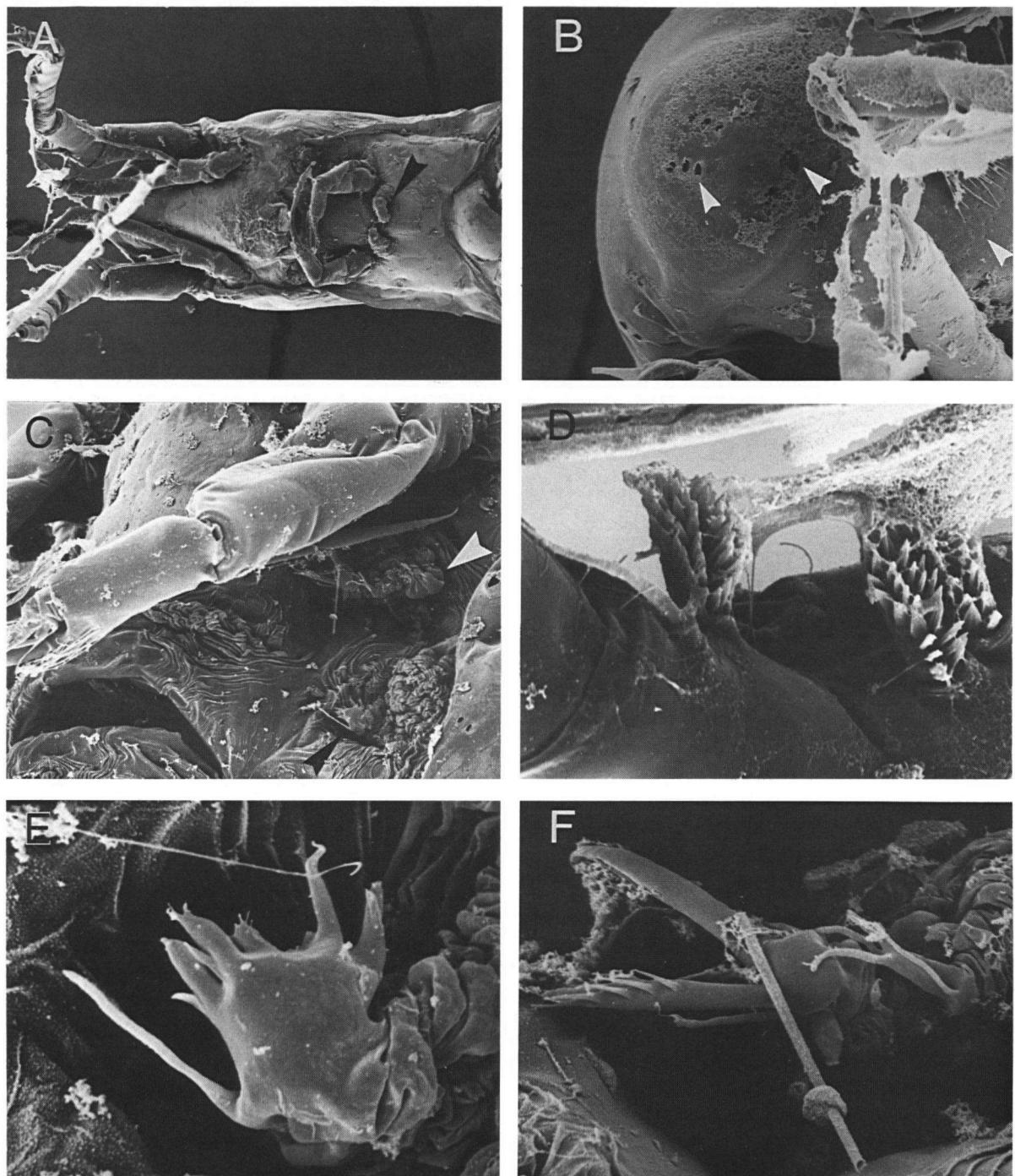


Fig. 9. *Aegisthus mucronatus* Giesbrecht, 1891 (SEM micrographs). Male: A, cephalosome, ventral view (arrow indicating maxillipeds); B, rostrum, anterior view (arrows indicating integumental pores); C, oral area with mandible (black arrow) and maxillula (white arrow); D, characteristic spines on antennular segments 4 and 5; E, mandible; F, maxillula.

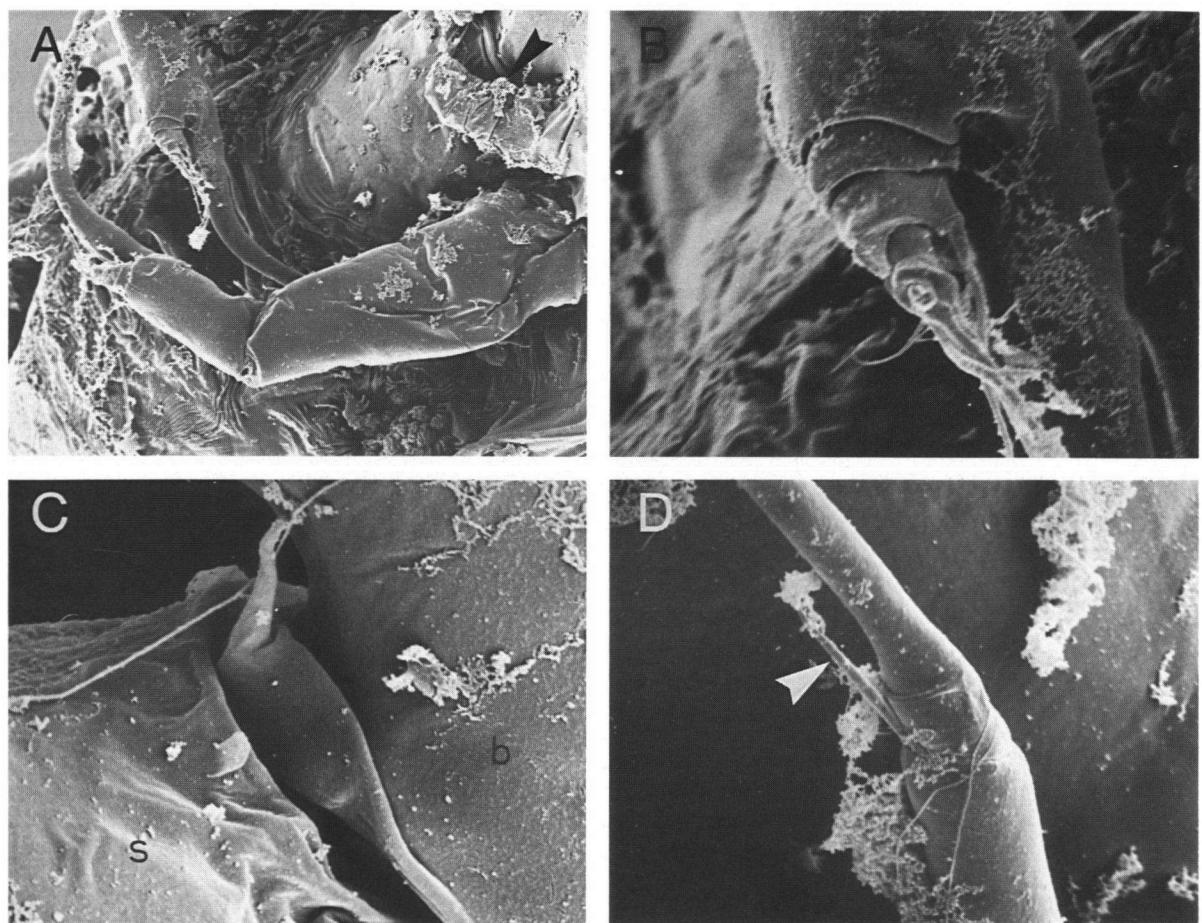


Fig. 10. *Aegisthus mucronatus* Giesbrecht, 1891 (SEM micrographs). Male: A, maxilla and maxilliped (arrow), posterior view; B, maxillar endopodite; C, baso-endite of maxilla (s = syncoxa; b = basis); D, antennal exopodite (arrow indicating minute seta on segment 1).

Rocco, 1972b; Volkmann, 1979); (3) with differently shaped endopodite claw as in the *T. gracilis*-group (Volkmann, 1979; Ho, 1982).

Another type of sexual dimorphism was found by Boxshall (1979) in the maxilliped of two new mesopelagic tisbid genera. Both *Volkmannia* and *Neotisbella* display a strong chitinous process on the endopodite in the male, a feature also shared by *Bathyidia* (Boxshall, 1979) and reinforcing the separate generic status of the latter (see also Volkmann, 1979).

In the same account Boxshall (1979) illustrates for the first time maxillipedal sexual dimorphism in the Clytemnestriidae (ex Pseudo-Peltidiidae). Males of both *Clytemnestra*

rostrata and *C. scutellata* can be differentiated from females by the length of the terminal claw. A similar phenomenon has been illustrated for *Miracia minor* by T. Scott (1893).

According to Vervoort & Tranter (1961), males of *Balaenophilus unisetus* (Balaenophilidae) have stronger maxillipeds, with the syncoxa and the basis slightly longer and more swollen than in the female.

The maxilliped of *Stenelia (Delavalia) noordti* differs considerably between both sexes (Schriever, 1982). The male maxilliped cannot be attributed to one of the three morphological types of the genus as recognized by Itô (1981).

The sexual dimorphism of the maxilliped noted in *Paranannopus variabilis* (Schriever,

1985a) is probably an artefact since the syncoxa of the female maxilliped has not been figured.

A character shared by all currently known *Metahuntemannia* males (Becker et al., 1979; Schriever, 1983, 1984) is the sexually dimorphic maxilliped showing various degrees of modification (e.g. rudimentary in *M. talpa*; Becker et al., 1979).

Maxillipedal sexual dimorphism in the Laophontidae is until now confined to two recently published accounts. *Laophonte confusa*, described by Decho & Fleeger (1986) from *Thalassia* beds of Florida, exhibits considerable variability between both sexes in the shape of the basis and of the terminal claw. This phenomenon is not found in any other member of the Laophontidae. All laophontid genera share an asetose maxillipedal basis and the spine figured by Decho & Fleeger is probably merely a chitinous thickening. In my opinion "...the species's unique but confusing mixture of taxonomic characteristics..." is best explained if the description is based on females and males belonging to distinct species. The only reliable reference of sexual dimorphism in the maxilliped of Laophontidae is that of Mielke (1985b), reporting the male endopodite claw of *Chilaophonte maiquillahuensis* to be more spinulose than in the female. This trait, however, was not observed in the second species of the genus, *C. conceptionensis* (see Mielke, 1985b).

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