

THE FEEDING MECHANISM OF *ANTARCTURUS* AND  
A REDESCRIPTION OF *A. SPINACORONATUS*  
SCHULTZ, 1978 (CRUSTACEA: ISOPODA: VALVIFERA)

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[Plates 1–5]

CONTENTS

	PAGE
1. INTRODUCTION	430
2. METHODS	431
3. REDESCRIPTION OF <i>ANTARCTURUS SPINACORONATUS</i> SCHULTZ, 1978	432
(a) Material	432
(b) Distribution	433
(c) Redescription	433
(d) Systematic position	438
4. BEHAVIOUR AND FEEDING MECHANISM	442
(a) General behaviour	442
(b) Feeding mechanism: collection of food	445
(c) Feeding mechanism: function of first pereopods and maxillipeds	446
(d) Structure and function of the filter-setae	451
5. BIOLOGICAL ACCOMMODATION: COMPARISON WITH <i>ARCTURELLA SAWAYAE</i>	454
6. DISCUSSION: EVOLUTION OF SUSPENSION FEEDING IN <i>ANTARCTURUS</i>	455
REFERENCES	456
ABBREVIATIONS USED ON THE FIGURES	458

The behaviour and feeding mechanism of valviferan isopods of the genus *Antarcturus*, exemplified by *A. spinacoronatus*, have been studied for the first time. This poorly known species is redescribed and details of its morphology, studied by light and scanning electron microscopy, are reported. Adaptations to its special habits include: cuticular spines on trunk segments and limbs which protect it from predators and

conceal its outlines; first pereopods with brushes of setae, the most important of which are the medio-ventral and dorsal setae of the propodus used for cleansing the filter combs of pereopods 2–4; long rows of setae on pereopods 2–4 used in passive sieving of phytoplankton; and stout pereopods 5–7 with their spines that are used for climbing.

The long setae of the filtering limbs are moved by a hydraulic mechanism. The structure of the basal articulation of these setae is described. The most conspicuous movements of the anterior limbs during feeding are recorded.

A comparison with *Arcturella sawayae* reveals the functional adaptations of the more specialized *Arcturella*. It is suspected that the family Arcturidae evolved in the Antarctic or Subantarctic Oceans.

## 1. INTRODUCTION

A series of studies on the biology and distribution of Antarctic isopods is currently being done to elucidate aspects of their biology and to clarify the position of some important species in the Antarctic marine food web. For this purpose isopods were collected during two expeditions of the R.V. *Polarstern* and in the 1984–85 season several species were kept in aquaria on board and later transferred to Germany. Feeding experiments with species of the valviferan genera *Antarcturus* and *Dolichiscus* led to the present paper.

In Antarctica the family Arcturidae is represented by about 75 species (Schultz 1981). These include some of the most conspicuous isopods of the benthic fauna. Often, several species occur in one locality. Such coexistence indicates that differences in their behaviour, food preferences or physiological adaptation must exist. That some of these adaptations can probably be recognized in morphological differences is shown in the comparison of *Antarcturus spinacoronatus* with *Arcturella sawayae*.

All Arcturidae have a remarkable specialization of their pereopods: pairs 2–4 (figure 33) have rows of very long setae on their podomeres that are obviously used to gather food. The posterior pairs (5–7) are used for climbing and walking (Schultz 1969). The various genera show important differences in thoracic morphology. Whereas genera like *Arcturus* Latreille, *Antarcturus* zur Strassen, *Spectrarcturus* Schultz, and *Dolichiscus* Richardson have anterior pereonites of similar length and somewhat shorter posterior segments; others, like *Arcturella* Sars and *Astacilla* Cordiner, have developed elongated fourth pereonites with simultaneously shortened anterior pereopods (2–4). Some phylogenetic trends can be guessed when comparing species that may have similar arrangements of cuticular spines, especially on the dorsal surfaces of their segments. Broadly defined genera like *Antarcturus* and *Arcturus* are obviously polyphyletic, but the quality of many descriptions and the lack of knowledge about functional morphology does not allow a satisfying phylogenetic analysis of this bizarre family.

Our knowledge about the biology of these animals is restricted to a few, brief, not always correct, observations. Goodsir (1941) reports that *Astacilla* ('*Leachia lacertosa*') 'frequently darts from its branch, with the rapidity of lightning, to seize with its long antennae some minute crustaceous animal, and returns to its resting-place to devour its prey at pleasure'. And '...swimming is the natural mode of progression'. Moreover, Goodsir observed that the antennae are cleaned by the 'anterior legs'. Concerning *Astacilla longicornis* (Sowerby) Sars (1899) writes that the animals use the hinder three pairs of legs for crawling, pleopods 1 and 2 for rapid swimming when changing their position, and reports that 'food is first seized by the long pediform inferior antennae'. In accord with these reports are the findings on the

animals' preferred substrata, namely among colonies of *Funiculina* (Pennatulacea), hydroids, *Alcyonium*, the spines of *Echinus* or *Cidaris*, in algae, and only rarely on bare bottoms (Sars 1899; Hult 1941). Sars (1899) also observed that females often carry their young on the body and antennae.

Fraenkel (1927) observed a Mediterranean *Astacilla* (obviously an *Arcturella*) and writes that these animals use their setae-bearing anterior pereopods for swimming, instead of the hidden pleopods. We must suppose that this mistake was based on the assumption that the beautifully armed pereopods 2-4 could only be useful for swimming and for nothing else. Fraenkel (1927) and later Moreira (1973*a,b*) observed the peculiar use of the antennae for climbing in *Arcturella*, and both also noted cleaning behaviour.

The concept found in some textbooks (see, for example, Kästner 1967) that these animals, which remind us of caprellid amphipods, live as well-camouflaged predators, waiting in their elevated positions for prey, is based on these few reports. It was not known whether this behaviour was typical for the whole family. Not until Moreira's publications (1973*a,b*) on *Arcturella sawayae* was it realized that this species was a passive filter-feeder, using the setae of pereopods 2-4 as sieves, and an active deposit-feeder, scratching up detritus with its antennae.

Others also had the impression that arcturids could be filter-feeders. M. White remarked in a discussion (in Holdgate 1970, p. 291) '... these [antarcturids] are certainly phytoplankton filter-feeders'. Schultz (1969) writes 'Arcturids are found in the deep sea, and indeed are filter-feeders characteristic of that extensive habitat'.

More detailed information on arcturid functional morphology is indispensable for the understanding of the ecological role of Antarctic species. Such is presented here. Many questions remain open, but it is clear that a more profound understanding of the interdependence of biology, morphology and ecology is possible. Most results were obtained from experiments with *Antarcturus spinacoronatus*, a species first described in 1978 by Schultz, which turned out to be very frequent in the Weddell Sea. A redescription of this species precedes an excursion into the special morphology of *Antarcturus*.

## 2. METHODS

During the expeditions 'Antarktis I' and 'Antarktis III' of the R.V. *Polarstern*, benthos was collected with an Agassiz-trawl at depths of between 100 and 1000 m. Samples were immediately sorted on deck to keep as many species as possible alive. Feeding experiments were done in aquaria, which were cooled in a temperature-controlled container ( $-1 \pm 0.5$  °C). Fresh, unfiltered Antarctic surface water and, later, artificial seawater was used, frequent changes being necessary to reduce mortality of *Antarcturus* after feeding. Living hydrozoans and anthozoans were not used as substrata. To keep the water clean, artificial 'trees' made of PVC and gauze had to replace them. Owing to the large size and slow movements of the isopods their activities could easily be observed with the naked eye. For documentation and reconstruction of feeding behaviour, especially the exact position of legs, numerous series of photographs were taken. The best pictures were drawn and are published here. Unfortunately, cinematographic methods were not at our disposal. A binocular Wild M5, a Leitz Dialux microscope with a camera lucida, and a scanning electron microscope Cambridge Stereoscan 180 were used for morphological studies. Semi-thin sections of Epon-embedded specimens revealed the inter-relations of mouthparts.

The behaviour described was observed not only in *A. spinacoronatus*, but also in a second common species, which is very similar to it and moves in the same way. This second species was used to prepare some of the drawings (figures 33c, 35 and 36). It too has a crown of spines on the cephalothorax, but some of the lateral pereonal spines are longer than in *A. spinacoronatus* and are arranged as in *A. polaris*, from which it differs by having longer spines and a less smooth pleotelson. Hitherto published descriptions do not allow a clear identification.

### 3. REDESCRIPTION OF *ANTARCTURUS SPINACORONATUS* SCHULTZ, 1978

It is assumed that the correct name of this species is *spinacoronatus*, as it refers to the crown of spines on the cephalothorax and is used in the *derivatio nominis*, the other spellings in the original description (Schultz (1978): '*spinacoronus*' in the map on p. 34, and '*spinacornatus*' on p. 38) being misprints.

#### (a) *Material*

For a list of stations at which *A. spinacoronatus* was found, see table 1.

The following specimens were used for comparison: *Antarcturus polaris* (British Museum (Natural History) (B.M.N.H.) 1921.11.29); *A. coppingeri* (B.M.N.H. 1879: 19, holotype); *A. antarcticus* (Musée National d'Histoire Naturelle, Paris, IS 1783, types).

TABLE 1. STATIONS WITH *ANTARCTURUS SPINACORONATUS*

position	depth	specimens	measurements
61° 20.58' S 54° 45.71' W	259–295 m	2 immature adults	29 mm, 46 mm
62° 38.81' S 55° 45.20' W	277 m	1 ovigerous female	35 mm
63° 28' S 54° 17' W	232 m	1 ovigerous female	32 mm
70° 26.94' S 8° 39.86' W	346 m	1 ovigerous female	41 mm
70° 29.85' S 8° 7.36' W	257 m	2 mature females	30 mm
70° 31.13' S 8° 1.01' W	219 m	1 immature specimen	(damaged)
72° 31.64' S 17° 34.97' W	242–246 m	1 immature adult	19 mm
72° 54.77' S 19° 39.94' W	429 m	1 immature adult	26 mm
73° 23.36' S 21° 30.37' W	465–481 m	1 ovigerous female	43 mm
73° 41.78' S 20° 55.5' W	191 m	1 manca	9 mm
76° 0.10' S 27° 27.12' W	322 m	3 ovigerous females	32–47 mm
76° 34.20' S 30° 53.5' W	335 m	1 ovigerous female	37 mm
77° 17.96' S 40° 5.47' W	745 m	1 immature adult	26 mm
77° 39.63' S 35° 23.91' W	439–444 m	1 ovigerous female	39 mm

*(b) Distribution*

Besides the stations of the *Polarstern* expeditions (see also figure 1) *A. spinacoronatus* is only known from the type locality (Schultz (1978): off Wilhelm II coast). It is very frequent in the Weddell Sea and it is astonishing that it has not been found more often elsewhere around Antarctica.

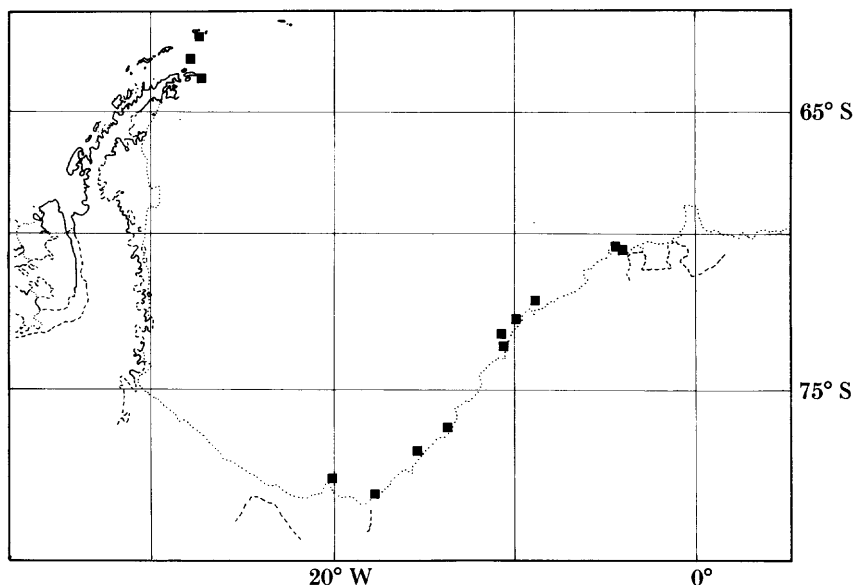


FIGURE 1. The distribution of *Antarcturus spinacoronatus* in the Weddell Sea. The localities reflect the activities of the R.V. *Polarstern* during the expeditions of 1982–83 and 1984–85.

*(c) Redescription (figures 2–12)*

Pereonite 1 fused with cephalothorax; pereonite 2 shorter than 3 and 4; pereonites 5–7 shorter than pereonite 2. Tergites of pereonites 5–7 with concave posterior border, into which the following segment fits when the animal bends dorsally. Pleonites fused with pleotelson. Cuticular spines as in figure 2 and figures 5–7, plate 1. The lateral supraocular spines of the cephalothorax do not surpass the eyes. Dorsal crown of spines, from which the species takes its name, formed of four transversal ridges which bear short, mostly blunt, spines. A small rostral spine projects dorsally between the peduncles of the antennules (A 1) (figure 3d); a broad rostral point, not seen in dorsal view, projects between the first articles of the antennae (A2). Terminal spines of pleotelson nearly as long as width of pleotelson. Ventral to these spines is a pair of very short spines (figure 7).

The arrangement of cuticular spines is similar in both sexes. Large specimens have more of the smallest spines.

Mature females with broader thorax than males or immature individuals. Oostegites on pereonites 2–4. Genital aperture ventrally on pereonite 5, outside of marsupium (figure 2b: G Ap). Mature female with a strong, medially directed spine on coxal sclerite of pereonite 4, forming a caudal breach for the marsupium (figure 2b: CS). Immature females with small coxal spines, males without (figure 2d).

Male genital aperture only visible after opening respiratory chamber. Two vasa deferentia

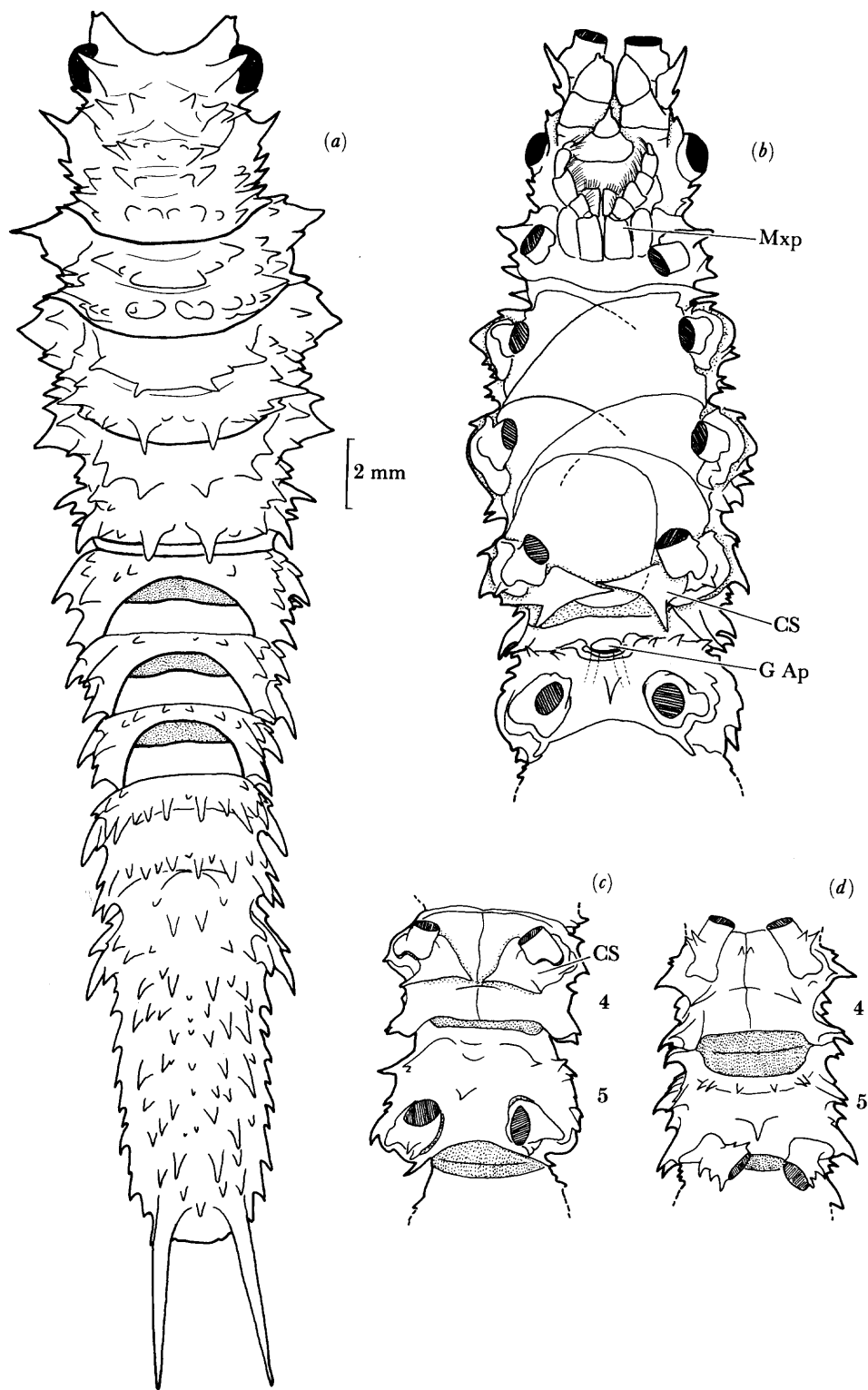


FIGURE 2. *Antarcturus spinacoronus*. (a) Dorsal view of ovigerous female. (b) The same specimen in ventral view, showing the coxal spines (CS) of pereonite 4 and the region of the genital apertures (G Ap) on pereonite 5. (c, d) Ventral views of pereonites 4 and 5 of an immature female (c) and a mature male (d).

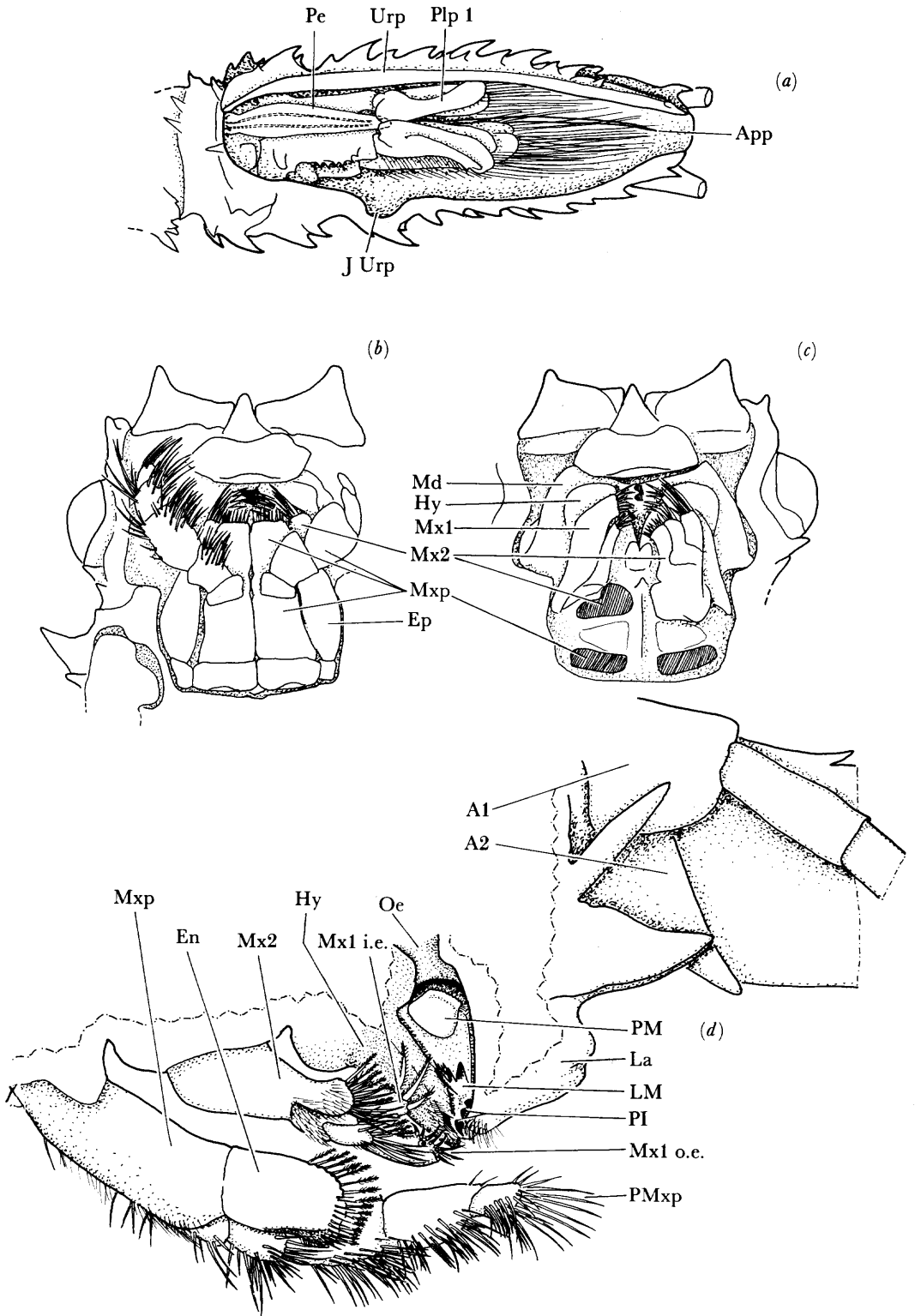


FIGURE 3. *Antarcticurus spinacoronatus*. (a) Pleotelson of male, ventral. Note how the distal end of the penis (Pe) is covered by lobes of the endopod of pleopod 1. Right uropod removed, left uropod opened. (b, c, d) Mouthparts in ventral (b, c) and medial views (d). In (c) both maxillipeds and the right maxilla are removed; (d) is a sagittal section showing the mouthparts of the left side.

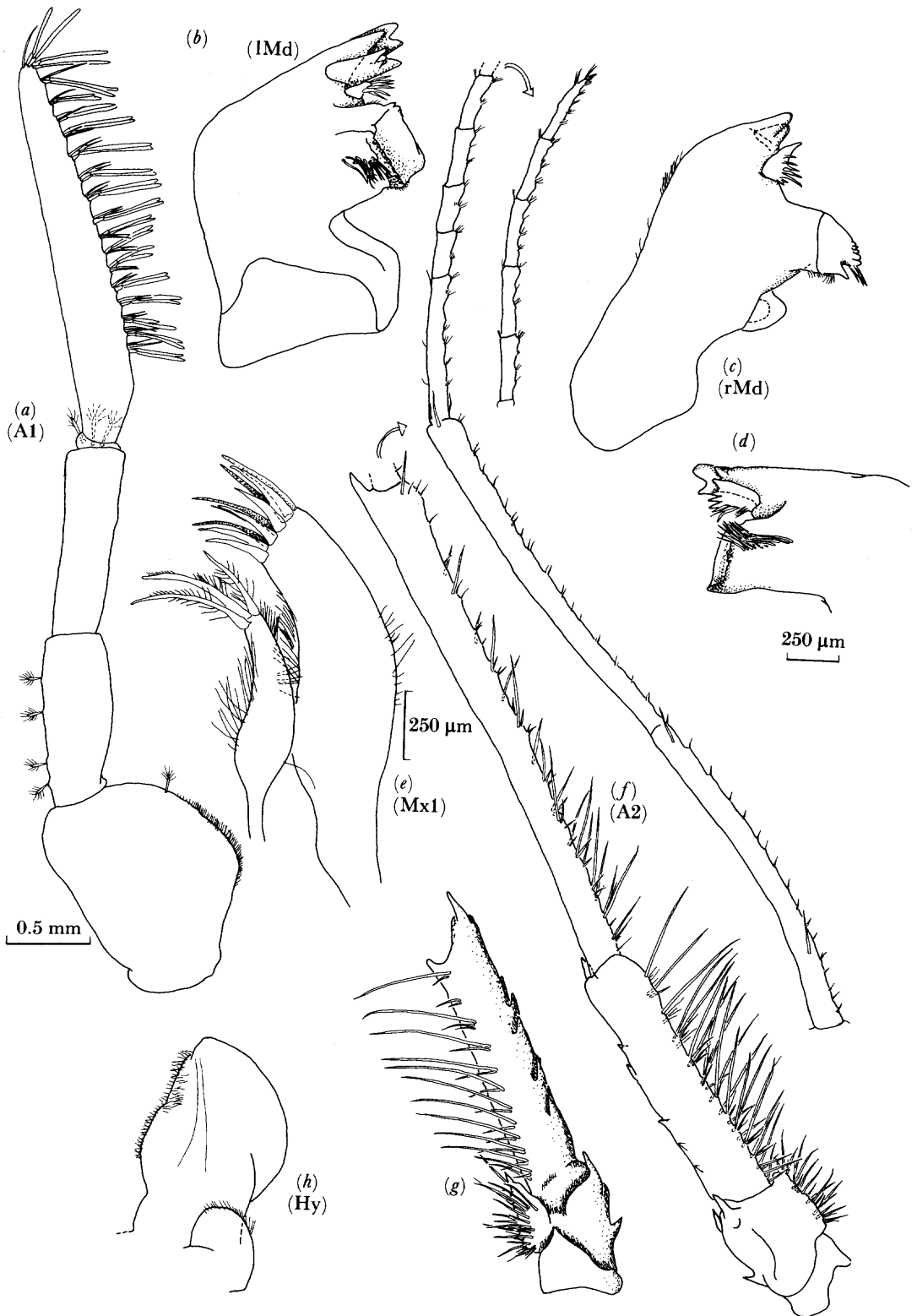


FIGURE 4. *Antarcticur spinacoronatus*, male. (a) Antennule. (b) Left mandible. (c), (d) Two views of right mandible. (e) Maxillula. (f) Antenna. (g) Lateroventral view of first peduncular articles of antenna. (h) Left half of hypopharynx.

## DESCRIPTION OF PLATE 1

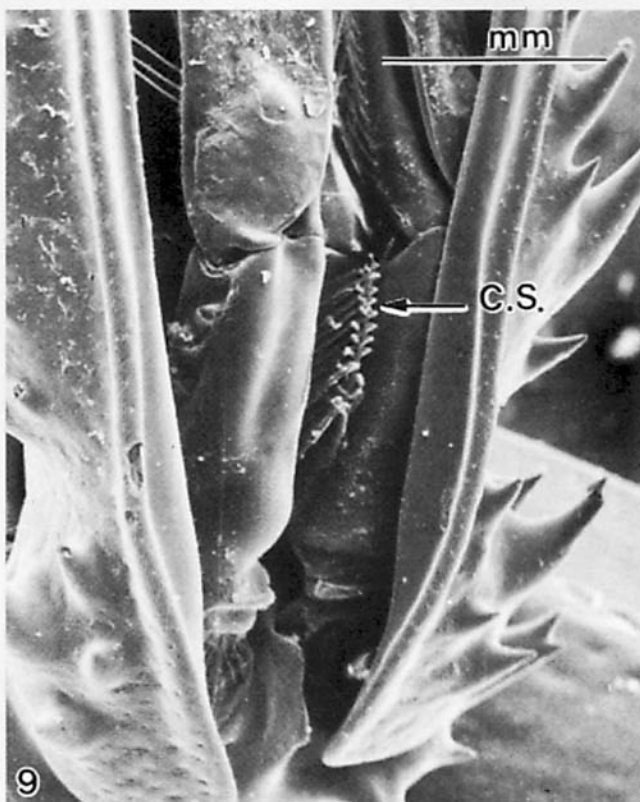
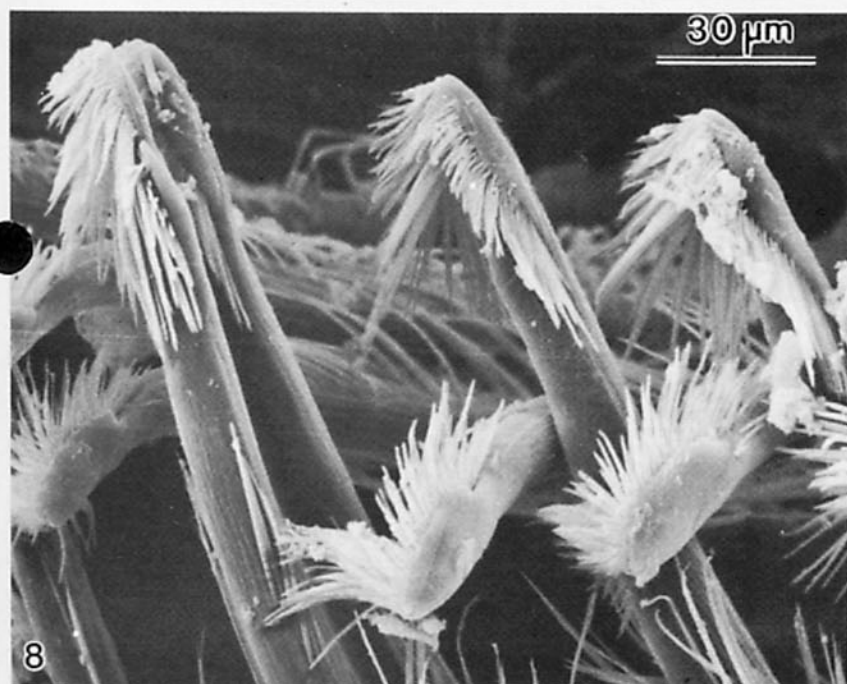
### *Antarcticur spinacoronatus*.

FIGURES 5 and 6. Cephalothorax with the crown of spines in lateral (figure 5) and dorsolateral (figure 6) views.

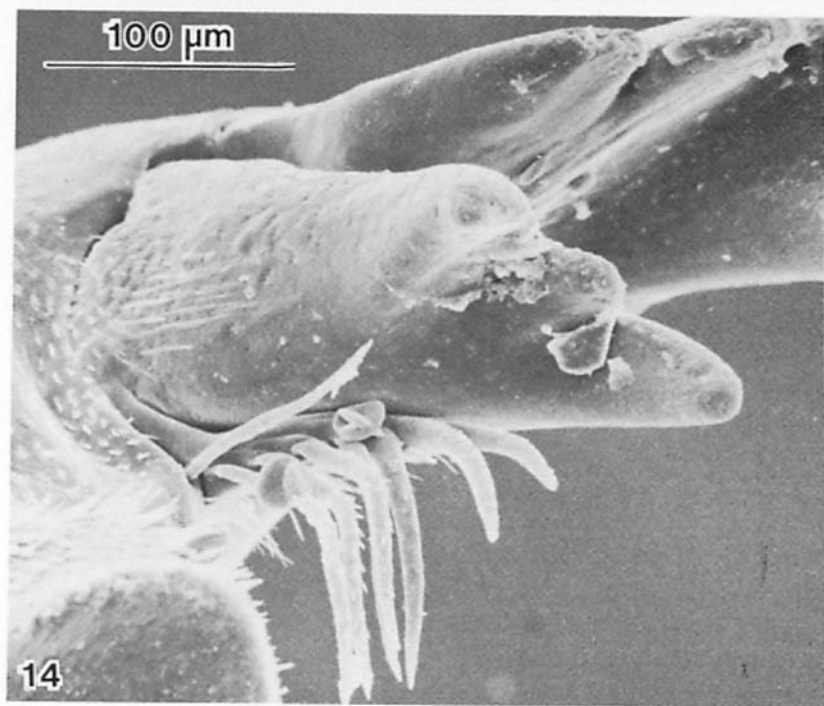
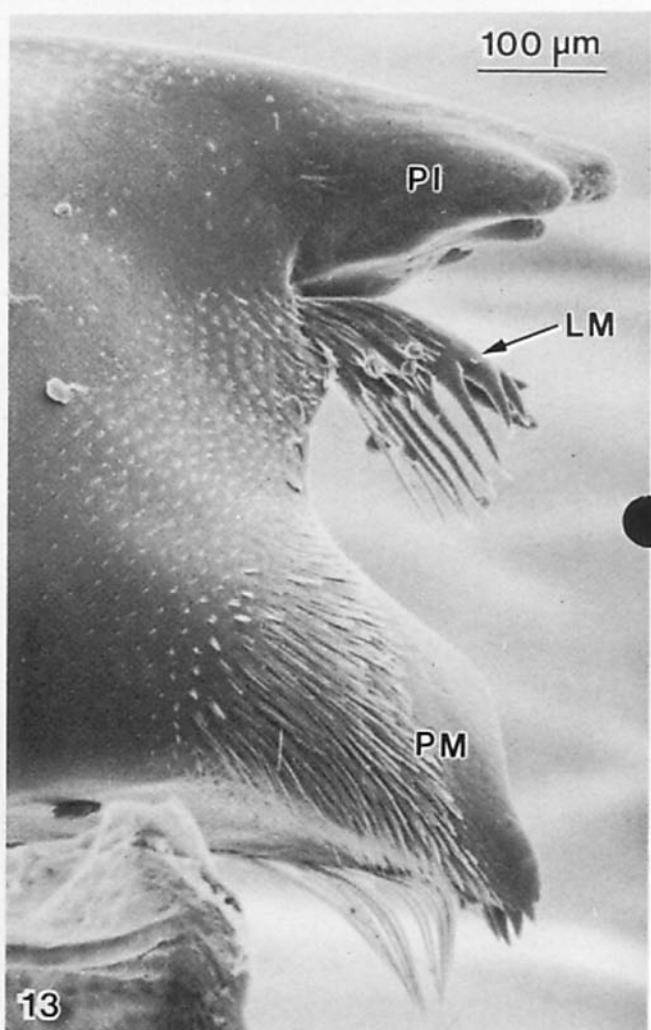
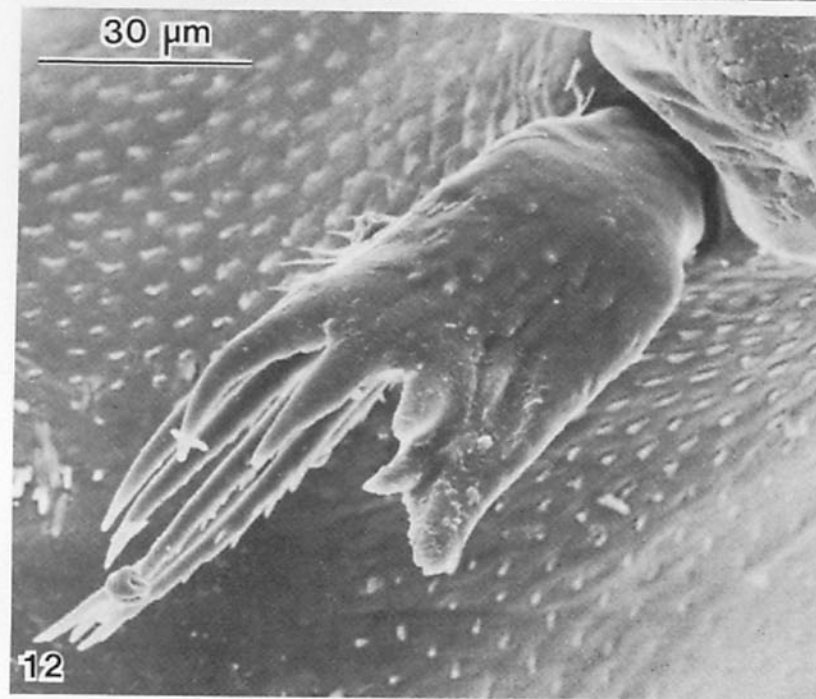
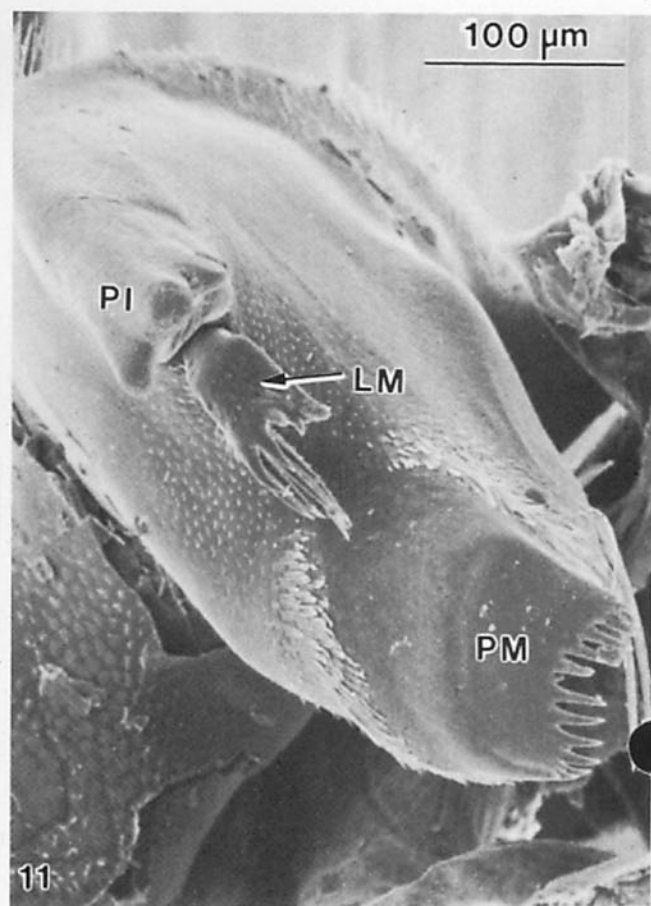
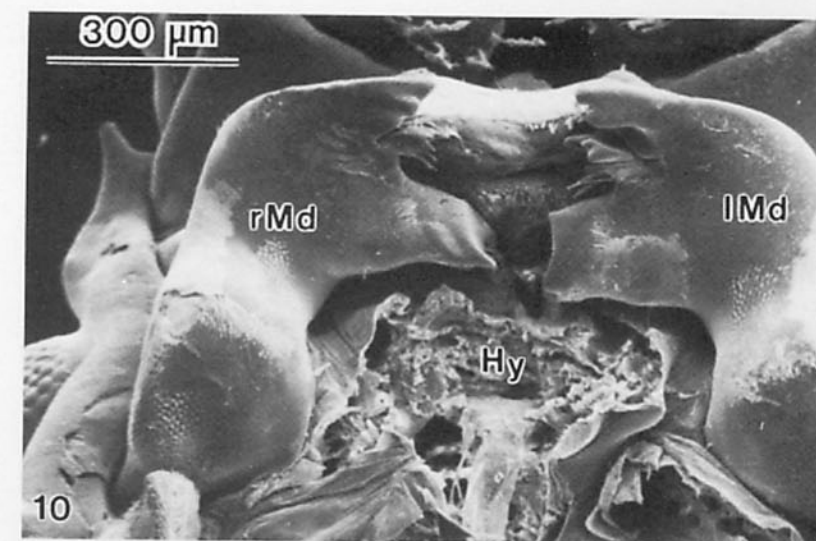
FIGURE 7. Distal part of the pleotelson in dorsal view, showing the characteristic armature of spines.

FIGURES 8 and 9. View into the ventral respiratory chamber, with the sympodites of pleopod 1 and the coupling setae (c.s.) and a detail of the distal interlocking structures of these setae (figure 9).





FIGURES 5-9. For description see opposite.



FIGURES 10–14. For description see opposite.

## DESCRIPTION OF PLATE 2

*Antarcturus spinacoronatus*: mandibles.

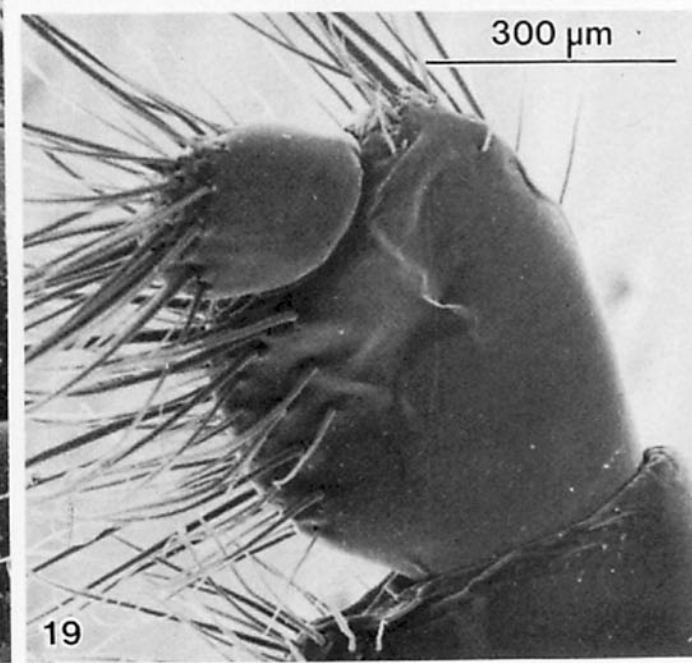
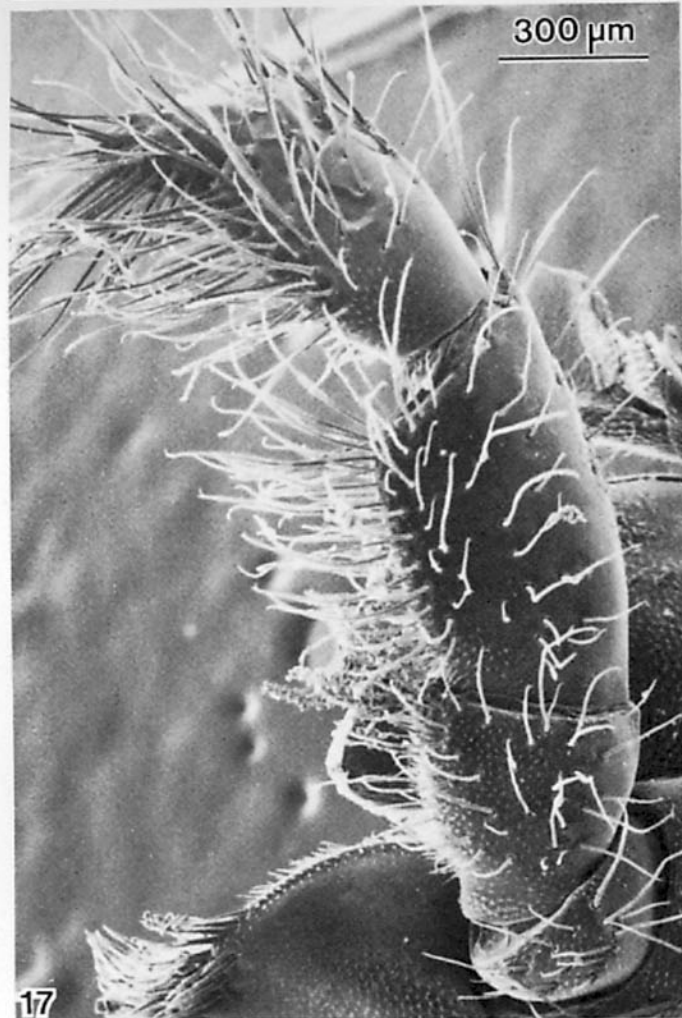
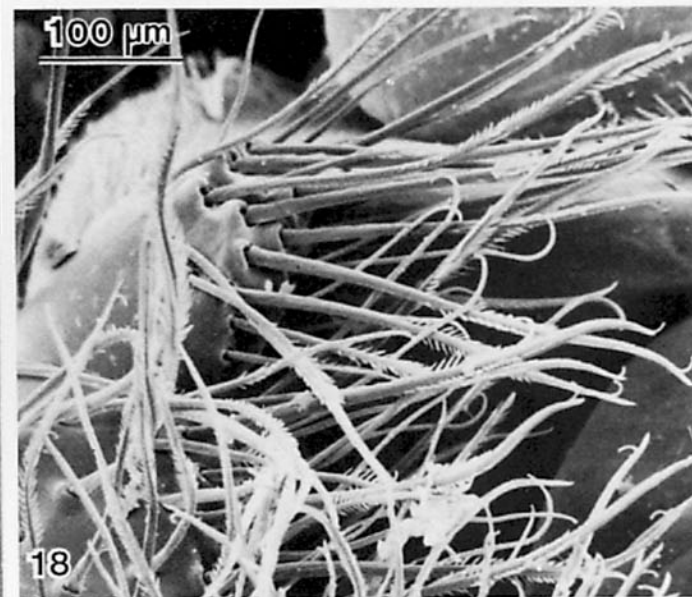
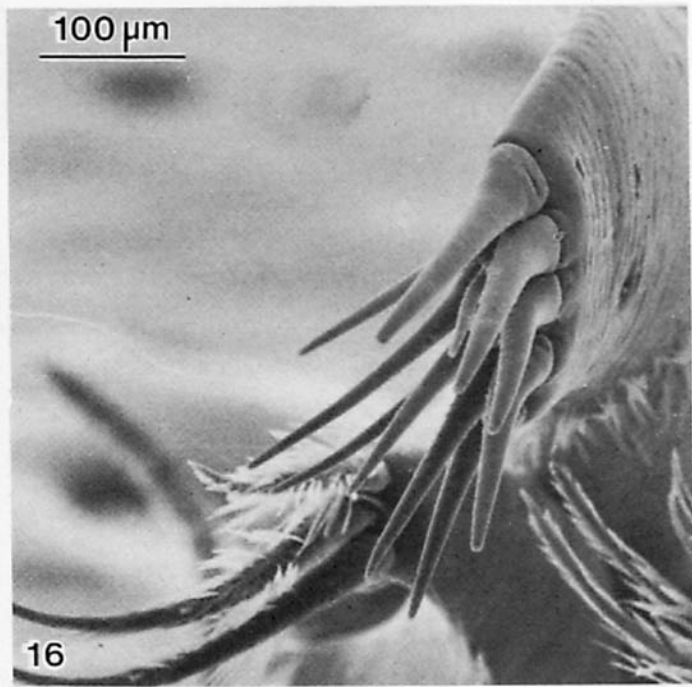
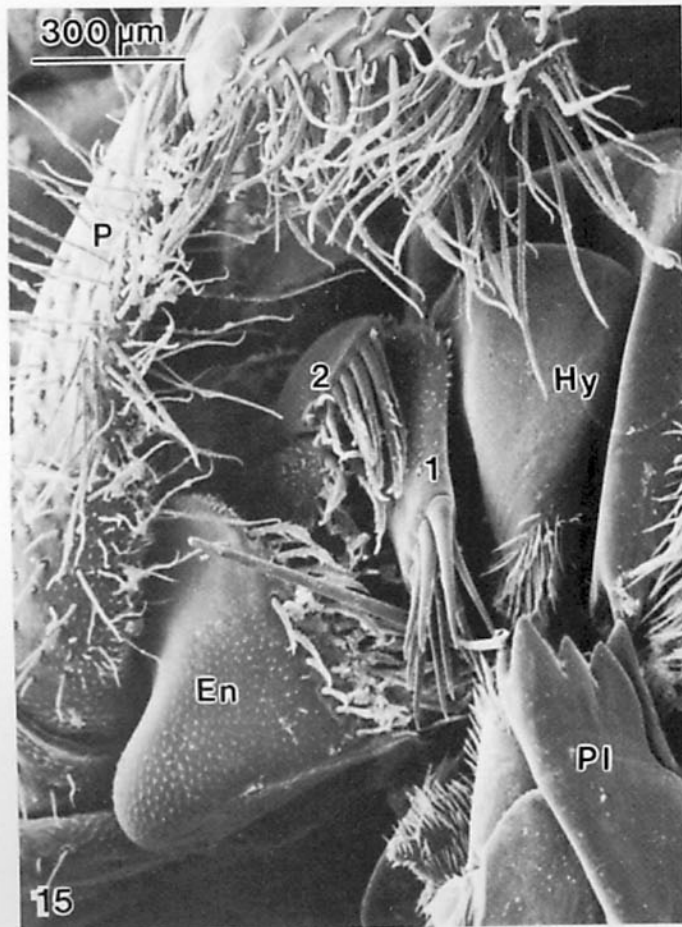
FIGURE 10. Both mandibles in ventral view; the hypopharynx (Hy) has been removed.

FIGURE 11. Right mandible.

FIGURE 12. Lacinia of right mandible.

FIGURE 13. Right mandible.

FIGURE 14. Lacinia of left mandible.



FIGURES 15–19. For description see opposite.

## DESCRIPTION OF PLATE 3

*Antarcturus spinacoronatus*: mouthparts.

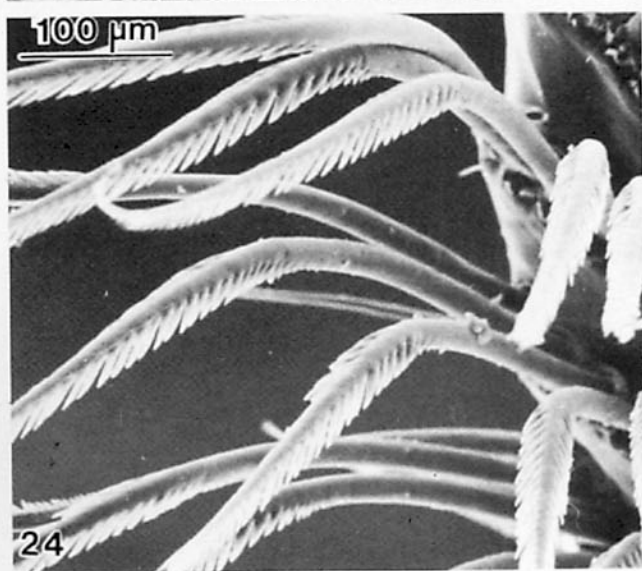
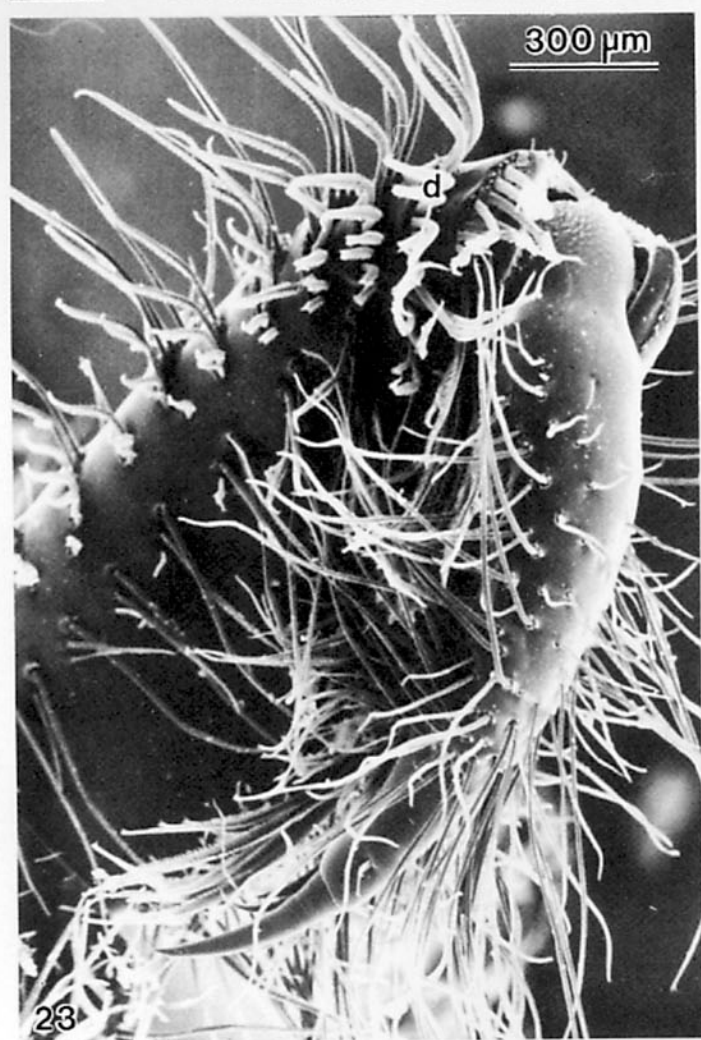
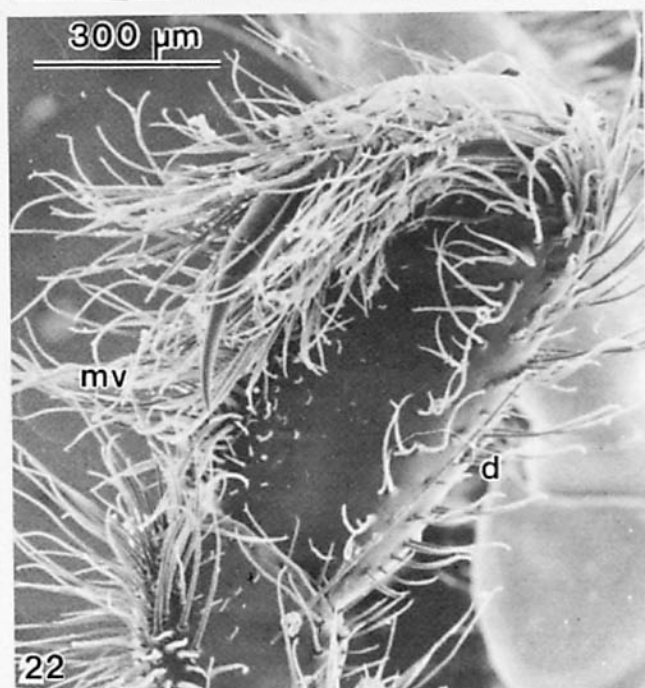
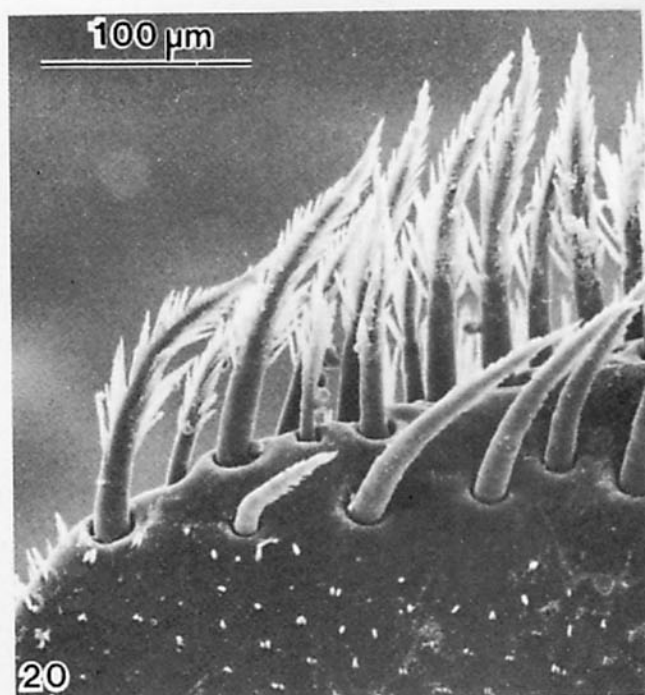
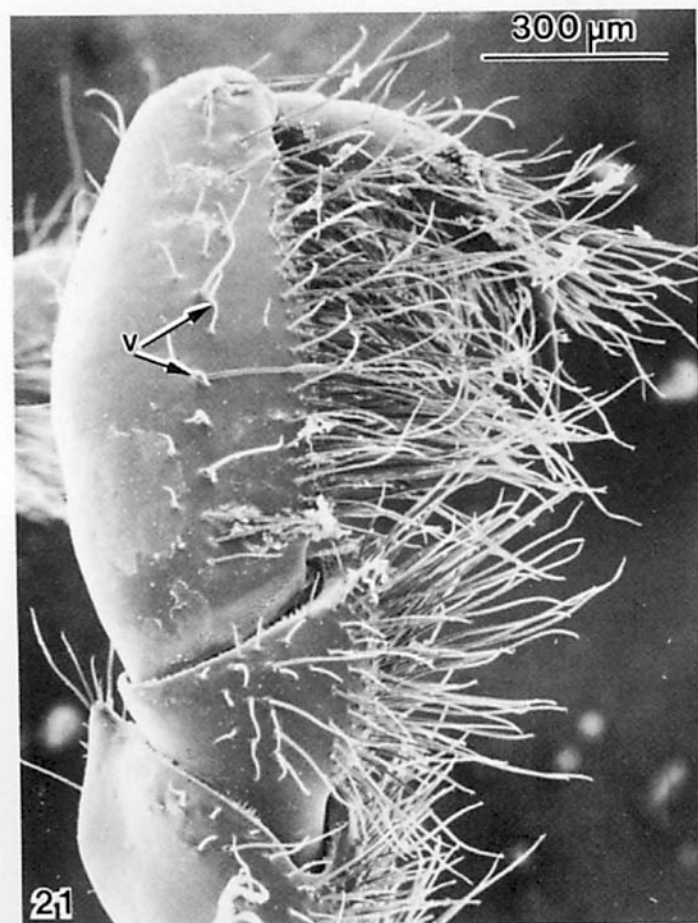
FIGURE 15. Mouthparts in medioventral view. 1: Lateral endite of right Mx 1; 2: lateral endite of right Mx 2.

FIGURE 16. Left maxillula in medial view.

FIGURE 17. Ventral surface of left maxilliped.

FIGURE 18. Last article of palp of right maxilliped with its mediodorsal setae.

FIGURE 19. Dorsal surface of palp of maxilliped.



FIGURES 20–24. For description see opposite.

## DESCRIPTION OF PLATE 4

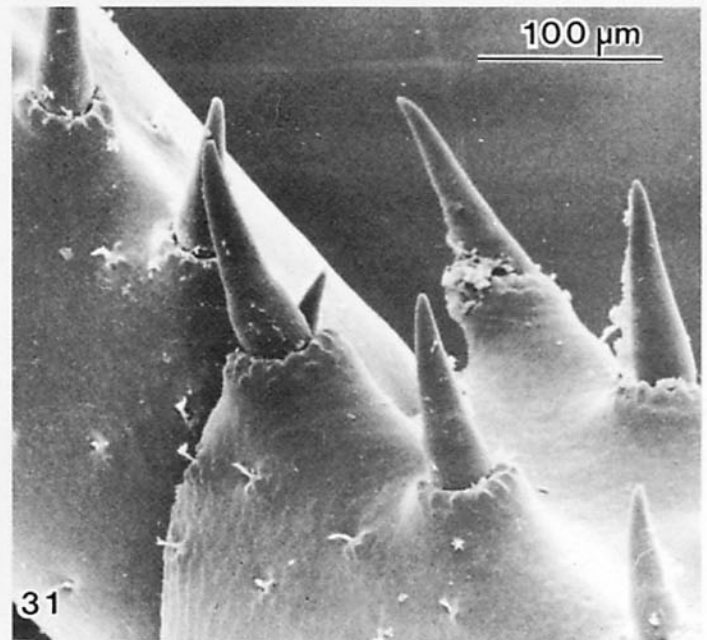
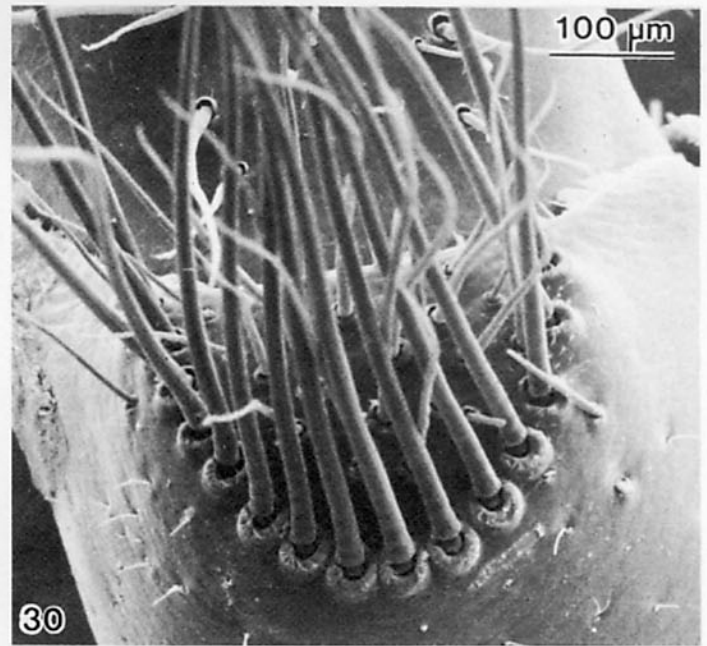
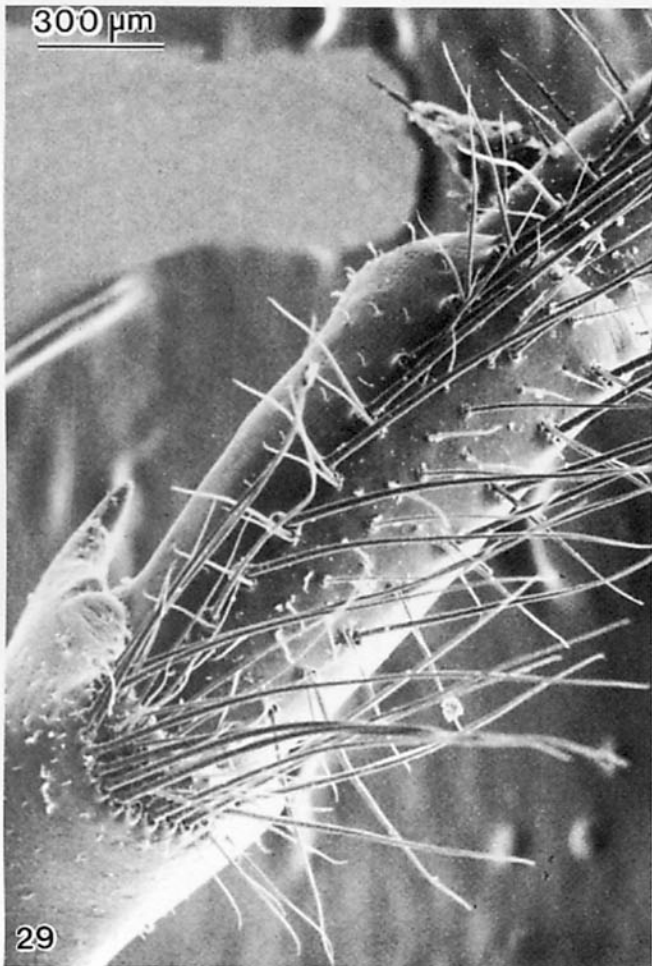
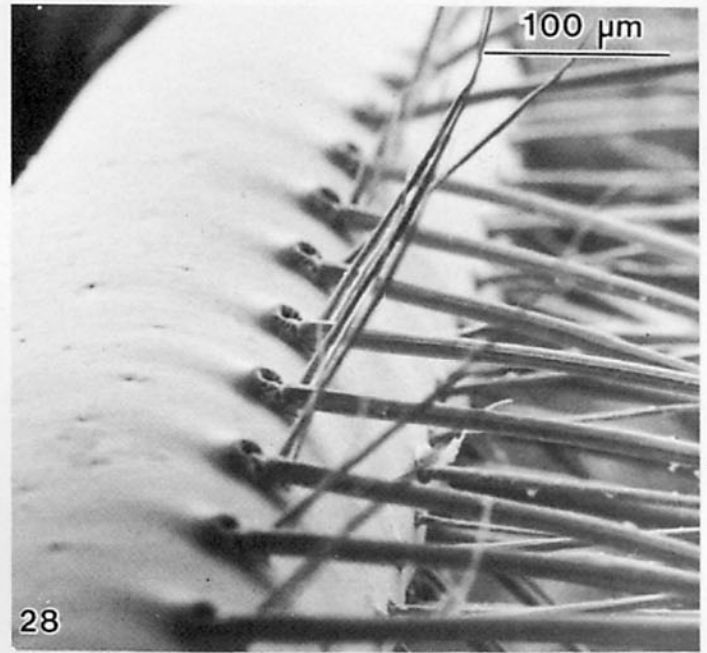
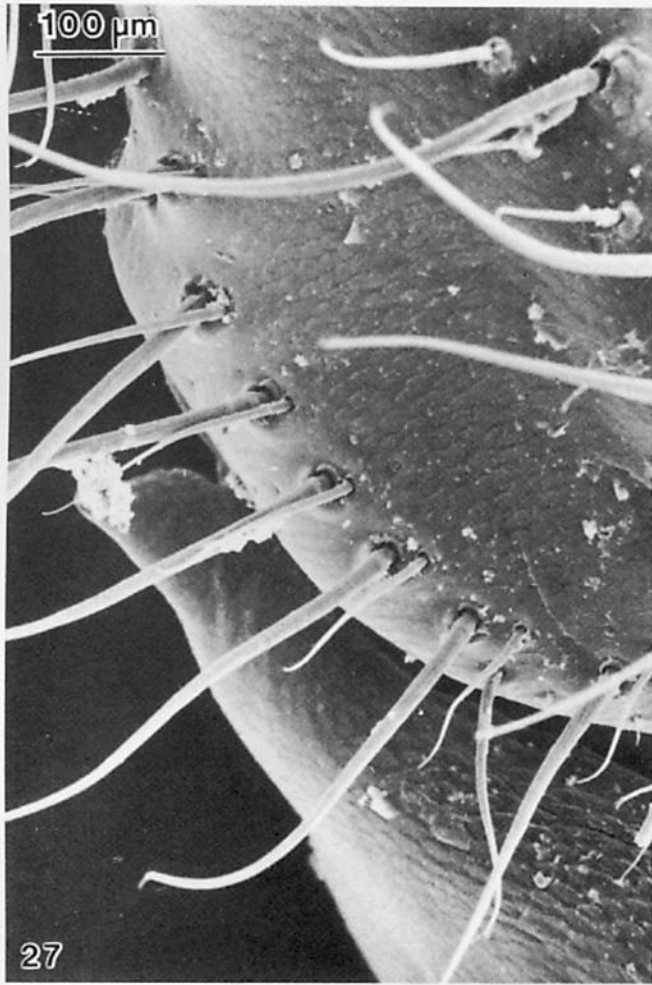
*Antarcturus spinacoronatus*: details of maxilliped and pereopod 1.

FIGURE 20. Spines on distal margin of the maxillipedal endite.

FIGURES 21 and 22. Distal podomeres of right pereopod 1 in ventral (figure 21) and dorsal (figure 22) views.

FIGURE 23. Left pereopod 1 with dorsal setae (d) of propodus.

FIGURE 24. Detail of dorsal setae of propodus.



FIGURES 27-31. For description see opposite.



end on the point of a large penis (Pe), its apex hidden under basal lobes of the endopods of the first pleopods (figure 3a).

Antennule with three subequal peduncular articles; first article broad; first flagellar article forming short ring, with three feather-like bristles, second article longer than two peduncular articles together, with fifteen groups of two aesthetascs and one or two simple setae; distally four aesthetascs and one seta.

Antenna longer than the animal's body. Peduncle (figure 4f) of six articles; first very short, without setae, second short, with ventral tuft of small setae and spines as in figures 4 and 6. Third peduncular article more than four times as long as broad, with two ventral rows of groups of setae, each consisting of one long and one or two short simple setae (plate 5, figure 5; figure 27, plate 5); lateral and medial surfaces each with five spines, lateral spines longer, distally one spine-like projection. Setal rows of fourth article as in third, but with wider spaces between groups of setae. Articles 4–6 long and slender, fourth with one distal spine-like projection and ventrally several simple setae, setae on articles 5 and 6 very short. Articles 4–6 each with one stout distal seta. Flagellum shorter than half of peduncle, of ten articles, bearing very short, small setae.

Mandibles (figure 4b–d; figures 10–14, plate 2) asymmetrical, without palp. Pars incisiva of right mandible (figures 4c, d, 11 and 13) narrower than left, with four teeth; lacinia mobilis smaller than pars incisiva, with short distal teeth and bristle-like proximal structures (figures 4c, d and 11–13). Below lacinia no further setae. Pars molaris stout, broad grinding surface with indented margin; row of setae on lower proximal side directed orally. Pars incisiva of left mandible with three teeth; lacinia mobilis stout, with three blunt teeth (figures 4b, 10 and 14; figure 15, plate 3), at its base a lobe bearing seven blunt spines. Pars molaris as in right mandible, indentation of lower edge of grinding surface less deep. Hypopharynx of two voluminous lobes, each bearing ventrally a smaller, lateral lobe; medial margins covered with fine setules. Lateral endite of maxillula with eleven strong, medially curved teeth (arrangement as in figures 3c and 4e; figure 16, plate 3), medial endite shorter, apex bearing three strong bristles with setules. Maxilla (figure 25a–d) of three endites; inner endite with twenty spines, most with two rows of spinules; medial endite with four long, serrated spines; lateral (outer) endite with nine spines. Apical margin of endite of maxilliped with two rows of short, spine-like setae, each with two rows of spinules (figure 20, plate 4; figure 25h). Endites touching in midventral line and projecting here dorsally (figure 37: En). Neither endite nor basis with coupling hooks. Epipod long, oval, surpassing second palpal article (figures 3b and 25h: Ep). Palp of five articles, third longest, last smallest; all with dense brush of setule-bearing bristles on ventromedial surface, dorsal surface smooth, without such armature (figures 17–19, plate 3; figure 25h).

Pereopod 1 (figures 25e–g) with long basis, short ischium, broadened merus, short trapezoidal carpus, broad-oval subchelate propodus; dactylus shorter than propodus, with a large apical

#### DESCRIPTION OF PLATE 5

*Antarcturus spinacoronatus*: details of setation.

FIGURE 27. Joint between first and second article of antenna, with row of filter-setae on second article.

FIGURE 28. Carpus of pereopod 4, with lateral row of filter-setae in focus.

FIGURE 29. Ischium of pereopod 4 with filter-setae and distal part of basis with semicircle of setae.

FIGURE 30. Semicircle of setae on distal end of basis of pereopod 4.

FIGURE 31. Spines on pereopod 5, joint between carpus and propodus.

and a short subapical claw. Articles densely setose. Ventral surface of propodus with few setae, most along a line a short distance from propodal palm (figures 21, plate 4; figure 25g) medioventral margin densely setose (fine structure as in figures 23 and 24, plate 4); the more distal setae with proximally directed tips, the proximal bent slightly in the direction of the dactylus (figure 22, plate 4); the outermost, somewhat shorter setae of this brush (on ventral side of propodus) standing as a row of single setae (figure 21). Mediodorsal side of propodus forming a slightly concave 'spoon', surface here nearly bare except for some short setae. Curved dorsal surface with long setae arranged in parallel transverse rows of combs (figures 22, 23 and 25f); between these combs and the mediodorsal concave 'spoon' are a few simple, medially directed setae.

(Being a thoracopod belonging to the cephalothorax 'pereopod 1' is not a true pereopod, but is called pereopod 1 in this paper to follow tradition and to avoid possible confusion with the homologue pereopod 1 of other isopods, where the first segment is not fused to the maxillipedal region.)

Pereopods 2–4 (figure 26) rather similar, but basis of pereopod 3 and pereopod 4 with strong proximal spine and ischium with long, spine-like projection not present on pereopod 1 distally, merus of pereopods 2–4 with a similar projection, carpus with only short distal projection. Carpus and propodus cylindrical, elongate. Dactylus shorter than propodus, slender, scythe-shaped, with one long and two short terminal claws. Setation of all legs similar: basis with posterodistal tuft of setae arranged in a semicircle (figure 26a, b, g, h: ST; figures 29 and 30, plate 5); ischium, merus, carpus and propodus with three longitudinal rows of setae on posterior surface, namely two lateral rows of groups of two or three simple setae, of which the outermost seta is very long, and a median row of single setae of medium size (figures 26c–e; figures 28 and 29, plate 5). The lateral rows of setae resemble those on the first articles of the antenna (figure 27). Dactylus lacking such armature, bearing only a few, short, slender setae.

Pereopods 5–7 shorter and stouter than anterior pereopods; basis always the longest article, cuticle forming long spine-like, blunt pegs (figure 32a–c); tread of ischium, merus, carpus and propodus with short, blunt spines (figure 31, plate 5; figure 32a–c), in two rows on merus and carpus, in single row of five spines on propodus.

Pleopods hidden in respiratory chamber (figures 8 and 9, plate 1) formed by pleotelson and uropods; in females and immature specimens all of similar form, with long branches, margins bearing long swimming setae. Males with modified pleopods 1 and 2 (figure 32d–g): endopod of pleopod 1 with a medially protruding basal lobe and a ridge running from this edge diagonally to the distolateral margin, where a tuft of modified setae inserts; most of these are feather-like; more distally is a row of setae with hooked tips, behind it a row of longer setae with setules only distally (figure 32d, e); medial and distal margins of endopod with over 30 swimming setae, lateral margin with simple setae. Endopod of pleopod 2 with long, stiletto-like appendix masculina and more than 30 swimming setae, exopod with about 80 setae. Uropod as in figure 32h, i, small distal branch with 5 setae.

#### (d) *Systematic position*

Specimens from the Weddell Sea agree well with the description of Schultz (1978), the shape of the supraocular spine and the arrangement of the shorter cephalothoracic spines being very characteristic. In Schultz's figures the antennule has no first flagellar article and the uropod has a slightly different number of cuticular spines. Schultz believes that *Antarcturus* sp. of Monod (1926) (from 70° S, 80° 48' W) could be identical with *A. spinacoronatus*, but Monod's specimens

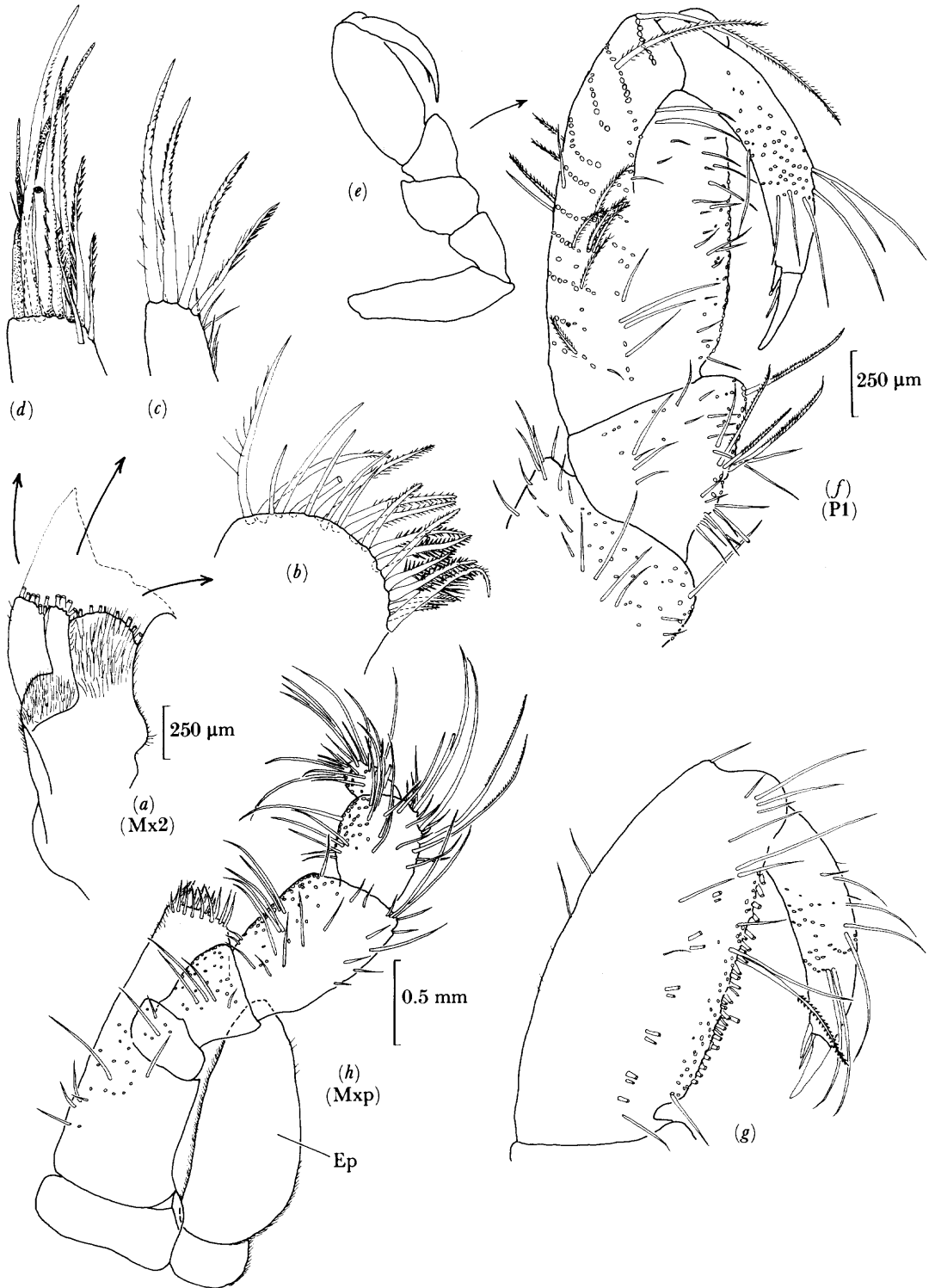


FIGURE 25. *Antarcturus spinacoronatus*, male. (a) Maxilla with details of setation of the endites (b, c, d). (e) Outline of pereopod 1. Last articles of pereopod 1 shown in ventral (f) and dorsal view (g). (h) Of the maxilliped only the ventral side can be seen. For many setae only the place of insertion is shown, other setae are cut off.

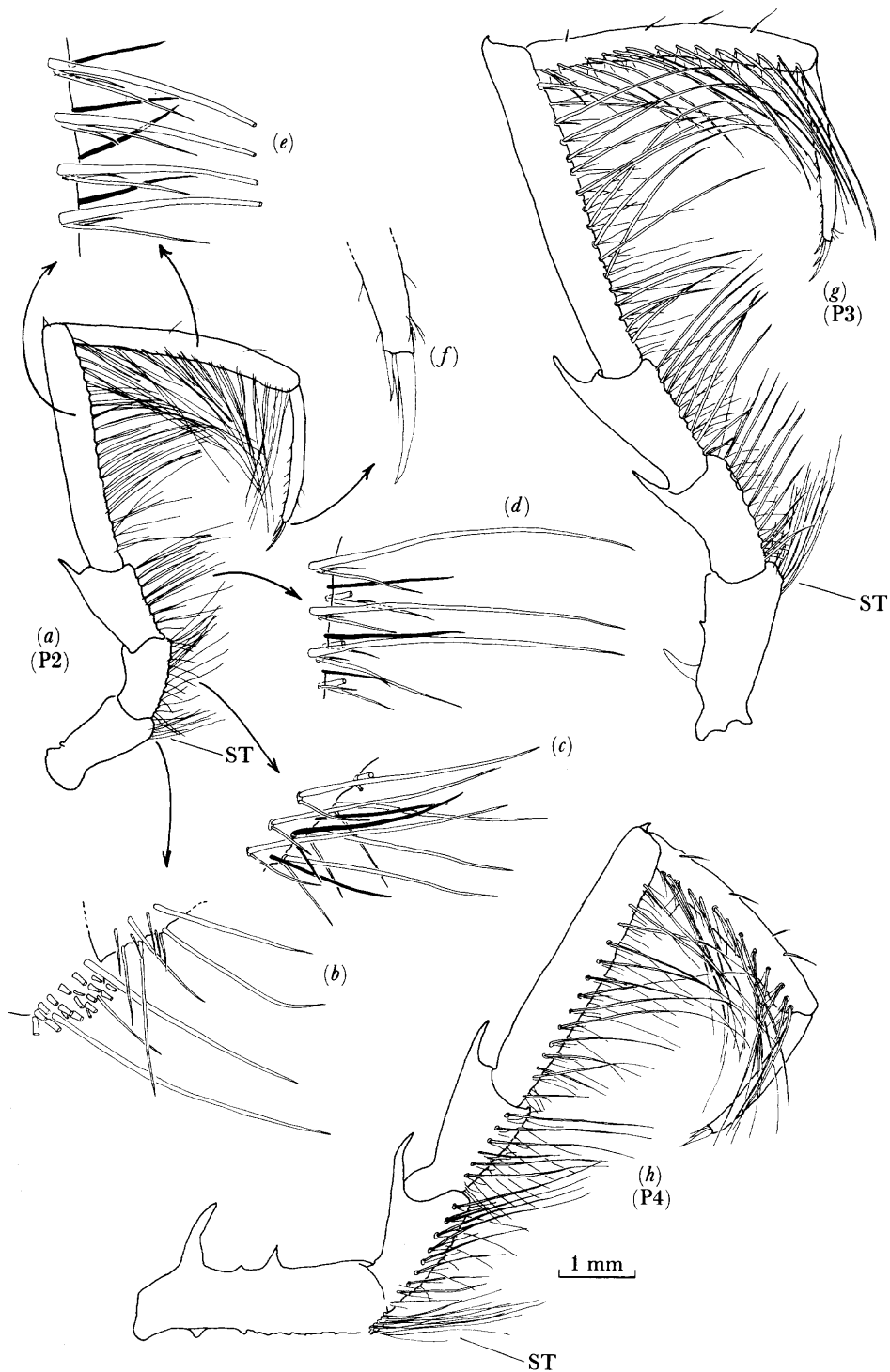


FIGURE 26. *Antarcturus spinacoronatus*, male. (a) Pereopod 2 with details of setation; only the filter-setae of one side of each podomere are shown in the detail of the carpus and propodus; central row of short setae black. (b) Setation of basis. (c) Detail of ischium. (d) Detail of merus. (e) Detail of carpus, identical with propodus. (f) Claws on dactylus. Pereopods 3 and 4 have a similar setation. (g) Pereopod 3. (h) pereopod 4.

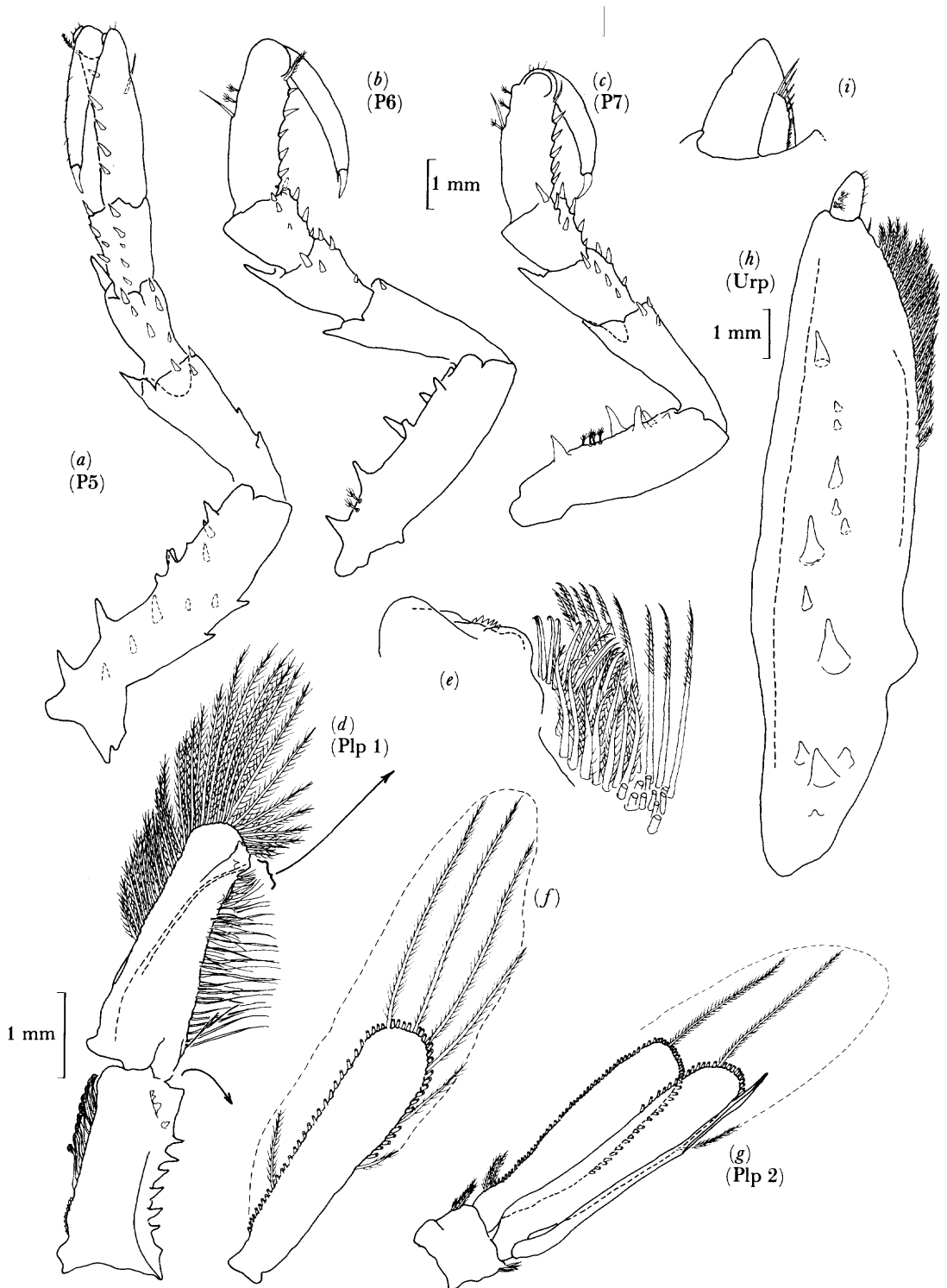


FIGURE 32. *Antarcticurcus spinacoronatus*, male. (a) Pereopod 5. (b) Pereopod 6. (c) Pereopod 7. (d) Pleopod 1 with detail. (e) The enlarged apical region of the endopod shows the complex setation of this area. (f) Exopod of pleopod 1. (g) Pleopod 2 with appendix masculina; (h) Uropod. (i) Distal branches of uropod.

have longer supraocular spines, which clearly surpass the eyes, a feature present only in very small individuals of *A. spinacoronatus*, never in adults. Similar also is *A. furcatus*, a species not very well described, as Schultz (1978) notes. Studer (1882) and Beddard (1886) figure for this species hook-like supraocular spines that are directed dorsally rather than laterally as in *A. spinacoronatus*. According to Hale (1946) and Kussakin (1967) the podomeres of *A. furcatus* are longer and bear more propodal spines (about ten) than *A. spinacoronatus*. *A. polaris* (Hodgson, 1902) has a similar outline and the lateral thoracic spines are probably homologous with some of the spines of *A. spinacoronatus*, but the smaller spines are lacking and the supraocular spines clearly surpass the eyes.

Several other species also have similar features, but differ in the number, size and arrangement of the cuticular spines, as far as can be judged from the published drawings (e.g. *A. adareanus* (Hodgson 1902); *A. alimus* (Schultz 1978); *A. americanus* (Beddard 1886)). All have two long terminal spines on the pleotelson, supraocular spines, additional acute or blunt cuticular spines or pegs, spine-like structures on the lateral side of the sympod of pleopod 1, and relatively short, spiny pereopods 5–7. However, for a further analysis of the natural relationships within the genus more exact descriptions are necessary, as they are to overcome difficulties with synonymies and the correct denomination of new specimens. Moreover, a better knowledge of morphology should help us to understand niche specialization in sympatric or neighbouring populations.

#### 4. BEHAVIOUR AND FEEDING MECHANISM

##### (a) *General behaviour*

The following behaviour seems to be typical for many arcturids. At least the observed species of *Antarcturus* as well as *Dolichiscus meridionalis* often moved in a similar way. To describe the subtle differences in behaviour more exact observations are needed.

As soon as freshly caught animals are placed in aquaria they climb on any elevated substrata they can find. Usually *A. spinacoronatus* avoids swimming. The antennae keep in contact with the surrounding ground, but optical orientation is also important; the animals react to a slowly approaching pipette when this is still about 15 cm away. When several individuals are resting close together, they use their antennae to touch each other and usually move away some centimetres until the antennae can move freely through the water. When exploring its surroundings the animal's body sways slowly from side to side. Changing position step by step with the pereopods 5–7, *Antarcturus* turns on the spot, moving the antennae in different directions, often towards close-by objects that are obviously detected by the eyes. In contrast to the antennae the antennulae are always held dorsally (figure 33c), probably to test the chemical properties of the water with their aesthetascs.

The antennae are also important for climbing (figure 33a). Animals moving slowly over substrata use pereopods 5–7 to grasp their support; the strong spines on the tread (figure 31) make it possible to hold thin threads, as well as smooth, thick spicules of sponges. Pereopods 2–4 can support the body on the dactyli, above all because, in contrast to the propodi, the dactyli bear no rows of long setae. But the dactyli cannot be folded against the propodi as in a subchelate leg and therefore an anterior pereopod alone cannot establish a firm hold: it can only be used like a walking stick. Support is found, as shown in figure 33a, when several of the anterior legs are pressed against the ground. The first pair of pereopods does not participate

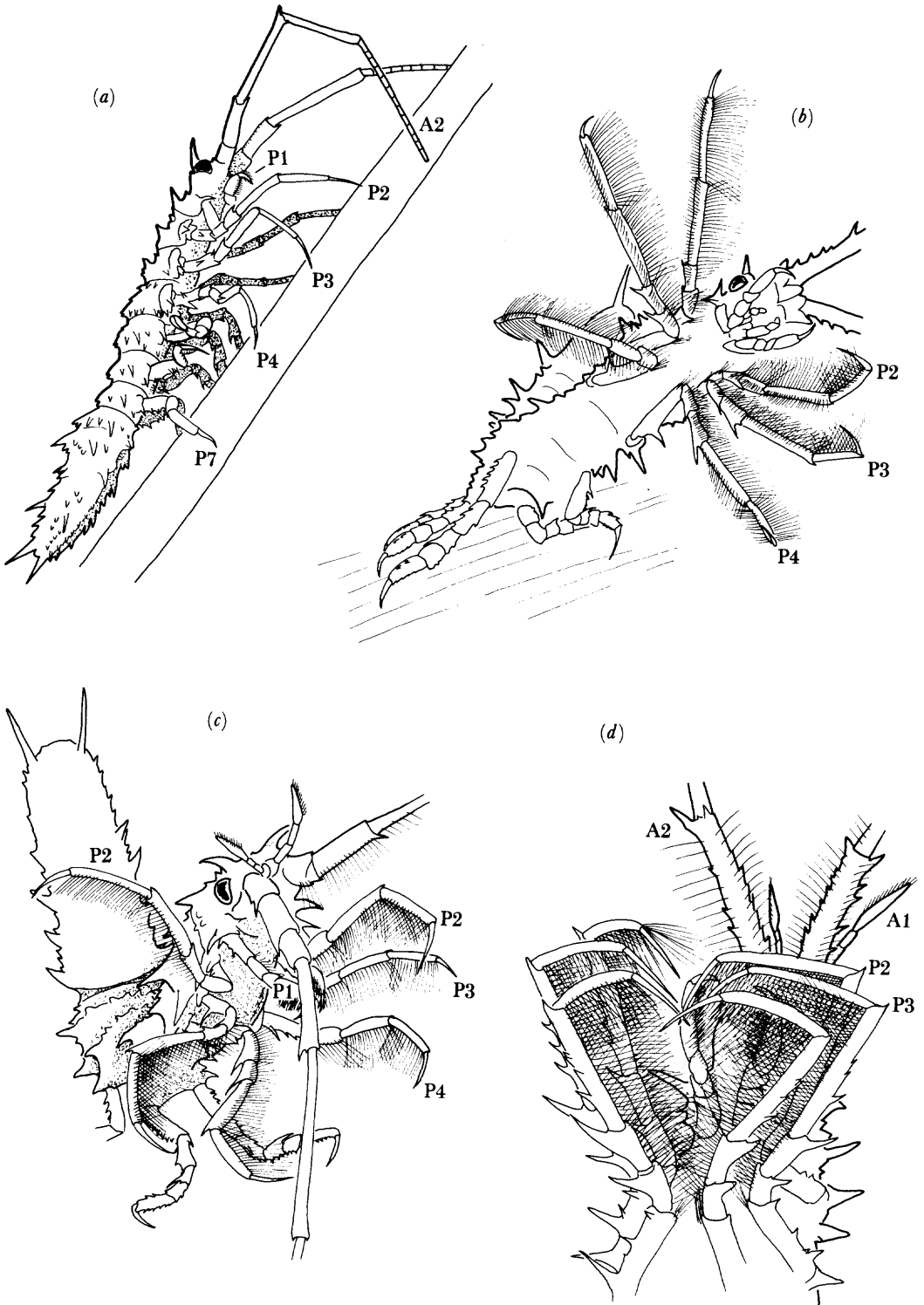


FIGURE 33. Behaviour of *Antarcticur spinacoronatus*. (a) Climbing with the help of the antennae and all pereopods (except pereopod 1). (b) Pereopods 2-4 in filtering position. The animal is inclined to the left to avoid an approaching pipette. (c) Vigorous movements of pereopods 2-4 in a suspension of food. (d) Ventral view of anterior pereopods. Resting position with folded filter.

in locomotion. The antennae are used as props for additional support. Similar behaviour was reported by Moreira (1973*a*) for *Arcturella sawayae* but, because in this species pereopods 2–4 are not used for climbing, the antennae are the only anterior support, and they grip while the posterior pereopods are drawn forward.

As long as *A. spinacoronatus* is undisturbed, it either does not move or it walks or climbs very slowly. Its movements are not much more lively than those of algae or hydroids that sway passively in the water. Movements are faster, but not well coordinated, when the animals are disturbed. They then often lose their foothold and fall to the bottom. To rise again the body is bent dorsally, the pleotelsonic terminal spines nudging the ground, while the peduncles of the antennae push against the substratum until the animal falls on its side and the hinder pereopods find a hold. Sometimes the pleopods beat to support the climbing movements. Only very short distances (a few centimetres) are traversed by jerks produced by the pleopods. Swimming distances longer than 10 cm are rarely observed. A species that swam more often than *A. spinacoronatus* is *A. antarcticus* Bouvier. This species can reach the top of a hydrozoan colony (15 cm), which the animals obviously could see, by swimming from the ground upwards, but even for this distance several attempts were necessary before success was achieved. When swimming horizontally *Antarcturus* keeps its ventral side down, in contrast to other isopods. The uropods are folded aside and the pleopods beat in the now open respiratory chamber. To reduce friction the antennae are held straight ahead and the legs are folded and pressed against the body. Pereopods 2–4 are held against the mouthparts, more tightly than is shown in figure 33*d*, and pereopods 5–7 are held against the ventral side of the hinder pereonites. The swimming position of *Arcturella sawayae*, which also seldom swims, is similar (Moreira 1973).

In summary, the locomotion of *Antarcturus* is not very effective; the animals lead an almost sessile way of life.

In their resting position the animals show a characteristic dorsal bending (figure 33*b,c*), with pereonites 5–7 nearly parallel to the ground, while the pleotelson and anterior segments are elevated. This posture is possible because of strong longitudinal thoracic muscles and the special dorsal articulations and elastic ventral intersegmental cuticles of pereonites 5–7 (figure 2*a,c,d*). However, it brings problems for ovigerous females. As the curvature includes pereonites 4–7, the reduced number of oostegites (three pairs, on pereopods 2–4) must be understood as an adaptation that avoids a distortion of the marsupium. The special caudal breach of the marsupium, formed by coxal spines of pereopod 4, has already been mentioned (figure 2*b*). A consequence is that the genital opening lies outside the marsupium; it is not known how the eggs are placed under the oostegites. In this posture the animals can resist currents, which they need for their nutrition. The slowly beating pleopods produce a current that leads the used respiratory water upwards and away from the animal.

The long terminal spines project like lances and probably serve for defence.

Resting and feeding animals remain in one place for many days; in nature they probably live for a long time on the selected substratum. The body sways from side to side and the antennae are extended. A large approaching object, in the experiments a finger or a pipette, provokes searching movements of the antennae, which try to touch it. If it comes nearer they react by bending the body to one side (figure 33*b*), but the foothold is kept, often even after having been touched. Escape is not normally attempted, but the pleopods stop beating and pereopods 2–4 are folded, protecting the long setae, and are pressed against the mouthparts (figure 33*d*). Only after more vigorous harassment may the animals swim a short distance or



climb to another place, but some still cling to the substratum and can only be removed by carefully opening the subchelae of pereopods 5–7 one by one. *A. antarcticus*, which is smaller than *A. spinacoronatus* and has a smoother cuticle without long spines, shows a different behaviour. It presses itself against the branch on which it was sitting. Lying along it only pereopods 5–7 hold the animal. The larger species relies on its camouflage and protective spines, the smaller species on cryptic behaviour. As in *Astacilla*, the camouflaged eye of *Antarcturus* is very transparent and shows a golden hue of reflected light, probably caused by a special structure of the ommatidia (see Nilson & Nilson 1983).

No differences in the behaviour of immature animals, mature males or ovigerous females were noted. The same is true of observations on the feeding mechanism.

(b) *Feeding mechanism: collection of food*

A zoologist observing *Antarcturus* will soon suspect that these animals can only live as plankton- or detritus-feeders. Their movements are far too slow to catch larger animals and furthermore they have no weapons. They are adapted in morphology and behaviour to a sedentary way of life. Their gut contents confirm this assumption: ingested material forms a greenish mass with some intact diatoms, silicoflagellates, small sponge spicules and a few sand grains.

For the feeding experiments, at first unsorted plankton from Antarctic surface water was used. As soon as a suspension of plankton is added to the aquarium, *A. spinacoronatus* reacts. It seems that the suspension is detected with the eyes or olfactory sense organs or both. However, typical feeding behaviour begins before any particle touches the basket of setae formed by pereopods 2–4. The animals stretch out the filtering legs (pereopods 2–4, as in figure 33*b*), the long setae are spread out and, as long as there is no current, the legs move vigorously. In a succession, for which no regular sequence was found, single filtering legs are bent dorsally (as in right pereopod 2 in figure 33*c*), drawn through the water with spread setae, then swung towards the mouthparts and first pereopods. The short first antennae are held dorsally and constantly move to and fro, the second antennae often make slow rotating movements. The animals may also start crawling around with pereopods 5–7, always staying close to their resting place. When no more particles are left in the water, movements cease and the animals remain in the resting position, pereopods 2–4 either stretched out (figure 33*b*) or folded (figure 33*d*).

Reactions are different when a light, constant current is produced in the aquarium (e.g. with a pump). The animals orientate the basket of setae transversely to the current and usually receive it with the ventral side of the anterior pereonites, although sometimes the current hits the dorsal side of these segments. When a current with food particles is produced with a pipette from above, the animals flex the anterior part of the body dorsally until it nearly touches the pleotelson and the basket of setae is held nearly horizontally to receive the food.

The filtering surface is nearly circular. The parallel rows of long setae on legs 2–4 form an obtuse angle to each other, the neighbouring setae of two legs nearly touching; the frontal area of the filter is formed by the setae on the first peduncular articles of the antennae. Basally on each leg the filter is completed by the semicircle of long setae on the distal part of the basis (figures 26*a, b* and 30).

The animals ingested almost any particle that adhered to the long setae. These came especially from the phytoplankton. Large, living calanid copepods were never caught, although they were often dropped into the filter basket. *Antarcturus* had no time to react before the copepod had left the trap with a few quick jerks. The much smaller, newly hatched nauplii

of *Artemia salina*, offered in several experiments, often could not escape and were ingested in the same way as flakes of phytoplankton. Artificial food – a suspension of triturated fish-food or flour of soya – was sieved out in the same manner as natural food. Of the flour only larger particles were caught; the majority of the smaller particles passed through the basket, the space between two filter setae in an adult *A. spinacoronatus* being about 100–150  $\mu\text{m}$ .

When larger flakes of fish-food the length of a podomere are placed in the basket of setae, the animals react by removing the flake, either by turning the leg, which is held aside until the flake falls by gravity, or by bending the anterior part of the body forward until the basket is turned down. This suggests that the filter-setae respond to mechanical stimuli and that no chemical sense organs are present on legs 2–4. Large flakes are ingested when they are placed on the mouthparts or on legs 1–2 in such a way that the first antennae can touch or come close to them. Species of *Antarcturus* as well as *Dolichiscus* pressed the flake against the mouthparts, holding it with pereopods 2–4 (as in figure 33*d*), then the subchelate pereopod 1 took parts of it or crumpled it and crammed it between the maxillipeds and within the reach of the other mouthparts. The animals never tried to pick up flakes that had been tasted and fallen to the ground, and they (*A. spinacoronatus* and *Dolichiscus meridionalis*) never tried to collect detritus by scratching the antennae or pereopods over the ground, behaviour common in *Arcturella sawayae* (Moreira 1973*a, b*).

For grooming, pereopods 1–4 are used. Individual filtering legs can be flexed dorsally (for example, the right pereopod 2 in figure 33*c*) and their long setae brush the cuticle as the leg is moved ventrally. The setae are not spread, but it is not clear whether the long setae or the somewhat shorter setae of the filtering rows are used as brushes. After each cleansing movement the filter-leg is directed towards the mouthparts, where it is cleaned by the first pereopods (see below). The collected material is ingested. The sides of the cephalothorax and the eyes are brushed directly by the first pereopods. To enable the first antennae to be cleaned they are bent downwards between the peduncles of the antennae until the first legs can reach them. As in *Arcturella sawayae*, the second antennae are brushed more frequently than the first. For this purpose a single antenna is moved ventrally until the anterior pereopods, sometimes only the first, can grasp it, and it is then pulled forward through the setal combs of the filter-legs and the setae of pereopod 1 (figure 34*b, c*). With their rows of setae (figures 4*g* and 27) the peduncular articles of the antennae collect particles of food in the same way as the filter-legs.

A feeding *Antarcturus* is constantly in motion. While the filter basket is spread into the water or the corresponding legs make rowing movements, the first pereopods clean an antenna or one of the filter-legs, or brush the dorsal cuticle of the cephalothorax. No regular succession of movements was observed. Any filtered or brushed-off particles are concentrated into a small ball or flake by the first pereopods and passed to the mouthparts.

(*c*) *Feeding mechanism: function of first pereopods and maxillipeds*

In the feeding mechanisms of *Antarcturus* the first pereopods and the maxillipeds play an important role. The main task of the filter-legs is to concentrate suspended particles on their setal combs. By their cleansing movements the first pereopods and maxillipedal palps concentrate these to small flakes that can be treated by the other mouthparts.

The first pereopods insert close to the basis of the maxillipeds (figure 34*a*). They are comparatively short and their corresponding body segment is fused to the cephalothorax, so that the first leg is almost a second maxilliped. Study of the movements of these limbs left certain

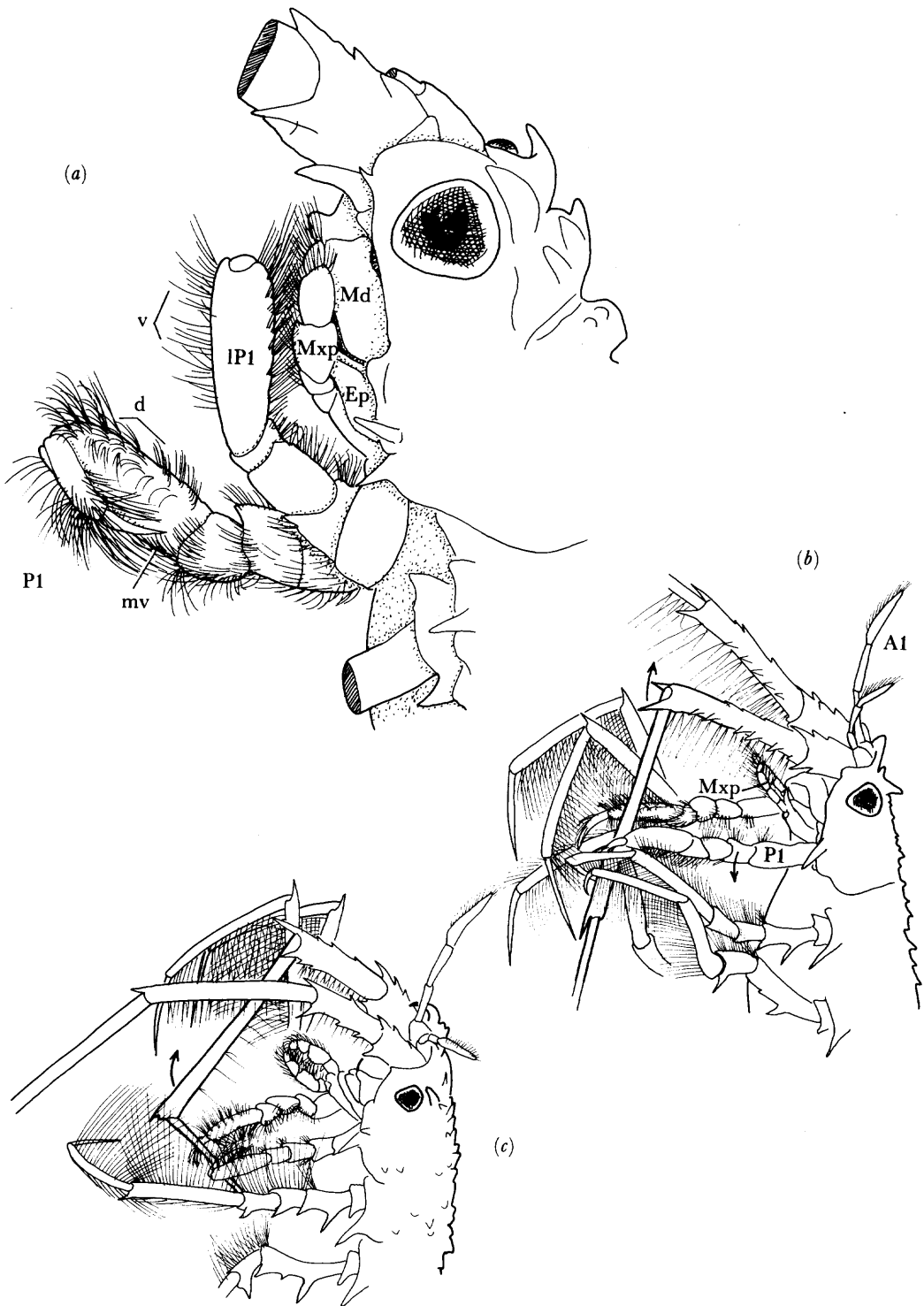


FIGURE 34. *Antarcturus spinacoronatus*. (a) Left side of cephalothorax. Note how the setae of the maxillipedal palp (Mxp) can brush through the dorsal propodal setae of pereopod 1 (here: left pereopod 1). (b) Anterior pereopods, including pereopod 1, cleaning the fourth article of the left antenna. (c) Pereopod 1 cleaning fifth article of right antenna.

problems unresolved; in particular the function of several groups of setae is not clear. However, it is obvious that the propodal groups of setae on the ventromedial margin (figures 25*f,g* and 34*a*: mv) and the dorsal transversal rows of setae (figure 34*a*: d) do much of the work. It is also important to remember that the palpus of the maxilliped is densely covered with setae on the ventromedian surface (figures 3*b,d* and 34*a*).

To brush off the particles collected by the filter, each of legs 2–4 must be cleaned individually. The leg is turned so that the long setae are directed to the mouthparts. Figure 35*a* shows how the left pereopod 1 passes over the combs of the left pereopod 2, brushing them from the base to the tips. During this movement most particles are collected by the propodal medioventral setae of pereopod 1 and probably also by the ventral setae of the dactylus. In this manner the medial row of setae of pereopod 2 is cleaned, and probably also the space between the two rows of filtering setae. To clean both rows simultaneously, both first legs pass over the filter-leg. In figure 35*b* the right pereopod 2 is cleaned by both the first legs. The particles are collected by the medioventral setae of the propodus of the right pereopod 1, but on the left pereopod 1 the dorsal propodal setae are used. Because of the different angle between comb and pereopod 1, the particles are caught by different groups of setae on the left and right legs.

From time to time the smooth dorsal surfaces of legs 2–4 are cleaned. In figure 35*c* the setae of the dactylus of the right pereopod 1 are passing over the outer surface of the propodus of pereopod 2.

It is not clear which of the propodal setae are most important for the cleansing of the antennae already described; in figure 34*b* propodal setae of pereopod 1 are used, in figure 34*c* the setae of the dactylus.

The result of the cleansing movements is a concentration of food on the setae of pereopod 1, especially on the medioventral and dorsal setae of the propodus and the setae of the dactylus. When larger particles are caught, these are passed directly to the maxillipeds (figure 35*d*). More often, small particles are scattered over the brushes of pereopod 1 and further concentration is necessary. This can be accomplished by the maxillipeds. As shown in figure 34*a*, the setae of the palp can comb through the dorsal propodal setae of the neighbouring pereopod 1, but the medioventral setae are out of reach. Therefore both first pereopods brush each other before the maxilliped starts to collect the particles. In figure 36*a* the medioventral setae of the left propodus are passing over the dorsal setae of the right propodus. Afterwards the left pereopod 1 brushes the medioventral setae of the right pereopod 1. These movements are repeated several times, then the maxillipedal palps collect the material concentrated on the dorsal setae. In figure 36*a* the palps are in the position just before brushing; in figure 36*b* the arrows indicate how the limbs are moved. Particles on other setae of pereopod 1 can probably be brushed off by the propodus of its partner.

The sequence of movements is summarized schematically in figure 38. The shorter setae accompanying the long filter-setae (figures 28 and 29) are omitted. Their role is not known, but one of their functions is probably to prevent large particles from floating against the cuticle of the podomere. These then sink, but there is a good chance that they may be caught by the shorter setae. Nevertheless, particles that sink may land in the semicircle of setae of the basis. Another function could be to clean the space between the bases of the long setae in the moment when the long setae swing back into a position as in figure 28.

The further fate of the particle could not be observed, but the morphology of the mouthparts and series of sections (figures 3*d* and 37) allow some deductions. It seems that the setulated

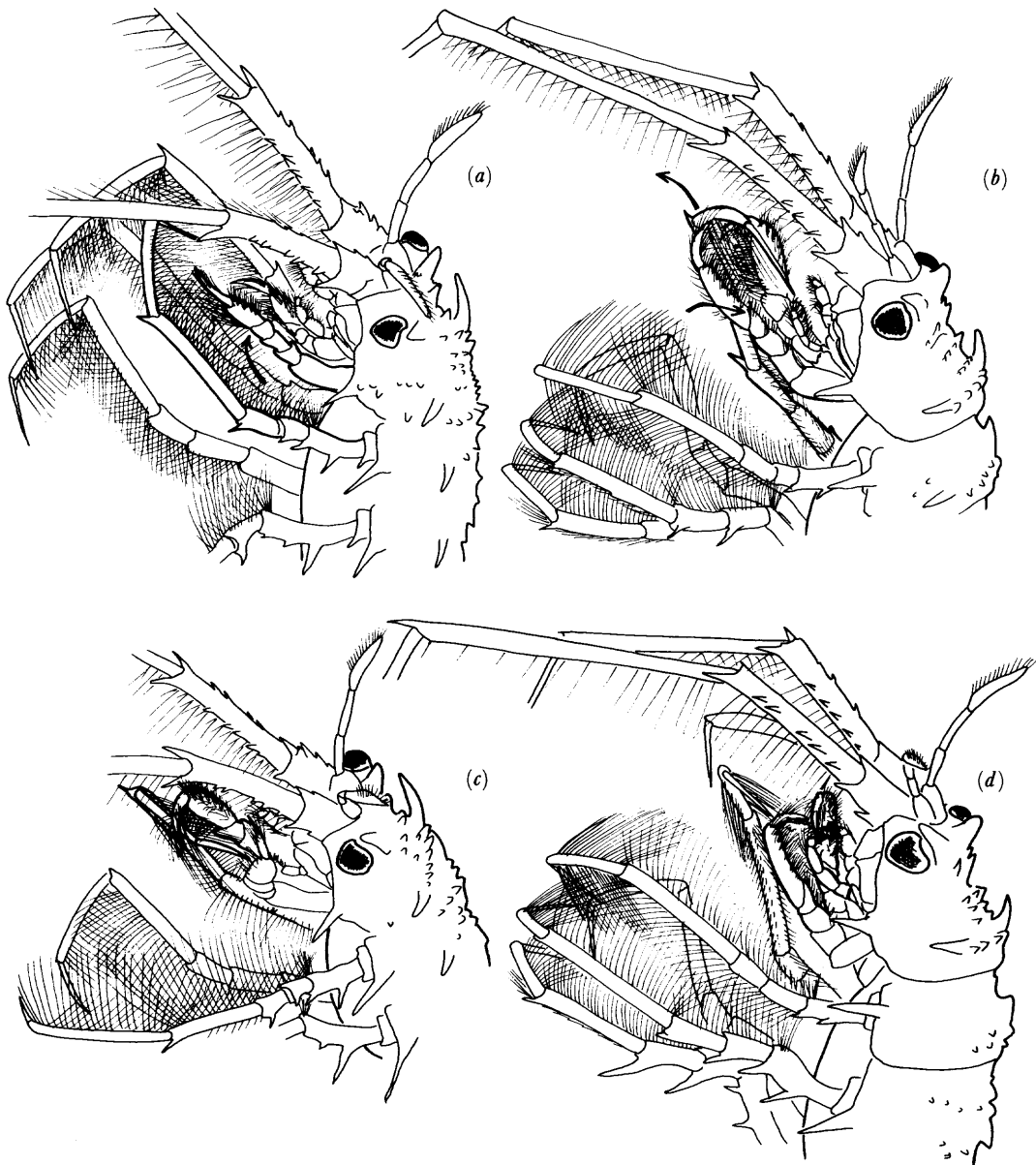


FIGURE 35. *Antarcturus*: feeding mechanism. (a) Medioventral setae of propodus and dactylus of left pereopod 1 passing over setae of left pereopod 2. (b) Both first pereopods cleaning the setae of right pereopod 2. Note that the right pereopod 1 works with the medioventral, the left predominantly with the dorsal propodal setae. (c) Dactylus of right pereopod 1 cleaning cuticle of right pereopod 2. (d) Shortly after the situation of c; the right pereopod 1 hands over a larger particle to the maxilliped.

bristles of the maxilla hold material against the chewing mouthparts (maxillula and mandible) that has been passed by the maxillipedal palps and prevent the escape of any particles. The stout spines of the lateral endite of the maxillula can pierce larger objects and hold them firmly until the closing mandibles seize them. The short distal spines on the maxillipedal endites limit the ventral space in front of the hypopharynx caudally (figure 37). Laterally this area is fenced in by the setae of the maxilla. This is the space in which the spines of the lateral endites of the maxillula work. The setae of the smaller, medial endites of the maxillula reach through

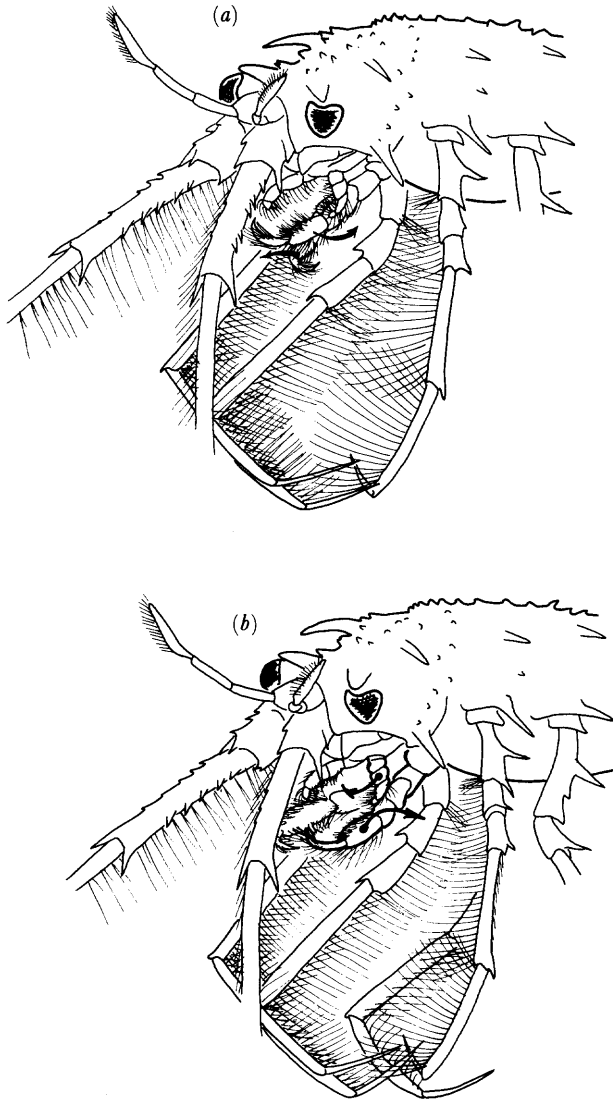


FIGURE 36. *Antarcturus*: feeding mechanism. (a) Right pereopod 1 brushing off particles from the ventral and medioventral propodal setae of the left pereopod 1 with its own dorsal brush of setae. (b) Movements (arrows) by which the palp of the left maxilliped cleans the dorsal setae of the left pereopod 1.

the slit between the lobes of the hypopharynx and can push particles into the grinding chamber between the mandibles. As seen in figure 3*d*, the mandibles work between labrum and hypopharynx, the pars molaris grinding near the entrance of the mouth. The movements of maxillula and mandible are probably well coordinated, each pair of limbs taking hold of the food in turn, as in other isopods (Naylor 1955; Wägele 1981). The function of the parts of a peracarid mandible is described by Cannon & Manton (1927) and Fryer (1965). The setae on the proximal (lower) surface of the pars molaris reach directly into the mouth and can push particles into it. The pumping activity of the stomach observed in other isopods (Scheloske 1976; Wägele 1981) probably plays an important role in the ingestion of food.

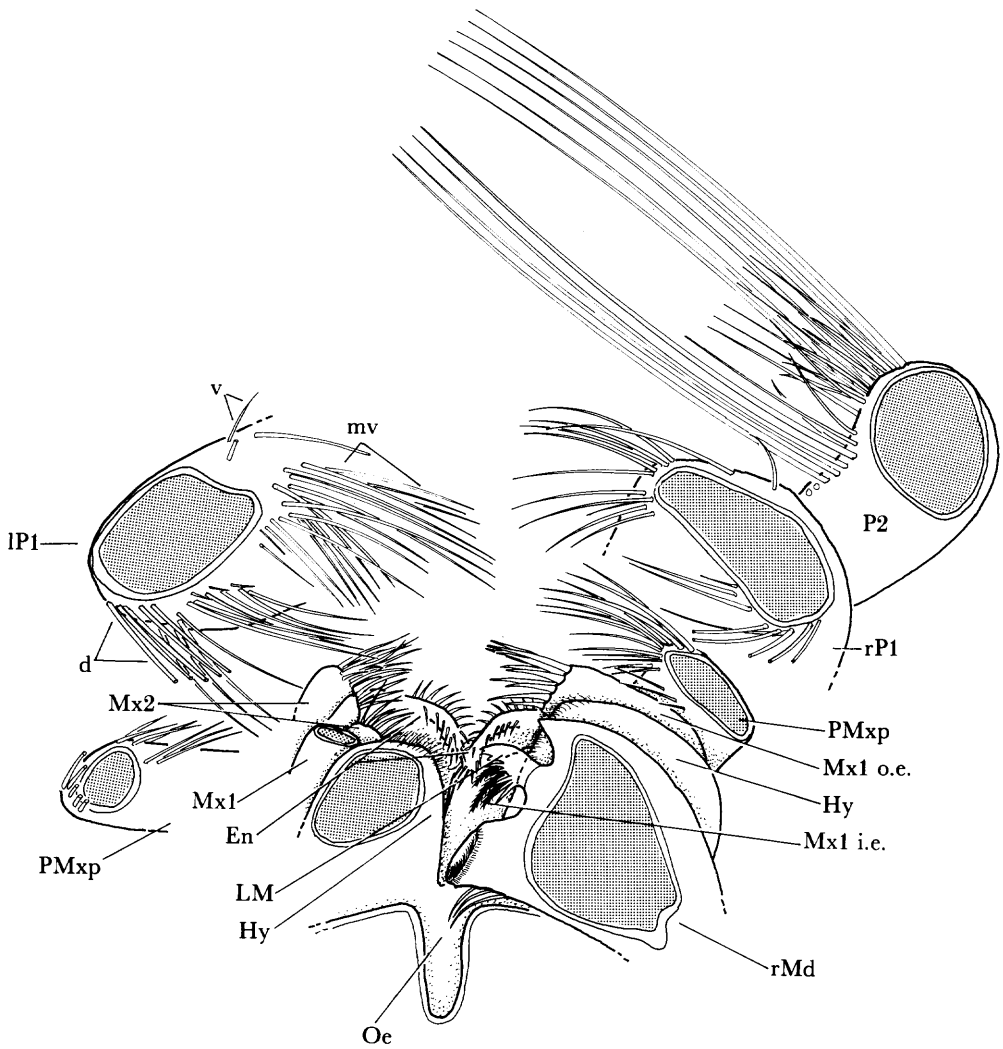


FIGURE 37. *Antarcturus spinacoronus*. Slightly oblique transverse-section of mouthparts, pereopods 1 and 2 in frontal view, at the level of the oesophagus, just behind the labrum. The left mandible is lacking, the apex of the left maxillule (Mx 1) is cut off, and the left pereopod 2 not shown. The right maxilla (Mx 2) is for the most part covered by the maxillula and is not shown.

(d) *Structure and function of the filter-setae*

The filter of *Antarcturus* can only work with movable setae. To sieve the water the setae are spread laterally, whereas for swimming, resting, cleaning of the filtering combs and in cryptic behaviour the rows of setae are folded together. However, no muscles insert at the base of the setae. Figure 39a shows that each seta is provided with a nerve, but no muscle or connections to the podomere-moving larger muscles are present. An understanding of the construction of the setal base (figure 39c) is essential for appreciation of the function of the filter.

Figure 39b shows a longitudinal section through the shaft of a filter-seta. The cuticle of the podomere has an opening that leads into the setal cavity. The base around the shaft is formed by a sclerotized cuticular ring, which has a lateral slight concavity and more distally an elevation. The ring bears some short setules that probably help to keep this joint clean. At the level of the elevation of the sclerotized ring the setal shaft is grooved. Its basal part is set

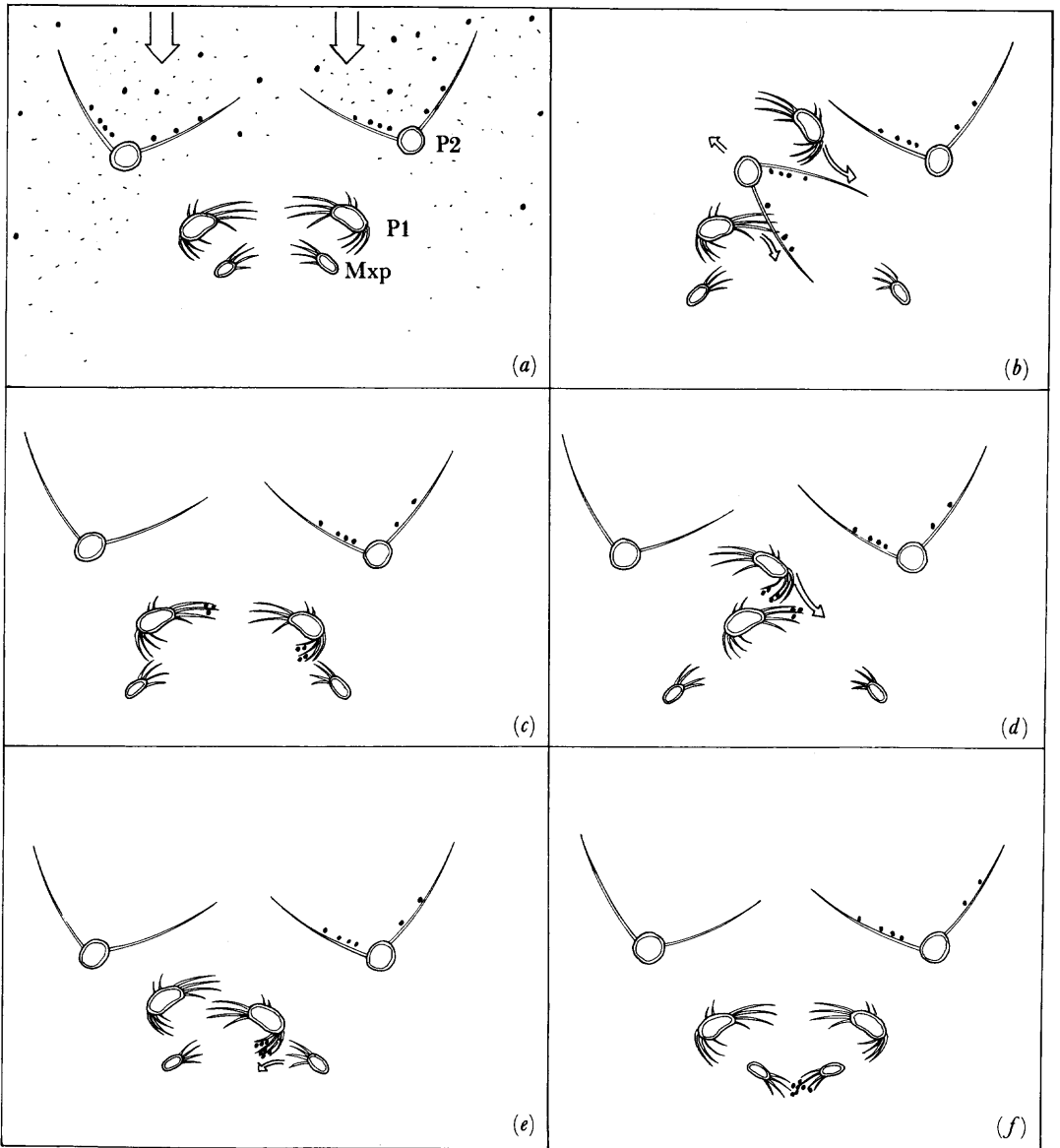


FIGURE 38. Schematic transverse-sections of pereopods 2, 1 and the palp of the maxilliped showing a sequence of movements during feeding. (a) Filter legs (P2) sieving plankton. (b) Both first legs (P1) brushing particles off the setae of the left pereopod 2; arrows indicate the direction of the movements. (c) Left pereopod 2 is cleaned, particles are now found on the medioventral propodal setae of the left pereopod 1 and dorsal propodal setae of the right pereopod 1. (d) Dorsal propodal setae of the right pereopod 1 collecting the particles on the medioventral setae of the left pereopod 1. (e) Maxillipedal palps brushing off particles from the right pereopod 1. (f) Maxillipedal palps just before passing particles to the maxillae.

in this ring where it is suspended by a thin cuticular membrane, which is thicker laterally than medially ('medially' here means towards the central row of single setae, which runs between the two rows of long filter-setae of each podomere).

The cuticle of the articulation has the same staining reaction as the exocuticle of methylene-blue-treated semi-thin sections and it is continuous with this darker, outer cuticle. In unstained preparations, the light microscope reveals a limit at the contact zone between the cuticular



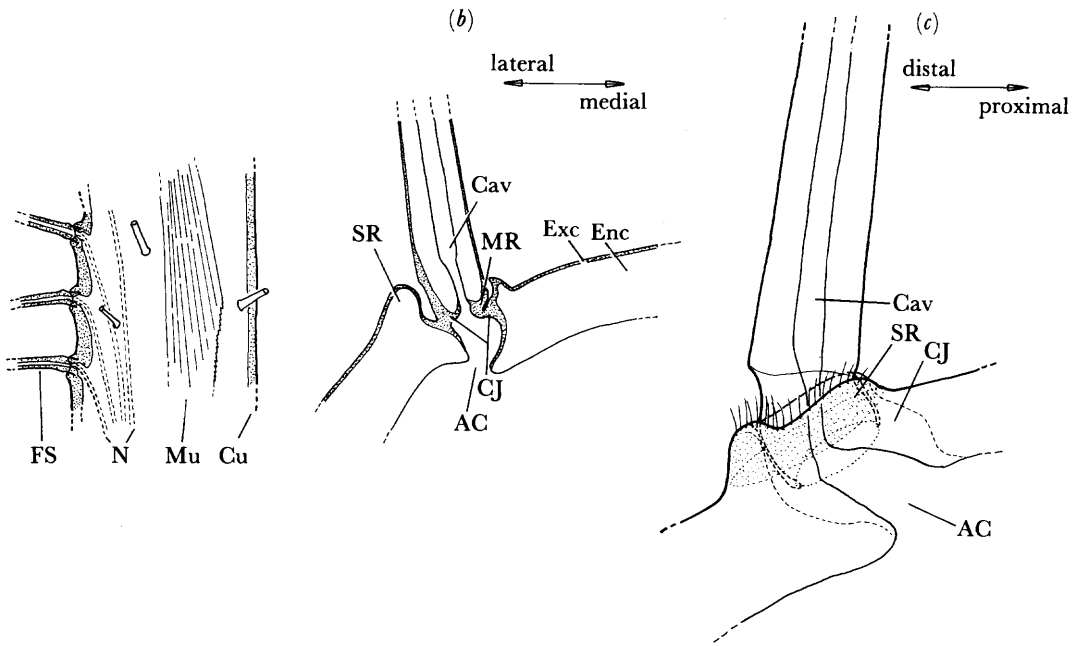


FIGURE 39. *Antarcturus spinacoronatus*. Structure of filter-setae. (a) Lateral view of a transparent propodus of pereopod 2 (optical section), showing innervation (N) of filter-setae (FS) and a muscle (Mu) which moves the dactylus. (b) Semi-thin section through the base of a propodal filter-seta. (c) Lateral view of base of a propodal seta through the transparent cuticle.

membrane and the neighbouring endocuticle, where the chitin fibrils probably change their orientation. The membrane obviously has special mechanical properties.

The spreading of the setae can only be achieved by an increase in blood pressure. As in a slack air-balloon in which the pressure is increased, the cuticle of the articulation is stretched by an increase in the blood pressure, probably especially in the medial area, which can be considered as a membrane reserve (MR in figure 39b). Thus the setal base is stretched medially more than laterally and the seta inclines to the side until the grooved shaft fits into the concavity of the sclerotized ring. Here the seta has a firm fit and thus all setae of one row are orientated exactly to form a sieve of a fairly constant mesh size. The elasticity of the membrane causes the seta to return to their original position as soon as the pressure is reduced.

A similar mechanism is known from a different group of crustaceans: some atyid prawns evolved unique fans or brushes of setae on the propodus and carpus of their chelipeds for collecting finely particulate detritus. The fans of setae are used by *Atya scabra*, *A. innocus* and *Micratya poeyi* for passive filtration (Fryer 1977). These setae are also moved by a hydraulic mechanism, the setal base of atyids having the same essential features as the setae of *Antarcturus*. They are suspended by a hinging cuticle that works as a spring, which gives way when the blood pressure is increased. The asymmetrical construction leads to an inclination of the setae; muscles are not present. Nevertheless several details described for atyid setae have not been found in *Antarcturus*; the structures are not homologous. The setal cavity of *Atya* is plugged by an occluded region, which prevents a leakage of haemolymph when a seta is broken distally. Such a plug does not exist in *Antarcturus*. The podomere forms no sclerotized ring around the shaft of *Atya*, the hinging cuticle is thinner and the setal basis has a thickened wall which is directly connected to the neighbouring cuticle at one side (Fryer 1977).

In *Atya*, as in *Antarcturus*, the mechanism of pressure regulation is not known. The hydraulic mechanism in combination with valves for the conservation of high pressure is possibly a system with very low energy-costs, in contrast to a system based on muscular action. Interestingly, no dead and fixed specimens of *Antarcturus* have any spread setae (compare figures 28–30).

*Antarcturus spinacoronatus* uses its setal combs for passive filtration, has no means of producing a strong current and therefore works with a low investment of energy, but it needs flowing, productive water to survive. The construction of the filter is characterized by the following data: the filtering area of a specimen of 35–38 mm length is about 190–260 mm<sup>2</sup>; the space between two setae, measured in fixed specimens is, at the setal base, about 100–150 µm wide; the diameter of the setae, almost circular in cross-section, is 20–25 µm (for comparison, the mesh size of the filter of *Euphausia superba* is less than 1 µm; Kils (1984)). In a current of 0.1–0.4 m s<sup>-1</sup>, such as occurs on the shelf area of the Weddell Sea (Deacon (1977); Gammelsrød & Slotsvik (1981), not measured directly on the seafloor), the filter will have to resist some friction, but this would be much higher with a smaller mesh size such as that of *Euphausia*. *Antarcturus* can without doubt easily cope with these frictional forces: its posture allows it to hold the filter into the current.

Of the possible filtering mechanisms discussed by Rubenstein & Koehl (1977) and La Barbera (1984) only the common 'sieving' will be effective in *Antarcturus*, although some planktonic organisms with sticky surfaces will adhere to a single seta. Many planktonic organisms, especially diatoms, are larger than the mesh size of the filter and will be sieved out passively. *Antarcturus* has a much more permeable sieve than *Euphausia* and will collect fewer particles, but without doubt its demand for energy is much lower than that of the constantly swimming euphausiids.

##### 5. BIOLOGICAL ACCOMMODATION: COMPARISON WITH *ARCTURELLA SAWAYAE*

Observations on the behaviour of *Arcturella sawayae* (Moreira 1973*a, b*) are in many respects consistent with the new data on *Antarcturus spinacoronatus*. *A. sawayae* also feeds on phytoplankton, whereas copepods only cause it to remain in the alert posture. But *A. sawayae* is more omnivorous, eating meat and debris as well as filamentous green algae (green algae do not exist in most areas where *A. spinacoronatus* was collected and no feeding experiments were done). *Arcturella* is able to collect food from the bottom, and it seems that deposit feeding is an essential ability of this genus, observed by Moreira (1973*a, b*) and (in Mediterranean species) by the author (unpublished observations). The instrument used for deposit feeding is the tip of the antenna, which scratches the bottom in a ventrally directed movement. After each movement each antenna is cleaned by the first pair of pereopods. This behaviour was not observed in *Antarcturus*, nor in *Dolichiscus*.

The reduced percentage of plankton in the food of *Arcturella* is expressed in the morphological differences between *A. spinacoronatus* and *A. sawayae*. Because of a longer fourth pereonite and simultaneously shorter pereonites 1–3 in *Arcturella* the distance between the insertion of the fourth pereopod and the mouthparts is shorter, the anterior legs are therefore shorter than in *Antarcturus* and without doubt the sieving surface is relatively small. In species of *Astacilla* the reduction of this surface is even greater. Interestingly, the claw and dactylus of legs 2–4 are reduced in *Arcturella*, so these legs are useless for climbing and the role of the antennae is more important than in *Antarcturus*. So the short claw-like flagellum of the antenna of *Arcturella* is an adaptation to the feeding habits and the different type of locomotion.

Conspicuous differences in the structure of the mouthparts are the broader maxillula of *Arcturella* with its shorter spines and fewer setae on the palp of the maxilliped, indicating a less fine type of food. The propodus of pereopod 1 is essentially as in *Antarcturus*, but there are fewer medioventral and dorsal setae and the article is shorter; the dactylus has no claw, the carpus is relatively long and, on the dorsomedial surface, as concave as the propodus. The function of the first pereopod is probably somewhat different in *Arcturella*, the larger carpus can possibly hold particles directly in front of the maxillipedal palp, but the propodal setae can be used in the same way as in *Antarcturus*.

Thus, in comparison with *Arcturella* the morphology of *Antarcturus* is less specialized, the anterior legs (1–4) are more similar to the primitive situation known from idoteids. Simultaneously, *Antarcturus* is less opportunistic, living predominantly on phytoplankton and without the capacity of *Arcturella* to exploit other food resources.

## 6. DISCUSSION: EVOLUTION OF SUSPENSION FEEDING IN *ANTARCTURUS*

Recalling the postulated original suspension feeding habits of malacostracan crustaceans, Moreira (1973*b*) suggests that within the Isopoda the Arcturidae have a primitive feeding mechanism, genera like *Idotea* or *Mesidotea* being more specialized in this respect. However, a cursory look at the functional morphology of some epibenthic or pelagic filter feeding Malacostraca (Leptostraca: Cannon (1927); Lophogastrida: Manton (1928); Mysida: Cannon & Manton (1927)) combined with generally accepted theories on the evolution of the Malacostraca (see, for example, Siewing 1957; Lauterbach 1973, 1975; Hessler 1983) reveals no similarities between primitive Malacostraca and the Arcturidae. The filtering elements of the limbs of Arcturidae cannot be homologized with the filter of primitive peracarids or leptostracans – the typical maxillary filter – which is still present in some syncarids (*Paranaspis*) and mysids (see information in Cannon & Manton (1929)). By transformation of the first thoracic limb into a broad, operculum-like maxilliped isopods can direct no current of water to the setae of the second maxilla, and the maxilliped cannot brush these setae as happens in *Gnathophausia* or *Lophogaster* (Manton 1928).

It is incontrovertible that the seven pereopods of isopods are primarily walking legs. The arcturids differ from the above-mentioned Malacostraca in being passive filterers without having the ability to produce a current. It would thus appear that the feeding habits of arcturids evolved secondarily within the suborder Valvifera, the idoteid genera representing a more primitive type (see also Kussakin 1973; Brusca 1984).

Comparison of *Arcturella* and *Antarcturus* reveals that within the Arcturidae the specialized phytoplankton-feeding forms are more primitive than those genera with an elongate fourth pereonite. Evolution leads from suspension feeders to more omnivorous animals with the ability to collect deposited material, and possibly to carnivorous species. Data on the behaviour of *Astacilla* are needed to confirm the scanty information published by Goodsir (1841). Interestingly, *Idotea* already displays some elements of the cleansing behaviour that leads to the evolution of the arcturid leg 1; combing spines used to remove debris from 'various appendages' are present on the first legs and on the inner border of the maxillipedal palp of some species of *Idotea* (Naylor 1955).

It is evident that this evolution took place in an ocean with streaming, probably highly productive water. Its end point is passive filter-feeding as in *Antarcturus*. Most Antarctic species of *Antarcturus* live in the shelf-area down to about 600 m (see Kussakin 1967), and within this

range appear to be eurybathic (*A. spinacoronatus*: 191–745 m), as is typical for many species of the Antarctic benthos (see, for example, Ushakov 1963; Arnaud 1974; Knox 1977). This zone of the sea-floor has a remarkable stock of suspension-feeders, especially of large sponges (see Ushakov 1963; Dearborn 1968; Koltun 1970). Only a few arcturids live in deeper waters (e.g. *Antarcturus beliaevi* and *A. anna*), but some of these are extremely eurybathic (e.g. *A. spinosus* and *A. furcatus* which range over 2500 m of depth). Thus while more data are required, we suspect a relation between hydrography, plankton content of the water, and the distribution of *Antarcturus*.

The Circumantarctic Ocean with its regular currents and high productivity would be a suitable place for the evolution of arcturid isopods. Therefore it is interesting that the Xenarcturidae Sheppard, 1957, presumably the less specialized sister-group of the Arcturidae (Brusca 1984), is only known from Patagonia. Unfortunately the biology of the Xenarcturids has never been studied.

Kussakin (1973) writes that the family Arcturidae '... is present all over the world, but its roots should also be sought in the Southern Hemisphere... the genus *Antarcturus*... is supposedly the most primitive of this family... the Antarctic ocean is inhabited by the greatest number of species...'. These statements of the experienced isopodologist fit into the mosaic-like picture we now have of the biology and evolution of the Arcturidae. Without an exact phylogenetic-systematic analysis this evolution cannot be studied, but it seems very probable that Kussakin's statements are correct and that the Arcturidae known from the deep sea and from many northern localities had their origin in the Antarctic.

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## ABBREVIATIONS USED ON THE FIGURES

A1	antennule	MR	cuticular area thought to be a membrane reserve
A2	antenna	Mu	muscle
AC	aperture in cuticle	mv	medioventral setae of pereopod 1
App	appendix masculina	Mx 1	maxillula
Cav	cavity of filter setae	Mx 2	maxilla
CJ	cuticle of setal joint	Mx 1 i.e.	inner endite of maxillule
CS	coxal spine	Mx 1 o.e.	outer endite of maxillule
c.s.	coupling spines of pleopod	Mxp	maxilliped
Cu	cuticle	N	nerve
d	dorsal setae of pereopod 1	Oe	oesophagus
En	endite of maxilliped	P	pereopod
Enc	endocuticle	Pe	penis
Ep	epipodite of maxilliped	PI	pars incisiva of mandible
Exc	exocuticle and epicuticle	Plp	pleopod
FS	filter seta	PM	pars molaris of mandible
G Ap	genital aperture	PMxp	palp of maxilliped
Hy	hypopharynx	rMd	right mandible
IUrp	insertion of uropod	r P 1	right pereopod 1
La	labrum	ST	setal tuft of basis (pereopods 2-4)
LM	lacinia mobilis of mandible	SR	sclerotized rim
lMd	left mandible	Urp	uropod
lP 1	left pereopod 1	v	ventral setae of pereopod 1
Md	mandible		