

# STUDIES ON THE FUNCTIONAL MORPHOLOGY AND ECOLOGY OF THE ATYID PRAWNS OF DOMINICA

BY G. FRYER, F.R.S.

*Freshwater Biological Association, The Ferry House, Far Sawrey,  
Ambleside, Cumbria*

(Received 6 May 1976)

[Plates 1-10]

## CONTENTS

	PAGE
I INTRODUCTION	59
II THE ECOLOGICAL BACKGROUND	62
III METHODS	64
IV GROSS MORPHOLOGY, ECOLOGY AND HABITS	64
(a) <i>Xiphocaris elongata</i>	64
(b) <i>Jonga serrei</i>	66
(c) <i>Potimirim glabra</i>	68
(d) <i>Atya innocous</i>	69
(e) <i>Atya scabra</i>	72
(f) <i>Micratya poeyi</i>	73
V THE FEEDING MECHANISM OF <i>XIPHOCARIS</i>	74
(a) The chelipeds and food collection	74
(b) The mouthparts and manipulation of food	75
VI THE FEEDING MECHANISMS OF THE NON-ACANTHOPHYROID SPECIES	83
(a) The chelipeds and their armature	83
(b) Food collection	94
(c) The mouthparts and manipulation of food	98
VII ATYID MANDIBLES AND THEIR MUSCULATURE	106
VIII THE EVOLUTION OF ATYID FEEDING MECHANISMS	108
IX THE FORE-GUT	110
(a) Introduction	110
(b) The fore-gut of <i>Atya</i>	111
(c) The fore-gut of <i>Xiphocaris</i>	118
(d) The remaining non-acanthophyroid species and a note on <i>Caridina</i>	120
(e) Structure and function of the decapod fore-gut and its relation to the mouthparts and feeding habits.	121
X ATYID ORIGINS, GEOGRAPHICAL DISTRIBUTION, ECOLOGY AND DISPERSAL	122
REFERENCES	126

Six species of atyid prawns, representing five genera, occur in streams on the West Indian island of Dominica (figures 1–6). The ecology and habits of each are described and the relation of features of gross morphology to ways of life noted.

*Xiphocaris elongata*, the most primitive living atyid, is a lightly built prawn whose adult habits are related to life in quiet pools in streams. An agile species and an excellent swimmer, it picks up individual small food particles with specialized chelipeds (figures 18 and 19) that differ from those of all other atyids and manipulates them with mouthparts (figure 77) which, while highly complex, are more primitive than those described for any other member of the family.

*Atya innocous* and *A. scabra*, representing perhaps the most specialized atyid genus, are very similar in gross morphology and are robustly built ambulatory species. *A. innocous* is common in a variety of situations: *A. scabra* is rare and has been found only in fast-flowing water. Both have chelipeds whose three distal segments are extremely specialized (figure 36) and whose propus and dactylus are armed with an exceedingly complex array of long, slender bristles. These can be used either as brushes for collecting finely particulate detritus (figures 58–60) or as filtering fans (figures 68 and 69) which, held passively in flowing water, extract suspended particles. The Atyidae is unique among the Malacostraca in having representatives that filter passively by means of the chelipeds.

The bristles (figure 40) are extended (figure 49), not by muscles, of which there are none in the distal parts of the propus and none anywhere in the dactylus, but by hydraulic forces. The return of the bristles to rest is by means of a cuticular spring. Some of the bristles of *A. innocous* are armed distally with minute denticles (figures 41 and 42) that facilitate scraping and sweeping: no such are present in *A. scabra*. The difference is related to the relative importance of scraping in the two species: *A. innocous* scrapes frequently, *A. scabra* seldom.

Finely particulate food is transferred and manipulated by the extremely complex oral machinery (figure 78). One of the most elaborate parts of this is a teaselling device in which components of the maxillae and first maxillipeds participate (figures 80 and 81). The feeding mechanism is described.

Morphologically and functionally *Micratya poeyi* can be regarded as a miniature version of *Atya*. It can both sweep and filter.

*Potimirim glabra* is rare in Dominica and its habits but little known. Morphologically it is similar to, but more primitive than, *Micratya*. Its cheliped bristles are clearly specialized for sweeping and show few signs of being used for passive filtration.

*Jonga serrei* occupies a separate and well-defined niche in the quieter parts of streams. For this it shows many morphological specializations and lacks such attributes as stout claws and robust walking legs that are the hallmark of its relatives living in fast-flowing waters. Its chelipeds are armed with distal scrapers that bear a remarkable similarity to those already described for African species of *Caridina*, to which animal it bears a general overall similarity. These are used for collecting food from substrates. It is incapable of passive filtration.

Atyid mandibles, while specialized – greatly so in the case of *Atya* (figure 83) – retain primitive features both of the skeleton and musculature such as are found even in the Branchiopoda. Retention of a large molar process is clearly associated with microphagous habits. Specialization for such habits has led to end points very different from those of advanced decapods such as crabs and crayfishes whose mandibles often slice material from large food masses. Specialization has been achieved by additions to and refinements of the primitive crustacean mandible whose salient features are still retained.

Comparison of *Xiphocaris* (primitive) and *Atya* (advanced) reveals many functional trends in the evolution of food manipulation. These two genera do not, however, simply represent primitive and derived conditions respectively but also end points of divergent specialisation. Likewise, *Jonga*, *Potimirim* and *Micratya*, while to some extent indicating stages on the route to an *Atya*-like condition, also indicate divergent specialization along that route.

All Dominican atyids have a complex two-chambered fore-gut. The most special-

ized, that of *Atya* (figures 91 and 92), is described in detail. The complex systems of ossicles developed in its walls are specialized, not for the crushing and grinding of large items of food as they are in many 'higher' decapods but for propelling fine particles posteriorly. Elaborately guarded channels (figures 114–119) from the gland filter that run along each side of the cardio-pyloric valve are presumed to be the route along which enzymes from the hepatopancreas pass into the cardiac chamber. Within the pyloric chamber a system of tubules made up from a delicate convoluted membrane (figures 111 and 112) ensures that there are wide spaces between the several strings of food particles thus separated (figures 105 and 106), thereby facilitating the digestive processes. The membrane is analogous to, and perhaps homologous with, a peritrophic membrane, but is permanent and not continuously renewed.

*Jonga*, *Potimirim* and *Micratya* have a fore-gut similar to that of *Atya*. That of *Xiphocaris* is different. Apart from a somewhat different arrangement of ossicles the method of spreading food particles so as to expose a large surface area for efficient digestion and absorption is not by means of a reticulated membrane but by a spinule-covered projection that confines particles to a narrow tunnel, crescentic in transverse section (figures 93 and 94).

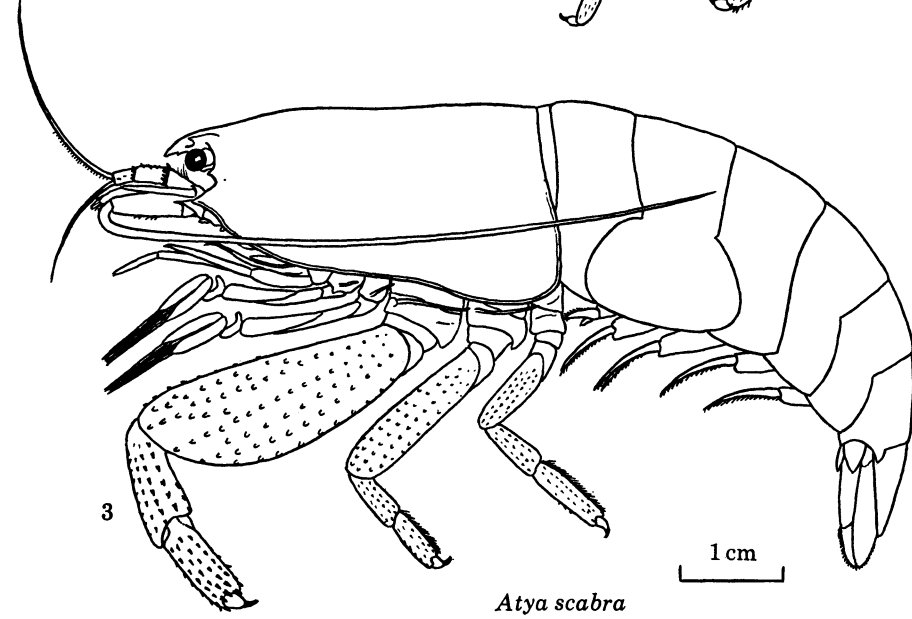
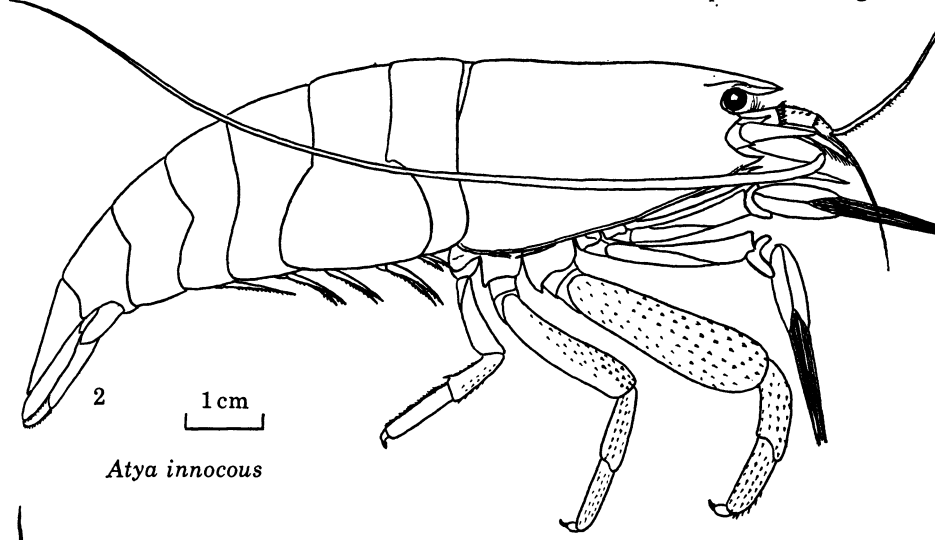
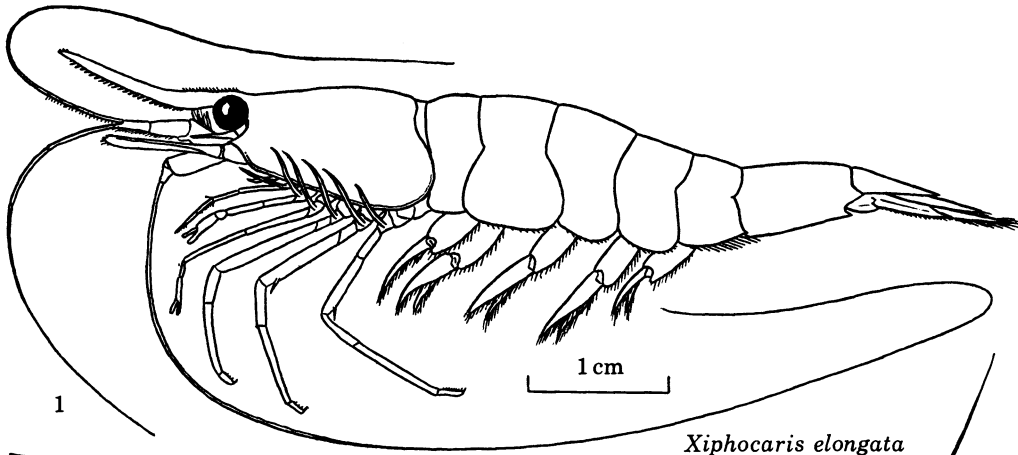
A decapod fore-gut lacking heavy teeth and grinding ossicles is not, as has been suggested, less efficient than one that employs such structures, nor is a large molar region of the mandible necessarily indicative of a crushing function, and non-crushing mandibles are certainly not inefficient. Different foods require different treatments by both mouthparts and fore-gut, both of which show appropriate specializations.

Atyids, of which there are no known marine species, have probably had a long history as freshwater animals. Fossils are known from freshwater deposits of Cretaceous age in Brazil. The occurrence of some species in brackish waters is not necessarily indicative of colonization of such habitats from the sea. Many continental species certainly reproduce in freshwater and it is likely that some of those living on islands also do so. Dispersal by sea as adults is virtually impossible and such physiological evidence as is available gives little confidence in the ability of larvae to serve as agents of dispersal across large tracts of ocean. Paradoxically atyids have colonized several remote oceanic islands, some of which have not been reached by truly freshwater fishes. Thus, while dispersal appears to have presented few problems in the past, how it was, or is, effected is uncertain.

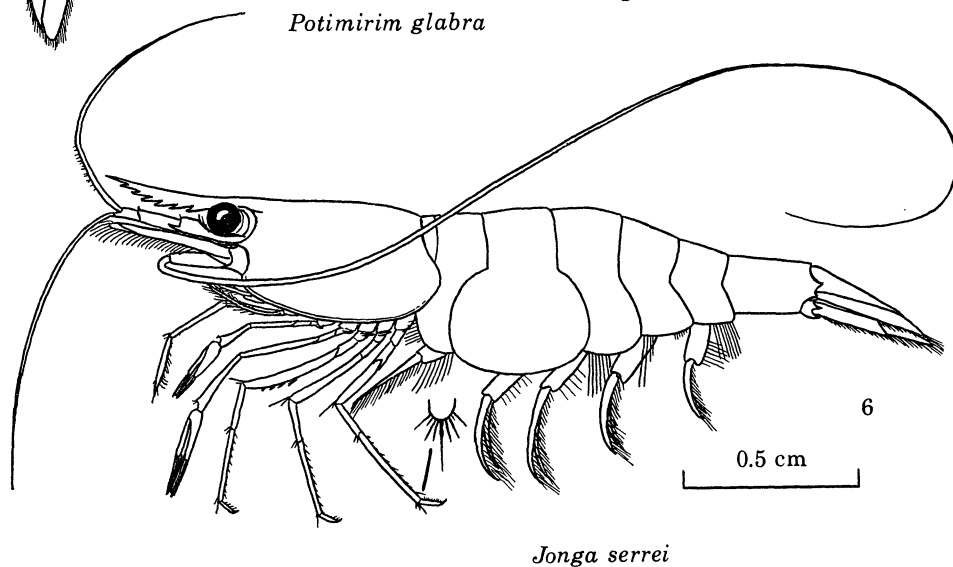
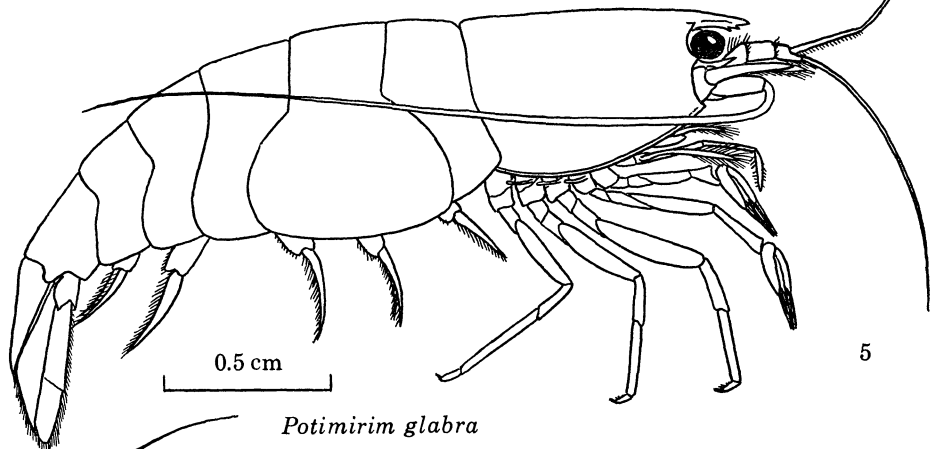
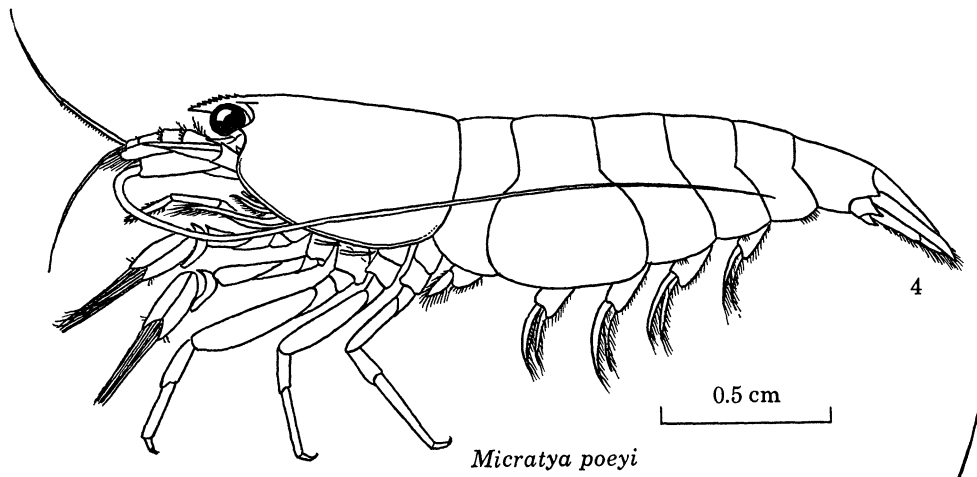
In the West Indies there is no correlation – such as holds good for example in birds – between island size and number of epigeal atyids. To these prawns each stream is the analogue of an island and it seems that a small island like Dominica, with many streams, may present a similar array of habitats to a large island such as Cuba. When ecological opportunities are increased by the provision of additional habitats, such as caves, the number of species of atyids is increased.

## I. INTRODUCTION

Although only about 300 square miles in area, the island of Dominica, West Indies, harbours no fewer than six species of freshwater prawns of the family Atyidae. This richness it shares with its now well-surveyed neighbour Guadeloupe (*ca.* 580 square miles) which has seven species (Lévêque 1974). Of the other West Indian islands only the much larger Cuba (*ca.* 44 000 square miles: nine species – of which two are subterranean), Jamaica (4400 square miles: eight species) and Puerto Rico (3400 square miles: seven species) have comparable numbers of atyids. Hispaniola is inadequately explored. Of the islands comprising the Lesser Antilles, Dominica and Guadeloupe have much the richest atyid faunas. While this may in part reflect less activity by investigators elsewhere, the relative richness of Dominica is undoubtedly real, and is a reflection of topography, climate, vegetation, and the lack of human interference.



For description see opposite.



FIGURES 1-6. The atyid prawns of Dominica. The arrangement of species is purely one of convenience. No phyletic affinities are implied.

Dominica is mountainous, enjoys a high and largely perennial rainfall, is for the most part forested, and has many permanent streams. Its topography has hitherto been conducive to the encouragement of only limited agricultural enterprises and, until recently, the little timber that has been felled has been replaced by secondary growth. Its streams have therefore escaped the unnatural scouring which has followed deforestation on neighbouring islands and are also for the most part unpolluted. The island's prawn fauna is therefore intact. By contrast, certain adjacent islands, while in some cases probably never so rich in this respect, have been subject to human interference, and some, like Antigua, have been devastated – woodland has been cut and soil eroded by the growing of sugar cane, streams flow intermittently, water shortages are experienced, and not a single atyid is reported.

The Dominican atyids, which are referable to five genera, are illustrated in outline in figures 1–6. These are:

<i>Xiphocaris elongata</i> (Guérin-Méneville)	<i>Atya innocous</i> (Herbst)
<i>Jonga serrei</i> (Bouvier)	<i>Atya scabra</i> (Leach)
<i>Potimirim glabra</i> (Kingsley)	<i>Micratya poeyi</i> (Guérin-Méneville)

Their taxonomy has been placed on a firm basis by Chace & Hobbs (1969). Here an attempt is made to give an account of certain aspects of their functional morphology and to relate these to ecology and habits. The account is based on material collected during a period of about four weeks spent in Dominica in February 1970, during which living specimens of all six species were observed. Field work was facilitated by the detailed information on localities provided by Chace & Hobbs (1969), which greatly reduced the amount of travelling and searching that was necessary. Live material of *Atya innocous*, *A. scabra*, *Micratya poeyi* and *Xiphocaris elongata* was successfully brought to England where more detailed observations were made.

From the point of view of phylogeny and adaptive radiation this assemblage is particularly interesting as it includes the most primitive of extant atyids – (*Xiphocaris elongata*) which is confined to the West Indies – as well as some of the most 'advanced' and highly specialized species. Further, these six species, while displaying many features of the common atyid plan, exhibit considerable diversity in body form, feeding habits and ecology.

## II. THE ECOLOGICAL BACKGROUND

Most Dominican streams, of which some account is given by Chace & Hobbs (1969) and for some of which chemical data are presented by Hart & Hart (1969), are fast flowing over much of their course, and for the most part stony. Only a few have short slow-flowing stretches near their mouths. Most arise in the very wet, relatively cool, central region at altitudes of over 1000, and sometimes as great as 4000 ft, and have short turbulent courses. Thus in spite of their tropical setting they tend to be cooler than streams in larger, less mountainous, land masses in similar latitudes. Chace & Hobbs (1969) quote temperatures within the range 21–26 °C but these are probably exceeded at the hottest time of the year, for which no data are available. Of the Dominican atyids, *Jonga* and *Xiphocaris* have been reported from water at 32 °C in neighbouring Guadeloupe (Lévêque 1974).

The rocks and boulders which occur in profusion in these streams were for the most part remarkably clean and free from algae at the time of my visit. Only in a few areas of limited extent were green growths observed. While this cleanness may be due in part to grazing by

the dense prawn fauna, there is no doubt that the bulk of the food consumed by the atyids comes not from the stones but consists of detritus derived mainly from the leaves of forest trees, though by the time it has been consumed this has been degraded to such an extent as to make precise identification extremely difficult. The importance of forest litter in the economy of streams in the nearby island of St Vincent has recently been noted (Harrison & Rankin 1975).

	slow flowing or lentic	pools in streams	fast flowing
	juveniles	adults	
<i>Xiphocaris elongata</i>			
<i>Jonga serrei</i>			
<i>Atya innocous</i>			
<i>Atya scabra</i>			
<i>Micratya poeyi</i>			
<i>Potimirim glabra</i>			
	riffles (rubble, small rocks and pebbles)	cascades (torrents)	accumulations of leaves
<i>Atya innocous</i>			
<i>Atya scabra</i>			
<i>Micratya poeyi</i>			
<i>Potimirim glabra</i>		--- ? ? ? ---	

FIGURE 7. The ecological preferences of the Dominican atyids. The upper part of the figure indicates general preferences; the lower part attempts to analyse further the habitats frequented in fast flowing water.

While all Dominican atyids frequent rivers and streams they differ markedly in the situations which they inhabit, and in abundance. Their ecological preferences, as revealed by the work of Chace & Hobbs (1969) and my own observations, are indicated in figure 7, further details being given in §IV. With the partial exception of *Xiphocaris elongata*, all are exclusively microphagous. The two species of *Atya* and *Micratya poeyi* have two methods of food collection at their disposal, as possibly has *Potimirim glabra*. *Jonga serrei* and *Xiphocaris elongata* have only one.

These atyids share the streams with five species of palaemonid prawns of the genus *Macrobrachium* which, however, differ greatly from the atyids in their food and feeding habits. Any competition is therefore probably for refuges rather than food. Likewise the aquatic and

semi-aquatic crabs of the genera *Guinotia* and *Sesamara* probably compete little, if at all, with the atyids, though *Guinotia dentata* (Latrielle) is possibly an occasional predator on them.

Dominican streams are dominated by malacostracans. Although not specifically sought, insects were clearly much scarcer than in comparable English streams. In some places they appeared to be virtually absent. Flint's work (1968) suggests that Trichoptera may be more plentiful at higher elevations than those frequented by prawns, but these and other typical aquatic orders seemed to be very sparsely represented. In their faunal composition therefore these streams are very distinctive and provide a startling exception to Hynes's (1970) generalization that 'the fauna of hard substrata in streams and rivers is remarkably uniform all over the world', but bear out his comment, based on but few surveys, that impoverishment of certain groups is a feature of isolated regions.

Of fishes only two species were seen. The little gobioid *Sicydium plumieri* (Bloch.) is often abundant and, being essentially a rock-cleaning detritus-feeder, may at times compete for food with the atyids. The somewhat larger eleotrid, *Eleotris pisonis* Gmelin, while common in the larger rivers and certain streams, was not seen in all streams. This is a carnivore which appears to feed largely on *Sicydium*, but part of an antennary flagellum of a prawn was seen in one of the few guts examined.

### III. METHODS

Animals were watched under various conditions in the field, and subsequently in aquaria. Flash photographs, in addition to those reproduced here, proved useful in elucidating certain habits. Material was fixed in either Zenker's fluid, alcoholic Bouin's fluid or 70 % alcohol. Animals treated by the first two were used for the preparation of thick, Mallory-stained sections cut in various planes from material embedded in low-viscosity nitrocellulose. Dissection was used where necessary. Exuviae sometimes proved useful in the study of skeletal features.

### IV. GROSS MORPHOLOGY, ECOLOGY AND HABITS

#### (a) *Xiphocaris elongata*

*X. elongata* (figure 1; figures 70 and 71, plate 4) (length to about 6.9 cm including rostrum) is the most primitive extant atyid, occupies an isolated phyletic position, and differs markedly in structure and habits from other Dominican species. Its strikingly divergent features were recognized by Bouvier (1925) who, without bestowing rank, designated *Xiphocaris* as an acanthophyroid atyid on account of resemblances to the oplophorid *Acanthophyra*. Without prejudice to taxonomic position it is convenient to refer to the rest of the Dominican atyids as non-acanthophyroid.

Juveniles and adults differ in ecology and habits. Juveniles occur, sometimes abundantly, in the lower reaches of rivers, where I found them particularly plentiful in marginal vegetation in slow flowing water, but also frequent exposed situations in shallow water. Adults, whose habits were studied in greater detail, seem only to occur further upstream, though not necessarily at any great altitude for they have been seen only about 200 ft above sea level. Here they can be watched in the quieter pools where they move about in the open, evidently feeding on the bottom, whether it be of rocks, coarse gravel, sand, or accumulations of dead leaves. From time to time they make more wide-ranging movements by swimming efficiently through open water. Adults were also found, but more rarely, in fast-flowing water, generally in the lee of



a rock, by Chace & Hobbs (1969), and by myself in a situation which suggested that they had sought the shelter of marginal – essentially terrestrial – vegetation.

*Xiphocaris* is a slender, lightly built prawn whose adaptations are related to tiptoeing delicately over a variety of substrates (figures 70 and 71, plate 4) and to swimming. Of the other Dominican atyids only *Jonga serrei* shares these habits to a significant extent. The body, especially the abdomen, is long and slender and protected by thin, largely transparent, cuticle. This and the remarkably transparent thoracic and abdominal muscles render it almost invisible.

The walking legs of Dominican atyids differ much from species to species and from leg to leg in individual species in accordance with functional needs, and are good indicators of habits. This applies both to general form (figures 1–6) and to dactylar armature. The legs of *Xiphocaris* are long and slender and in a walking animal the ischium-merus region is usually extended horizontally or directed somewhat ventrally. While obtuse, the carpus-merus angle frequently approaches 90° (figures 70 and 71, plate 4). Thus, unlike many walking arthropods, *Xiphocaris* ‘stands up’ on its legs and does not ‘hang down’ as, for example, does *Atya* (q.v.). Because of this and the elongate nature of the three distal segments the body is elevated well above the substratum, a habit more suited to life in still than in rapidly flowing water. Furthermore *Xiphocaris* rests and walks on the clawed tips of the dactyli and does not use them to any extent for gripping as do *Atya* and others. Even if, for any reason, the body is pressed against the substratum, only the claws of the dactyli make contact: no other segments are used for gripping.

The dactyli are illustrated by Bouvier (1925) and are similar in general form to those of *Jonga* shown in figures 8 and 9, the differences in proportions being apparent by comparison of these figures with figure 1.

Rapid walking movements can be executed, and walking in reverse can be practised when necessary. The tail fan, habitually spread as an aid to balance in the walking animal, is never used as a prop as it is in the largely ambulatory *Atya*. While a much alarmed individual kept in a confined space may cower against the substratum, prolonged observation of an undisturbed animal reveals that almost never do the pleopods make contact with the bottom. When walking the animal holds the abdomen more or less horizontal and well clear of the substratum with the pleopods pressed against it in the forward position (figure 71, plate 4).

The pleopods, more powerfully developed than in any other Dominican atyid, are the main propulsive organs when swimming, though the well-developed exopods of the chelipeds and walking legs also apparently always assist. Thus, although the possession of exopods is a primitive feature, their retention is of functional significance. When the animal swims the body is kept straight and the chelipeds and third maxillipeds are bunched together beneath the mouthparts and directed forwards, but the walking legs hang below the thorax as an undercarriage which is used as it alights. Besides being an able swimmer, *Xiphocaris* can hover motionless and also swim in reverse. Movements of the thoracic exopods have been seen in a hovering individual but their exact rôle has not been ascertained.

The eye is better developed than in any other atyid, the visual field is virtually a sphere, and the visual sense is highly developed. Movements of an observer are detected from a considerable distance. The elongate rostrum may provide some protection for the eyes, though one suspects that its main function is that of a stabilizer during swimming. *Xiphocaris* is also extremely adept at evading capture. It swims rapidly away from an approaching net, often in reverse, and frequently rises to the water surface whence it leaps into the air and, with what are presumably further flexions of the abdomen, may make one or more additional leaps before disappearing

beneath the surface. No other Dominican species exhibits such behaviour, but it appears that the Californian *Syncaris pacifica* (Holmes) has a similar ability (Hedgepeth 1968).

*Xiphocaris* is provided with very long flagella both on antennules and antennae – longer than those of crevice-frequenting species. Those of the antennae in particular can be swung so as to explore a large area around the animal, including a region behind the body.

The third pair of legs is used for grooming as in *Caridina* (Fryer 1960). For this the dactyli possess a comb of spines, much like that of *Jonga* shown in figure 9, by means of which the whole of the abdomen can be cleansed. At times the pleopods are systematically combed. When this happens they are sometimes stretched so that their tips touch the substratum. In order that the tail fan may be reached the abdomen is flexed. The third pair of legs may also assist in pushing off the old cuticle during ecdysis, for an individual which had been paying considerable attention to what at the time was taken to be grooming of the abdomen was then seen to flex its abdomen into an acute hairpin bend and apparently comb the tail fan. A few minutes later the animal was seen to have moulted though the process was not witnessed.

The second chelipeds and third maxillipeds are also used for grooming. The former, which clean by a series of nips which follow each other with great rapidity, are extremely mobile and can reach the dorsal parts of the carapace. They are also used for cleaning the eyes, antennal scales and apparently the mouthparts for they are sometimes persistently applied to the latter when the animal is not feeding. They also reach back and help to clean the pleopods. The third maxillipeds are used to clean at least the second walking legs, antennules and antennae. The two latter appendages are flexed to allow the third maxillipeds to comb them.

The delicacy of balance was well shown by an individual engaged in active grooming. Both right and left first legs were held clear of the bottom and the left third leg was used, as were the second chelipeds, for grooming the abdomen. Only the second left and second and third right legs were used for support but the animal appeared perfectly balanced.

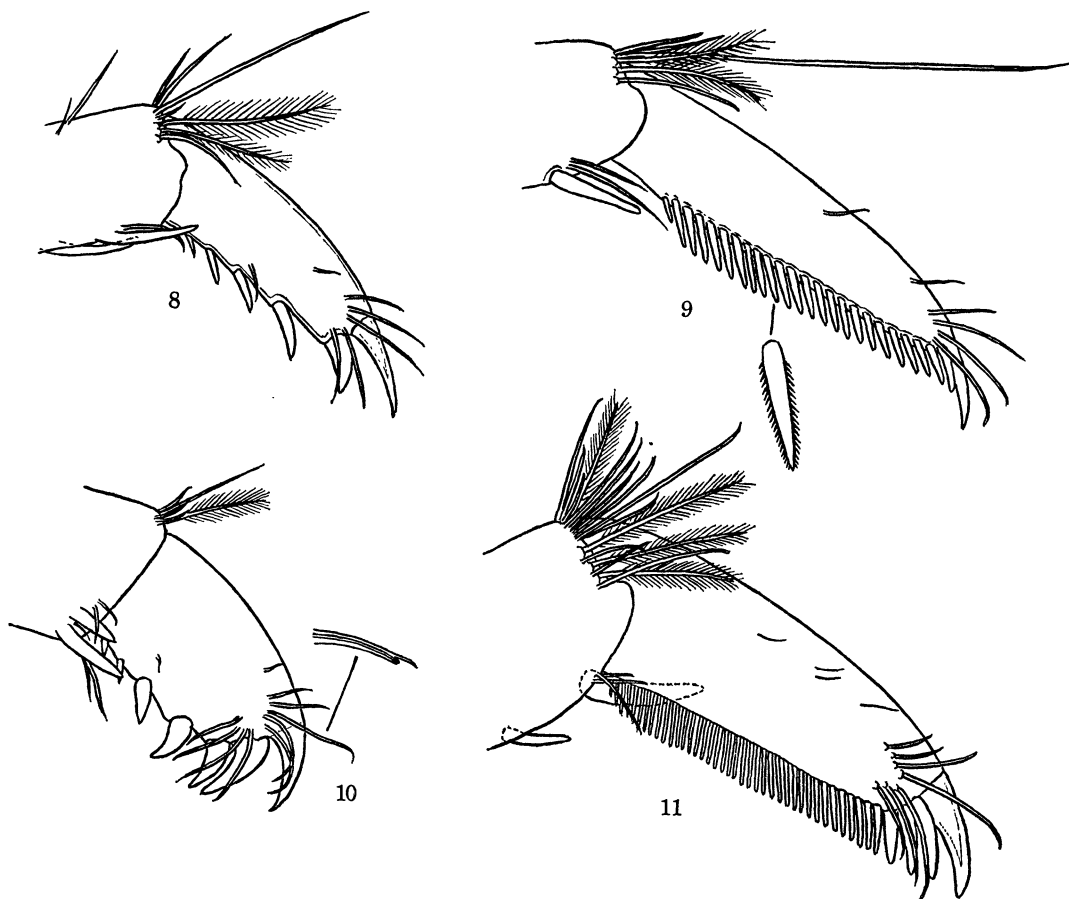
Notwithstanding its distinctive method of food collection (§V(a)) *Xiphocaris* feeds largely on detritus, as do other Dominican atyids, but is probably able to utilize sources not available to at least such specialists as *Atya* and *Micratya*. Plant fragments of terrestrial origin were numerous in the guts examined and one contained large numbers of unidentified spore cases. It is impossible to know how much the fine division of many of the plant fragments is due to the size of collected particles and how much to mandibular action. In some cases the contents were more 'gritty' than those of *Atya*, the many inorganic particles doubtless having been picked up with food from sandy areas such as are scarcely frequented by *Atya* and *Micratya*. Diatoms, so few as to be insignificant, were the only food items that could be attributed to production within the streams. Occasional windfalls are probably utilized. In Dominica a small *Atya* kept in the same vessel as a large *Xiphocaris* died and was partly eaten by the latter. At least partial disintegration is, however, probably necessary before such food can be utilized. (See also notes on feeding mechanism, §V(b).)

An adult lived for over 20 months in captivity, which suggests a potential life span of several years.

#### (b) *Jonga serrei*

Although found only in riverine habitats, *Jonga serrei* (figure 6) (length to about 2.48 cm including rostrum) is confined to slow-flowing, often virtually lentic, situations such as exist near certain river mouths where sandspits provide a barrier and give rise to almost lacustrine conditions of restricted extent. As Chace & Hobbs (1969) point out, it is absent from Dominican

streams which are fast-flowing to their mouths. Where suitable slow-flowing conditions exist it frequents marginal and submerged vegetation, sometimes in great abundance. Lévêque (1974) found it frequently among vegetation in Guadeloupe. His statement that it 'semble limité aux eaux courantes et n'a jamais été observé dans les mares' is not an indication that it lives in fast-flowing water for a glance at his map shows that all 18 stations from which he collected it are in low-lying regions where (as the presence of vegetation suggests) flow is generally slow.



FIGURES 8-11. Tips of walking legs of *Jonga serrei* and *Potimirim glabra*.

FIGURE 8. *J. serrei*, leg 1. Leg 2 is very similar.

FIGURE 9. *J. serrei*, leg 3. Note the long sensory seta of the distal end of the propus. (The distal claw is only slightly sclerotized.)

FIGURE 10. *P. glabra*, leg 2. Leg 1 is very similar. Several of the distal setae are like that shown in the inset.

FIGURE 11. *P. glabra*, leg 3. The distal claw is very lightly sclerotized - only a little more than in *Jonga*.

Bouvier (1925) has suggested that *J. serrei* is derived from a *Caridina* of the *nilotica* group (which is an Old World and Australian complex) and Chace & Hobbs also remark that it is more similar to *Caridina* than is any other American atyid. Certainly its habits are very similar to those of *Caridina africana* Kingsley and *C. nilotica* Roux observed in Africa (Fryer 1960). It is more slender and lightly built than any Dominican species other than *Xiphocaris*, and its adaptations are those of a species which walks lightly over surfaces - plants and debris - and does not usually have to withstand fast-flowing currents. It also swims well. How it copes with floods

is not known, but the seeking of crevices is likely, and it is possible that it at times suffers severely from such events. Thus near the mouth of the Castle Bruce River are beds of *Potamogeton* in which Chace & Hobbs record the presence of large numbers of *J. serrei*, but in which I failed to find a single specimen in spite of intensive search.

Although less slender than *Xiphocaris*, and differing markedly from it in its method of food collection, *Jonga* exhibits certain similarities in its morphology which reflect similarities in habits. These include long, slender walking legs and chelipeds, powerful pleopods, somewhat elongate antennules, well-developed antennal scales, long antennary flagella and a long rostrum. The functional significance of the last attribute is not entirely clear, but it may facilitate straight swimming and is certainly unsuited to life in fast-flowing streams.

The dactyli of legs 1 and 2 are very similar (figure 8) and strikingly different from those of *Atya* and *Micratya* (q.v.). Although much less sclerotized than those of these genera their distal claws appear not to become worn with use, being employed largely for walking lightly over surfaces or at times grasping plant material. The dactylus of leg 3 has a well-developed grooming comb (figure 9). At the distal extremities of several leg segments, and especially of the merus and propus, are long sensory setae (figures 6, inset, 8 and 9), directed laterally and anteriorly in life. These are much longer than their counterparts – where these exist – in other species (cf. figures 8 and 9 with figures 12–14) and are related to life in still water and probably to wandering among vegetation.

*Jonga* holds its chelipeds with the tips directed downwards towards the substratum (cf. *Potimirim*), not bunched together and directed forward as does *Atya*, but tends to lift them into a somewhat *Atya*-like position when swimming.

The food consists of material swept from the surfaces of plants and other objects and perhaps from the bottom. While largely embraced by the term 'detritus', that collected in the one locality where it was investigated (the lower part of the Layou River) differed from that of other Dominican species. Many inorganic particles were present, obviously from the sandy bottom, and in some cases diatoms of various species as well as unidentifiable organic debris. One suspects, however, that in such a detritus feeder the nature of the food is determined not only by the food collecting apparatus but by what is available.

#### (c) *Potimirim glabra*

*Potimirim glabra* (figure 5) (length to about 3.1 cm) is not common in Dominica and its ecology is but little known. As did Chace & Hobbs (1969) I found only a few specimens. Like *Micratya poeyi* (q.v.) it frequents fast-flowing water – moderately swift to swift according to Chace & Hobbs – and, again like *M. poeyi*, seeks situations among small stones. In spite of these similarities it is less specialized than *M. poeyi* – which may help to explain its greater rarity. The single specimen collected by Holthuis (1954) in El Salvador also came from clear fast-flowing water between rocks and boulders on a sandy bottom and Davis (1964) obtained specimens 'from their shelter beneath rocks in a small stream' in the same country. In Guadeloupe Lévêque (1974) found it twice, both localities being on the mountainous Basse Terre, once in a stream cascading among rocks and once in rocky pools among waterfalls. No ecological data are available for the animal from Brasil of which Villalobos (1959) gave an excellent morphological description and named *P. brasiliiana* and which is regarded as a synonym of *P. glabra* by Chace & Hobbs (1969).

Superficially *P. glabra* resembles *Micratya*, (§IV (f)) but its walking legs are more slender

(cf. figures 4 and 5) and the dactyli of legs 1 and 2 (figure 10), whose inner armature was used for gripping stones in the vessel in which individuals were observed in Dominica, are in some ways intermediate between those of *Jonga* and *Micratya*. If the comparison is confined to atyids about whose ecology something is known, then dactyli such as those of *Jonga* and *Xiphocaris*, and of at least two African species of *Caridina* (Fryer 1960, figure 1) are adapted for life in still water; those of the type found in *Atya* and *Micratya* (§IV (d), (e), (f)) for life in fast-flowing water. Other species with slender legs and *Jonga*-like dactyli, such as the subterranean *Stygio-caris* and the endemic genera of the Lake Tanganyika also presumably frequent still water for the most part. On this basis *Potimirim* shows less morphological adaptation to life in torrential situations than do its Dominican relatives *Atya* and *Micratya* yet it is under such conditions that it has been found. From a functional point of view the differences between it and *Micratya* otherwise concern particularly the food collecting chelipeds.

*Potimirim* was found in company with juveniles of *Atya innocous* from which it was separable at a glance, not only by the blue spots described by Chace & Hobbs (1969), but by the fact that it held its chelipeds with their bristles directed towards the substratum and not bunched together and forward as does *Atya*. The food consisted of detritus, similar in nature to that of *Atya* and *Micratya* (§IV (d-f)) but, in the three specimens examined in detail, the admixture of large fragments was rather high. One contained the remains of an insect exuvium (no tissues were detected), presumably of terrestrial origin, which were very prominent within the gut, which indicated that relatively large objects are occasionally collected. Two or three diatoms – an infinitesimal proportion of the whole – were suggestive of scraping.

(d) *Atya innocous*

This species (figure 2) (length to about 12.2 cm) is widely distributed in Dominica where it occurs, often plentifully, in a diversity of habitats from sea level to altitudes of at least 2500 ft (Chace & Hobbs 1969). Unlike *Xiphocaris*, which regularly swims, and occurs particularly in pools, *A. innocous* is essentially an ambulatory species that can cope with a wide range of conditions. It frequents such different situations as torrential streams, where it lurks beneath stones, in crevices, and among accumulations of leaf debris, and quiet pools such as those frequented by *Xiphocaris*. Many juveniles were found clinging to the matted roots of trees over which water was flowing very rapidly. That it can exploit such different habitats can be attributed to a considerable extent to its ability to collect food by two very different methods.

That its tolerance exceeds the range of natural conditions in Dominican streams was indicated by its occurrence in a pond whose bottom was composed largely of soft ooze. When this pond, which had been constructed on a stream, was drained, hundreds of individuals were collected for human consumption. Although it frequented such a situation, many of its adaptations are to clinging to and clambering over hard substrates. In nature I found it plentiful in water as cool as 21 °C and it occurs at altitudes where lower temperatures must prevail at times. In aquaria it has remained healthy in spite of falls in temperature to 14 °C. By contrast, individuals taken from running water survived for over two weeks in confined conditions in which temperatures at times rose to at least 32 °C, withstood a trans-Atlantic air journey, and then flourished in aquaria.

The behaviour of *A. innocous* was studied in a quiet pool on a stream at Springfield (altitude about 1500 ft), in an ornamental pond where a large population was established, and, more intensively, in aquaria. In the Springfield pool individuals of various sizes were watched as

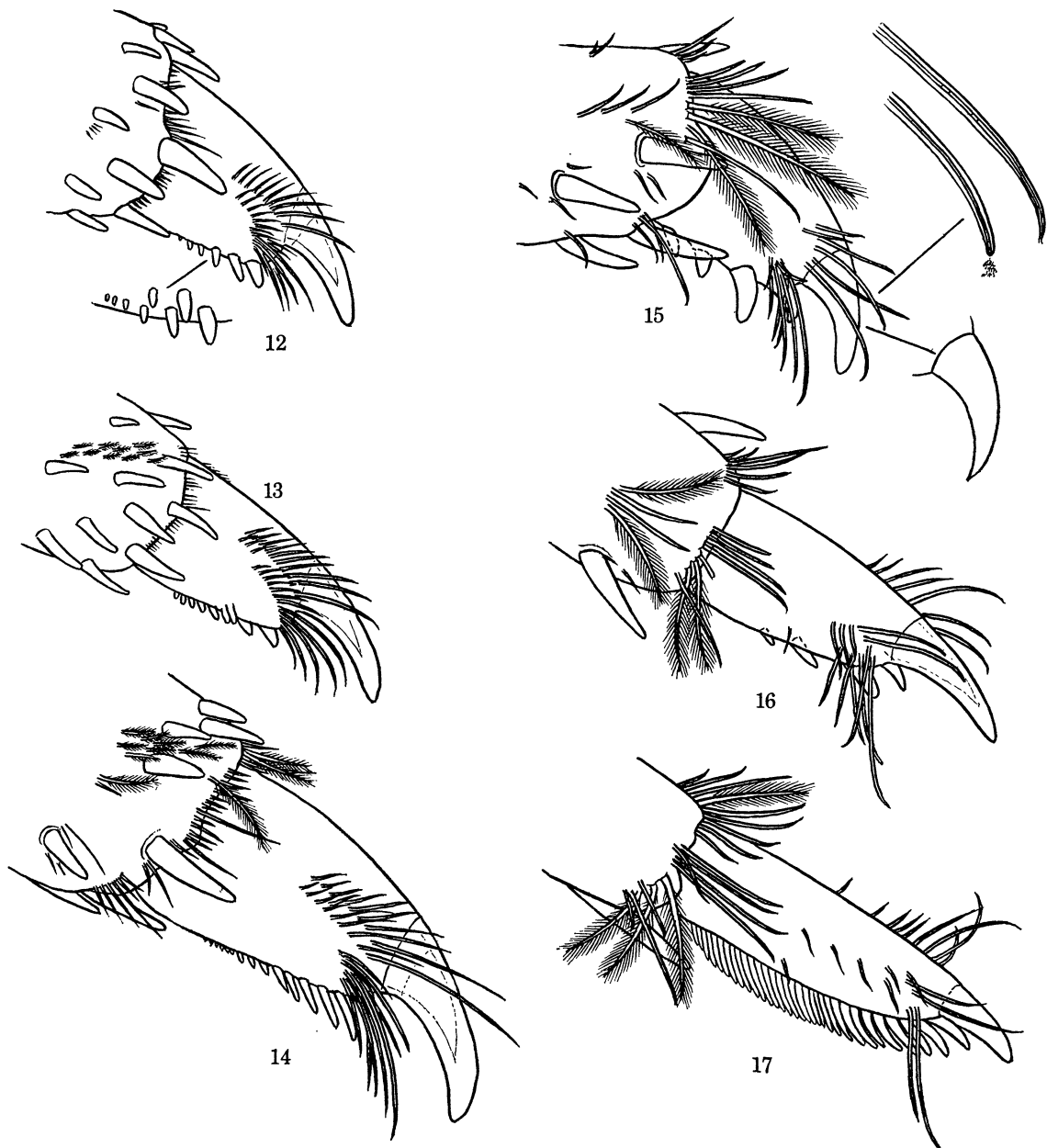
they moved, usually slowly, over a bottom composed of small stones, gravel and coarse sand. Large bare rocks were largely, but not entirely, shunned. These prawns were active in daylight, as were others seen elsewhere, but observations in the ornamental pool, which had artificial illumination, revealed greater nocturnal than diurnal activity. By night many feeding animals frequented the walls of the pool which were almost deserted by day. Although to be seen in pools, its abundance beneath stones, of which baskets of individuals collected for human consumption bear witness, suggests that vastly larger populations exist in stony situations in fast flowing water than in pools.

*A. innocous* is a robust prawn whose form is that of a true bottom dweller. The abdomen is relatively shorter and much less slender than that of *Xiphocaris*, and is flexed ventrally so that the tail fan almost always makes contact with the substratum in a walking, feeding or resting animal (figure 63, plate 2). Its pleopods are less well developed. It seldom swims unless disturbed. Progression is often associated with feeding by scraping and it generally walks slowly, but a rapid scuttle can be achieved over short distances. The typical macruran backward escape reaction by rapid flexion of the abdomen is practised, and a seriously disturbed individual seeks refuge beneath or between stones. In sharp contrast to that of *Xiphocaris* the cuticle is thick and often darkly tanned. While all individuals have a similar colour pattern (which changes with age as described by Chace & Hobbs 1969), colour polymorphism is exhibited, there being brown and green morphs. Many individuals, especially the larger ones, however, are so dark as to appear almost black.

*A. innocous* appears to pay less attention to grooming than *Xiphocaris*, but this activity may be carried out particularly by night or when the animal is hidden beneath stones, for individuals are usually clean. Some from the mud-bottomed pool, however, carried a light burden of algae and detritus. Nevertheless the third pair of legs is used for grooming the pleopods which are deliberately swung forward and ventrally to facilitate this, and grooming of the more ventral parts of the carapace has also been seen. Grooming may be more important in young than old individuals for while juveniles have a well-developed grooming comb on the dactylus of the third walking leg this becomes less accentuated in larger individuals (figure 14).

Reciprocal grooming of the cheliped bristles and the mouthparts also takes place, sometimes over a prolonged period. The chelipeds are closed so that their bristles form a long tuft rather like an artist's paint brush (figure 2; figure 63, plate 2) and these are systematically passed between the mouthparts, each cheliped being dealt with in turn, the point of the brush repeatedly being pushed posteriorly along the anterior-posterior axis of the body and between the mouthparts and then withdrawn. During this process the mouthparts operate vigorously. Although details cannot be observed it is likely that the maxilla and first and second maxillipeds all play a part in grooming the cheliped bristles and are themselves perhaps cleaned in the process. Occasionally a cheliped is opened, thereby momentarily expanding its fan (§VI (a)). Wiping movements of the third maxillipeds are also involved at times. These appendages are used to comb the cheliped bristles and to cleanse the mouthparts and the region near the base of the antennae.

The walking legs are robust. The ischium/merus region, especially of legs 1 and 2 is usually directed somewhat dorsally (figures 58-60, plate 1; figure 62, plate 2; figure 66, plate 3), and the backwardly inclined carpus, propus and dactylus are short - relatively shorter than in *Xiphocaris* - so that the body 'hangs down' from the legs and is generally kept close to the substratum. The axis of the coxa/body joint is aligned differently in each leg so that the coxae of



FIGURES 12-17. Tips of walking legs of *Atya innocous* and *Micratya poeyi*.

FIGURE 12. *A. innocous*, leg 1.

FIGURE 13. *A. innocous*, leg 2.

FIGURE 14. *A. innocous*, leg 3.

FIGURE 15. *M. poeyi*, leg 1. Insets show hollow distal setae from one of which what may be a secretion is exuding, and the sharp terminal claw of a presumably recently moulted individual before much wear has taken place.

FIGURE 16. *M. poeyi*, leg 2.

FIGURE 17. *M. poeyi*, leg 3.

Different scales have been used for convenience of illustrating different limbs. Size is best appreciated by comparison with figures 2 and 4.

the two posterior legs are directed more posteriorly than the first, and the axis of the coxa/basis joint differs similarly in alignment from leg to leg to give a good spread of the leg axes. The dactyli are armed with a powerful, highly sclerotized claw (figure 63, plate 2) and, on each side of it, with an array of slender spines (figures 12–14). These are hollow and conceivably exude secretions distally in some cases (see *Micratya*). The terminal claws are inclined somewhat towards the body so that the animal can exert a pull on each, the body thus being firmly anchored by legs that are under tension. That such a pull is exerted can regularly be seen in an animal walking over a stone. Unless the claw can be hooked over its edge, as in figures 58–60, plate 1, each footfall of legs 1 and 2 is followed by a sliding towards the body of the dactylus until the claw finds a grip. The grip is extremely effective. When individuals crawling on and feeding from the vertical cement walls of the ornamental pond were slightly disturbed a rapid backward retreat of several body lengths along the wall took place, following which a new grip was achieved with apparent ease. Some wear of the claws takes place: individuals with rather sharp pointed claws are presumably recently moulted. Although the dactyli of legs 1 and 2 are provided with several, more proximal, stout spines (figures 12 and 13) these are seldom employed during ordinary progression, but may well be called upon when the animal is crawling in fast-flowing water on shingly substrata.

When a suitable retreat is available *A. innocous* may rest for long periods suspended in an inverted position beneath a stone gripping with the dactylar armature of its legs. Even in such a position, one of the third pair of legs at least may release its hold for grooming purposes.

The eyes are relatively smaller, and the flagella of the antennules and antennae shorter, than in *Xiphocaris*, reflecting different ways of life.

The food consists, apparently entirely, of particulate detritus. Among the mass of largely unidentifiable brownish material with which the gut is usually packed, many plant fragments, mostly minute but occasionally of almost macroscopic dimensions, have been detected – leaf cells, vessels with spiral thickening, part of a fern sporangium, etc. – the origin of which, like that of most of the other organic particles, is undoubtedly the forest trees and associated vegetation that surround the streams in which the animals live.

An individual brought to England when small, but of unknown age, lived for about 6 years and 9 months in an aquarium and had not achieved its maximum size at the time of death. Several others lived for 3 or 4 years.

In aquaria adults readily mated and produced fertile eggs from which larvae emerged, but never survived. Even experienced prawn-rearers at Conway failed to keep these for more than 10 days. As Bordage (1908) and Edmondson (1929) successfully reared other species, their death was probably due to an inability to provide suitable food or adequate space.

(e) *Atya scabra*

Very few specimens of *A. scabra* (figure 3) (length to at least 10 cm) were found, and Chace & Hobbs (1969) also testify to its rarity in Dominica. As were their specimens, mine were collected among stones in rapidly flowing water. Of these one adult was kept for 2½ years in an aquarium with several specimens of *A. innocous*. Here, by day at least, it had more retiring habits than *A. innocous*, making few appearances from the stones under which it took refuge, save to filter as described below. I never saw a specimen in the open in the field, nor did Chace & Hobbs (1969) – (cf. *A. innocous* which was so observed both by Chace & Hobbs and myself). Likewise Darnell (1956), who carried out much field work on a Mexican stream where *A. scabra* was



plentiful, never saw one by day outside the riffle in which they lived, but did so occasionally at night.

The walking legs are more robust than those of *A. innocous* (cf. figures 2 and 3), perhaps enabling it to withstand more torrential conditions. The individual kept in the aquarium collected food more frequently by filtering and much less frequently by scraping (§VI(b)) than did *A. innocous*. Only very rarely was it seen to scrape rocks with its chelipeds. Such behaviour is in keeping with habitat preferences. *A. scabra* frequents situations in which passive filtering might be expected to be practised more readily than active scraping. A very small but highly significant difference in the nature of the cheliped bristles is correlated with this difference in behaviour (§VI(a)).

The rarity of this species in Dominica may be due to its habitat preferences and habits or to its inability to compete with *A. innocous*, which is better equipped for collecting food by scraping. In Jamaica, where both species occur, Hart's (1961) records reveal that there also *A. innocous* (recorded by him as *A. occidentalis*) is more plentiful than *A. scabra* and the same is true of Guadeloupe (Lévêque 1974). A study of the habits of *A. scabra* in areas from which *A. innocous* is absent would throw light on this problem. In the Mexican locality whence Villalobos (1943) obtained his material of *A. scabra* (and where it was unaccompanied by any other member of the genus?) it evidently occurred in greater numbers than in Dominica. This was certainly the case in the riffle in a Mexican stream where it was the only atyid present and where Darnell (1956) estimated its numbers at about 10/m<sup>2</sup>.

The food, like that of *A. innocous*, consists of detritus, and in general I was unable to recognize differences between the gut contents of the two species. Larger pieces of vegetable matter were found in *A. innocous* than in *A. scabra* and may reflect different feeding methods but the number of *A. scabra* examined was too small to be significant and the most important aspect of the comparison was the similarity of the gut contents of these species. Darnell (1956) found 'a large quantity of unidentifiable detritus and some plant remains, mostly bits of leaves' in specimens from a Mexican stream. He also found arthropod fragments, in most cases apparently derived from exuviae, but in one case probably from live insects, and numerous diatoms and other algae mostly derived from outside the frequented habitat. Significantly, he also noted that algae growing in abundance on rock surfaces were scarcely eaten (though the possibility that these were unpalatable cannot be excluded) and, although clearly unaware that these animals can filter, concluded that they fed, not from the uppermost rocks, but on detritus and other material that found its way to the bottom of the riffle.

(f) *Micratya poeyi*

As its name suggests, and the following functional account shows, *M. poeyi* (figure 4) (length to about 2.35 cm) can in many respects be conveniently regarded as a miniature *Atya*. It is very common in Dominican streams and near the edges of rivers where it occurs in fast flowing riffles and among small stones. It is also a very constant inhabitant of piles of fallen leaves which accumulate among rocks in rapidly flowing water. Chace & Hobbs (1969) also report it from rapidly flowing drainage ditches. Although very common, its habits are so cryptic that few individuals were seen moving openly over the bottom. Those disturbed by collecting operations quickly sought shelter, both swimming and crawling – with and against brisk currents – being employed. Aquarium observations have been more revealing.

Great agility and acrobatic prowess are shown as the animal crawls over rocks and squeezes

through cranies, unhesitatingly crawling upside down if need be. Like *Atya*, *Micratya* habitually employs the tail fan when crawling. Although flight is the ultimate means of escape, a frequent response to interference is to cling tightly to the object being gripped. Individuals kept in containers were several times lifted out of the water as they clung to a stone or leaf.

The general form is robust and the abdomen is that of an ambulatory species. The pleopods are, however, well developed, as demanded by the need to combat fast flowing water. The walking legs are robust. Although relatively less so than in adults of *Atya* spp. (cf. figures 2–4) their form is comparable with that of young *A. innocous* of similar dimensions, the increased girth of the legs in adult *Atya* being the result of allometric growth – presumably necessitated by the relatively greater increase in bulk than in length as size increases. Like those of *Atya* the short dactyli are provided with stout sclerotized claws (figures 15–17) and, on each side, with fine curved spines. The method of gripping with the claws is also similar to that of *Atya*. *Micratya*, however, also regularly presses the inner surface of the dactylus, and sometimes also of the propus, against the object to which it is clinging. Except in the case of the dactylus of leg 3 both these segments are provided with short stout spines, those of the dactyli of legs 1 and 2 being shown in figures 15 and 16. The inner face of the propus is flat, each edge being armed with a row of widely spaced spines which can be pressed against a stone, leaf or other object. The fine curved spines adjacent to the dactylar claws are thick-walled. Each has a very narrow duct which appears to open at its tip (figure 15, inset). In some cases what may be traces of secretions are to be seen here, and sometimes material can be seen in the duct so it is possible that adhesive material is used for attachment. The claws become rounded with wear (figures 15–17). In what are presumably recently moulted individuals they are needle sharp (figure 15, inset). The dactylus of leg 3 is modified for grooming (figure 17).

*M. poeyi* exhibits a complex colour polymorphism (Chace & Hobbs 1969) involving three distinct colour patterns of which one occurs as two distinct colour morphs. Superimposed on this polymorphism is individual variation in colour.

As in *Atya* the food can only be described as detritus. This appeared similar to that of *Atya* but lacked larger fragments and was possibly more flocculent, but differences are almost impossible to define. Two diatoms only – in separate individuals – emphasize the scant importance of autochthonous material, most food obviously deriving ultimately from the vegetation of the forests.

An individual collected as an adult survived for over 14 months, which suggests a potential life span of at least 2 years, possibly considerably more.

## V. THE FEEDING MECHANISM OF *XIPHOCARIS*

### (a) *The chelipeds and food collection*

The chelipeds of *Xiphocaris*, illustrated by Bouvier (1925), are long, slender (figure 1) and very mobile, the posterior being the longer and more slender pair. The carpus/propus joint, is essentially monocondylic – which grants mobility – but is clearly derived from a pivot joint and shows little of the excavation so characteristic of all other Dominican species and displayed in an extreme form by *Atya* and *Micratya* (§VI (a)). The dactylus arises rather distally and is much shorter than the propus with which it articulates by a typical pivot joint to form a pincer such as is found in many decapods (figures 18 and 19). This pincer, however, exhibits specializations. Distally each cheliped is armed with flattened sclerotized denticles (figure 21,

FD), rather like human finger-nails in form, and so arranged that when the chela is closed they can cut as well as grip (see also Bouvier 1925; figures 22, 23 and 26). By opposition of a stout tooth (figures 20 and 23, LD), and a thickened lateral part of a nail-like denticle some crushing can also be achieved. Furthermore, on its inner side the face of the dactylus bears contiguous blade-like spines (figure 20, BS), mentioned without reference to function by Bouvier, which, when the pincer is closed, oppose a chitinous blade (CBP) which runs along the inner side of the face of the propus. A few such spines are present distally on the outer face of the dactylus but here the blade is very short. The structures are clearly derived from spines on whose posterior edge a blade-like extension has developed. Two proximal spines of cheliped 1 (figure 20) are particularly illuminating in this respect as they are less modified than the rest. Adjacent to each blade is a row of setae which, like many of those that form a distal tuft, have thin walled tips (figure 20, inset) that, unlike their non-staining stems, stain pink with Mallory. These, clearly derived from the more typical sensory setae of which many clothe the propus and dactylus, perhaps serve both the tactile and gustatory senses.

The opposing faces of the propus and dactylus are not parallel to each other but make an acute angle whose apex is on the inner, denticulate and bladed side (figures 22 and 23). To the outside are arcs of setae. Thus when the chela is closed a wedge-shaped space whose open end is guarded by setae is enclosed between its component segments.

The sclerotized distal claws are used for picking up, and perhaps crushing, small particles, and for pulling and 'biting' small fragments from large food masses, while the rest of the chela is used for collecting detritus. As the pincer closes, loose particles will be enclosed within the chamber so formed. The inner blade-like spines are presumably used to scrape detritus from firm substrates, and probably to sever attached material for they clearly function as shears when their blades come together. Collected material is conveyed to the mouthparts, sometimes with many successive rapid movements of the chelipeds, sometimes more slowly.

The posterior chelipeds usually reach forward beyond the anterior and are also sometimes flexed to reach backward. They explore the bottom more than the first pair and are swung over a wide area. At times they can be seen 'nipping' with great rapidity when not apparently collecting food. When large accumulations of detritus are available large loads are transferred to the mouthparts, particularly by the robust anterior chelipeds. On such occasions while food is being manipulated by the mouthparts one, or more usually both, of the anterior chelipeds may hold a further load or loads while the second pair explore the substratum.

Only occasionally are the third maxillipeds involved in the handling of food – essentially the removal of excess material. From time to time they make very rapid movements that appear to be for cleaning the chelipeds, for which their armature is suitable.

(b) *The mouthparts and manipulation of food*

Of all Dominican atyids, and almost certainly of all members of the family, *Xiphocaris* has the least specialized mouthparts. Likewise the feeding mechanism, while complex and elegant, shows fewer refinements than that of the non-Acanthoephyroid species, but displays a level of organization from which, by elaboration, that of other species could have been derived.

Individual mouthparts have been sketched by Bouvier (1925) but few details are shown. Their arrangement in situ is shown in figure 77 (located on page 100 for ease of comparison with *Atya*) the inner face of the left appendages being revealed by removal of their partners. The spatial relations of the individual components are made clear by comparison of this figure with

figures 24 and 25, and figures 28 and 29. These render a description unnecessary but certain features demand emphasis. The mouthparts are directed antero-ventrally as indicated in the inset of figure 77. They are small, the length of the post-mandibular masticatory complex being only about 2.5 mm in a 5 cm prawn.

The proximal endite of the maxillule bears a row of orally directed spines (figures 77 and 28, SSMxllle). The sparsity – there are only 25 in all – and stoutness, particularly of the distal 10 of these spines, is noteworthy. Towards the posterior end of the row (beyond the limits of figure 77) the spines progressively diminish in length and diameter. Stout armature is an attribute also of the distal endite of the maxillule (figures 77 and 24, DE Mxllle) and of the distal endite of the maxilla (DE Mx) whose large size in relation to the rest of the appendage is also noteworthy. By contrast what, following the usage employed for *Caridina* (Fryer 1960) is called the teaselling lobe (TL) of the maxilla is short and sparsely armed with relatively stout spinules. These are seen in section in figure 28. The long distal endite of the first maxilliped (figure 77, Mxp 1) bears, immediately below the teaselling lobe of the maxilla, a thicket of spines, arranged in rows. The tips of some of these are spatulate, otherwise there is no elaboration.

Although not all details of the feeding mechanism have been elucidated by observation, the general process is clear and some of the points not observed can be inferred with confidence from anatomy and by comparison with other atyids. Material collected by the chelipeds is passed to the mouthparts and held by the opposed first and/or second maxillipeds. The degree to which the latter participate is uncertain. In *Caridina* these appendages are sparsely setose and are by-passed by the food: here they are provided with stout spines, some of considerable length (figure 77, Mxp2, and figure 29, Mxp2 and S Mxp2) that can reach dorsally between the overlying mouthparts and are almost certainly employed at times for pushing food material, perhaps more especially large particles, but whether they ever strip material from the chelipeds is not known. Should they do so it would be a simple matter to pass it to the first maxillipeds whose distal endites, either by such receipt or by direct removal from the chelipeds, hold material in the mid line. From here it is swept orally by the teaselling lobes of the maxillae (TL), the return of any particles on the backstroke being prevented by the small, but significant, modifications of the tips of some of the spines of the first maxilliped.

Figure 25 shows very clearly how material lying towards the posterior end of the teaselling lobe is guided orally by the proximal fences of the maxillae (F Mx), and figures 77, 25 and 29 show the spinules of the proximal endite of the maxillules (LS Mxllle) – some located dorsally,

FIGURES 18–23. The chelipeds of *Xiphocaris elongata*.

FIGURE 18. Anterior cheliped, inside.

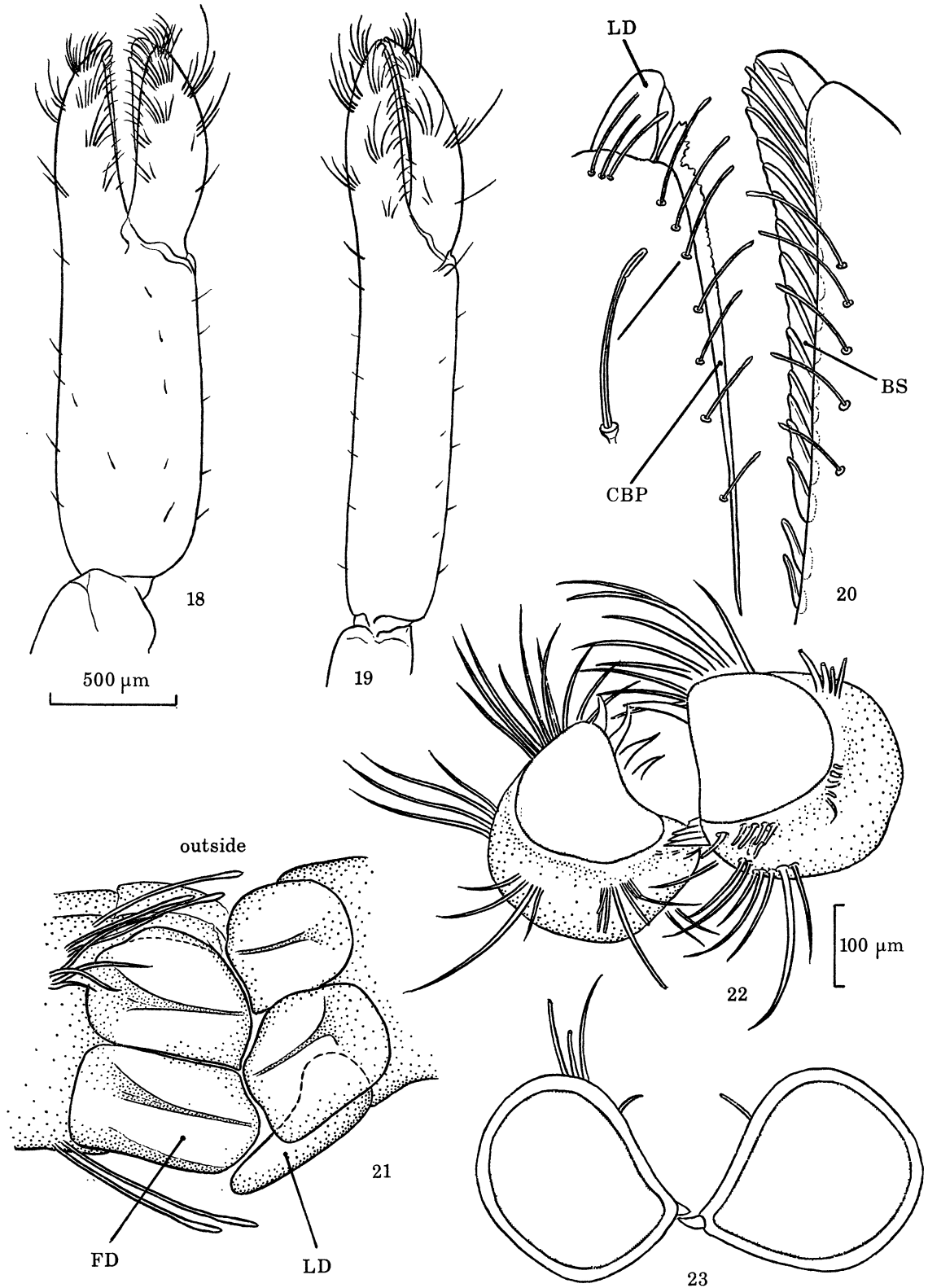
FIGURE 19. Posterior cheliped, inside.

FIGURE 20. Inner face of distal extremity of anterior cheliped showing how the blade of the dactylus is made up of individual blade-like spines. Note also the chitinous blade of the propus. The inset shows one of the fringing sensory setae with a thick-walled stem and a thin-walled distal region.

FIGURE 21. Distal extremity of posterior cheliped seen end on, showing the finger-nail-like distal denticles and lateral tooth. Many setae omitted.

FIGURE 22. Transverse section through distal region of dactylus and propus of posterior cheliped to show the space enclosed when the cheliped closes.

FIGURE 23. The same, more posteriorly.



FIGURES 18-23. For description see opposite.

others in a more ventral longitudinal row – that strip and clean this region and sweep particles on their way. The tips of some of these can be seen in figure 25, and others seen by deeper focusing are shown in the inset. Material is lifted from the teaselling lobes by the overlying distal endites of the maxillules and passed to the incisor processes of the mandibles or, to a lesser extent, pushed within the orbit of the stout spines (SS Mxlle) of the anterior end of the proximal endites of the maxillules and thence to the mandibles.

It is not clear whether particle size influences treatment, but at both its distal and proximal extremities the armature of the ‘masticatory’ part of the maxilla is heavy (figure 77), and in the case of the robust proximal elements, adjoins the most robust elements of the maxillules. Direct pushing by the second maxillipeds or deliberate placement by the chelipeds would

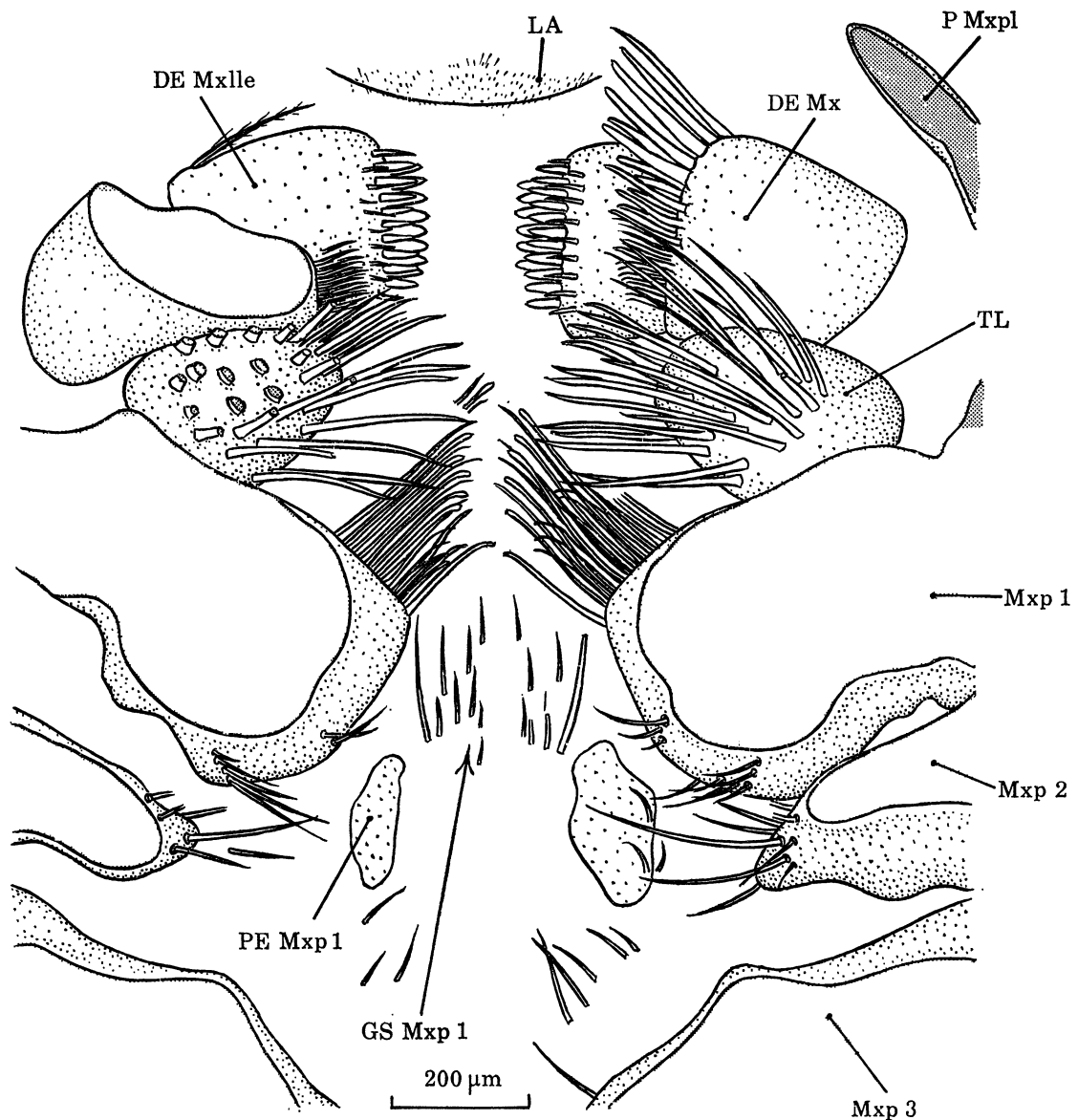


FIGURE 24. *Xiphocaris elongata*. Thick oblique horizontal slice through the mouthparts, viewed ventrally. On the right (left-hand side of animal) the level is as indicated by X-X in figure 77, somewhat deeper-lying region being indicated on the left.

enable coarser elements to be dealt with here and, in the case of the distal armature, passed directly to the mandibles, but there is no evidence that such discrimination occurs.

Food is received from the chelipeds by the distal endites of the mouthparts. Elaborate armature ensures that it is kept there and that little finds its way posteriorly as it moves towards the mandibles. The armature of the proximal endite of the first maxilliped that plays an important part in this is shown in figures 77, 24, 25 and 29, GS Mxp1. The last two of these show very clearly how effective this must be. It is only during the final stages of dorsal transport, involving the

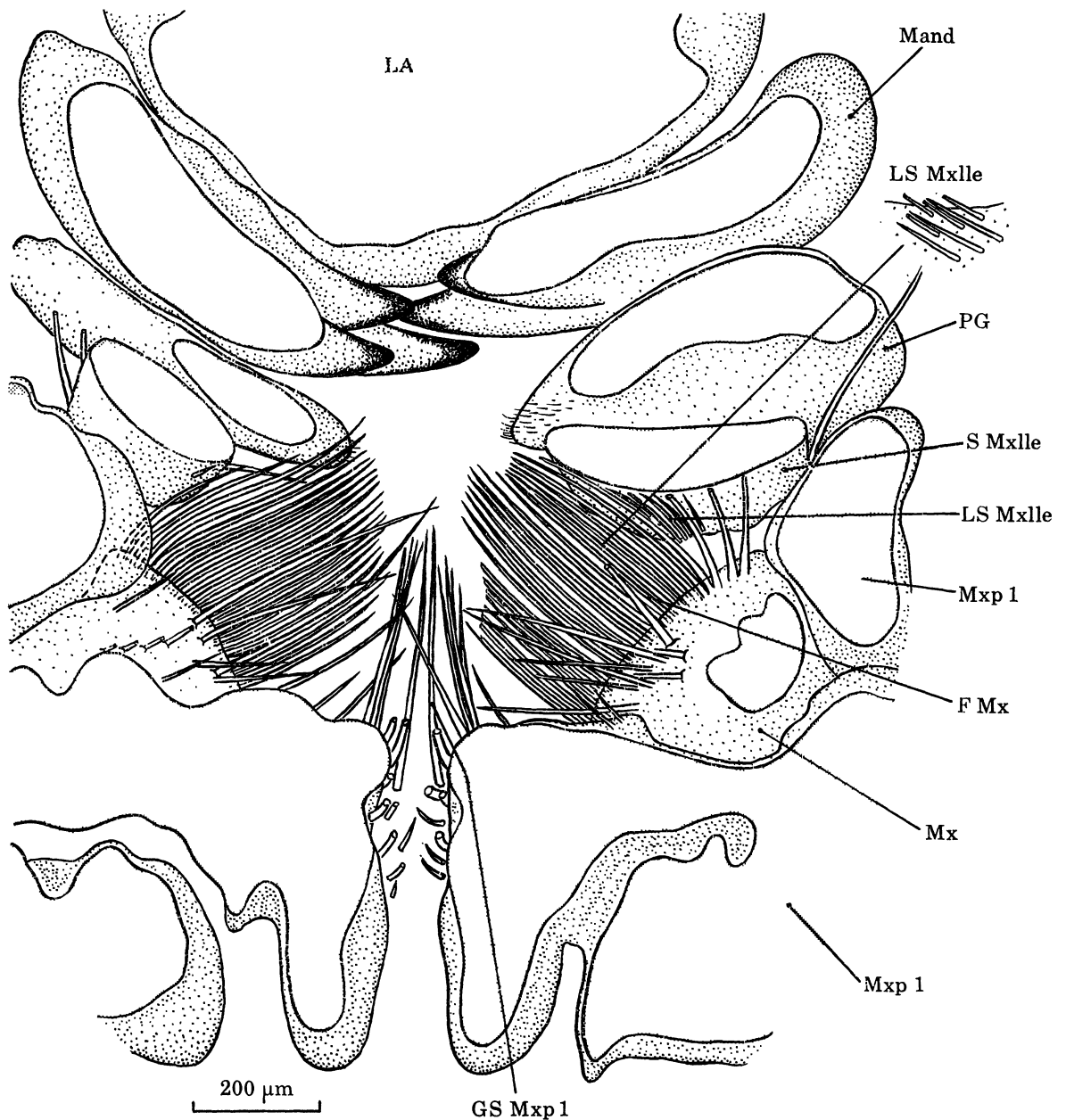
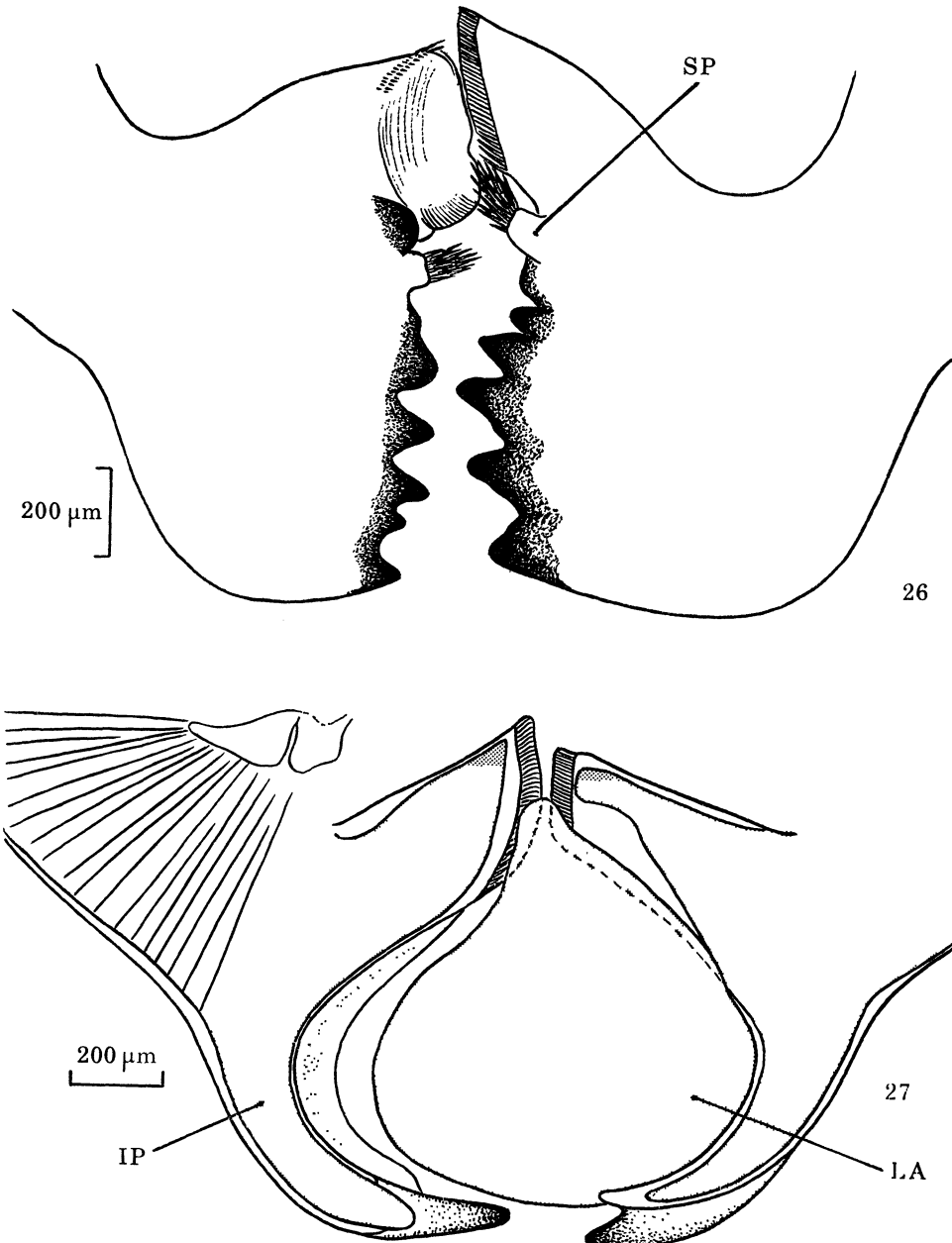


FIGURE 25. *Xiphocaris elongata*. Thick oblique horizontal slice through the mouthparts at the level indicated by Y-Y in figure 77, ventral. The inset shows the spinules of the proximal endite of the maxillule as seen by deeper focusing beneath the fence of setae of the proximal endite of the maxilla. Some of these could be made out at the level of the main figure but are omitted for clarity.

maxillules and maxillae, that the proximal endites are directly involved. Although no direct observations have been made it appears evident that it is the distal parts of these appendages that are the most important.

In skeletal features the mandibles (figures 26 and 27) differ from those of the non-Acantho-phyroid atyids (cf. figures 83, 87 and 88). The armature of the incisor region is relatively more massive, its teeth are not confined to the distal extremity but extend over much of the length of



FIGURES 26 and 27. *Xiphocaris elongata*.

FIGURE 26. The molar and incisor processes of the mandibles *in situ*. Seen from behind.

FIGURE 27. Transverse slice through the mandibles and labrum, viewed from in front, showing how the incisor processes of the former embrace the latter. Most cut surfaces are indicated by stippling but muscles of the right mandible are shown in a simplified manner.



the blade (itself thicker than in other atyids), the molar surfaces are smaller, but nevertheless well developed, and there is no row of lifting spines between the incisor and molar regions. The armature of these regions is almost confluent but there is on each mandible a spinous projection (figure 26, SP), perhaps the homologue of the lifting spines in other atyids. The incisor process is a crushing and biting rather than a sweeping and lifting device. While this condition

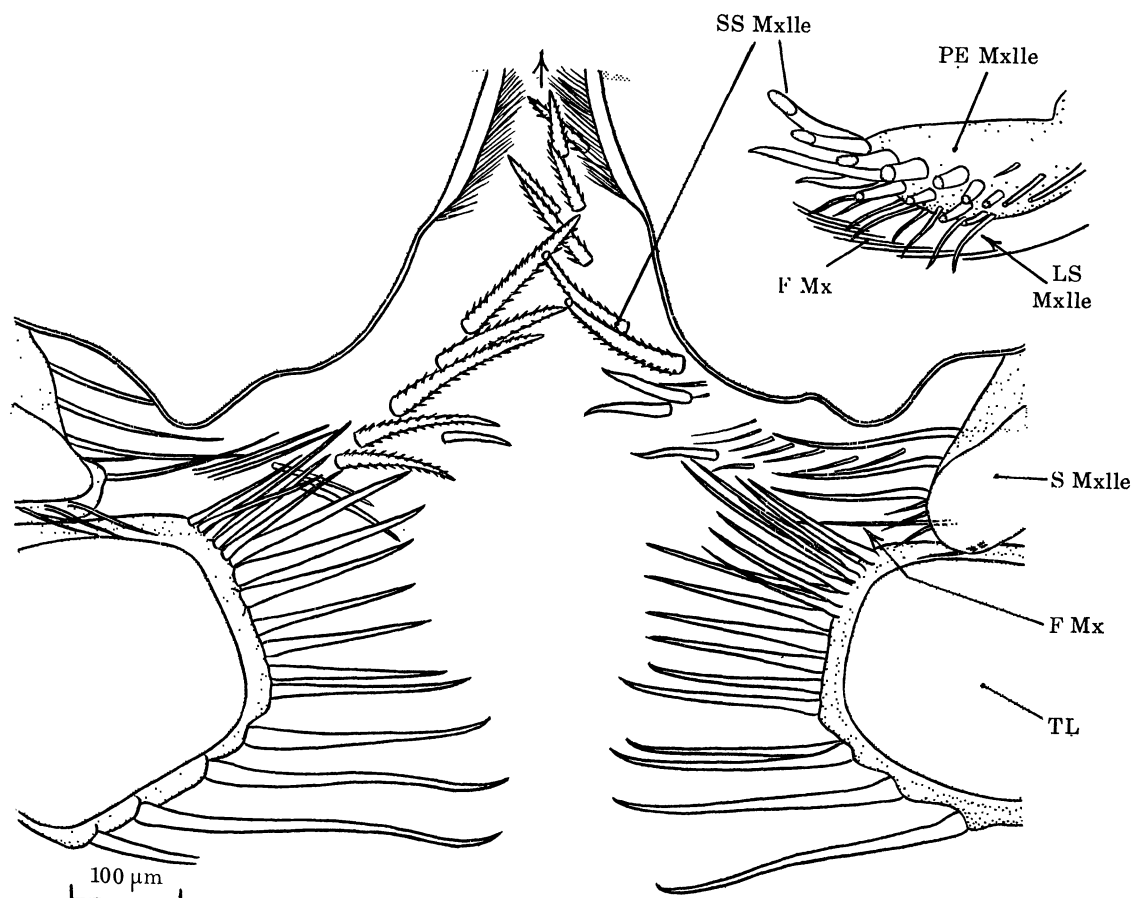


FIGURE 28. *Xiphocaris elongata*. Transverse slice through the more anterior mouthparts cut just anterior to the tip of the proximal endite of the maxillule (cf. figure 77), viewed from in front. The arrow indicates the direction of the oesophagus. On the left-hand side of the figure some spines of the teaselling lobe of maxilla, visible because this is a thick slice, have been omitted for clarity. Because the slice is thick more than one row of teaselling spines can be seen. On the right-hand side the fence of fine setae of the maxilla (F Mx) is just coming into view, one seta being visible. The inset shows a very slightly more posterior slice through the extreme tip of the proximal endite of the maxillule the lifting spines of which can be seen protruding between the setae (F Mx) that make up the fence of the proximal endite of the maxilla.

is probably more primitive than that of *Atya* (§VI(c)) and shows resemblances to that in the euphausiid *Meganyctiphanes*, regarded by Manton (1928) as having a generalized type of mandible, some of the differences reflect differences in food, that of *Xiphocaris* being less finely particulate than that of *Atya*. The shape of the incisor process (IP) and the way in which it embraces the labrum is best appreciated from transverse sections (figure 27). The significance of such association in relation to mandibular movement is discussed with reference to *Atya* in §VI(c).

The cuticle adjacent to the oesophageal entrance and that of the labrum in the same region is much thickened and here are developed many stout spinules directed towards the oesophagus (figure 28). These serve to guide food particles orally. Deformation of the labrum, several of whose basically dorso-ventral muscles insert in the vicinity of the armed area, may even contribute actively to their propulsion.

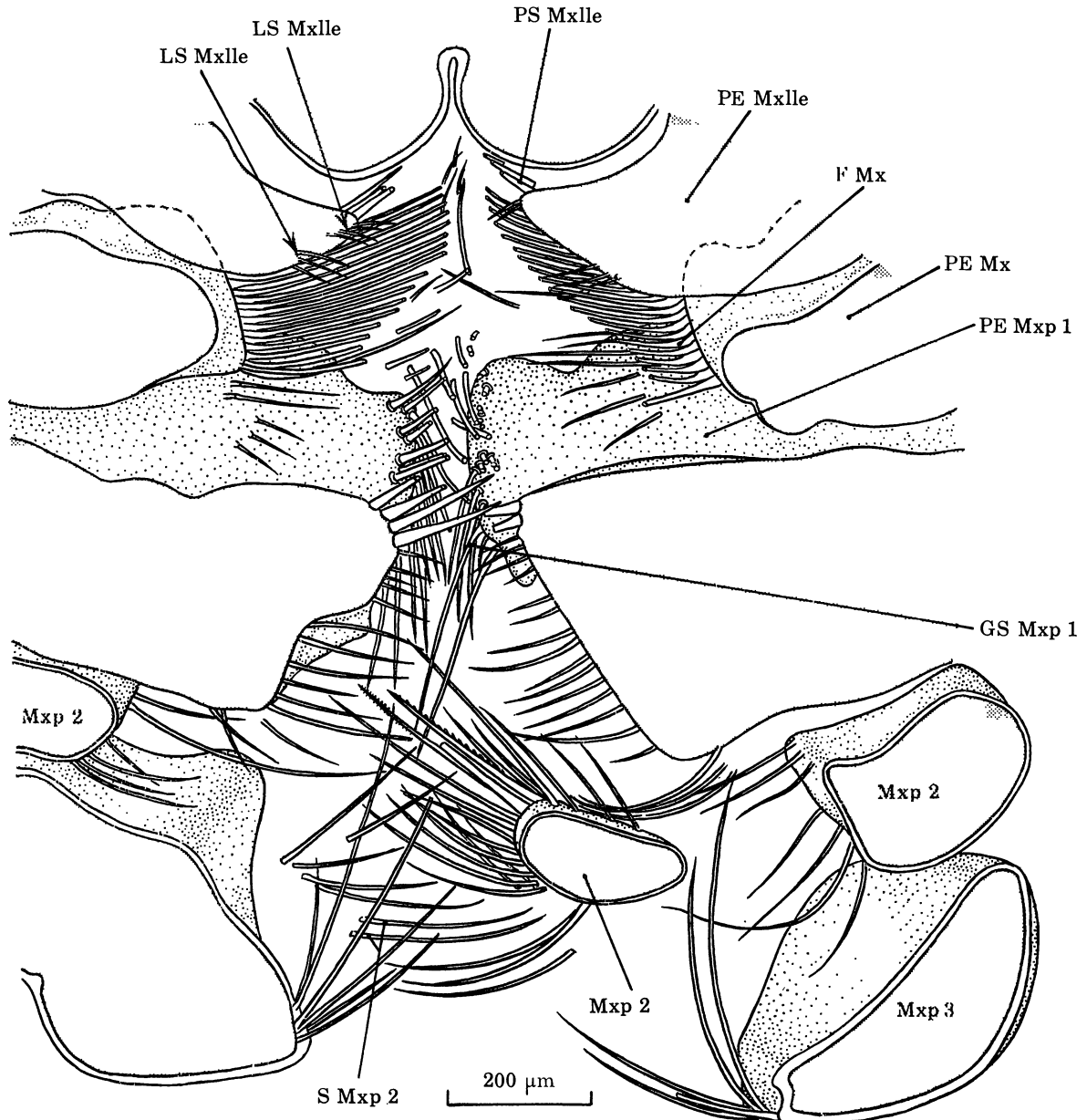


FIGURE 29. *Xiphocaris elongata*. Transverse slice through the mouthparts at the level indicated by A-A in figure 77, viewed from in front. Where the cuticle is thin it is indicated by a single line. Note that the second maxilliped is reflexed and the left appendage is therefore cut twice, the inner section being near its tip. On the other side only some of the setae from near the tip are present. The spines of the proximal endite of the maxillule (PS Mxlle) lie posterior to those stout spines (SS Mxlle) shown in figures 28 and 77, with which they form a continuous row, but are less stout.

VI. THE FEEDING MECHANISMS OF THE NON-ACANTHOPHYROID SPECIES

(a) *The chelipeds and their armature*

All atyids save *Xiphocaris* possess an array of distal spines or setae on the propus and dactylus of the chelipeds that is unique to the family. The spines and setae (described collectively as bristles) are used to collect food. Although it can be inferred from anatomy that adaptive radiation in the employment of this apparatus by the family as a whole is greater than that shown by the Dominican species, the latter nevertheless exhibit some of the most widely divergent and most specialized end points of this radiation.

The possession of distal bristles is undoubtedly a specialization, yet atyids are in many ways primitive decapods. Whatever its evolutionary history the chela of a primitive bristle-armed atyid cheliped may be envisaged as having the properties shown diagrammatically in

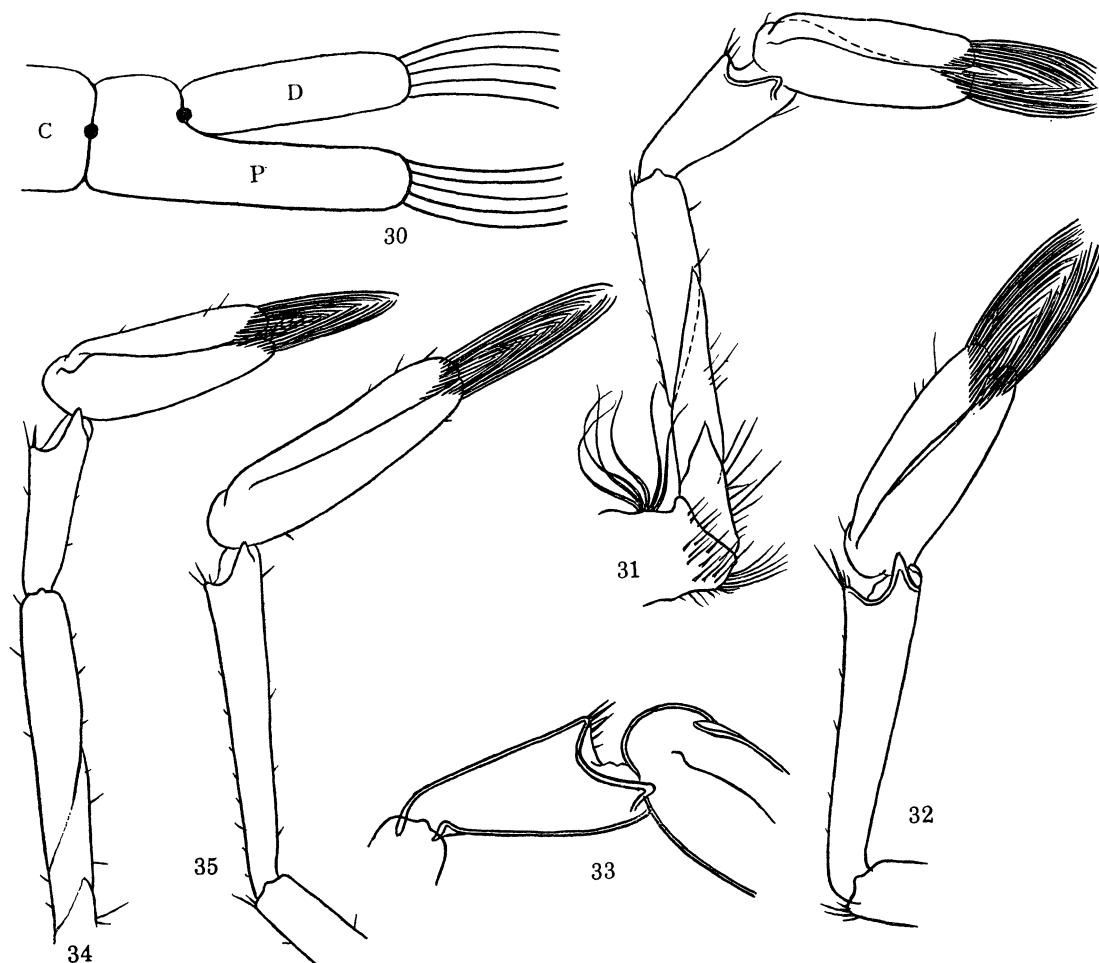


FIGURE 30. Diagrammatic representation of a primitive, bristle-armed atyid cheliped. Joints are indicated by black spots.

FIGURE 31. *Potimirim glabra*. Cheliped 1 from the inside.

FIGURE 32. *P. glabra*. Cheliped 2 from the inside.

FIGURE 33. *P. glabra*. Cheliped 1 from the inside to show the carpus/propus joint.

FIGURE 34. *Jonga serrei*. Cheliped 1 from the inside.

FIGURE 35. *J. serrei*. Cheliped 2 from inside.

figure 30, namely a carpus/propus joint located at the proximal end of the propus, a carpus lacking any conspicuous emargination, a propus/dactylus joint located some distance from the base of the propus, and an array of relatively unspecialized distal bristles. For obvious functional reasons specialization of the bristles has always occurred but chelipeds bearing many resemblances to this primitive type are displayed by the West African *Caridinopsis* (figured by Bouvier 1925).

The chelipeds of the Dominican species are specialized to differing degrees and in strikingly different ways. Those of *Potimirim* (figures 31–33) and *Jonga* (figures 34 and 35) in part retain certain primitive features though in each the carpus/propus joint has shifted some way from the proximal end of the propus, correlated with which the carpus has become somewhat emarginated. Further, the propus/dactylus joint has moved backward towards the base of the propus. The chelipeds of *Jonga* are modified for scraping in a manner closely resembling that employed by the two most closely studied species of *Caridina* (*C. africana* and *C. nilotica*) (Fryer 1960); those of *Potimirim* are referred to later. In complete contrast those of *Atya* and *Micratya* are modified for the collection of food by passive filtration in a manner otherwise unknown among the whole of the Malacostraca, but which does not prohibit their employment as sweepers. These differences are also related to life in different situations.

The chelipeds of *Atya* (figures 36–38) and *Micratya* (figure 39) stand furthest from the ancestral type. The propus has become slewed so that the carpus/propus joint is now located about half-way long the propus; the much shortened carpus is deeply excavated on its anterior (dorsal) face to receive the proximal region of the propus; the propus/dactylus joint has shifted proximally, the dactylus has elongated so that it and the propus are approximately equal in length, and the elongate distal bristles show extreme specialization.

The nature of the chelipeds and the methods of food collection are essentially the same in both Dominican species of *Atya* and in *Micratya* but the cheliped bristles differ slightly in ways that are of considerable ecological importance. The following description applies in essentials to all three species. A cheliped is shown in outline in figure 36. Lateral swinging is effected at the coxa/body joint: elevation and depression at the coxa/basis joint. The basis, ischium and merus are fused to form a single functional unit, the former ischium/merus joint being extremely oblique, presumably for strength, and representing an accentuated version of what is seen in *Caridina* (Fryer 1960). This compound segment is flattened from side to side (figure 36, insets). The Dominican atyids present an evolutionary series in this respect, beginning with *Jonga*, passing through *Potimirim*, and culminating in *Atya* and *Micratya*. The three distal segments are remarkably modified. The carpus, which articulates with the merus by a pivot joint that grants ample flexure, is excavated dorsally into a deep cup (figure 37, CC) and itself rests in a less obvious cup excavated at the distal end of the merus when the limb is extended. In this position the carpus/propus joint 'locks' and has greater strength than at any degree of flexure. The lateral walls of the dorsal carpal cup are of rigid cuticle. Its lining is for the most part thin, mostly blue-staining with Mallory and therefore soft. Only proximally is it thick and sclerotized: distally it is thrown into folds to permit free movement of the propus. As is typical of the Natantia there is only one fixed point in the carpus/propus joint which, while clearly derived from a pivot joint, is now so loosely articulated as to render the pivots more or less obsolete. Of the pivots the outer has virtually disappeared, as in *Caridina* (Fryer 1960): the inner is more reduced than in that genus. Skeletal-wise the propus is united to the carpus only by arthro-dial membrane and, when flexed upon it, is in no way constrained by rigid exoskeleton.

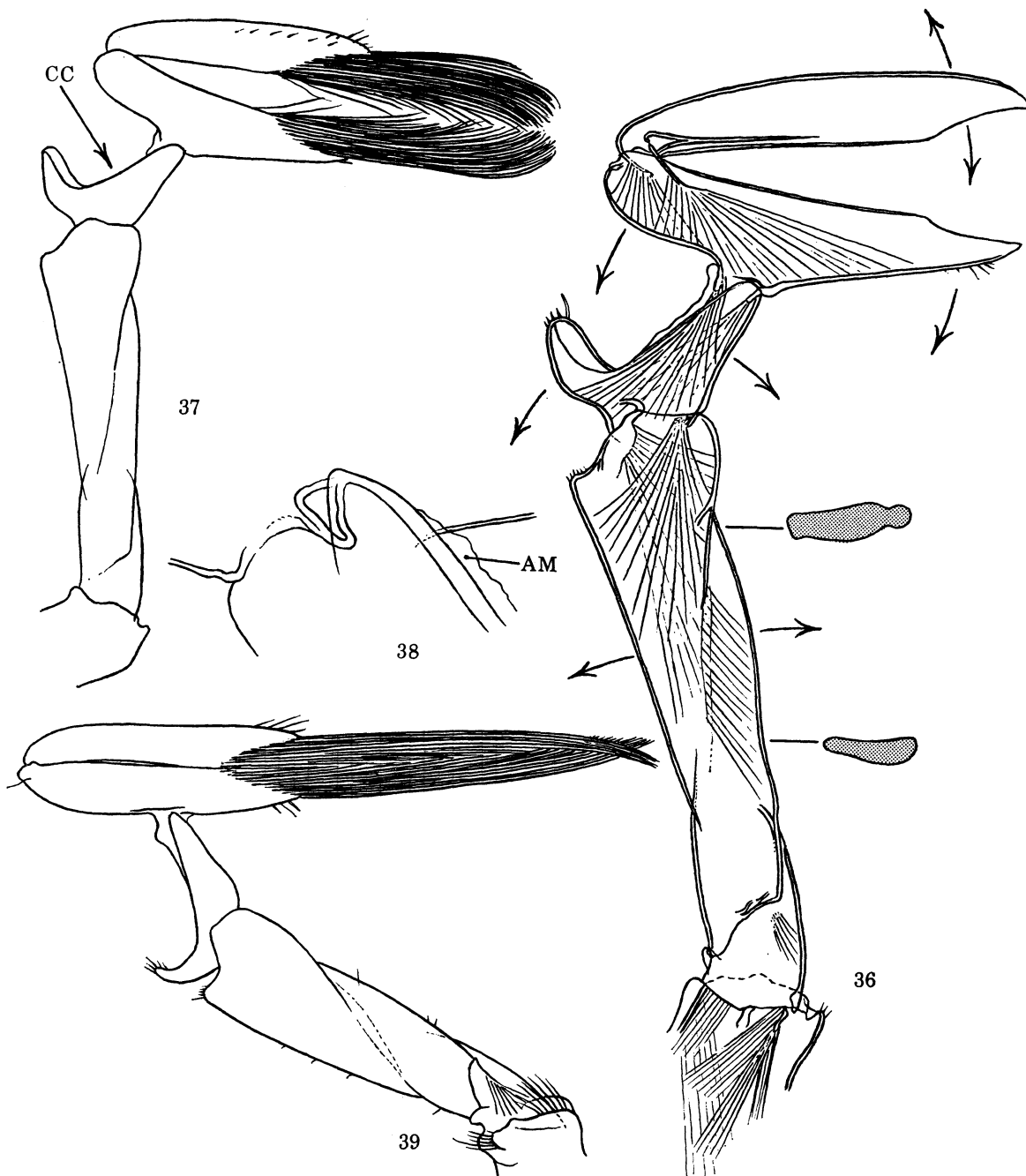


FIGURE 36. *Atya innocous*. Cheliped 1 from the outside to show the musculature. Arrows indicate movements. Distal bristles omitted. In the insets, which show sections at different levels, the inner face is uppermost.

FIGURE 37. *A. innocous*. Cheliped 1 from the inside.

FIGURE 38. *A. innocous*. The carpus/propus pivot from the inside.

FIGURE 39. *Micratya poeyi*. Cheliped 1 from the outside.

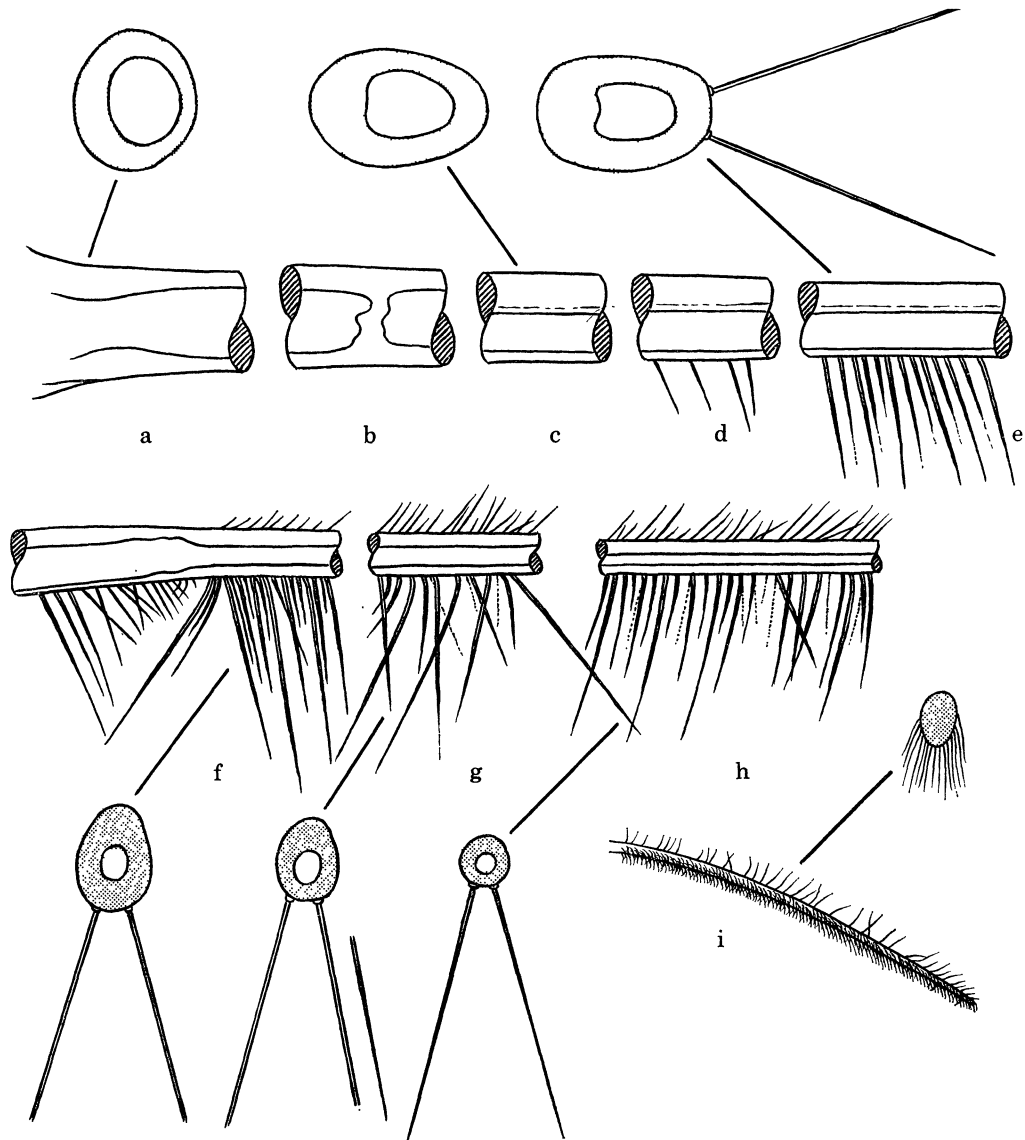


FIGURE 40. *Atya innocous*. A typical cheliped bristle shown at various points along its length and with transverse sections at some of them to show the change in form and armature from base to tip. All portions of the bristle are to the same scale: the transverse sections are to a larger scale, the first and the last differing from the rest which are all to the same scale. The gaps are vastly greater than shown here.

FIGURES 41–48. Cheliped armature.

FIGURE 41. *Atya innocous*. Tip of a bristle provided with scraping denticles from the cheliped of an individual about 7 cm in length. The fine setules, shown only distally, continue proximally.

FIGURE 42. *A. innocous*. An example of a double row of teeth on a scraper. The row of teeth to the right lies beneath the shaft but for clarity the proximal three are shown as if the shaft was transparent.

FIGURE 43. *A. innocous*. The tip of a bristle that serves as a brush seta in face view.

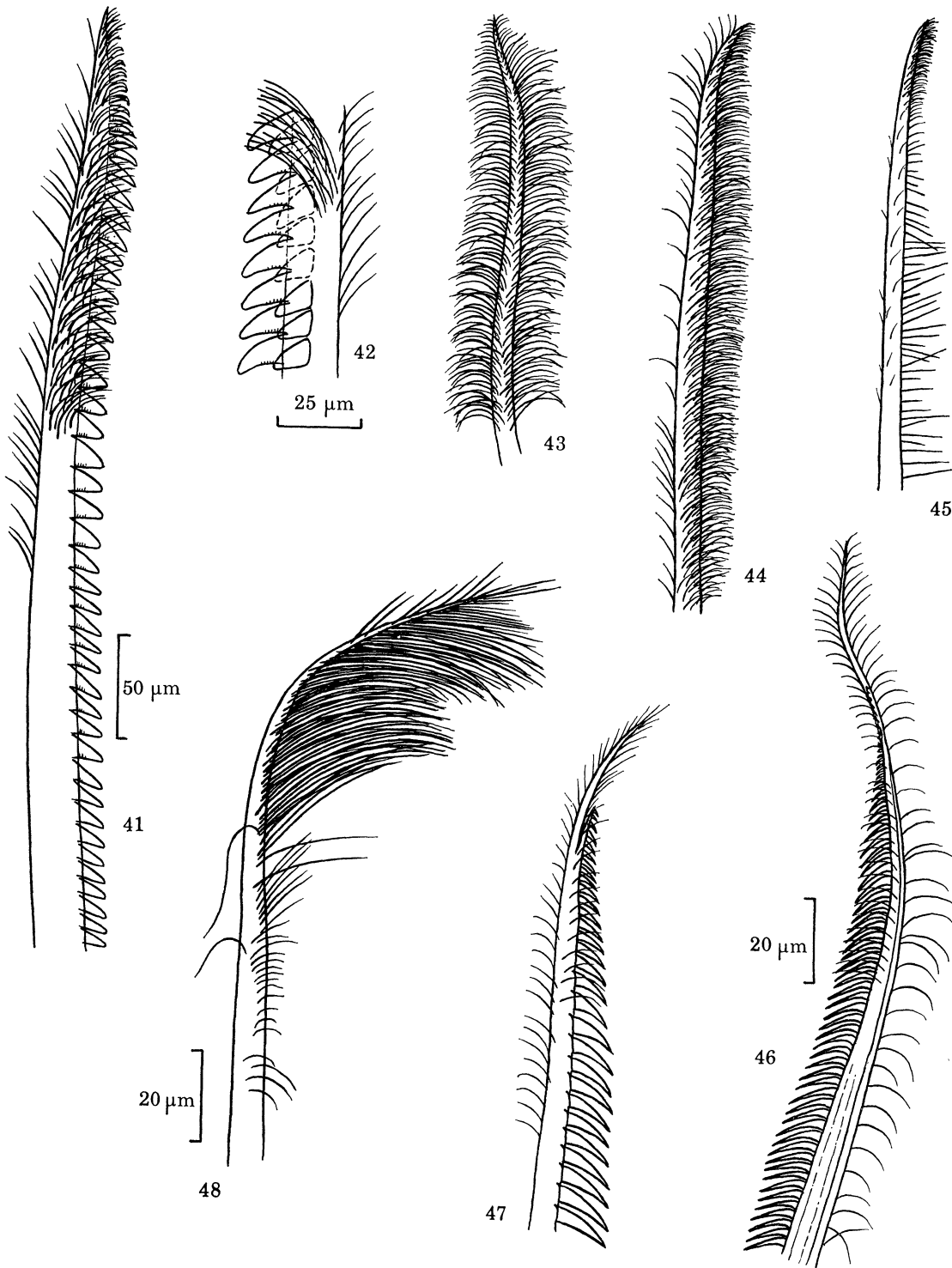
FIGURE 44. *A. innocous*. The same from the side. Others are less setose than this and somewhat stiffer distally.

FIGURE 45. *A. scabra*. The tip of a typical bristle (a brush seta) from the side (cf. figure 44).

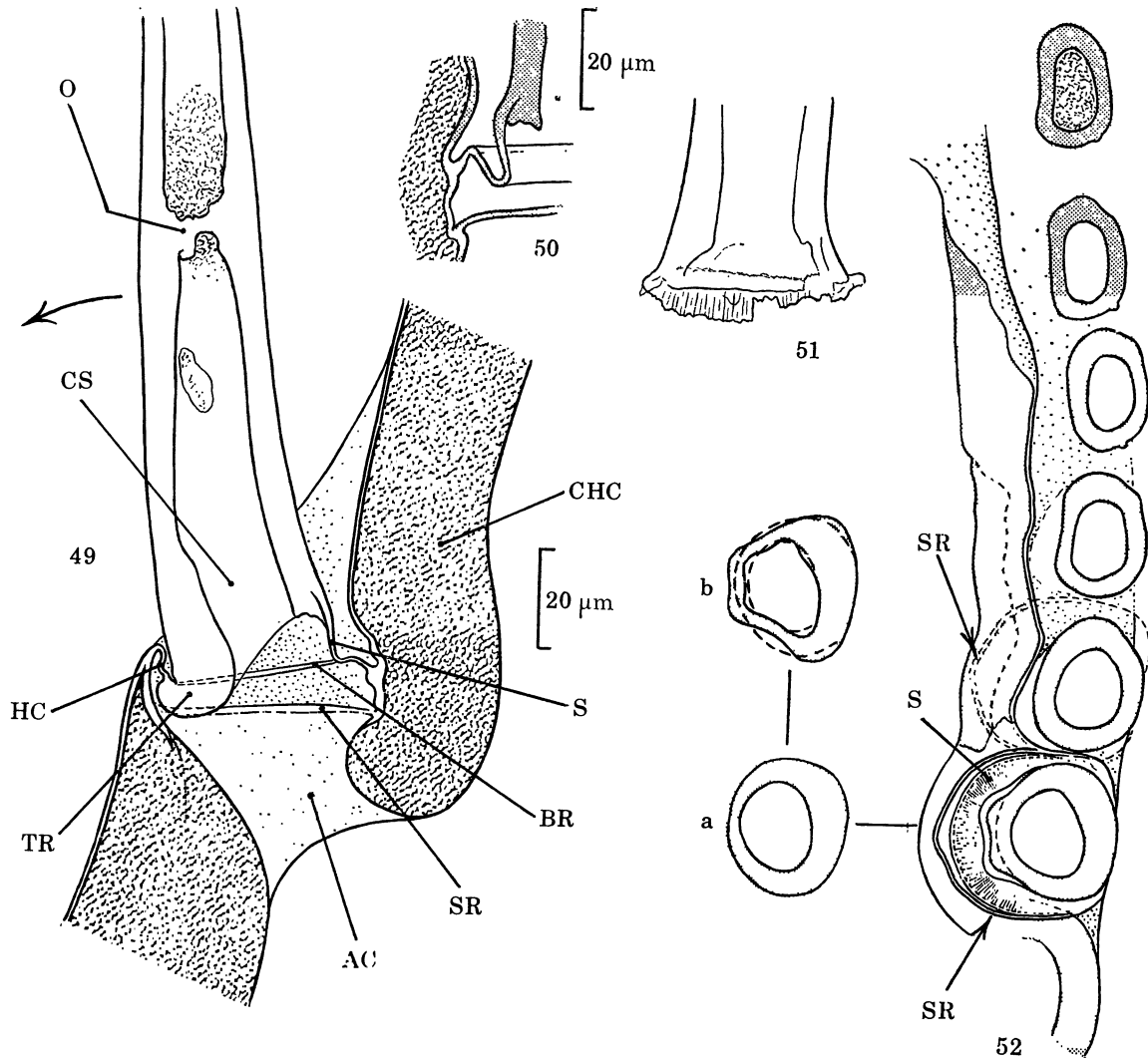
FIGURE 46. *Micratya poeyi*. A brush seta. The armature here approaches that of a very fine comb. Other setae have much finer denticles than those shown here and these extend to the tip of the seta.

FIGURE 47. *M. poeyi*. A comb bristle.

FIGURE 48. *Potimirim glabra*. A brush seta.



FIGURES 41-48. For description see opposite.



FIGURES 49-52. The structure of the cheliped bristles of *Atya*.

FIGURE 49. Longitudinal section, cut along the plane of bilateral symmetry, through the base of a cheliped bristle *in situ*. (*A. scabra*).

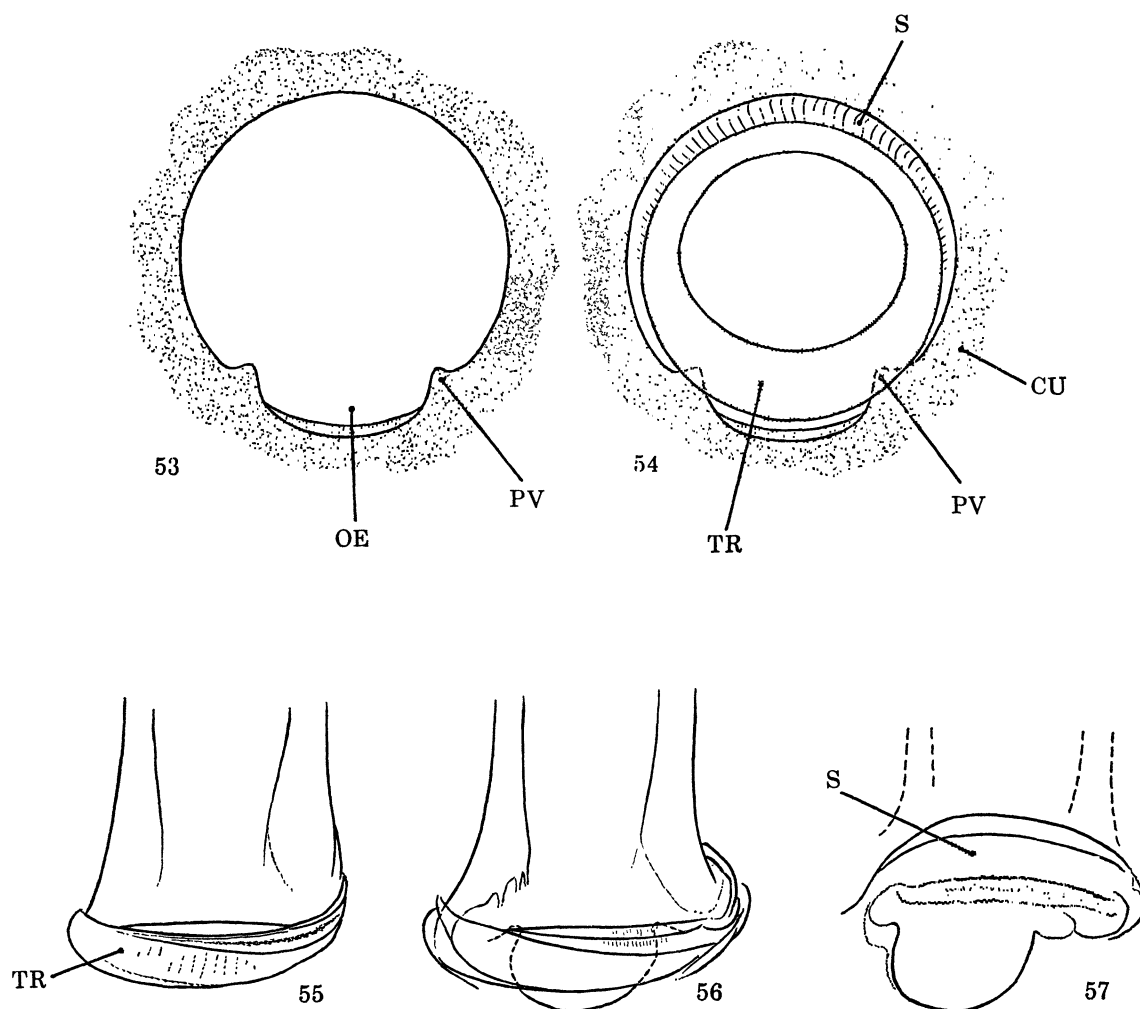
FIGURE 50. Longitudinal section through the spring of another seta on the opposite side of the cheliped (and therefore extending in the opposite direction to the seta shown in figure 49).

FIGURE 51. Base of a seta torn from its cheliped and viewed from the spring side. (*A. innocous*.)

FIGURE 52. Transverse section through a row of cheliped bristles near their bases. Because these are arranged in oblique rows (figure 64, plate 2) each is cut at a slightly different level from its nearest neighbours, the region covered here extending from the base of the bristle (lower end of figure) to the occluded region. When the surface of this thick slice is in exact focus the contour of the bristle at the lower end of the row is as shown in inset *a*. In the spring region this level is indicated by a dashed line in the main figure and the spring itself (S) is shown as seen by slight focusing down. The position of the supporting ring (SR) of the adjacent bristle, as seen by focusing down yet further, is shown by dashed lines. The supporting ring of the nearest bristle actually lies below the cut cuticle which is here not shown in the interest of clarity. The 'overlap' of adjacent supporting rings is permitted by the staggering of the insertion of each seta relative to its neighbours in the row (figure 65, plate 2). Note that the apparent 'hole' seen near the second and third bristles in the series is not the excavation for the thickened rim but represents the out-of-focus spring region. The 'ridging' of the spring is over-emphasised for clarity. Inset *a* shows a transverse section of the nearest bristle as seen at the level of focus of the main figure. Inset *b* shows the same at a deeper level of focus showing how the shape changes markedly over a very short distance in this region. (*A. scabra*.)



This is not the case when the limb is extended. Its proximal end then dips into the cup of the carpus (see arrow in figure 36) into which it fits snugly and receives support. Equally remarkable is the proximal shift of the articulation between propus and dactylus which is such that the propus/dactylus joint actually lies proximal to that of the carpus/propus, and is located at the proximal extremity of the propus, which is itself free of the carpus. A propus/dactylus pivot



FIGURES 53-57. The pivoting region of the cheliped bristles of *Atya*.

FIGURES 53 and 54. Diagrammatic representation of the relation of the base of a cheliped bristle to the supporting cuticle. Figure 53 shows the hole in the cuticle and figure 54 shows a transverse section of the bristle *in situ* above this hole. This seta would swing towards the observer during extension.

FIGURES 55-57. Base of a bristle *in situ* on the cheliped, looking at the thickened part of the rim (figure 55) and then at successively deeper levels so that in figure 57 the inner face of the spring is seen (*A. innocous*).

joint enables the chela, whose arms are of equal length, to be opened widely – to more than 100°. The shift of the propus/dactylus joint is easy to appreciate by a consideration of a series of atyids of which, in this respect, *Caridina* is the most primitive and has chelipeds whose propus and dactylus have relations to each other similar to those of many decapods. Stages intermediate between *Caridina* and *Atya* are shown by *Jonga* (figures 34 and 35) and *Potimirim* (figures 31 and 32).

Cheliped musculature is shown in figure 36 which also indicates the direction of movement of the various segments. Antagonistic muscles and pivot joints are responsible for movements of the carpus, propus and dactylus. As in other decapods the basis/ischium and ischium/merus joints are (or were) dorso-ventral hinge (not pivot) joints, which have flexor, but no extensor, muscles. Manipulation suggests that slight movement – employing resilin for extension? – is possible at the ischium/merus joint but the muscles here may serve as much for bracing the compound leg ‘segment’ as for causing movement.

Distally both propus and dactylus are fringed by numerous extremely long bristles whose arrangement is shown in figure 37 and figures 64 and 65, plate 2. When the cheliped is at rest these are bunched together in a manner recalling the bristles of an artist’s paint-brush (figure 63, plate 2). When the cheliped is extended they are spread in a remarkable manner of great functional significance, alternate spreading and closing being directly concerned with the collection of food. For convenience the bristles of *A. innocous* are described first, though the principles involved, and in some cases anatomical details, are the same in all cases (so much so that some of the illustrations used in the functional account are of *A. scabra*). Attributes of individual species are mentioned later.

While superficially simple each bristle is a complex structure which articulates proximally with the segment from which it arises by means of an elaborate joint. Each is basically a tube of sclerotized cuticle (non-staining with Mallory over most of its length) whose shape in cross-section differs from one region to another (figure 40). There is also diversity among the bristles (see below) and diversity of armature from species to species (figures 41–48) but generalization is possible. The central duct is occluded for a short distance not far from its base (figures 40*b* and 49, O) – a matter of great functional significance. The basal articulation allows each bristle to swing through a wide angle, not far short of a right angle in some cases, but only in one plane. This is here called extension. The plane of extension differs from bristle to bristle so that when the entire assemblage is extended the bristles spread out to form a fan-like, semi-circular array on both propus and dactylus (figures 58–61, plate 1). The two semi-circles together make up a basket-like arrangement best appreciated by reference to figures 68 and 69, plate 3.

The joint (figures 49 and 52, lower end, and figure 65, plate 2) can best be visualized by considering the base of the seta to consist of a more or less circular rim which sits above a basically circular hole in the thick cheliped cuticle, pivoting being accomplished by means of a device akin to the gimbals of a ship’s compass. At each side of the hole and directed into it arises a pivot (figures 53 and 54, PV) supported by a local thickening of the cuticle. These pivots are not located diametrically opposite each other but somewhat towards what for convenience of description can be called the outer face of the bristle. That part of the bristle that lies between the pivots, and is therefore somewhat less than a semi-circle, is thickened (figures 49, 54 and 55, TR) and is attached to the supporting cuticle by a hinge (figure 49, HC) of thinner, flexible but tough cuticle that permits movement. When the bristle is extended the thickened rim dips down into the hole whose edge here is somewhat excavated. That part of the rim that lies internal to the pivots is bound to the cheliped cuticle over much of its circumference by a band of tough cuticle, here termed the spring (figures 49, 52, 54 and 57, S). When the bristle is at rest this band is thrown into a fold in a manner best appreciated from sections (figures 49 and 50): when the bristle is extended the band of cuticle straightens out and, as its behaviour shows, is then under tension. Between the spring and the thickened rim, the bristle is united to the cheliped cuticle by a continuous sheet of thin cuticle that fulfils the same functions as an

arthrodial membrane at a limb or body joint. This is tough, flexible and non-ductile. Strength is given to the joint by a sclerotized supporting ring (SR) seen bisected in figure 49 and, by focusing down, almost in its entirety in figure 52. What appears to be a toughened basal ring (BR) can sometimes be made out in the folds of the spring. The supporting ring is fixed: the basal ring moves with the bristle.

As shown in figure 64, plate 2, the cheliped bristles are inserted in rows around the distal extremities of the propus and dactylus. This enables bristles of one row to lie between those of adjacent rows when the chela is opened so that, although some of the soft tips of some bristles may curve over their neighbours, the result of full extension is an essentially uniseriate fan of bristles (figures 58–61, plate 1; figures 66–69, plate 3).

There are no muscles attached to any of the bristles; indeed the cavity of the dactylus is devoid of muscles, those responsible for the opening and closing of the chela being housed entirely within the propus (figure 36). Extension of the bristles is therefore not the result of direct muscular action. Equally it is not a passive response to water currents – an apparently feasible means of extending the fans in flowing water – for extension can be accomplished in still water and is under the precise control of the animal. Extension is clearly caused by an increase in blood pressure as is the momentary opening of the movable hooks of the labium of nymphal dragonflies (Amans 1881), the extension of the cirri of pedunculate barnacles (Cannon 1947) and the legs of spiders and many myriapods. In spiders, according to Ellis (1944), Parry (1957) and Parry & Brown (1959, 1959*a*), extension may be due entirely to such pressure, and certainly is when the fourth legs are extended in unison during the jump of jumping spiders, while Manton (1958*a*), who agrees that this is so when the limb tip is off the ground, argues for assistance by the indirect action of depressor muscles during the propulsive stroke in a walking animal, as she believes to be the case also in myriapods (Manton 1958). Whichever system operates, spiders were shown by Parry & Brown to be capable of producing surprisingly high transient pressures – as much as 8 times the pressure maintained at rest, which was itself deemed adequate to extend an unloaded leg. Production of adequate pressures by arthropods thus appears to present few problems.

Although the precise origin of this increased pressure in *Atya* has not been located it is obviously localized within the cheliped and is not a mere generalized increase like that involved in the hydraulic mechanism of spiders' legs (Parry & Brown 1959). Increased pressure overcomes the resilience of the spring and extends the bristle. All the bristles of a given cheliped extend simultaneously and at the same rate, as is inevitable with such a mechanism, but each cheliped can operate independently. Full extension is maintained for as long as pressure is sustained. As soon as pressure is released the spring of each bristle, under tension during extension, returns the bristle to its resting position. Each cheliped has ample blood-filled haemocoelic spaces whose volume need change but little to cause extension of the bristles. Extension of the bristles is invariably associated with extension of the cheliped (see, for example, figures 58–60, plate 1) and is not practised when the cheliped is at rest. An observation made on *Micratya poeyi* in Dominica before the mechanism was appreciated showed that nipping of the ischium/merus region stimulated a cheliped to open and its bristles to be extended.

Extension of the bristles has a parallel in the erection of the leg spines of spiders mentioned in passing with reference to pressure exerted on a drowned, and therefore turgid, mygalomorph by Ellis (1944) and observed to take place immediately prior to a jump in salticids by Parry & Brown (1959*a*). In spiders spine erection seems to be an inevitable consequence of an increase

in pressure in the limbs concerned and is of no known functional significance. Neither the details of erection nor the nature of the articulation of the spines were investigated by these authors. In *Atya*, that region of the base of the bristle that bends is composed of non-staining refractile cuticle continuous with the refractile outer layer of the cheliped cuticle. From her extensive studies on myriapods Manton (1958) concluded that this is the most elastic and least ductile cuticular state. These properties are those demanded of cuticle located here. The spring appears to be of essentially similar composition though traces of pale blue are sometimes detectable in Mallory-stained sections. This bespeaks of flexibility, but the amount of blue-staining, when detectable, is small and observations are difficult to make on this thin region. The thick, supporting cheliped cuticle of the pivoting region (figure 49, CHC) is very different, being made up largely of blue- and red-staining layers.

In *Atya innocous* each bristle is of great length and differs in its nature from base to tip, and from bristle to bristle. The extreme base is approximately circular in section (figures 40*a*, 52*a*, *b*). Very near the base, however, most bristles become oval in section (figures 40*b*, *c*, 52) and are very clearly so in the region where, not far from the base, the lumen is completely occluded by a plug of chitin (figures 40*b*, 49, 52). Complete occlusion is invariable. Always towards the distal side of the plug (O) and sometimes, but not always, to the proximal side, there is what gives the impression of an accumulation of only partially consolidated chitinous debris (figure 49). When such is present to its proximal side the amount is generally small. Transverse sections confirm that this is an accumulation of material bound together in an amorphous mass and not merely an optical effect of roughened walls of the lumen in this region.

The constant presence of the occluded region bespeaks its importance. As the bristles are sealed structures there appear to be no theoretical reasons why an increase in pressure should not extend them even if no such plug was present. The plug, however, ensures that no leakage of haemocoelic fluid occurs should a bristle be broken distally. Although the material collected indicates that such breakage is a rare event – and *Atya* takes great care of its cheliped bristles when these are not in use (figure 63, plate 2) – it is inevitable at times. It is doubtful whether any significant increase in strength or rigidity is conferred by the plug. In his excellent account of the setae of the crayfish *Austropotamobius pallipes* (Lereboullet) Thomas (1970) describes a variety of what he calls septate setae with a similar septum or plug, but much nearer the base. However, he says this is always perforated. Nevertheless some of his figures suggest a complete plug and in some crayfish setae that I have examined I have been unable to detect any aperture. The setae concerned are not extensible in the manner of the atyid bristles and the septum here clearly has a different function.

Beyond the plug is a long, very straight, hollow region, more or less oval in section, whose outer wall is much thicker than the inner (figure 40*b–e*). Initially this straight region is unarmed, but a short way along its length setules arise on its inner side (figure 40*d*). Proximally these are sparse and short; more distally they are more numerous, much longer, and regularly arranged in two rows which are directed obliquely inwards (figure 40*e–h*) so that when the entire fan is spread the gaps between adjacent bristles are spanned by a meshwork of setules. This fan therefore forms a more efficient network in a filtering animal (see below) than is apparent to the naked eye.

The straight region terminates at a pseudo-joint of which figure 40(*f*) shows a typical example. Up to and including this region all the bristles are basically similar but differ in length and in the details of their armature. More distally there is considerable individual variation

such as is not apparent on casual examination but which is of great functional significance. Just as was described in detail for *Caridina* (Fryer 1960) the bristles are arranged in a series that shows a gradual transition in form from the innermost to the outermost rows. As in *Caridina*, the innermost terminate in scrapers, the outermost in brushes. In *A. innocous*, however, the scrapers, while formidably armed on a micro scale, are much less robust in relation to the size of the animal than in *Caridina* – or some of their Dominican relatives. They are made up of long rows of small teeth (figure 41) – less than 20  $\mu\text{m}$  in length in a 7 cm individual – on the inner face of the bristle, double on some bristles (figure 42). Only the distal part of a row is shown in figure 41. These, while able to scrape (§VI (b)), are less specialized for this than the short rigid scrapers of *Caridina* (Fryer 1960) and of some of the Dominican species described here. In all there are about 28 scrapers in each fan in *A. innocous*.

Beyond the pseudo-joint the setae tend to curve towards their partners on the opposite half of the cheliped, this being especially so at the tips of some of the outer, brush-bearing types. Many of these are straight for a considerable distance beyond the pseudo-joint and their armature continues the filtering network of the more proximal regions almost to their tips. Here the nature of their armature changes and they are provided, in some cases profusely, with setules which arise not only on the inner face, as do the filtering setules, but also laterally. On some bristles, particularly those located laterally, these are short; on others, particularly those located medially (most distally) they are longer and curved. All are directed inwards to form a brush (figures 40*i*, 43, 44). Beginning at the pseudo-joint additional setules are also present towards the outside of the bristle (figures 40*f-i*). These extend to the tip. The pseudo-joint marks the boundary between a rigid proximal and a more flexible distal portion of the bristle. Here the properties of the cuticle change, for though the entire bristle is made up of refractile chitin a difference is apparent optically when the bristles are viewed *en masse*, the distal portions having a brownish, the proximal a golden, tinge. This can be seen in figure 63, plate 2, where the chelipeds are at rest. Likewise the extreme distal brush-bearing portion stains faintly pink with Mallory and when setae are mounted in polyvinyl lactophenol containing cotton blue the distal portion rapidly stains an intense blue while the proximal portion stains only slowly and much more faintly. Approximately 280 such bristles in each fan are present in *A. innocous* so that when it is spread the gaps between adjacent bristles are small (figures 68 and 69, plate 3) and these in turn are spanned by the long filtering setules.

On casual inspection the bristles of *A. scabra* appear identical to those of *A. innocous*, but differ in certain important respects. There are no comb-bearing scrapers. Further, the sweeping bristles – some 280–290 in number – never have such a conspicuous terminal brush as those of *A. innocous*, that shown in figure 45 being typical (cf. figure 44). These differences are directly related to feeding habits, and perhaps also to the relative abundance of the two species in Dominica. As bristles differ among themselves in both species it is scarcely possible to compare the arrangement of the filtering setules, which are essentially similar in both. However, because the distal brushes are much shorter in *A. scabra* than in *A. innocous* the filtering regions somewhat more closely approach the tips of the bristles.

*Micratya poeyi* one of whose chelipeds is shown in figure 39, employs the same means of food collection as *Atya* (§VI (b)). Its bristles are constructed on the same principles but differ in detail. Not more than 120 are present in each fan, of which about 36 are combs. The combs are similar to those of *A. innocous* but individual denticles are relatively longer and more slender and are set more obliquely on the bristle (figures 46, 47). As *Micratya* is smaller than *A. innocous*,

however, the denticles are smaller than those of any but very small *A. innocous*. The comb bristles terminate in a short brush (figure 47). The long, brush-like setae differ among themselves. Those that arise laterally have tips that resemble those of *A. innocous* but are somewhat less setose: those that arise medially, while functionally brushes, are structurally more akin to extremely fine combs (figure 46). A strict quantitative comparison of the filtering setules is not possible, but those of *Micratya* are certainly fewer and more widely spaced than in either species of *Atya*.

The chelipeds of *Potimirim glabra* (figures 31–33) display an array of some 150 bristles akin to those of *Caridina* (Fryer 1960) with an inner arc of some two dozen coarse scrapers, a more distal arc of finer scrapers, arcs of bristles combining the attributes of scrapers and brushes and, most distally, an array of brushes. These latter are particularly well developed (figure 48) more so than in *A. innocous* (or *Caridina*). A striking difference between *Potimirim* and all species of *Atya* and *Micratya* is the absence of filtering setules from the long sweeping bristles. Only a few scattered setules are present.

*Jonga serrei* has more slender chelipeds than *Potimirim* (cf. figures 34 and 35 with 31 and 32), the propus and dactylus being also much narrower. Each is fringed by only about 70 bristles the arrangement and form of which is remarkably similar to those of *Caridina*, for which detailed illustrations are available (Fryer 1960; figures 26 and 28). There are no filtering setules but scattered setules are present as in *Potimirim*.

#### (b) Food collection

*Atya innocous*, *A. scabra* and *Micratya poeyi* can collect food both by scraping/sweeping and by a method of passive filtration unknown in the Malacostraca outside the Atyidae, but the relative importance of these methods differs from species to species. For convenience food collection by *A. innocous*, the best studied species, is described first.

Sweeping by *A. innocous* is similar in principle to that employed by habitual scraping/sweeping atyids such as *Caridina* and *Jonga* and is best appreciated by reference to figures 58–61, plate 1, figure 62, plate 2, and figures 66 and 67, plate 3. Animals sweep either while stationary or, more usually, moving forward. An individual simultaneously advancing and collecting food is shown in figures 58–60, plate 1. The white material is the proprietary food 'Bemax', particles

### DESCRIPTION OF PLATE 1

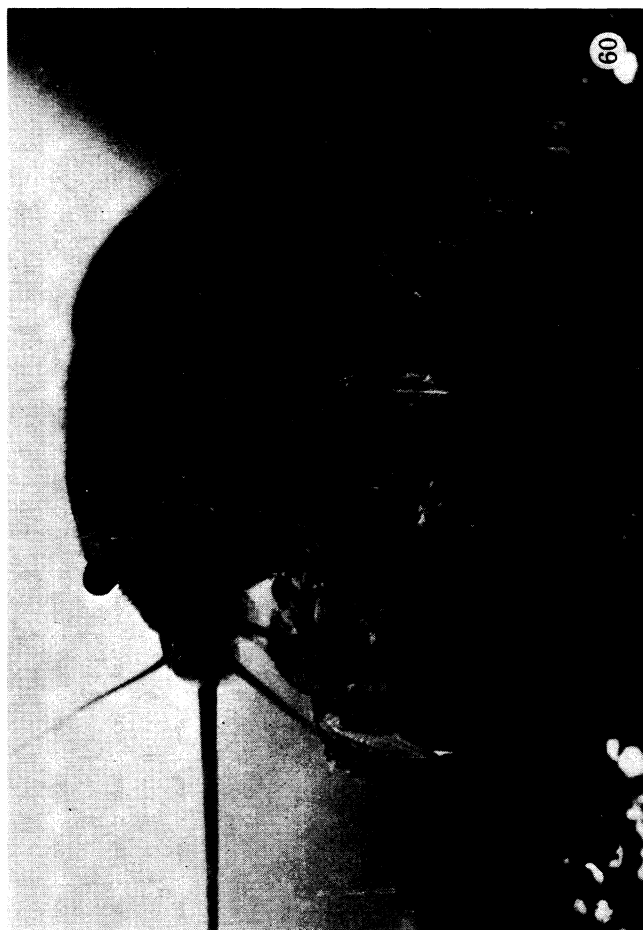
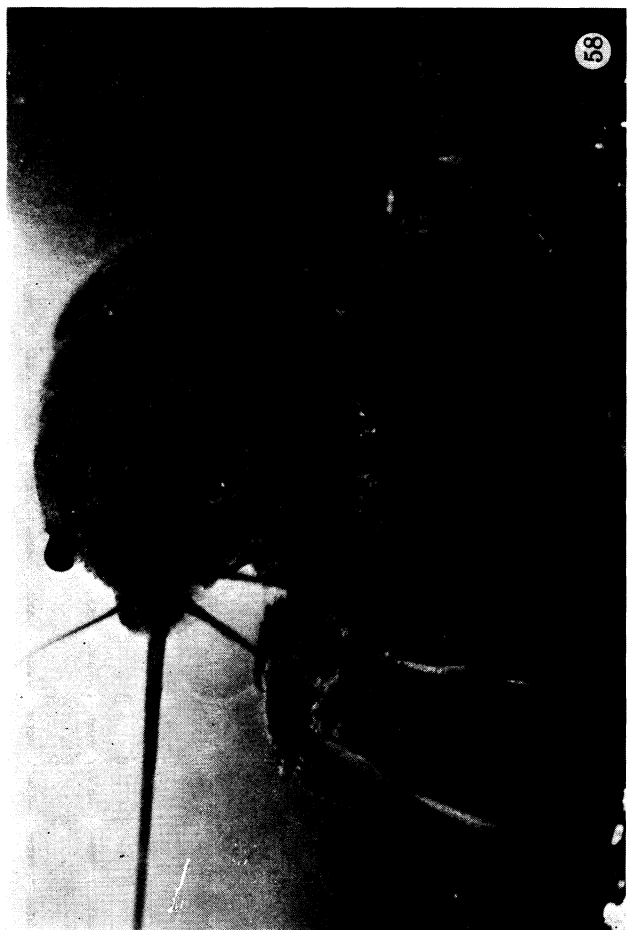
FIGURES 58–61. Figures 58–60 comprise a sequence.

FIGURE 58. *Atya innocous* advancing over a stone, scraping material from it as it does so. The white material is 'Bemax' that has been scattered as food. Three chelipeds are spread, the right anterior showing clearly how the bristles are bent and scrape with considerable force as the cheliped is closed. The left posterior cheliped has swung under its anterior companion and is passing food to the mouthparts.

FIGURE 59. The left anterior leg has been swung forward – note how its claw is employed – as scraping continues. Here the left anterior cheliped is conveying food to the mouth, its flexibility being clearly revealed, and the other three are in various stages of the sweeping process.

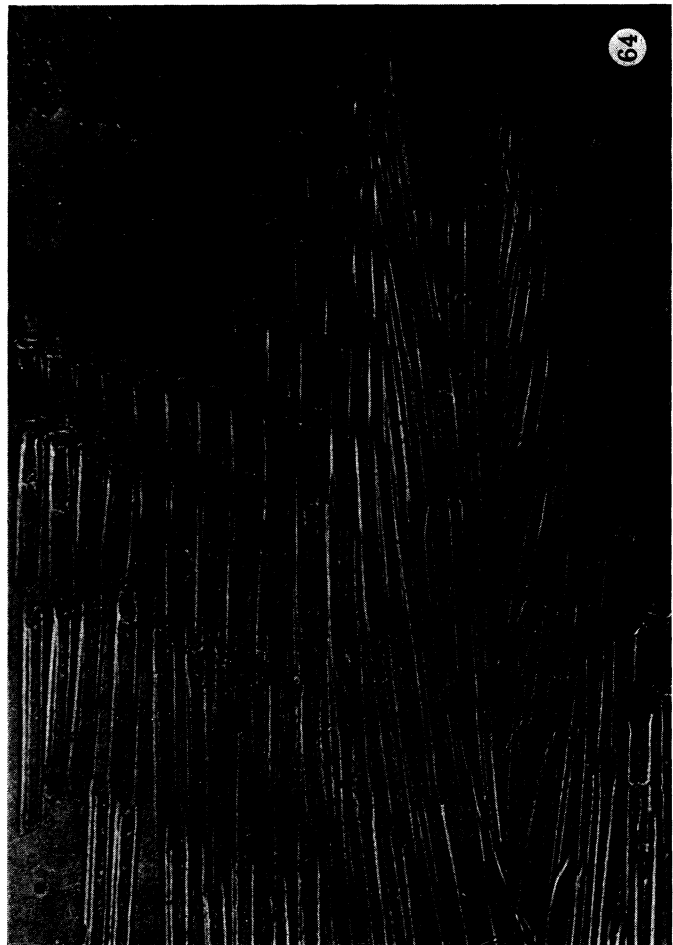
FIGURE 60. The animal has advanced a little further forward and here all four cheliped fans are partly or fully spread. The right posterior fan is about half open and is being advanced prior to scraping. The two left chelipeds, seen from different aspects, enable the whole fan to be visualised. Note how the antennules explore the rock ahead of the sweeping fans.

FIGURE 61. *A. innocous* advancing over a stone and scraping surfaces approximately at right angles to each other. Note how the antennules and antennae explore an extensive area ahead of and around the advancing prawn.



FIGURES 58–61. For description see opposite.

(Facing p. 94)



FIGURES 62-65. For description see opposite.



of which are being collected. All four chelipeds are employed simultaneously but at any given instant each is likely to be at a different stage of the process. The initial stage is a reaching towards the substratum by a cheliped and opening of a chela, which is accompanied by extension of its armature of bristles. This is shown particularly clearly by the anterior chelipeds on the left-hand side of figures 58 and 60, plate 1, where fully spread fans of bristles are seen just before scraping begins. These fans are then applied to the surface to be scraped – in nature almost invariably a stone – and begin to close. Successive stages are shown by the left posterior cheliped in figures 60 and 59, plate 1, and by the right anterior cheliped in figures 59 and 58, plate 1. Figure 58, plate 1, shows very clearly how, as the fan closes, the distal portions of the long brushes sweep the surface of the stone. The fine-toothed scrapers that lie internal to these sweeping brushes also pass over the stone and do so before the brushes. Thus, exactly as in *Caridina*, brushes are available to collect any particles dislodged by the scrapers. This principle is indeed widely applicable within the Crustacea, having been evolved in what are otherwise exceedingly diverse mechanisms employed by animals of remote phyletic affinity including the Anostraca (Fryer 1966), Cladocera Anomopoda (Fryer 1963, 1968, 1974) and Thermosbaenacea (Fryer 1965). As the fans close they collect and embrace particles. Almost closed fans can be seen in figure 61, plate 1, and figure 66, plate 3. A closed cheliped is then passed quickly to the mouthparts and its load removed. The left posterior cheliped is in this position (or just leaving the mouthparts) in figure 58, plate 1, and figure 67, plate 3.

There is no rigid sequence of application of the chelipeds to the substratum, different situations being met by different sequences, but at times the same sequence may be repeated many times. Thus when scraping rapidly the sequence left 1, left 2, right 1, right 2 may be many times repeated. The rate of application to the mouthparts varies much according to circumstances. When large accumulations of food are available long pauses ensue between successive applications; at other times a rate exceeding 1/s may be maintained for up to at least a minute. On one occasion, when food was plentiful, scraping with the second chelipeds only was observed and this at infrequent intervals. The chelipeds are extremely mobile and versatile, can be used while the animal is standing or hanging at various angles, can be used anterior to it (figures 58–61, plate 1) or swung so that three of them scrape towards the same side (figure 63, plate 2).

Although in nature food particles seem to be largely (perhaps almost exclusively) derived from the breakdown of forest leaves and are therefore seldom likely to be firmly attached to a surface, *A. innocous* can nevertheless remove material so attached. At certain times of the year individuals kept in aquaria were supplied with stones collected from the littoral region of

#### DESCRIPTION OF PLATE 2

FIGURE 62. *Atya innocous* sweeping a stone and displaying the great mobility of its chelipeds, the right anterior having been swung across to operate on the left side of the animal. Note the employment of the claw on the first walking leg.

FIGURE 63. *A. innocous* at rest, showing the way in which the chelipeds are held with their distal ends bunched together and their bristles directed forward. This individual (which is of the 'green' morph) shows the characteristic colour pattern of this species which is much clearer in some individuals (as here) than others.

FIGURE 64. *A. innocous*. Longitudinal section through the tip of a cheliped showing the arrangement of the bristles of the propus and dactylus.

FIGURE 65. The same showing the basal pivots of a few of the bristles. Note the apertures in the cheliped cuticle which place the cavity of each bristle in continuity with that of the appendage, and also the occluded region some way proximal to the base of each bristle.

Windermere on which a dense growth of firmly attached filamentous algae was growing. This was efficiently removed, the rocks being completely cleaned.

The other method of food collection employed by *A. innocous*, passive filtration, can be practised only in flowing water. Such filtration was first mentioned very briefly by Müller (1881) for '*Atyoida potimirim*' (= *Potimirim potimirim* (Müller)) where it is clearly subservient to scraping and is indeed not referred to in a more detailed paper on the morphology and habits of this prawn given later (Müller 1892). It was subsequently reported for *Atya molluccensis* de Haan by Cowles (1915) who succinctly explained the essence of the process in two paragraphs and gave a simple but informative sketch. This obscure publication has either escaped attention or incurred disbelief, one eminent carcinologist having expressed verbal scepticism that such filtration takes place at all. Filtration by *A. innocous* has been observed many times.

A filtering animal takes up a position usually facing, but sometimes oblique to, the direction of flow, raises its chelipeds, opens their chelae, and spreads their fans to the maximum extent, more or less at right angles to the current. Each cheliped contributes a filtering basket and, being held adjacent to the baskets of its three companions, forms part of a large, continuous filtering meshwork (figures 68 and 69, plate 3; figures 72–76, plate 4). Suspended particles are caught by the baskets which from time to time close rapidly and are applied to the mouthparts just as they are after collecting a load by sweeping/scraping. The application rate is lower than when scraping and differs according to circumstances. As an example, one series, measured over 3 min 32 s in an aquarium in which currents were set up by a bubbling device, gave an average of one application every 6.4 s. Sometimes at least 20 s may elapse without any cheliped being moved. There is no regular sequence in the order in which chelipeds are applied to the mouthparts. The same cheliped has not, however, been seen to be moved twice in succession but it may be applied after only one other cheliped has been in action, or may remain passive until the other chelipeds have, between them, been used up to at least five times. When a suitable site has been located, an individual may remain there filtering for long periods, certainly for more than 6 h, sessions of more than 2 h being common.

As the various plates show, the propus/dactylus chela of a cheliped does not always – and indeed when the animals feed in the rather weak current set up in an aquarium, seldom – receive

### DESCRIPTION OF PLATE 3

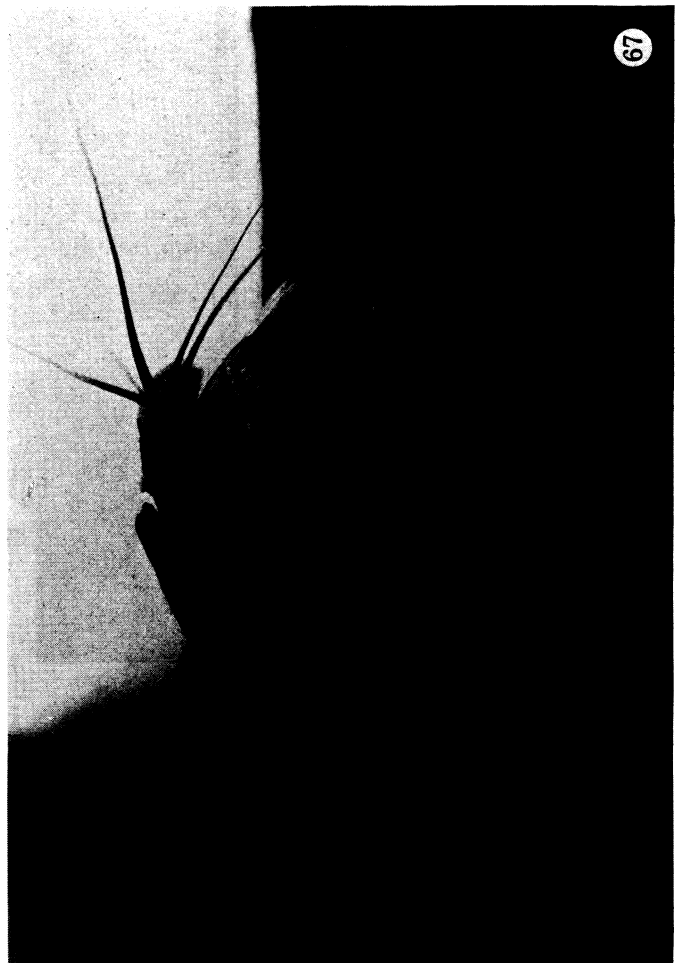
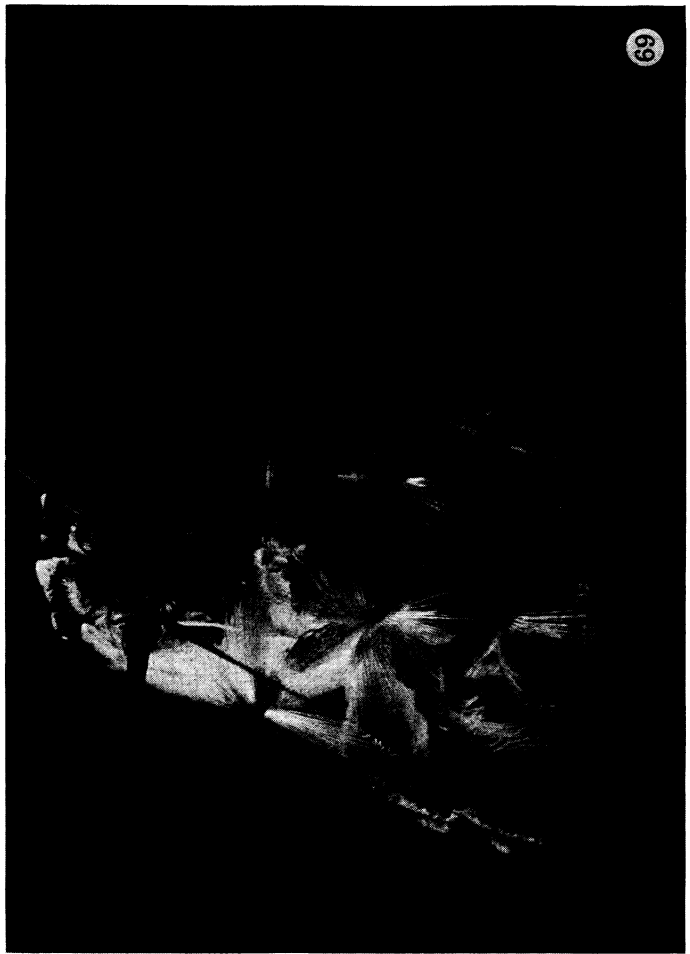
FIGURE 66. *Atya innocous*. Lateral view of an individual walking over a stone and sweeping food from it as it does so.

The right anterior cheliped is open and its fan of bristles is sweeping the substratum. The right posterior cheliped is held just clear of the substratum and is being opened prior to application in the manner of its partner. One of the left chelipeds is closed and is either being brought to or withdrawn from the mouthparts. Note how the claws of the walking legs are employed. Another prawn can be made out hiding beneath the stone – a typical refuge.

FIGURE 67. *Atya innocous*. Lateral view of an individual emerging from a crevice and scraping a stone with its chelipeds which are operating in different planes. The two right chelipeds are sweeping, the left anterior, almost closed, has just conveyed a load to the mouthparts and is being extended forward before being applied to the stone, and the right posterior is in the process of passing material to the mouthparts. Its propus/dactylus joint, directed anteriorly, lies immediately above the right anterior cheliped. Note how the third maxillipeds are extended forward.

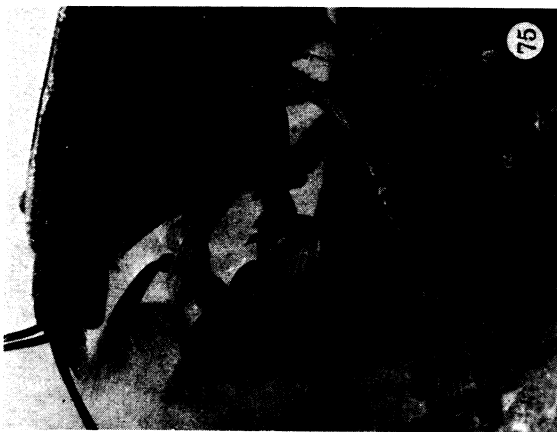
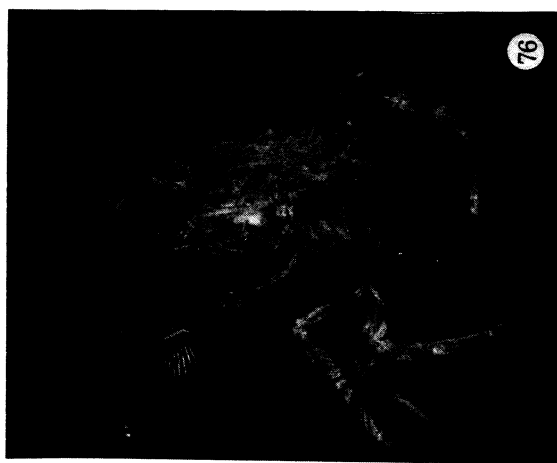
FIGURE 68. *Atya innocous* viewed from in front as it stands with all four cheliped fans spread so as to make an almost continuous filtering surface which collects particles drifting towards it. To the left is an individual of *Xiphocaris elongata*, also seen from in front, which, although largely out of focus, conveniently reveals the great difference between it and *Atya*.

FIGURE 69. *Atya innocous*, as above, showing the cheliped fans in greater detail.



FIGURES 66-69. For description see opposite.

*Facing p. 96)*



FIGURES 70-76. For description see opposite.

support from the excavation in the carpus. (This applies equally to *A. scabra*.) It is clear, however, that any increase in the load borne by the fans would have the effect of forcing the propus into the carpal excavation, which would inevitably help to hold it firm, and it can scarcely be doubted that this is important in nature where the animals often live in fast-flowing water. The bilateral compression of the stem of the cheliped (figure 36, insets) is here important. By being held 'edge-on' to the current, maximum strength and minimum resistance to pressure are achieved.

Although *A. innocous* most frequently faces the current when filtering this is not obligatory and, such is the versatility of the chelipeds, the filters can be placed at right angles to a current almost irrespective of the orientation of the trunk. All can be swung to one side of the animal or can be held so that the filtering surface is more or less parallel to the ventral surface of the body, such a position being approached in figure 76, plate 4. An individual has also been seen filtering while hanging upside down within a tube through which a current was flowing.

In nature *A. innocous* obviously selects regions of optimum flow as was beautifully demonstrated by a semi-natural situation in Dominica. Many individuals of this species had been introduced into an ornamental pool which was from time to time freshened by the opening of a valve which allowed a powerful jet of water to pass down a vertical pipe which opened beneath the water surface and some distance above the bottom. From this region, therefore, water flowed outwards over the bottom with diminishing velocity, points equidistant from the outlet having the same velocity. Shortly after the valve had been opened prawns began to assemble around the pipe and to feed by filtration. Many eventually did so and all were arranged in a perfect circle at whose centre was the pipe, thereby indicating that all preferred the same current velocity.

The relative importance of sweeping and passive filtration in nature is unknown. With two methods at their disposal the prawns no doubt use that most appropriate to a particular situation. Individuals kept in an aquarium where a current was constantly in existence regularly employed both methods. As expected filtration occurred infrequently when an abundance of particulate food (or an algal mat) was available for collection by sweeping/scraping. The readiness with which animals began to filter in the artificial pool when the opportunity presented itself, and where sweeping was also observed, perhaps indicates that filtering is used more in nature than in aquaria.

---

DESCRIPTION OF PLATE 4

FIGURE 70. *Xiphocaris elongata* seen from in front. Note how the animal 'stands up' in contrast to *Atya* which 'hangs down'.

FIGURE 71. *X. elongata* from the side.

FIGURE 72. *Atya innocous*. A filtering individual seen from above. The left posterior cheliped fan is not fully extended and is either just beginning to be withdrawn or is about to be re-expanded after carrying material to the mouthparts. The dorsal colour pattern is clearly seen in this individual.

FIGURE 73. *A. innocous*. An antero-lateral view of an individual with all four cheliped fans spread for filtering.

FIGURE 74. *A. scabra*. A filtering individual at the entrance of a Perspex tube through which a current of water is flowing.

FIGURE 75. *A. innocous*. A lateral view showing all four cheliped fans spread for filtering.

FIGURE 76. *A. innocous*. Antero-ventral view of an individual filtering in a region of eddies at the end of a tube through which a current of water is passing. Three fans are fully spread; the left anterior cheliped is passing food to the mouthparts.

*A. scabra* filters by a method indistinguishable from that of *A. innocous* (figure 74, plate 4). Intermittent observations made in an aquarium over a period of 2½ years showed that, under these conditions, it filtered more persistently than did *A. innocous*, with several individuals of which it shared its domicile. On the other hand sweeping took place extremely seldom. This is clearly related to the complete absence of even the fine scrapers found in *A. innocous* and to the rudimentary nature of the brushes on the long filtering setae. As does *A. innocous*, this species often filters continuously for many hours, and the frequency with which it applies its chelipeds to the mouthparts also varies greatly according to circumstances, intervals of as short as 2 and as long as 35s between successive applications having been noted. Likewise the chelipeds are not employed in a fixed sequence.

*Micratya poeyi*, of which an adult was watched intermittently in an aquarium over a period of more than 14 months, scrapes in the same way as *A. innocous* but does so more rapidly. It was also often seen to scrape persistently with its second chelipeds while keeping the first pair either in the resting position or somewhat open. *A. innocous* was only once seen to use the second chelipeds alone. It also filters as do the species of *Atya* and was seen to hold the first pair of chelipeds open for this purpose at the same time as it scraped with the second pair. On another occasion it filtered with the second pair while the first made occasional scraping movements and were at times half spread. Such a combination of activities was not seen in either species of *Atya* but the general principles of food collection whether by scraping or filtration are the same in all cases.

The way in which *Caridina* collects food by scraping surfaces with its cheliped bristles has been described in detail (Fryer 1960). Observations on living *Jonga* were limited but revealed what appeared to be an exactly similar process. It is also apparent that *Jonga* is incapable of passive filtration in the manner described for *Atya* and *Micratya*; nor does it frequent a suitable habitat in which to indulge in this practice. Not only is the cheliped armature specialized for scraping and sweeping, and totally unsuited to filtration, but the chelipeds themselves, while eminently suited to passing food to the mouthparts, which they do with great rapidity, are too lightly and delicately constructed to withstand the forces involved during passive filtration (cf. figures 4 and 6). Lightness and mobility rather than robustness has governed their design.

Although some observations were made on living *Potimirim* its food collecting habits were not observed, though it was seen to apply its chelipeds to its mouthparts as anticipated. In spite of the fact that it occurs in fast-flowing water it seems unlikely that it employs passive filtration though the possibility that it has begun to practise this cannot be entirely ruled out and the congeneric *P. potimirim* apparently does so at times. One individual was seen to raise its chelipeds to something like the position in which they are often held by filtering *Atya* but did not spread them in an *Atya*-like manner. Although its cheliped armature is clearly specialized for scraping, and the long sweeping bristles that would be employed for filtering (were such to be practised) lack an armature of filtering setules, there are about twice as many such bristles as in *Jonga* – a condition to be expected in a filterer. The chelipeds themselves, while less specialized than in the filtering *Atya* and *Micratya*, are more similar to these forms than are those of *Jonga* and, like their bristles, show incipient development of features that could lead to filtering.

(c) *The mouthparts and manipulation of food*

The mouthparts of *Jonga* and *Potimirim* are so similar to those of *Caridina* (Fryer 1960) that the more specialized *Atya* is described first. The mouthparts of *A. innocous* (figure 78) and *A. scabra*

(figures 79–82, plate 5) are virtually identical. *Micratya* is also very similar but perhaps less specialized in certain respects. In comparison with *Caridina*, (Fryer 1960, figure 2) and especially with *Xiphocaris* (figure 77) the most striking feature is the great elongation of the teaselling apparatus of the maxilla and first maxilliped (TL and G Mxp1) and the concomitant increase in the number of rows of spines and setae involved. In absolute terms (number of rows of spines per unit length) the teasel of *Atya* is very slightly coarser than that of *Caridina*, but as the animal is much larger it has a relatively finer teasel. Thus the animal from which figure 78 was prepared had a length approximately twice that of the *Caridina* used in the preparation of figure 2 in Fryer (1960), and was therefore very much more bulky, yet had a grid only very slightly less fine. The ‘fineness’ or ‘coarseness’ of the device cannot, however, be measured simply by the number of elements involved as its ability to deal with fine particles is much enhanced by specializations of the grid setae of the first maxilliped which, in *Atya*, enable even large animals to deal with extremely fine particles.

As in *Caridina* food is passed to the mouthparts by the chelipeds from whose bristles it is stripped by the grid setae of the first maxillipeds (figure 78, G Mxp1). The cheliped bristles are of ample length to by-pass the second maxillipeds (Mxp2) which protect and groom the more anterior mouthparts. Because of its reflexed nature, the tip of each second maxilliped lies not at the anterior limits of the mouthparts but beneath the posterior part of the teaselling apparatus, and is directed backwards. The most anteriorly lying setose part (S2 Mxp2) is actually the penultimate segment. The distal segment (S1 Mxp2) is very mobile and armed with numerous spines and combs, including a stout toothed terminal spine (figure 78, CLS; figure 82, plate 5) which enable it to clean adjacent structures. It is possible that at times the second maxillipeds may strip some material from the chelipeds, though this has not been established. Although they are suitably equipped to catch any particles that may fall onto them, and which could then be passed back to the first maxillipeds, any such function seems to be expressly ruled out by a ‘safety net’ of setae borne ventrally by the first maxillipeds (figure 78, SN) which is seen especially clearly in transverse sections (figures 80 and 81, plate 5). From this the spines of the teaselling lobe of the maxillae (TL) can sweep food dorsally if necessary. That the second maxillipeds do not regularly play a part in food transfer is indicated by the different nature of those parts that lie adjacent to the essentially uniform grid of the first maxilliped. Were such transfers made one would anticipate a similar structure throughout the relevant section of the appendage. Posterior straying of food particles is prevented by fences of setae on the proximal portions of the third (GS Mxp3) and second maxillipeds (GS Mxp2) and, a little more dorsally, by a less conspicuous row of setae on the ventral part of the proximal endite of the first maxilliped (GS Mxp1): cf. *Xiphocaris*.

Particles held between the opposed rows of grid setae are swept dorsally and to some extent anteriorly by spines of the long teaselling lobes of the maxillae which fit with great precision between them (figure 78, and especially figures 80 and 81, plate 5). As they pass orally, particles which lie towards the posterior end of this apparatus are deflected forward by an array of very long setae that arise from the dorsal face of the proximal endite of the first maxilliped (L Mxp1) and are funnelled orally by a fence of fine curved setae borne on the proximal endite of each maxilla (F Mx). The fencelike nature of these is best seen in figure 78; their curved form in transverse sections (figures 80 and 81, plate 5). Orally directed transport of particles coming to lie in this funnel is ensured by a device analogous to that of the teaselling apparatus. Fine setae borne on the lower face of the proximal endite of the maxillule – indicated

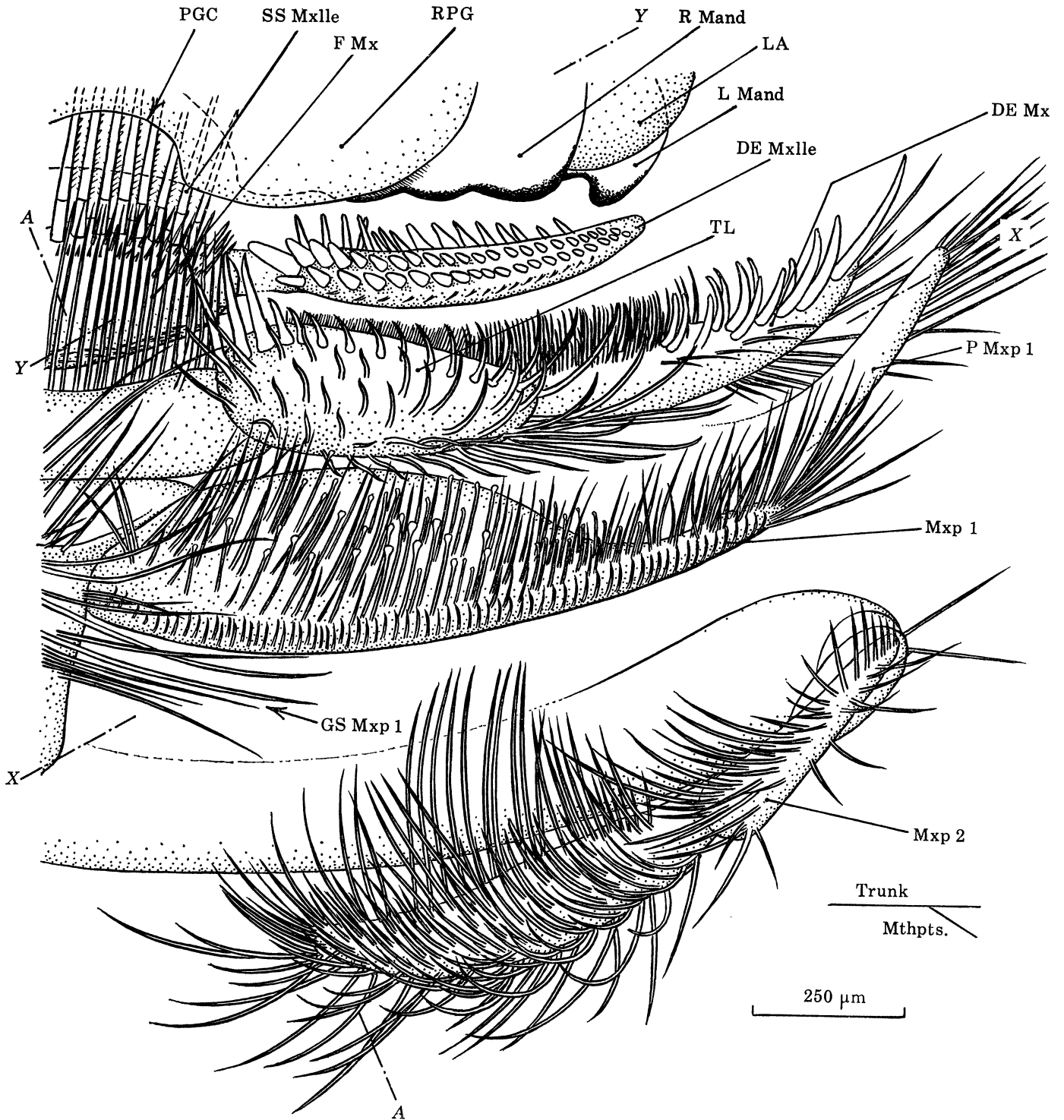


FIGURE 77. *Xiphocaris elongata*. The mouthparts of the left hand side *in situ* of an individual *ca.* 5.1 cm in length including rostrum. The most proximal parts of the post-mandibular appendages are not shown and maxilliped 3 is omitted, as are the more lateral parts of maxillipeds 1 and 2 that can be seen by deeper focusing. The right paragnath (RPG) is left *in situ* but part of it has been cut away to reveal the stout anterior spines of the proximal endite of the maxillule (SS Mxlle) that it would otherwise obscure. Likewise the right mandible (R Mand) is left *in situ* so that the tips of the incisor processes of both mandibles, which embrace the labrum (see figure 27), are seen.



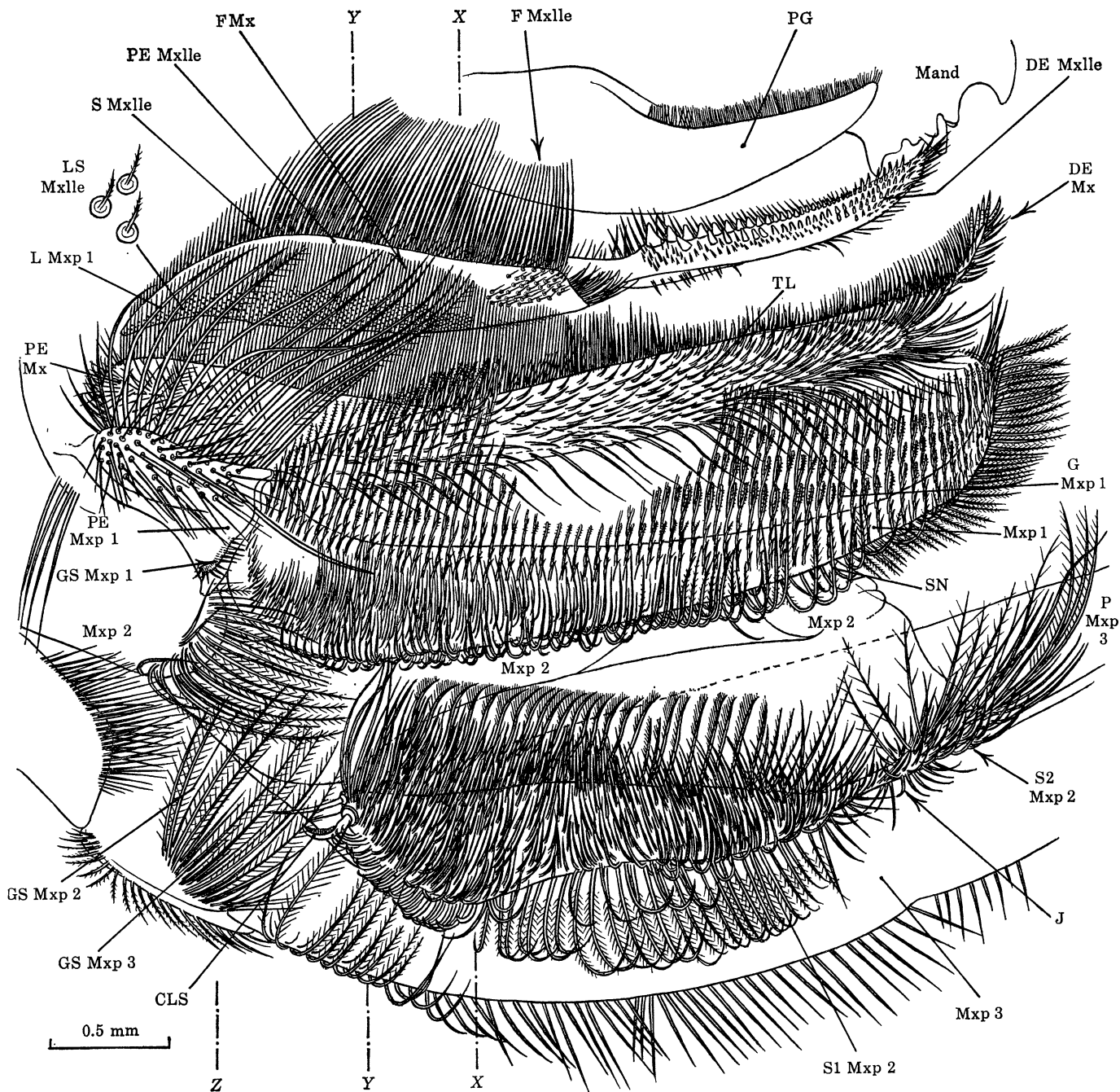


FIGURE 78. *Atya innocens*. The mouthparts of the left hand side of an individual *ca.* 4.7 cm in total length (carapace length 1.5 cm) *in situ*. In order to display certain features the individual appendages are separated from each other more widely than in life. In particular the teaselling lobe of the maxilla (TL) has been largely eased out of the grid of the first maxilliped (G Mxp1) between the rows of spines of which its own spines fit (as can be seen proximally), and the second maxilliped (Mxp2) is also pulled ventrally. In the interests of clarity some of the grid setae of the first maxilliped in the middle of the grid are cut short thereby giving an uninterrupted view of the teaselling lobe. All the long setae of the proximal endite of the first maxilliped (L Mxp 1) bear setules but these are shown only in a few cases. Note that, because the second maxilliped is reflexed, the portion that lies near the proximal parts of adjacent appendages is actually its distal extremity, and that the long setae that lie below the distal extremity of the first maxilliped actually arise from the penultimate segment (S2 Mxp2). The joint between these two segments (J) is difficult to see from the angle at which the mouthparts are viewed here. The outline of a more proximal part of the appendage as it here passes from view behind the first maxilliped can be seen in this region. The distal cleaning spine (CLS) of the second maxilliped is directed partly towards the observer and therefore appears somewhat foreshortened. The paragnath and incisor process of the mandible are not lying exactly as in life, having been disturbed by the dissection, but their general location is much as shown here. Approximate levels of the sections shown in figures 80-82, plate 5, are indicated by X-X, Y-Y, and, ventrally, Z respectively. In figure 82 the distal endites of the second maxillipeds on each side are lying further back than in figure 78, so that the cleaning spines appear in the sections.

by spots in figure 78 and whose form is shown in the inset (LS Mxllle) – protrude between the gaps in the fence of setae as is very clearly shown in transverse slices (figures 80 and 81, plate 5). These inevitably lift particles, which eventually come within reach of the marginal setae of the proximal endite of the maxillule. Of these there is a row of short setae (S Mxllle) as well as that of longer conspicuous setae (F Mxllle) that reach between the paragnaths towards the mandibles. The movement of this endite is a swing along the arc indicated by its marginal setae. Distally it has two sets of fine setae, directed anteriorly and somewhat orally (figure 78), which can assist in the movement of particles emerging from somewhat more anterior regions of the teaselling apparatus. Adjacent to the gap between the endites of the maxillule the setae of the dorsal margin of the teaselling lobe of the maxilla are particularly long – a functional necessity. Still more anteriorly the teaselling apparatus passes material to the distal endite of the maxillule (DE Mxllle) which lies within reach of the mandible. In this it is assisted anteriorly by the much reduced distal endite of the maxilla (DE Mx). One suspects that most food passes orally via the more anterior parts of the mouthparts and that relatively small amounts take a more posterior course. Certainly it is only the distal portion of the proximal endite of the maxillule that can reach food material emerging from the teaselling apparatus and sweep it orally, and it is difficult to see how more than stray particles find their way to the extreme posterior end of the long funnel of setae borne by the maxilla. Although this region is clearly able to cope with material in the way described it seems likely that it serves chiefly as an efficient posterior cleansing device rather than as an important contributor to the transport of food.

In both the teaselling apparatus and the distal endite of the maxillule the most robust armature lies posteriorly, as it does in *Xiphocaris*, and gradually becomes finer distally. It is difficult to see how, if they collect particles of various sizes as must often be the case, the chelipeds could place coarse particles posteriorly and finer ones anteriorly. It is equally difficult to see how sorting according to size could occur during the teaselling process. Currents set up by the various palps (as described for *Caridina* – Fryer 1960) could conceivably carry small particles anteriorly at times, but this seems very unlikely. It is of course possible that if collecting predominantly coarse material the prawn can insert its chelipeds towards the posterior end of the grid; if collecting predominantly fine particles more anterior, but this is purely conjectural.

Food is swept from the maxillules by the incisor processes of the mandibles (figure 78, Mand) details of which are shown in figure 83. Its passage from the incisor to the molar processes is

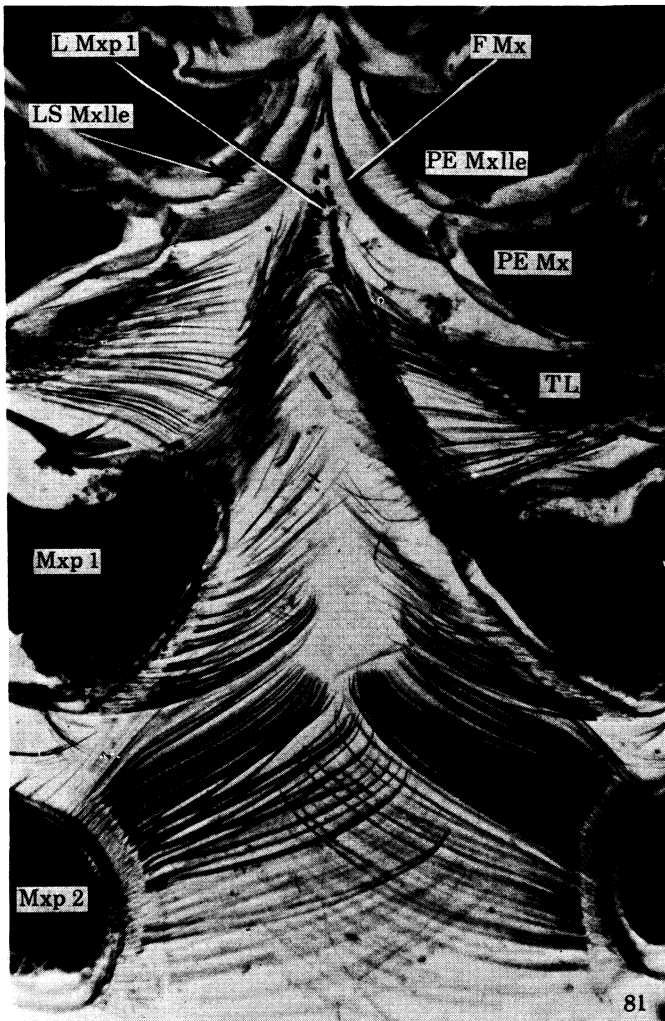
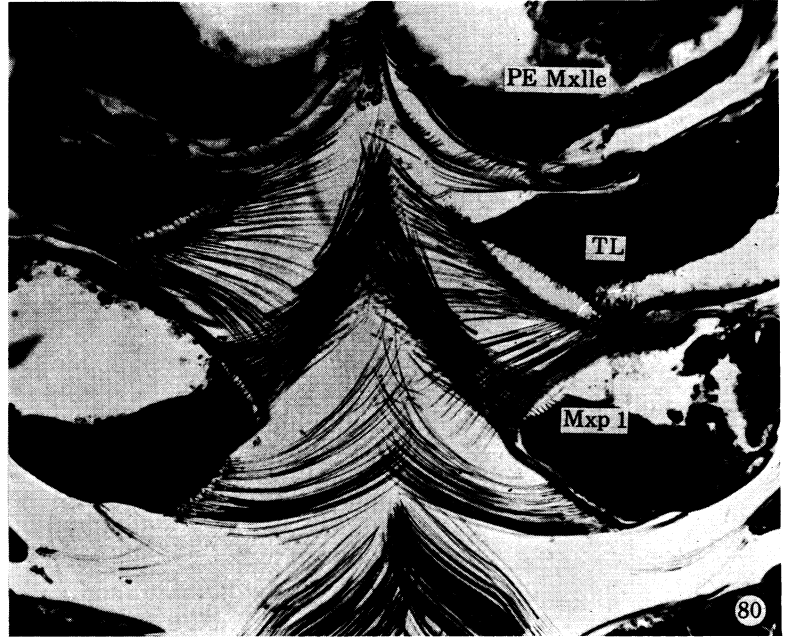
#### DESCRIPTION OF PLATE 5

FIGURE 79. *Atya scabra*. Transverse section through the molar processes of the mandibles between which a sliver of food particles, coming from below, is passing.

FIGURE 80. *A. scabra*. Transverse section through the mouthparts (dorsal and ventral portions omitted) at the level X–X in figure 78 showing the teaselling lobes of the maxillae (TL) and how their spines fit between the grid setae of the first maxillipeds (Mxp 1). Note the ‘safety net’ of setae immediately beneath the grid setae.

FIGURE 81. *A. scabra*. Transverse section through the mouthparts at the level Y–Y in figure 78. This shows the chute formed by the fence of setae (F Mx) of the proximal endite of the maxilla (PE Mx) and the long setae (L Mxp1) of the proximal endite of the first maxilliped. It also shows the dense array of spines of the second maxilliped (Mxp2) whose tip is here extended somewhat more posteriorly than in figure 78.

FIGURE 82. *A. scabra*. Transverse section through the first and second maxillipeds at the level Z in figure 78. Here, however, the scrapers and associated spines of the tip of the very mobile second maxillipeds are swung more posteriorly and dorsally than in that figure and reach towards the proximal endite of the first maxilliped. The proximal endite of the second maxilliped lies too far laterally to be seen in this figure but some of its setae (GS Mxp 2) are visible.



FIGURES 79-82. For description see opposite.

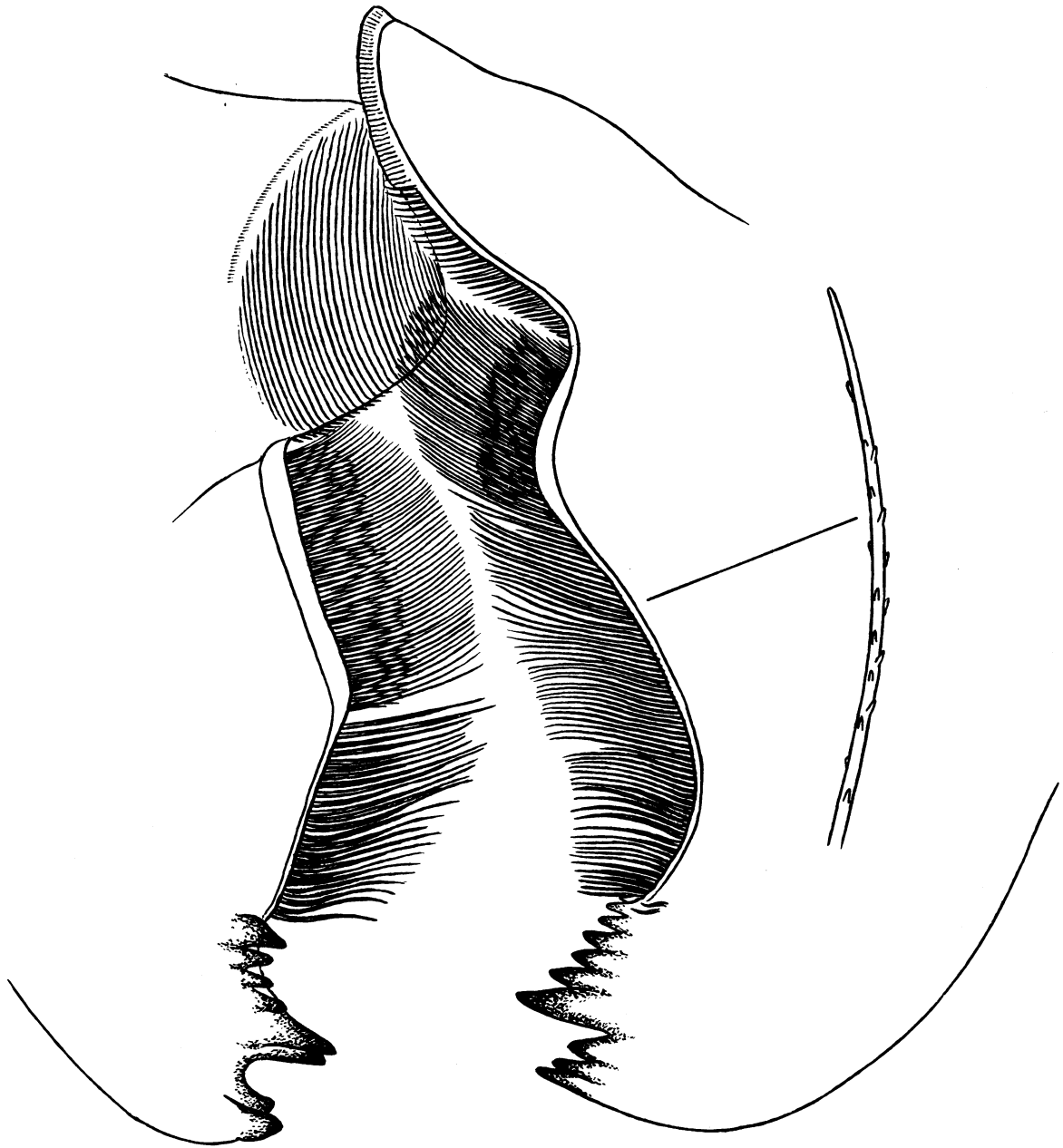
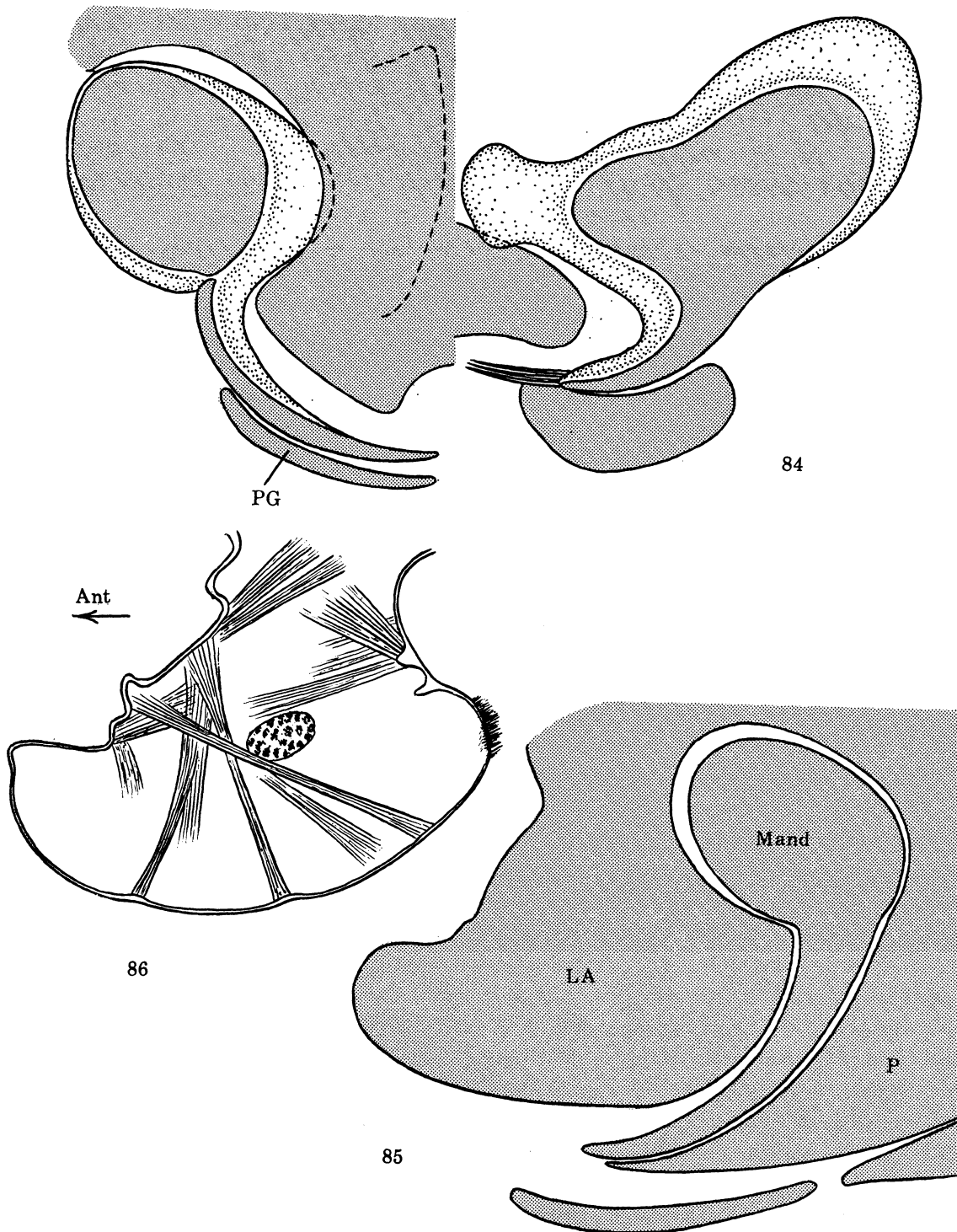


FIGURE 83. *Atya innocuus*. The molar and incisor processes of the mandibles from behind. The inset shows the distal end of one of the lifting spines of the ventral series of the right mandible.



FIGURES 84-86. *Atya innocous*.

FIGURE 84. Transverse section through the labrum, mandibles and paragnaths. Although drawn from actual slices the figure is much simplified. The left hand half shows a more anterior region than the right, and the dashed line shows the approximate position of the molar process, which lies more posterior than either of the sections. Note how the incisor process is confined within a curved slit whose walls are formed by the labrum and paragnaths (cf. figure 85).

FIGURE 85. Longitudinal section through the labrum, and mandible and paragnath to show how the incisor process lies in a narrow slit. Although diagrammatic and simplified this is based on a section. In reality, in a thick section the incisor process curves so much in what is here the vertical plane as to be partly 'overlapped' by the paragnath. For clarity it is shown as it would appear if a very thin slice had been cut (cf. figure 84). Near its edge - where arise the lifting spines - the incisor process is thinner than at the level shown here.

FIGURE 86. Longitudinal section through the labrum showing the arrangement of the muscles.

made possible by the elaborate development of what in *Caridina* were called lifting spines (Fryer 1960) which, like the processes themselves, are markedly asymmetrical in arrangement, the better to facilitate transfer of the food sliver. A simple arrangement of lifting spines is seen in various malacostracans – amphipods, isopods, *Monodella*, etc. – but no case so elaborate as that of *Atya* appears to have been described. The spines, which dorsally consist of double rows, are not only asymmetrical with respect to each other, but those of the left mandible lie anterior to those of the right so as to permit more effective cooperation in lifting the food sliver. The arrangement of the stouter ventral series is not entirely regular. Here and there two spines arise very close together, and there is some overlap.

The lifting spines can operate efficiently only by virtue of their close association with the labrum and paragnaths. Each incisor process is a relatively thin, blade-like extension of the mandibular corm whose shape is like that of a segment broken from a sphere. The concave anterior face lies adjacent to the posterior face of the labrum and the convex posterior face is embraced by the paragnaths, the whole blade thus lying within a narrow slit which, because part of a sphere, appears curved in both longitudinal and transverse planes (figures 84 and 85). The labrum is provided with muscles running largely fore and aft (figure 86) that enable it to deform its posterior face and thus, by movements akin to those of peristalsis, perhaps to aid movement of the food, though its part in this respect can be only minor.

Although the mandibles are completely hidden, this arrangement confirms absolutely the inferences made from articulation and musculature concerning their movements (§VII). In spite of the deformation of which the labrum is capable (which is probably only slight) the plane of movement of the curved incisor process through the slit is restricted to that conferred by rolling movements of the body of each mandible. No large adduction or abduction movements are possible. Even if the musculature and articulation were capable of granting such movements – which they are not – they would cause the incisor process to jam in the slit.

The lifting spines carry food particles through the slit to the posterior end of the molar surfaces (figure 79, plate 5) whence, by typical rolling movements such as are found even in branchiopods, it is swept between them and forward to the entrance of the oesophagus. The ridging of the molar surfaces (figure 83) is such as to assist such forward transfer with little tendency to carry material back on the return stroke.

Of the non-acanthophyroid Dominican atyids *Jonga* has what are interpreted as the least specialized mandibles (figures 87, 88). In basic form and musculature they employ exactly the same principles as those of *Atya* but the armature of the incisor processes is simpler and indicates the sort of stage through which *Atya* probably passed during its evolution. Two sets of lifting spines are present on each mandible. These are fewer and relatively stouter than in *Atya*. Distally the left incisor process has a distinct cutting blade (figure 87, CB) rendered effective by virtue of the asymmetry of the mandibles and perhaps helpful in chopping small fibrous items. In this respect it may be more specialized than *Atya* but a strict assessment is not possible as the efficacy of the cutting blade of *Atya* may be enhanced by the greater muscular power available.

The mandibles of *Potimirim* and *Micratya* are very similar to each other and bridge the gap between those of *Jonga* and *Atya*. In each the number of lifting spines in each series is greater than in *Jonga* but less than in *Atya*. There are, for example, almost twice as many spines in the ventral series of the right mandible as in *Jonga*, but less than a third of the number in *Atya*.

A more primitive atyid mandible than that of *Jonga* is probably that of *Halocaridina rubra* Holthuis from Hawaii, sketched by Holthuis (1963). Here the left appendage bears only a single

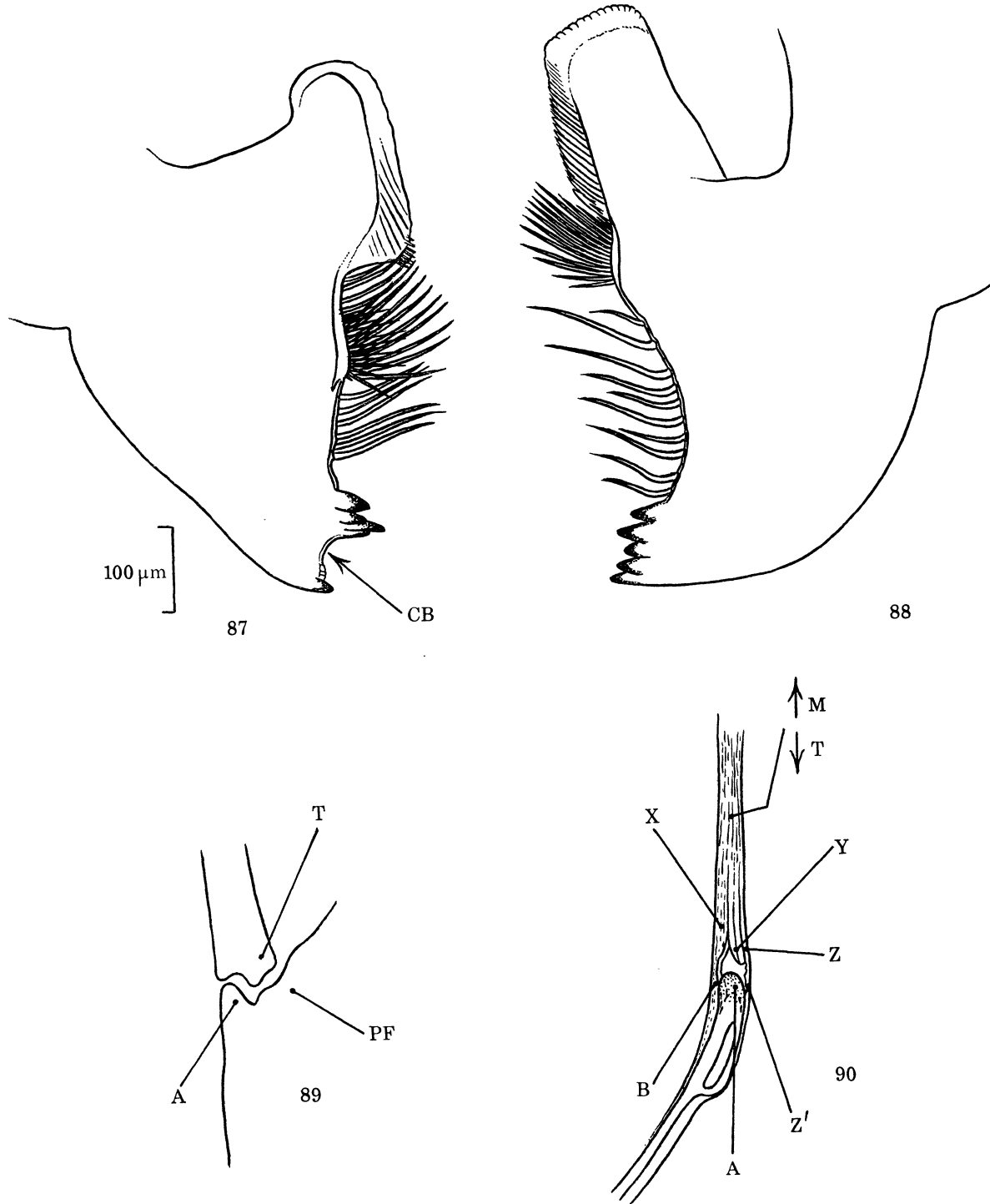


FIGURE 87. *Jonga serrei*. Molar and incisor processes of the left mandible from behind.

FIGURE 88. *J. serrei*. The same, right mandible.

FIGURE 89. *Atya innocous*. The union of the tendinous extension of muscle 4 with the apodeme of the posterior face of the mandible.

FIGURE 90. *A. innocous*. Longitudinal section through the region shown in figure 89. The tendinous rod shown dorsally merges still more dorsally with muscle 4. Material in the vicinity of X stains red with Mallory, at Y there is a region of essentially non-staining amber-coloured material tinged with red in places, at Z blue staining is apparent, and from about Z' the blue gradually disappears ventrally.

group of spines – ‘a tuft of spinules’ (Holthuis) – equivalent to the dorsal group of *Jonga*, the right a dorsal group and what appears to be a single spine in the position of the ventral row of *Jonga*.

#### VII. ATYID MANDIBLES AND THEIR MUSCULATURE

Our understanding of mandibular mechanisms in the Crustacea has been greatly extended by the work of Manton (1964) by reference to which the grade of organization of atyid mandibles can be assessed. While those of *Atya* in particular display great specialization, all retain many primitive features and are very different from those of such advanced decapods as crabs and crayfishes whose specializations, largely for cutting material from large food masses, have taken them far from the primitive condition from which they were derived. Information on mandibular mechanisms of lower decapods (Eucarida) is confined to a few forms described by Berkeley (1928) and Snodgrass (1950). Those of atyids prove to be more like those of primitive malacostracans of other divisions – Syncarida: Anaspidacea (Manton 1964), Peracarida: Mysidacea (Cannon & Manton 1927) and Thermosbaenacea (Fryer 1965) – than of advanced members of their own group, the Eucarida. Atyid mandibles indeed retain many attributes described for branchiopods (Snodgrass 1938, 1950; Fryer 1963; Manton 1964) but also show more advanced features. Atyids have developed a large incisor process – absent in branchiopods – but nevertheless retain a large molar region – clearly related to microphagous habits. The axis of swing of the mandible is oblique, about 45° to the long axis of the body, much as in *Anaspides*, and is nearer to the anterior than the posterior margin. Functional reasons for these features, associated with transverse biting of the incisor process, have been discussed by Manton (1964).

In microphagous branchiopods and syncarids finely particulate food arrives at the molar surfaces of the mandibles from behind: in ‘higher’ peracarids and eucarids larger food masses are passed to the mandibles from below – e.g. see Manton (1964, Figure 5), and Manton (1973, Figure 1). To this generalization atyids, especially the non-Acanthophyroid forms, are a specialized exception. In *Xiphocaris*, most primitive in this as in many other respects, food passes obliquely antero-dorsally. In the non-Acanthophyroid species, in spite of their microphagous habits, food travels to the molar surfaces of the mandibles not from behind but below as is clearly seen from figures 78, 83 and 85 and figure 79, plate 5. Nevertheless this dorsal transfer, effected in the more advanced forms by the lifting spines, carries the food to the posterior end of the molar surfaces, whence by their rolling action it is passed between them just as in branchiopods. Because of the oblique set of the mandible and the shape of the molar surfaces, however, what was primitively a forward transfer of particles now includes a considerable dorsal component.

Although the mandibles lie too deep to be observed in action in life it is possible with care to dissect out the entire ensemble intact. Manipulation shows very clearly not only that rolling is the predominant movement, as one would infer from structure, musculature and the observed movements of the mandibles of branchiopods, with whose musculature those of atyids have much in common, but that such movements will pass food between the markedly asymmetrical molar processes whose shape and ridging are beautifully adapted for sweeping material towards the oesophageal entrance.

As in branchiopods, syncarids (*Anaspides*) and lower peracarids (*Monodella*; *Hemimysis*) there is a transverse mandibular tendon and two suspensors from the dorsal head cuticle which pass



on either side of the fore-gut. In branchiopods and the minute *Monodella* these endoskeletal elements are thin tendinous sheets: in atyids, where the mandibles are much larger, they are massive and extremely tough fibrous structures. Their retention here is interesting as in 'higher' members of both the Peracarida (Isopoda) and Eucarida Decapoda (crabs and crayfishes) they have been lost in relation to changes in mandibular function (Manton 1964). As in *Anaspides* and *Monodella* the cavities of the mandibles are filled by muscles of the 5a, b and d series, particularly the first mentioned, which are remotor rollers. The amount of muscle present is greater than in the lightly built *Monodella* (see Figures 12–14 in Fryer 1965) but similar to that shown diagrammatically for *Paranaspides* by Manton (1964, Figure 9).

It is noteworthy that in all cases this musculature is bilaterally symmetrical. Although the development of skeletal asymmetry of both the molar and incisor elements of the mandibles has played a part in mandibular evolution, the exploitation of muscular asymmetry – so well defined and so important in mandibular evolution in the most successful of all branchiopods, the Cladocera (Fryer 1963, 1968, 1974) – has been precluded for reasons referred to in the discussion of the mandibular mechanism of *Monodella* (Fryer 1965). Such asymmetry would preclude effective biting by the incisor processes.

Just as in *Anaspides*, muscle 4 of atyids (undoubtedly homologous with muscle 4 of branchiopods) originates dorso-laterally and inserts via a long tendinous rod onto a hollow apodeme on the posterior margin of the mandible. In *Xiphocaris* this tendon merges imperceptibly with the mandibular apodeme. In *Atya* the union between the tendon and the apodeme is specialized, a true articulating joint being formed. The apodeme itself is very small (figure 89, A). The ventral extremity of what is functionally the tendon is expanded and strengthened, being pale brown in colour in contrast to its shining white colour elsewhere. Where it articulates with the apodeme the intervening joint is made up of pliable, whitish to colourless, translucent, tendinous material. There is a binding tendinous layer (figure 90, B) internally and a cuticle-like band (Z and Z') externally that responds to Mallory by staining pale blue or remaining colourless and is therefore soft. Staining reactions at the extremity of the tendon are indicated in figure 90. Its cuticle-like nature suggests that this region may be part of the apodeme and that the joint arose within it rather than at the point of union of apodeme and tendon. Whatever its origin an such an articulation enables the muscles to pull the tendon always in one plane while the edge of the mandible swings through a wide arc.

Although the body of the mandible has a very thick cuticle this is perforated by minute pores and its outer surface bears numerous fine, sometimes setose, setae whose function is presumably to inform the central nervous system of the position of the mandibles during a cycle of movement. The cuticular surface of the mandible is kept clean by feathered cleaning setae arising from the adjacent cuticle. In one region setae of the distal endite of the maxillule can reach the outer face of the incisor prolongation and clean it.

The evolutionary interest of the mandibles of atyids and certain other primitive decapods observed by Snodgrass (1950) is that we can now recognize that the primitive basic type of malacostracan mandible possessed by the Syncarida Anaspidacea is found also among the Eucarida even in the Decapoda – the group that has given rise to the most 'advanced' of all crustaceans. Thus while peracarids such as isopods, and eucarids such as crabs and crayfishes, display highly specialized endpoints of mandibular evolution, there still exist members of these groups – themosbaenaceans, mysids, atyids and certain other decapods – that share with the primitive Syncarida a mandibular mechanism whose derivation from that of the branchiopod

type is readily apparent. Particularly striking is the fact that the mandible of *Atya*, while extremely specialized, has achieved this specialization by additions to, and refinements of, the primitive type of crustacean mandible whose salient features it still to a large degree retains.

#### VIII. THE EVOLUTION OF ATYID FEEDING MECHANISMS

It is clear that the feeding mechanism of *Xiphocaris* represents the least, and that of *Atya* the most, specialized among Dominican atyids, and almost certainly of the family as a whole. While as a broad generalization this is undoubtedly true, the mechanism of *Xiphocaris* is nevertheless complex and exhibits specialized features. Indeed some of the striking differences between *Xiphocaris* and *Atya* – as of the chelipeds and mandibles – represent not simply primitive and derived conditions respectively but end-points of divergent specialization. *Jonga*, *Potimirim* and *Micratya* reveal less specialized conditions than those seen in *Atya* and indicate not only stages along the route to an *Atya*-like condition but divergent specialization along that route. In respect of their feeding mechanisms, however, they all stand much nearer to *Atya* than to *Xiphocaris*, as they do in basic anatomy. This is not entirely the case habitwise, in which respect *Xiphocaris* and *Jonga* show certain convergent similarities.

The mouthparts of atyids are constructed on the basic caridean plan: even the basic decapod plan is discernible throughout. There are clear similarities between those of *Xiphocaris* and of the recently described and undoubtedly primitive *Procaris* (Chace & Manning 1972; Holthuis 1973) for which a new family and superfamily had to be erected. From a functional point of view the most significant feature of this similarity is that *Procaris* lacks chelipeds – all its pereopods being pediform – and must therefore either collect its food directly with its mouthparts or have material swept or lifted towards them by pediform appendages. No information is available on this. Indeed the significance of the enormous evolutionary step involved in the incorporation of chelipeds into the feeding mechanism seems largely to have escaped the attention of those considering decapod evolution.

If food is collected directly by the mouthparts of *Procaris*, then, provided its mouthparts are arranged in a similar manner to those of other carideans, it is only the more posterior members – maxillipeds 1 and 2 – that can have access to the substratum. If the characteristic decapod flexure of maxilliped 2, which grants mobility, is associated in *Procaris* with food collection then we may gain an insight into the original reason for this curious yet very persistent feature. If it is the first maxillipeds that collect food they presumably do so by whisking material towards the maxillae. One can, however, only guess how *Procaris* feeds and express the hope that its feeding mechanism – which could throw much light on decapod evolution – will receive attention.

One is on much firmer ground in comparing *Xiphocaris* with other Dominican atyids. Many functional trends in the manipulation of food can be clearly recognized here, but the differences in the chelipeds are so great as to offer few clues to the origin of the non-Acantho-phyroid type, and the mandibles also present problems. Although of necessity speculative, cheliped evolution nevertheless merits brief mention. A primitive chelate appendage armed distally with denticles (or thickened sclerotized cuticle) and an array of, originally, sensitive or protective bristles, could have given rise to both types. Accentuation of the denticles in relation to the precise seizure of individually selected small food particles would lead to the condition seen in *Xiphocaris*: accentuation of the bristles for sweeping and, ultimately, filtering, to

the condition seen in the non-Acanthophyroid genera. Alternatively the ancestors of the group may have had no chelipeds (a possibility made less fanciful by the discovery of *Procaris*) and the non-Acanthophyroid forms perhaps acquired them by a route already suggested and illustrated diagrammatically with reference to *Caridina* (Fryer 1960). *Xiphocaris* could either have acquired its chelipeds independently by flexure of the dactylus against a projection of the propus, or diverged from what was to lead to the mainstream of atyid evolution by developing distal teeth on the primitively sweeping cheliped before it became very specialised.

A clue as to how extensible bristles came to be used for food collection is provided by the observation that leg spines of jumping spiders are automatically erected when pressure increases prior to a jump (Parry & Brown 1959*a*). A similar erection of originally protective or sensory spines or setae with an increase in pressure, for whatever reason it was developed, may have initiated their incorporation into the system.

Among the non-Acanthophyroids emphasis has been on the collection of fine particles, and exploitation of such a food source has clearly been highly successful. The evolutionary sequence of specialization in the chelipeds has been outlined in §VI(*a*). The mouthparts and the way in which they deal with food show this equally well, *Jonga*, *Potimirim* and *Micratya* (and *Caridina*) being illustrative of changes on the route to the condition seen in *Atya*. Evolutionary (but not phyletic) trends, of which a primitive condition is shown by *Xiphocaris* and a specialized derivative by *Atya* (often with *Jonga* and *Potimirim* displaying a less specialized stage than *Atya*), include the following, appreciation of which is facilitated by a comparison of figures 77 and 78.

- (1) Reduction in the stoutness of the denticles of the distal endite of the maxillule.
- (2) Reduction in the stoutness, and a great increase in the number, of orally directed spines on the proximal endite of this appendage.
- (3) Extreme development of the proximal lobe of the distal endite of the maxilla. This is achieved both by an anterior extension at the expense of the distal lobe, which becomes much reduced, and by a posterior extension so as to underlie not only the distal but much of the proximal endite of the maxillule.
- (4) An increase in the number of regularly arranged rows of its armature of spines to form an elaborate teasel.
- (5) Reduction in stoutness, and an increase in number, of the setae that make up the fence on the proximal endite of the maxilla.
- (6) Elongation of the grid section of the first maxilliped, an increase in the number of setae that it bears, their arrangement in more definite rows, and great elaboration of the setae themselves.
- (7) The development of finer and more numerous spines and setae on the distal segment of the second maxilliped.

All these trends, like that towards the development of fine lifting spines on the mandible (§VI(*c*)), are related to increased efficiency in the manipulation of fine particles by animals whose most specialized representatives also show a trend towards an increase in size. While the post-mandibular mouthparts of *Xiphocaris* indicate what could be precursors (albeit modified precursors) of the condition seen in *Atya*, it is unlikely that the immediate ancestors of the latter had such heavy crushing denticles on the incisor process of the mandible as does *Xiphocaris*. Although this arrangement is less specialized than that of *Atya*, the differences here also reflect divergent specialization just as they do in the chelipeds.

The less specialized nature of *Jonga*, *Potimirim* and *Micratya* than of *Atya* is best illustrated by reference to the teaselling apparatus. In these three genera the teasel is made up of only 16–18 oblique rows of spines (far more than in *Xiphocaris* but far fewer than in *Atya*) and the grid has only about 32 rows of setae in *Jonga*, about 36 in *Potimirim* and about 40 in *Micratya*, plus in each case a number of distal setae that are not obviously arranged in rows. In these respects they exhibit a level of specialization about the same as *Caridina*. There are more than 70 rows of setae in the grid of *Atya*.

That sweeping in *Atya* and *Micratya* preceded passive filtration as a means of food collection is clear. The latter habit is possible only in flowing water and calls for robust walking legs armed with stout claws as well as robust and highly specialized chelipeds. These attributes contrast strongly with those of *Jonga* which is a specialized scraper and lives in still or slow-flowing water. The much larger size of *Atya* than other atyids is also clearly advantageous in this respect and must permit the colonization of situations where smaller forms could venture only by virtue of keeping very close to the bottom – thereby restricting opportunities to filter.

An interesting parallel with *Atya* is shown by the larvae of simuliid flies which also live in fast flowing water and filter food particles by means of fans developed on outgrowths of the labrum. Davies (1974) has investigated the larva of a primitive member of this family, *Crozetia*, and found that its rudimentary fan is used not for passive filtering but for scraping. Thus two very dissimilar groups of arthropods, employing structures of different anatomical origins, have exploited similar conditions in similar ways and have evidently followed routes which show considerable functional similarities. This is a striking example of ecological convergence.

## IX. THE FORE-GUT

### (a) Introduction

The armature of the fore-gut of 'higher' decapods was noticed by Aristotle and has subsequently been the subject of enquiry by several investigators. Less attention has been paid to the 'lower' forms but Bonnier's study (1899) of the penaeid *Cerataspis* and the monumental work of Mocquard (1883), who studied a wide range of decapods, are notable exceptions. Interesting contributions have also been made by Patwardhan (1934, 1935–1935*d*) and Reddy (1935). A species of *Atya* was included among the forms studied by Mocquard but, although he gave a long and detailed description, his minute illustrations and the lack of a figure showing the armature of the fore-gut *in situ* make it difficult to appreciate just how the apparatus is arranged. His account concerns chiefly the ossicles elaborated within the wall of the fore-gut, best studied in an entire preparation examined from without. From a functional point of view the internal arrangement is more informative. A terminology for the ossicles, based on a study of 'higher' forms, modified from that of Huxley (1880) and Mocquard (1883), has recently been given by Maynard & Dando (1974) and, so far as possible, is utilized here though, as Mocquard noted, while most ossicles of the atyid fore-gut can be homologized with those of 'higher' forms, some parts are problematic. Not all the ossicles developed in 'higher' forms are represented. Although the fore-gut of *Atya* is more specialized than that of *Xiphocaris* it has been the subject of more detailed study and is therefore dealt with first.

(b) *The fore-gut of Atya*

An intact fore-gut of *A. innocous*, seen from above, shows the arrangement of the dorsal ossicles (figure 91). The major internal features are revealed by a longitudinal bisection (figure 92). As is typical of decapods an anterior cardiac (CCH) and a posterior pyloric chamber (PCH) are clearly recognizable. The walls of each are for the most part of membranous but tough chitin elaborated into what for convenience of description and purposes of homology can be called ossicles, but which in no case have the massive tooth-like nature displayed by those of many 'higher' decapods. The cardiac chamber is a spacious sac, but much smaller than in an *Astacus* of similar size, somewhat expanded laterally and narrowing posteriorly. Its most conspicuous armature consists of two distinct sets of somewhat posteriorly located rake-like spines (ACS and PCS) which are borne on stout chitinous supports (ACP and PCP) on each ventro-lateral wall. The spines reach out into the chamber towards their partners on the opposite side as can be seen most clearly in figure 91. The homologies of the supports are in some doubt (see Mocquard 1883): here they are referred to as anterior (ACP) and posterior (PCP) comb plates – names which describe form and function and are non-committal homology-wise. The anterior comb plate bears a uniseriate row of spines some of whose robust ventral members (ACS) have multitined tips. More slender spines (DR) continue the row dorsally. The posterior plate is much larger and more complex. On its anterior margin it bears a uniseriate row of stout spines (PCS) often with elaborated tips; more posteriorly a dense pad of spinules (SCP) that become ever finer and more setule-like towards its base (figure 92; figures 98 and 99, plate 7). These are mostly directed postero-dorsally so as to direct food particles towards the narrow cardio-pyloric aperture. Near the base of each posterior comb plate is a channel (LC), well screened by setules, that is referred to below.

In the roof of the pyloric chamber are ossicles, armed with spines or setae. Anteriorly, and running more or less transversely, is a narrow, sparsely armed, mesocardiac ossicle (figures 91 and 92, MO) which is basically a folded and somewhat sclerotized region of the wall. Articulating with this are two oval, domed pterocardiac ossicles (PO). These are armed with a single row of spines on their outer margins (LPO). Posteriorly the spines follow the inwardly curving margin of the ossicle towards the mid-line (PPO). Laterally each pterocardiac ossicle is 'hinged' to the wall by a well-defined ligament (L). Posteriorly they articulate with a median urocardiac ossicle (UO) which in turn articulates by means of a transverse ligament (L) with a median plate, the pyloric ossicle (PY). From above only a trace of the ligament is visible in the mid-line (figure 91, L), but in fact it extends transversely along the line of union of urocardiac and pyloric ossicles, being obscured at each end by the latter which overlies the posterior edge of the urocardiac. According to Mocquard (1883) the urocardiac articulates with a pre-pyloric ossicle, which he describes, but in *A. innocous* I cannot distinguish such a separate ossicle which, I assume, is fused to the pyloric or has disappeared. The armature of the urocardiac ossicle is enabled to extend posteriorly and ventrally into the cardiac chamber partly by virtue of an invagination. From near its posterior ventral extremity a bifid media tooth (figure 92, MT, figure 100, plate 7) projects downward into the now rapidly narrowing cavity. Posteriorly the urocardiac ossicle also gives rise to two lateral lobes (LL) that abut on the zygo-cardiac ossicle (see below) and whose long stiff setae extend postero-ventrally into the narrow posterior end of the cardiac chamber.

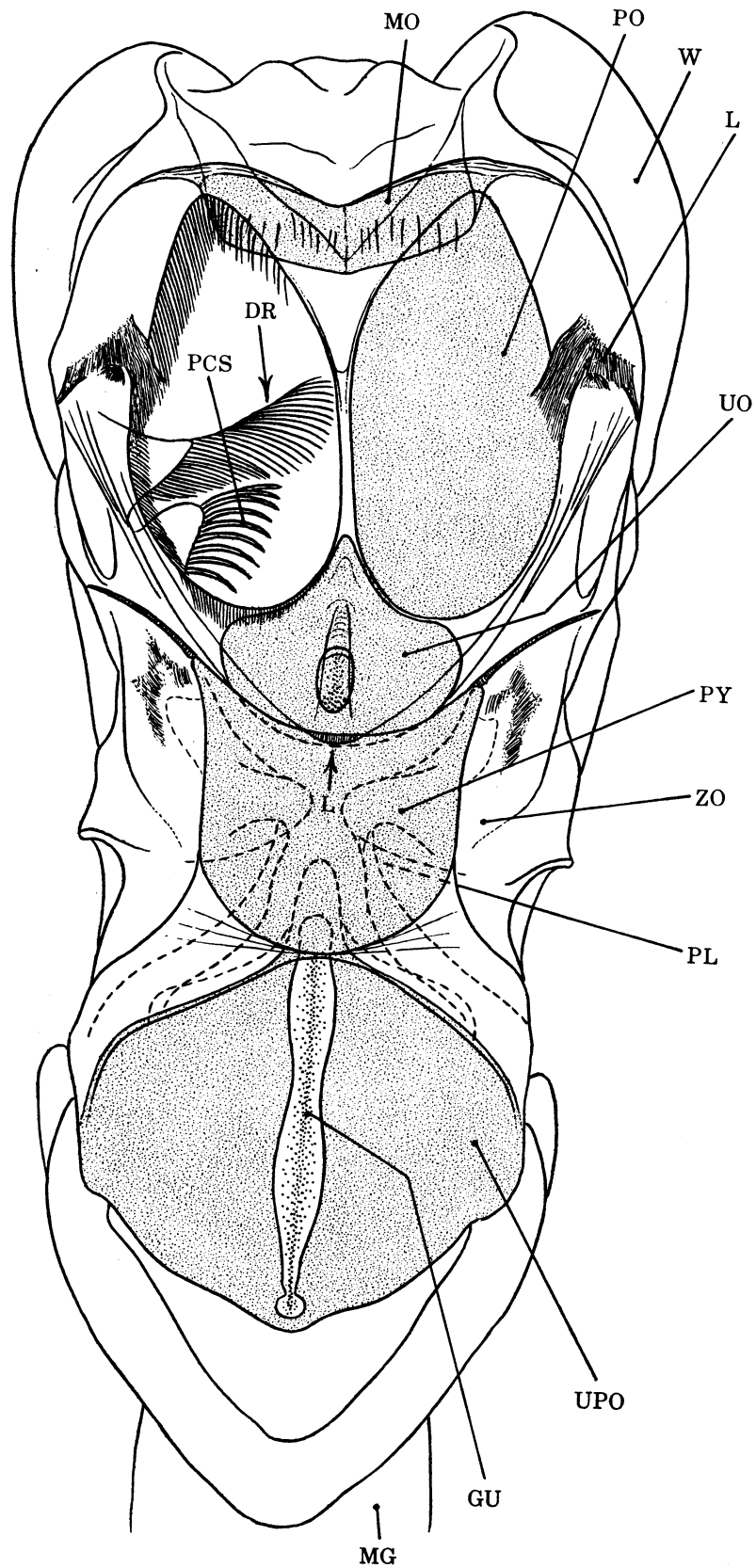


FIGURE 91. The fore-gut of *Atya innocous* seen from above after removal of all attached and investing muscles. On the left the pterocardiac ossicle (PO) is shown as a transparent window – which indeed it virtually is – and the distal row of spines (DR) of the anterior comb plate and the spines of the posterior comb plate (PCS), as seen through it, are shown in a simplified manner, elaborations of their setae being omitted. The armature of the left pterocardiac ossicle only is shown. Mechanical stippling is used purely for convenience to show the limits of certain ossicles.

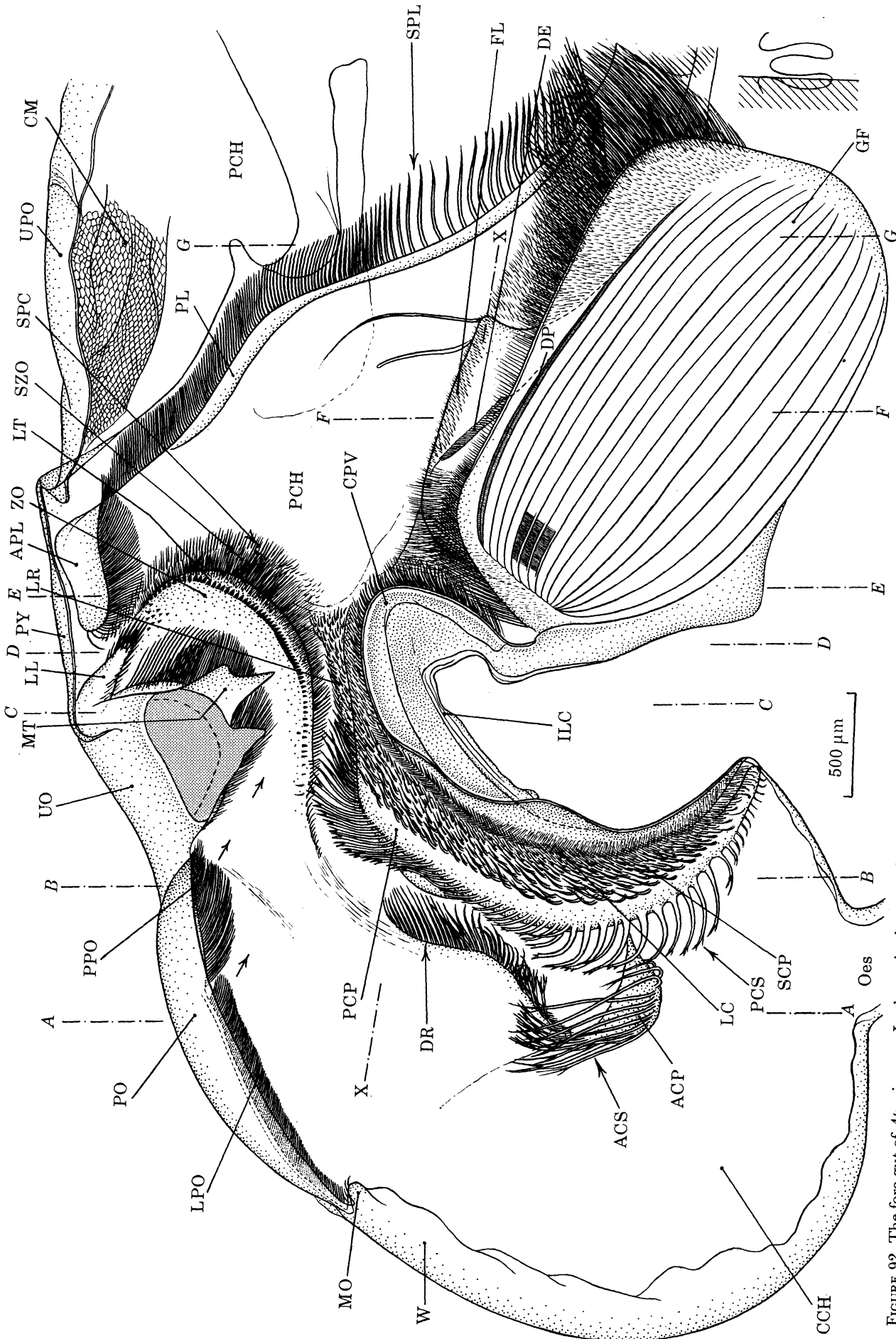
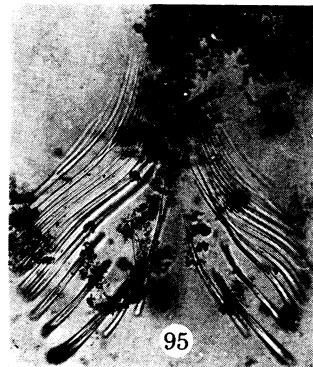


FIGURE 92. The fore-gut of *Atya innocuous*. In the main the organ has been bisected and the left half removed, but of the gland filter (GF) - bottom right - which consists of an inner and two outer 'leaves' (see text and inset which shows this diagrammatically) only the left outer leaf has been removed to reveal the left face of the inner leaf. A fragment of the convoluted membrane (CM) is shown schematically in the dorsal part of the pyloric chamber. The urocardiac ossicle (UO) is cut to the viewer's side of the mid-line and its invagination indicated in a simplified manner. Positions A-A to G-G indicate the levels of transverse sections shown in figures 95-107, plates 6-9, and X-X the level of the horizontal section in figure 114, plate 10. The scale refers to an individual 6 cm in length but no significant size related changes in form have been noted.



FIGURES 93-97. For description see opposite.



On each side of the urocardiac ossicle is a broad zygo-cardiac ossicle (ZO) which bears posteriorly and ventrally a row of about 60 small but stout sclerotized teeth, the lateral teeth (LT), opposed to their neighbours on the opposite side, and is also armed with numerous slender spines (SZO). Immediately below the zygo-cardiac ossicles there is, on each side, a longitudinal spine-covered ridge on the lateral wall of the cardiac chamber (figure 92; figures 100 and 101, plate 7, LR). On each side the median tooth and zygo-cardiac ossicles lie above the posterior end of the posterior comb plate, which is borne on a stout chitinous support, the infero-lateral cardiac plate (ILC) of Mocquard. This plate also supports a broad tongue-like cardiopyloric valve (CPV) that occupies the floor of the narrow region between the cardiac and pyloric chambers. This is provided with a carpet of backwardly directed spinules (figure 92; figure 102, plate 7).

The narrow cardio-pyloric aperture, best appreciated from transverse sections (figures 100–102, plate 7), opens into the pyloric chamber (PCH) which is divided into upper and lower compartments. Along the floor of the upper compartment runs a median longitudinal slit that gives access to the so-called gland filter (GF) – a structure similar in essentials to that present in a variety of decapods of diverse feeding habits. This slit is guarded throughout its length by fine spines arising from its elongate flanking lips (figure 92, FL), the arrangement being different in the anterior and posterior portions (figures 103, 105, 106, plate 8; figure 108, plate 9). It is also guarded by similar fine spines borne along the length of the dorsal ridge of a median projection (figure 92, inset) that divides the filter into equal halves along its length and is directed towards the median slit. The latter spines (figures 103, 105, 106, plate 8; figure 108, plate 9) are directed dorsally through the slit and, acting in concert with those of the lips, effectively seal the slit-like opening against the entry of all save exceedingly minute particles. The inner face of each outer wall, and both faces of the median projection, are armed by rows of exceedingly close-set spinules whose layout is indicated semi-diagrammatically in figure 92 and whose nature can be appreciated from figures 108–110, plate 9. Anteriorly, where the outer wall rises above the median projection, it is provided with a row of close-set chitinous denticles (figure 92, DE; figure 106, plate 8; figure 109, plate 9), which help to guard, and can perhaps seal, the slit-like entrance. Dorsally the median projection bears a row of even finer denticles (DP).

The roof of the pyloric chamber is covered anteriorly by the pyloric ossicle (which also covers part of the cardiac chamber), posteriorly by the uropyloric ossicle (UPO). Beginning

DESCRIPTION OF PLATE 6

FIGURE 93. *Xiphocaris elongata*. Transverse section through the pyloric chamber of the fore-gut showing the spinous elongate median projection (MP) that restricts food particles to the lateral walls of the upper compartment. Immediately beneath this projection is the slit-like opening to the gland filter.

FIGURE 94. *X. elongata*. The same showing how the entrance to the gland filter is guarded by spinules. The ‘ghost’ spinules beneath the cuticle from which these arise are the Anlagen of those that will serve as their replacements at the next moult.

FIGURE 95. *A. innocous*. Transverse section showing the tips of the spines of the anterior comb plates of the cardiac chamber of the fore-gut.

FIGURE 96. *A. innocous*. Transverse section through the cardiac chamber of the fore-gut cutting through the anterior comb plates at about the level A–A in figure 92.

FIGURE 97. *A. innocous*. The same a little more posteriorly cutting through the posterior comb plates.

(Note: plates 7 and 8 continue this series of sections, all of which are of the same individual. The last member appears on plate 9.)

under this roof (figure 92; figure 104, plate 8, APL) and twisting so as to allow it to run obliquely backward down each lateral wall of the upper compartment is another, possibly compound, ossicle that bears a long row of spines (figure 92, SPL), very fine dorsally, coarser and more widely spaced ventrally (figure 107, plate 9). This is the pleuropyloric (PL). Some of its antero-dorsal spines are curved and reach into the adjoining recess (figure 104, plate 8). Antero-dorsally the walls of the chamber bear spinous pads (SPC) – largely obscured by the zygo-cardiac ossicle in figure 92 – some of which can be seen in figure 104, plate 8.

The lumen of the chamber is divided into a series of convoluted ducts or tubules (figures 105, 106, plate 8; figure 107, plate 9) by folds of exceedingly flimsy cuticle (figures 111, 112, plate 9), here referred to as the convoluted membrane, which displays characteristic reticulation. A fragment only of this is shown in figure 92 (CM). Basically this is a cellophane-like sheet on which the margins of the hexagons are elaborated from undulating ridges of cuticle. In certain marginal regions there are small areas of unelaborated sheet. Between here and the hexagon-covered regions is a narrow transition zone where ridges arise, become larger and more numerous, tend to overlap, and gradually sort themselves out into hexagons, thereby illuminating the nature of the latter. Between the tubules are wide spaces (figures 105, 106, plate 8). Food particles are confined to the tubules whose thin walls, one suspects, act like a peritrophic membrane, being readily permeable both to enzymes and the products of digestion which can move freely in the spaces and the more readily gain access to the food mass. By this means a more efficient system of digestion and absorption can be achieved than would be the case if the particles passed through the chamber as a single compact mass. Laterally, over a broad area food particles are in direct contact with the lateral walls of the chamber (i.e. are not separated from it by a reticulated membrane) so that the spines of the pleuropyloric ossicles can operate directly on the food mass. The tubules in no way prevent the entry of fine particles into the gastric filter whose slit-like opening is in direct contact with an unenclosed stream of particles just as are the lateral walls of the pyloric chamber. The system of tubules extends throughout the pyloric chamber but does not extend into the mid-gut.

The musculature of the decapod fore-gut varies much in detail from species to species but, as was observed by Mocquard (1883), a basic arrangement is recognizable throughout. Three 'higher' forms have recently been treated by Maynard & Dando (1974) who gave clear, simple illustrations. Although *Atya* is much smaller than any of these and the muscles not always easy to

---

#### DESCRIPTION OF PLATE 7

For ease of comprehension the approximate levels of several of these sections are indicated on figure 92, where all relevant structures are labelled. All photographs are of thick slices, focused on the most significant features of the section, and viewed from in front. Thus in some cases, as in figure 102, backwardly directed spinules are seen by focusing through the cuticle from which they arise.

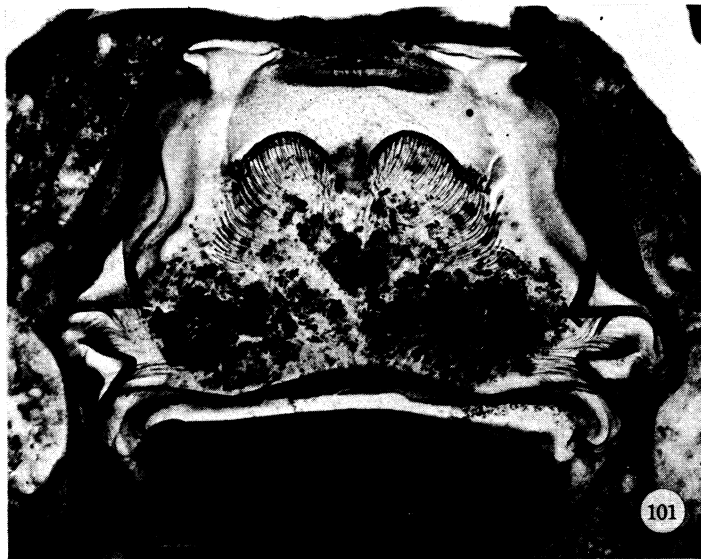
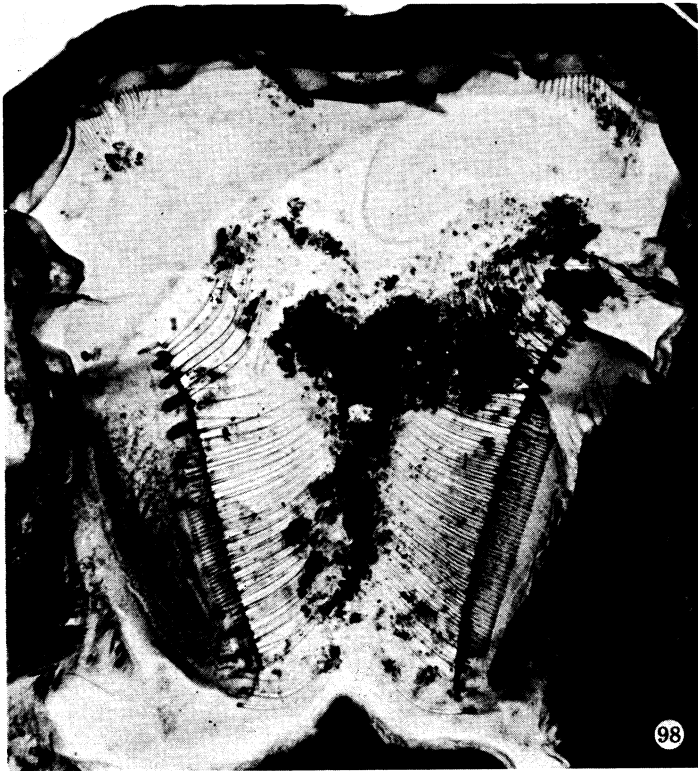
FIGURE 98. *Atya innocous*. Transverse section through the cardiac chamber of the fore-gut cutting through the posterior comb plates at the level *B-B* in figure 92. Dorsally some of the posterior armature of the pterocardiac ossicles can be seen (cf. also figure 91).

FIGURE 99. The same a little more posteriorly. Dorsally the median projection of the urocardiac ossicle is just coming into focus.

FIGURE 100. The same at about the level *C-C* cutting through the bifid median tooth of the urocardiac ossicle.

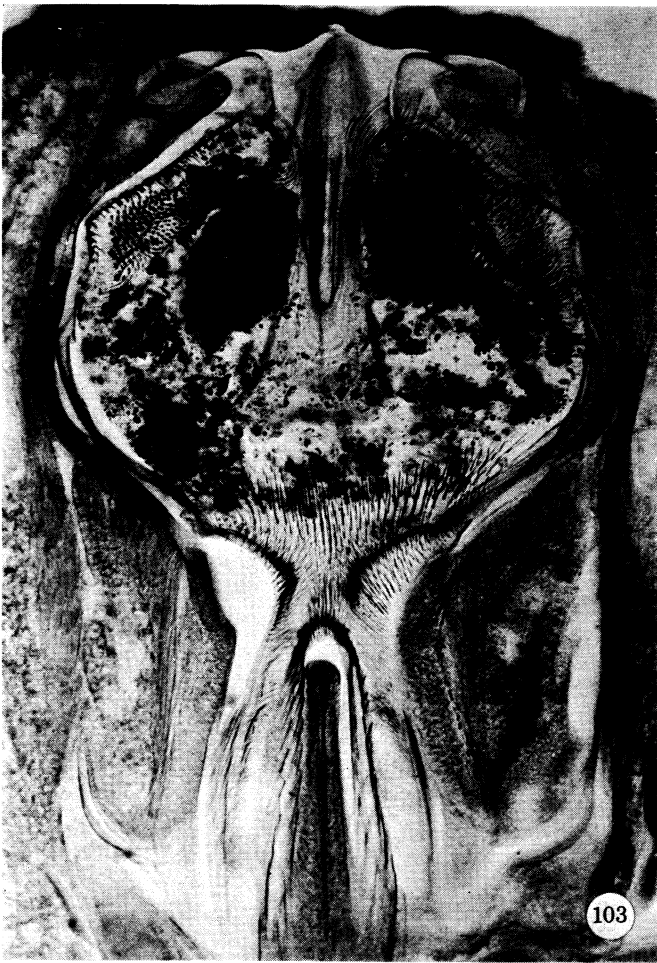
FIGURE 101. The same at about the level *D-D* where the chamber is narrowing.

FIGURE 102. Transverse section of the fore-gut at the level *E-E* where the cardiac chamber opens into the pyloric chamber. The large, median spinous pad is the cardio-pyloric valve. Some of the lateral teeth of the zygo-cardiac ossicle can be seen dorsally on the left. The first traces of the gastric filter appear ventrally.



FIGURES 98-102. For description see opposite.

(Facing p. 114)



FIGURES 103-106. For description see opposite.

trace, the principles elucidated by Maynard & Dando are applicable and only a brief outline account is necessary here. Although movements of the fore-gut cannot be seen in the living animal much can be inferred from anatomy and from manipulation. The greatest movements take place in the cardiac chamber. Its volume can be increased by the contraction of dilator muscles which take their origin on various rigid elements of both endo- and exoskeleton and insert on various anterior parts of the thin but tough cardiac wall. Its volume can be decreased by contraction of various intrinsic muscles that invest its walls, both originating and inserting on the ossicles of which it is in part comprised. More striking, however, are movements of the dorsal series of ossicles, especially the paired pterocardiacs and the urocardiac. These and the mesocardiac are pulled forward and away from the pyloric ossicle by anterior and posterior gastric muscles, and backward by intrinsic cardiopyloric muscles that are antagonistic to these. Manipulation of a skeletal fore-gut shows that contraction of the cardiopyloric muscles pulls back the pterocardiacs and that a relatively slight depression of these ossicles, which are laterally hinged by conspicuous ligaments (figure 91, L), causes the urocardiac – which is hinged by a single median ligament (L) to the pyloric ossicle – to swing under the latter and, more particularly, to slide downwards into the narrow cardio-pyloric passage as indicated by arrows in figure 92. Even unaided by the anterior gastric muscles the natural elasticity of the skeletal assemblage returns the dorsal ossicles to the position from which they are depressed: muscular contractions may therefore draw them even further and thereby increase the amplitude of movement. In *Astacus*, where true mastication is practised, the median tooth moves forward and ventrally (Huxley 1880), and this appears to be generally the case, at least in higher decapods. In *Atya* the swing is clearly in a different plane. A forward and downward movement would here serve no useful purpose and any forward movement is inevitably accompanied by a rise in the position of the tooth. That the zygo-cardiac ossicles swing towards each other and towards the median tooth is clear; but the amplitude of their movement is not known. Manipulation suggests that it is slight – as is indeed inevitable for the ossicles lie not far apart.

Food passing up the oesophagus (figure 92, Oes) enters the cardiac chamber from below. Almost immediately it comes within the field of operation of the anterior and posterior comb plates. The latter are borne on rigid supports – the infero-lateral ossicles – which can, however, be opposed by means of transverse muscles, thereby bringing the comb plates together and moving particles postero-dorsally. Manipulation reveals great elasticity ventrally which returns the posterior comb plates to the limits of abduction when the muscles are relaxed. The anterior

DESCRIPTION OF PLATE 8

FIGURE 103. *Atya innocous*. Transverse section through the pyloric chamber of the fore-gut a little posterior to level E-E in figure 92.

FIGURE 104. Left side of the dorsal compartment of the pyloric chamber at the same level as in figure 103, to show some of the details. The anterior dorsal extremity of the pleuropyloic ossicle (APL) is to be seen dorsally with its curved anteriormost spines reaching into the antero-dorsal recess from which they are well suited to rake particles.

FIGURE 105. The same more posteriorly. Here the food particles have entered the ducts formed by the convoluted membrane. Note, however, that no such membrane intervenes between the laterally lying particles and the wall of the pyloric chamber where the spines of the pleuropyloic ossicle, here seen more or less in transverse section, can just be made out.

FIGURE 106. The same at the level F-F in figure 92. Some parts of the convoluted membrane can be made out just above the slit-like opening to the gastric filter, whose chitinous denticles can also be seen.

comb plates appear to be more passive in their action. However, movements of the wall of the cardiac chamber will churn particles – which are in any case being forced through by material arriving from the oesophagus – and the comb plate spines, even if they never moved, would serve to direct particles dorsally and posteriorly and prevent their return. Dilation of the cardiac chamber will, however, draw the anterior comb plates apart and its contraction will bring them together. Muscle fibrils, detectable in sections, by pulling at the base of these plates, may perhaps somewhat alter their angle of attack, and swing their tips dorsally.

That the posterior armature of the posterior comb plates is much finer than that of the anterior part of the pads suggests the possibility of a grading of particles – fine material being extracted and propelled more effectively than coarse particles which thus remain longer in the cardiac chamber exposed to enzymatic action (see below). While mechanically feasible, proof of this is lacking, though there is a hint in sectioned material that the finest particles are dealt with by the finest setules (figure 99, plate 7).

An important contribution to the transport of the food particles is certainly made by the dorsal ossicles whose armature and movements are specialised for this function. The mesocardiac ossicle probably plays an insignificant role in this respect, but the setae of the pterocardiac ossicles sweep material backward and the ossicles themselves press it in this direction. (The cardiac chamber is often crammed with food.) A very positive contribution is made by the urocardiac ossicle whose bifid median tooth and setose lateral lobes propel material towards the narrow cardio-pyloric aperture. (This can be most clearly envisaged by reference to figures 100 and 101, plate 7.) Throughout the cardiac chamber the various spines and setae are so orientated as to guide or sweep particles posteriorly and to prevent their return. While the general action of the teeth of the zyocardiac ossicles is self-evident their effects are uncertain. These are the homologues of the major grinders in 'higher' forms, but here, while they may be involved in the tearing of such large food particles as occasionally ingested leaf fragments, relatively little breaking up of material is necessary, and they are not suited to grinding.

Food material entering the pyloric chamber passes into the ducts formed by the convoluted membrane. It should be noted, however, that such material as initially lies dorsally and, more posteriorly, lies laterally, can be acted upon directly by the spines of the pleuopyloric ossicle (figure 92; figure 107, plate 9). That these rake it posteriorly towards the mid-gut is self-evident.

#### DESCRIPTION OF PLATE 9

FIGURE 107. *Atya innocous*. Transverse section through the pyloric chamber of the fore-gut at the level G-G in figure 92. On the right the pleuopyloric ossicle has conveniently been torn away and clearly reveals the arrangement of its spines. The convoluted membrane which forms ducts in the lumen of the chamber is clearly seen.

FIGURE 108. *A. innocous*. Transverse section through the dorsal part of the gastric filter near its anterior end showing the elaborate array of guarding setae and spines.

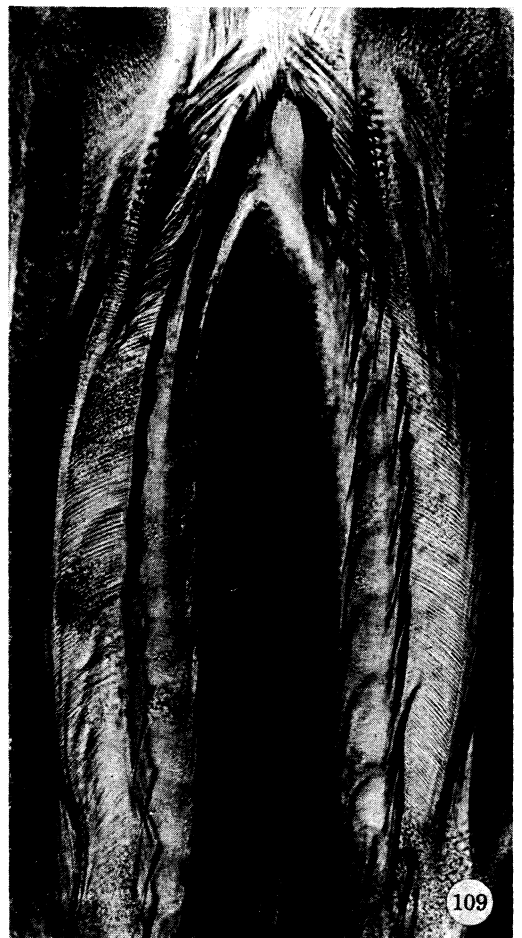
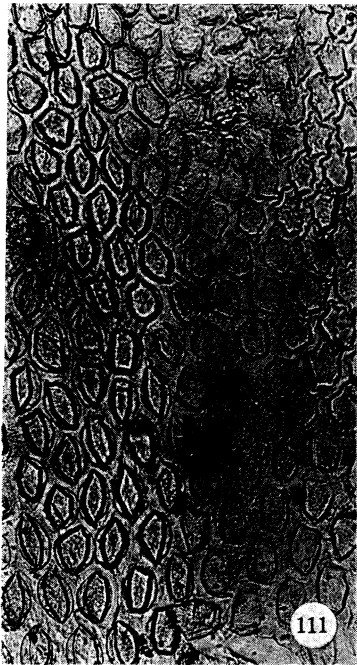
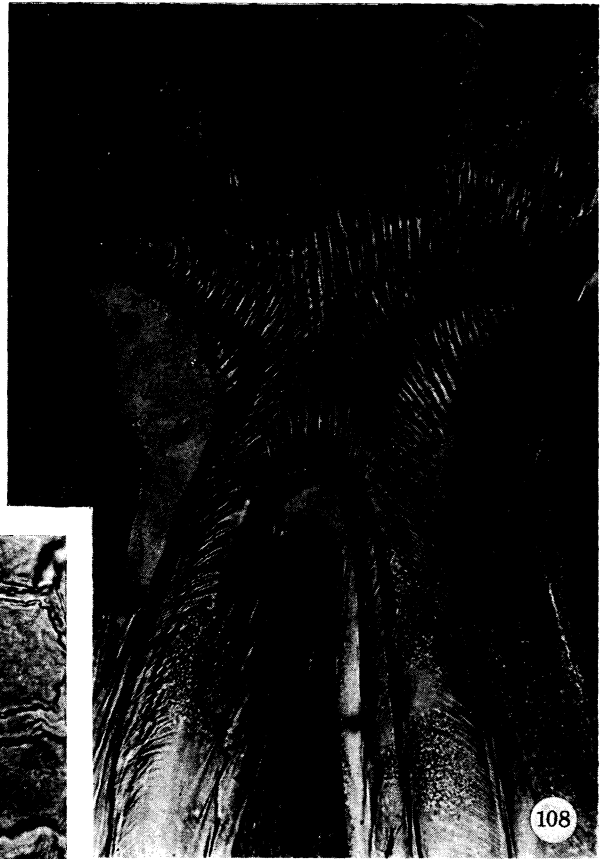
FIGURE 109. *A. innocous*. Transverse section through the gastric filter posterior to figure 108. Note the very fine spinules that line the walls of its chambers and the exceedingly fine particles that have found their way into these chambers.

FIGURE 110. *A. innocous*. Some of the armature of the gastric filter and food particles within it.

FIGURE 111. *A. innocous*. A portion of the convoluted membrane. Because of its shape this cannot be laid perfectly flat.

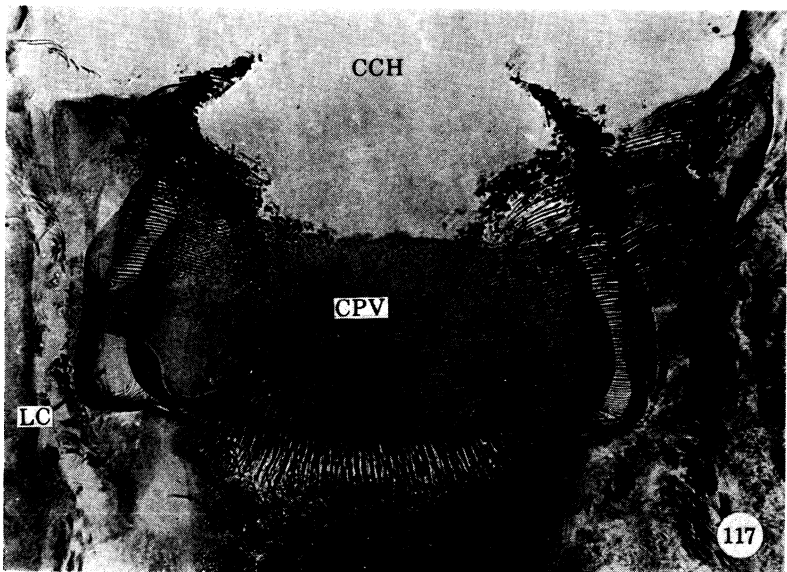
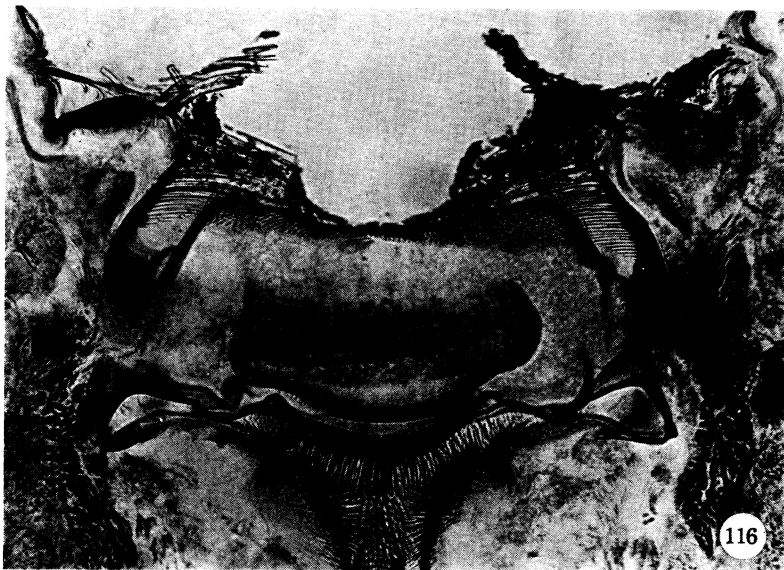
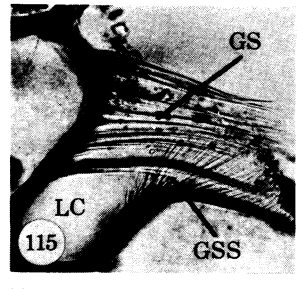
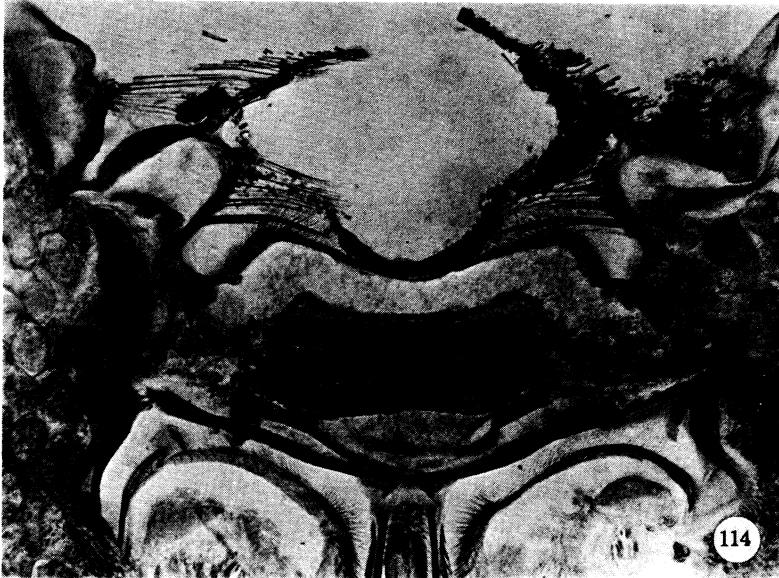
FIGURE 112. Details of the convoluted membrane.

FIGURE 113. *Xiphocaris elongata*. Transverse section through the gastric chamber of the fore-gut showing the posterior comb plates.



FIGURES 107-113. For description see opposite.

*(Facing p. 116)*



FIGURES 114-119. For description see opposite.



In the mid-gut it forms a compact mass. It seems possible that material enclosed in the ducts proper may move more slowly than that subject to raking by the pleuropyloric ossicles.

The actions so far described have been purely mechanical but studies of other decapods make it clear that within the cardiac chamber food particles are also subjected to the action of digestive enzymes originating in the hepatopancreas. This organ, which is as conspicuous in *Atya* as in other forms, serves both as a seat of enzyme secretion and of absorption. Its secretions pass via the gland filter to the cardiac chamber, in this case almost certainly via two narrow, almost duct-like channels one on each side of the cardio-pyloric valve around the tongue of which they curve. Anteriorly these run along the basal part of the posterior comb plates (figure 92 LC). Their course around the edge of the cardio-pyloric valve can be traced in both transverse and horizontal sections, most clearly in the latter (figures 114–117, plate 10). Throughout their length they are guarded by spines that overhang them and interlock with spinules arising from the cardio-pyloric valve or, anteriorly, the floor of the cardiac chamber (figures 100, 101, plate 7; figures 114–119, plate 10). The photographs show how effective is the screen of interlocking spines and spinules and how, although food particles lie adjacent to the channels, none are to be seen within them†. It is an almost certain inference that it is along these grooves that hepatopancreatic secretions pass forward into the cardiac chamber. As food is passing backwards through the central aperture there is in fact no other means whereby such secretions, whose presence in the cardiac chamber of decapods is apparently universal (e.g. see Yonge (1924) on *Nephrops*), can pass forward to it. Within the cardiac chamber, enzymes, assisted by mechanical action, will break down the often already very fine food particles. It is now well established (e.g. Yonge 1924) that minute particles and material in solution are taken into the hepatopancreas via the gland filter. In *Atya* it is clear that only exceedingly fine particles can gain entry to the gland filter, and this is readily confirmed by microscopical examination of the chamber within it. Here little more than a mucus-like haze is detectable (figures 108–110, plate 9).

If the mid-gut of *Atya* functions like that of such decapods as have been investigated some absorption, but no digestion, takes place there. In this respect attention is directed to the doubtful identity of the animal studied by van Weel (1955). Although designated as *Atya spinipes* Newport, he classifies it in the title of his paper as 'Decapoda-Brachyura' (*Atya* belongs to the Macrura) and refers to it throughout as a 'tropical freshwater crab'. Further he refers to

---

DESCRIPTION OF PLATE 10

FIGURE 114. *Atya innocous*. Horizontal section through the cardiac chamber of the fore-gut, the cardio-pyloric valve and the dorso-anterior extremity of the gland filter at about the level X-X in figure 92, which therefore cuts the dorsal part of the posterior comb plates more or less transversely. Note how the lateral channel on each side is guarded by overhanging spines that combine with fine spinules arising from the floor of the chamber to exclude particles from it. (See figure 115.)

FIGURE 115. The lateral channel (LC) in greater detail, showing the guarding spines (GS) and spinules (GSS).

FIGURE 116. The same a little more dorsal. Here the lateral channels are beginning to run more horizontally.

FIGURE 117. The same a little more dorsally. Here the way in which the lateral channels pass around the edges of the cardio-pyloric valve (CPV) and place the cardiac and pyloric chambers in communication is clearly seen, as is the way in which these grooves are guarded by fine spines.

FIGURE 118. As figure 117, to show the way in which the lateral channel is protected by a fence of fine spines.

FIGURE 119. Further details of the guarding spines.

† Screening is in fact even more efficient than is apparent as the spines bear lateral rows of close-set spinules, too fine to be revealed in the photographs, which bridge the gaps between them.

feeding his experimental animals on meat – with which *Atya*, a detritus feeder, could not cope. The physiological and cytological observations recorded in this paper therefore lose much of their value as it is not known to which animal they refer. They clearly cannot refer to *Atya*.

(c) *The fore-gut of Xiphocaris*

While showing many resemblances to that of *Atya*, the fore-gut of *Xiphocaris* differs in several conspicuous ways; most notably perhaps in the way in which food material is passed through the pyloric chamber. The cardiac chamber is much more elongate and tubular than that of *Atya* and the arrangement of its dorsal ossicles differs, but like that of *Atya* is provided ventrally with anterior and posterior comb plates (figure 120). Of these the anterior pair (ACP), unlike

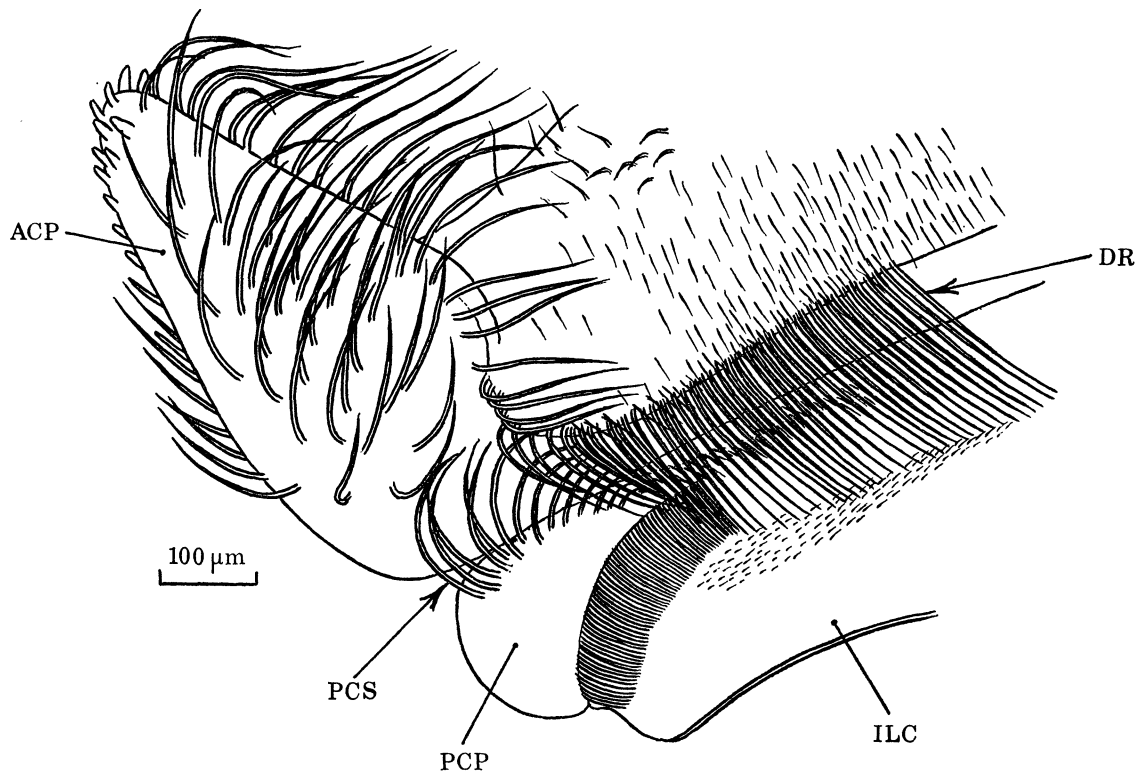


FIGURE 120. *Xiphocaris elongata*. The anterior comb plate (ACP) and the anterior part of the posterior comb plate (PCP) of the cardiac chamber of the fore-gut as revealed by dissection.

the flattened plates of *Atya*, are finger-like projections covered with spines and spinules some of which are shorter and more robust than those of *Atya*, others elongate and slender. As in *Atya* a row of fine spines (DR) extends from the anterior comb plate. Here it is associated with the posterior plate (PCP). Because the chamber is elongate, the posterior comb plates, which, like those of *Atya*, are borne on an infero-lateral cardiac ossicle (ILC), are straight over much of their length and only curve as they merge with the cardio-pyloric valve. The row of stout spines seen in *Atya* is represented by much shorter spines and the rest of the spinules with which they are provided form a less broad pad. Some details, and the relation of the spinules to the food mass, are shown in figure 113, plate 9.

Dorsally the mesocardiac ossicle, like that of *Atya*, consists of a fold in the wall, but is here somewhat more robust and has more spinules. The pterocardiac ossicles, instead of making up

the roof, are narrow and lie to each side of a roof which consists of a single unelaborated sheet of smooth chitin which is however thicker than the anterior lateral walls of the cardiac chamber. (An alternative, but I believe less likely, explanation is that the median sheet represents an anterior extension of the urocardiac ossicle which therefore articulates directly with the mesocardiac as in many higher decapods.) The urocardiac ossicle is provided with a single median tooth (figure 121, MT) and the lobes at each side of it are armed with short denticles (cf. the sweeping setae of *Atya*), these features being related to the coarser nature of the food particles in *Xiphocaris* than in *Atya*.

The location of the zygocardiac ossicles is much as in *Atya*. Each has a row of lateral teeth whose size, relative to that of the ossicle, is about the same as, or a little longer than, in *Atya*.

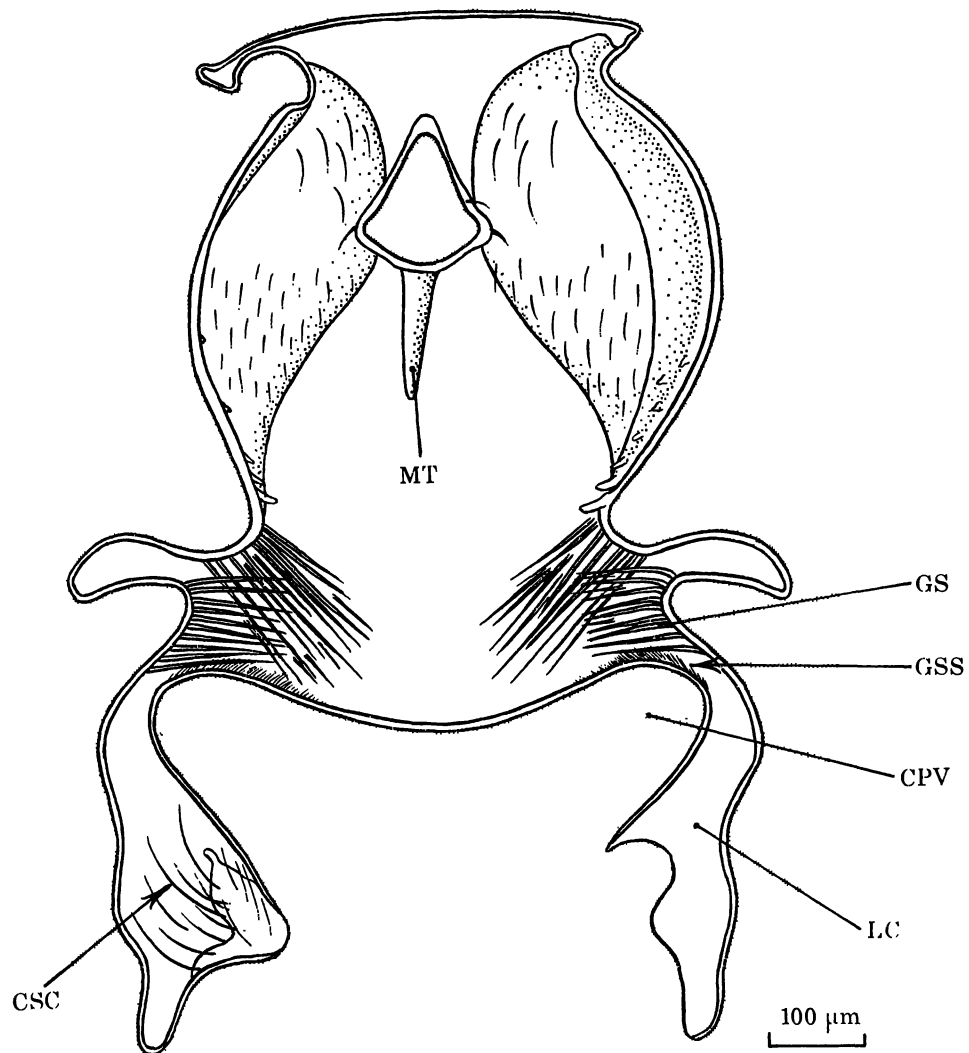


FIGURE 121. *Xiphocaris elongata*. Transverse section through the fore-gut at the level of the median tooth, to show especially the channels (LC) at each side of the cardio-pyloric valve (CPV) which unite the pyloric and cardiac chambers, and the spines (GS) and spinules (GSS) that exclude food particles from them.

Dorsal to these there is, over much of the inner face of the ossicle, a scattering of small denticles rather like the few found postero-dorsally in *Atya*. The greater prevalence of such denticles in *Xiphocaris* than in *Atya* is presumably related to the coarser nature of the food particles that it ingests. The zygocardiac ossicles are also armed with numerous long, backwardly and ventrally directed setae similar to, but relatively longer than, those of *Atya*. These serve to sweep material towards the pyloric chamber. As in *Atya* the cardio-pyloric aperture is narrow and, again as in *Atya*, there are screened channels (figure 121, LC) that run around the sides of the cardio-pyloric valve (CPV) and presumably permit hepatopancreatic secretions to pass, via the gland filter, to the cardiac chamber. Long, fine setules within these (CSC) probably serve a cleaning function. The gland filter is similar in principle to that of *Atya* but relatively smaller.

It is the upper part of the pyloric chamber that differs most strikingly from that of *Atya*. Its cavity is circular in section and little different in diameter from that of the mid-gut with which it is continuous. Running longitudinally along its floor is an elongate slit, guarded by spinules, which opens into the gland filter (figure 93, plate 6) as in *Atya*. The pyloric ossicle is small and articulates with a larger uropyloric which, like that of *Atya*, has a median longitudinal invagination. In *Xiphocaris*, however, this extends deeply into the chamber as an elongate projection (figure 93, plate 6, MP) so as more or less to divide it along its length. Furthermore, the projection is armed with long spinules that radiate outwards towards the walls of the chamber to which they approach closely but do not touch. Thus there is only a narrow crescentic channel between these spinules and the wall through which food particles can pass (figures 93, 94, plate 6). There is no trace of any convoluted membrane such as is found in *Atya* but, physiologically, the median plate serves the same purpose: it ensures that food material is spread as a thin layer so that material in solution and, perhaps, minute particles can diffuse freely through it. Such material presumably enters the gland filter as in *Atya*, and, ultimately, the hepatopancreas.

A pleuropyloric ossicle is elaborated in each lateral wall of the upper compartment of the pyloric chamber. Like that of *Atya* this is elongate and armed with a single row of spines and, as in *Atya*, begins in an antero-dorsal position and follows a similar course obliquely backward along the lateral walls. It can just be seen dorsally in figure 93, plate 6. Ventrally, from the posterior end of the pyloric chamber, there extend into the mid-gut two long conical projections similar to those to which, in other decapods, a valvular function has been attributed. Whether or not this is their function they are much longer than those of *Atya*.

(d) *The remaining non-Acanthephyroid species and a note on Caridina*

The fore-guts of *Micratya*, *Potimirim* and *Jonga* closely resemble those of *Atya*. All have a convoluted membrane in the dorsal compartment of the pyloric chamber and not, as does *Xiphocaris*, a median plate. Such differences as exist are quantitative rather than qualitative, and while some of them, such as the presence of fewer, relatively stouter, lateral teeth on the zygocardiac ossicle of *Micratya* and *Jonga* are doubtless of ecological significance they in no way alter the principles on which the apparatus is built or operates.

Among the animals whose fore-gut was studied by Patwardhan (1935c) was an alleged Indian atyid that he called *Caridina brachydactyla* de Man, which is regarded as a form of *C. nilotica* Roux by Bouvier (1925). Of its fore-gut he gives a simple sketch and brief description. This differs so much from the fore-gut of the atyids described here, and from the description given by Mocquard (1883) of the Algerian animal that he called *C. longirostris* H. Milne-Edwards,

which is also regarded as a form of *C. nilotica* by Bouvier, as to be puzzling. Fortunately I have been able to examine two sets of transverse sections of the closely related *Caridina africana* that I prepared many years ago and find that, as anticipated, the fore-gut of this animal is very similar to the Dominican non-Acanthophyroid species and bears little resemblance to that figured by Patwardhan. For example, *C. africana* has conspicuous comb plates. No such are shown by Patwardhan for his alleged *Caridina*. It also has a convoluted membrane in the pyloric chamber. Patwardhan's observations on other species are of a sufficiently high standard to suggest that he would not have missed such things as the comb plates and it can be tentatively concluded that the animal he studied was not a *Caridina*, nor indeed an atyid, but some other locally collected caridean.

(e) *Structure and function of the decapod fore-gut and its relation to the mouthparts and feeding habits*

In a series of papers dealing with a variety of decapods Patwardhan (1934, 1935–1935*d*) drew two conclusions: first, that the forms regarded as primitive on other grounds have the simplest types of fore-gut (generally referred to as a gastric mill in higher forms); second, that what he called the 'efficiency' of the gastric mill is related to the ability of the mouthparts, especially the mandibles, to masticate the food. He regarded a mill able to tear and masticate the food as most 'efficient'. With these conclusions Reddy (1935) concurs. While both contain an element of truth, with neither is it possible to agree in entirety.

It is true that some primitive Natantia have a very simple fore-gut and that primitive forms as a whole tend to display a simple condition in this respect, but this generalization is not applicable to the Atyidae whose members, while regarded as 'lower' decapods, have a complex and highly specialized fore-gut. Complexity here is related to the need to cope with finely particulate food – feeding habits entirely different from those of most 'higher' forms.

Both Patwardhan and Reddy regarded forms with cutting and tearing mandibles as having less efficient oral apparatus than those whose mandibles have large molar processes, which they believed to be efficient crushers of food. Both also associated habits with the degree of 'efficiency' of the fore-gut – 'timid' species being said to ingest large lumps of food which could later be macerated and digested while the animal occupied a secure retreat. While these conclusions appear attractive, and there is an undoubted correlation between the presence of cutting and tearing mandibles, which pass large lumps of food into the fore-gut, and the development of crushing and grinding ossicles therein, it is not always correct to assume that a large molar process bespeaks of efficient crushing, and certainly wrong to regard non-crushing mandibles as inefficient or to refer to them as 'simple', as does Patwardhan 1935*d*, or 'feebly developed' as does Reddy (1935). On the contrary large molar processes are often indicative of a primitive condition and are not necessarily able to effect much crushing, while biting and slicing mandibles are the outcome of evolutionary specialization towards entirely different functions and are often extremely efficient at carrying out the tasks they have to fulfil. Although the mandibles of *Atya* have massive molar processes these are not related to the grinding of food material. Only minute particles are collected and little trituration is either necessary or practised.

Some general conclusions can be drawn. Decapods that feed on large lumps of food – with which powerful chelipeds and efficient slicing and biting mandibles, and in some cases robust post-mandibular mouthparts, enable them to deal – require a complex gastric mill for their

subsequent maceration. Forms whose food does not require such treatment in the fore-gut lack such apparatus, but the development of complex and highly specialized machinery for the treatment of ingested material is not precluded in 'lower' forms should the necessity for such arise. Such machinery, very different from that used for tearing and grinding, but equally specialized, is necessary for handling minute particles such as are utilized by most atyids. It is no accident that many larger decapods feed on large food masses. Their large size, giving greater muscular power than in smaller forms, lends itself to the utilization of such sources of food. Atyids are unusual in having given rise to some relatively large (but not enormous) species that are able to subsist on small particles. The key to their ability to have done so lies in their extremely specialized and efficient means of food collection, which has also demanded a specialized fore-gut.

#### X. ATYID ORIGINS, GEOGRAPHICAL DISTRIBUTION, ECOLOGY AND DISPERSAL

Several lines of evidence indicate that atyids are ancient inhabitants of freshwater. Their enormous area of distribution and the occurrence of fossils of Cretaceous age in freshwater deposits in Brazil (Roxo 1940; Buerlen 1950) testify to this, as does the fact that there has been much differentiation in freshwater, including the production of endemic genera in Lake Tanganyika. Today they are widespread throughout the freshwaters of the tropics, but a few have penetrated cooler regions. There are no marine atyids. On the other hand they have colonized freshwater in places like Hawaii and the Galapagos Islands that lack true freshwater fishes and amphibians. Further, some species occur in brackish pools, and these and certain of the cavernicolous forms, of which there are several, some belonging to purely cavernicolous genera, may indicate direct colonization from the sea. In some cases at least, however, colonization of such waters from freshwater is possible. As long ago as 1894 Ortmann felt that it was wrong to regard the ability of certain East Indian species of *Caridina* to tolerate brackish water as indicative of immigration from the sea. He considered this to be a case of adaptation to such conditions by members of an old element of the freshwater fauna. More recently Schminke (1972, 1973, 1974, 1975) has convincingly argued that those members of the Bathynellacea (Syncarida) that inhabit polyhaline waters (all members of the genus *Hexabathynella*) are derived, not directly from marine invaders, but from more primitive freshwater forms with a very long history in such waters, which they colonised perhaps as long ago as the Carboniferous. It might also be noted that among the branchiopod Crustacea – freshwater animals par excellence – the otherwise exclusively freshwater Anostraca includes *Artemia* which has colonized salt lakes and salt pans that are far more saline than the sea. Salt-tolerance or life in proximity to the sea is therefore not an automatic criterion of immediate marine ancestry, especially in a large family with no present-day marine representatives.

Habits also bespeak a long ancestry in freshwater. Thus, in *Atya*, passive filtration involves complex adaptations to life in flowing water which are indicative of long residence in such situations. In spite of these anatomical and ecological specializations the genus has a virtually circumtropical distribution including such isolated places as Mauritius and Hawaii. Its absence from certain large areas, such as East Africa, may be due to ecological factors rather than inadequate means of dispersal. Its adult specializations are of such complexity as to preclude the possibility that they were independently acquired in several different places. Equally they are of a kind that would be useless in, and effectively preclude its dispersal by, the sea – from which it is not reported – even if its physiology would permit this.

In considering means of dispersal much depends on the degree of tolerance of salt water. Atyids have few attributes that would enable them to disperse by other means. Overland dispersal can have played little part and they do not possess resistant eggs or other stages. Not only are adult atyids confined to freshwater but some are certainly unable to survive in seawater. Thus, while showing some degree of euryhalinity, adults of the Hawaiian *Atya bisulcata* (Randall) are incapable of withstanding 12 h immersion in seawater (Edmondson 1929). Likewise the Californian *Syncaris pacifica* was shown by Hedgepeth (1968) to be incapable of living in full seawater though able to survive at salinities of up to 24‰. Hedgepeth, without mentioning larvae, thinks that *S. pacifica* cannot have achieved its present – very restricted – distribution in separated streams by migration from one to the other via the sea.

Interest therefore centres on larvae as potential agents of dispersal and much depends on their ability to tolerate seawater. Many atyids, such as *Caridina* and the endemic forms of Lake Tanganyika, habitually reproduce in freshwater yet have larval stages such as one associates with marine forms. Many larvae of *Atya bisulcata* of Hawaii were successfully reared in freshwater by Edmondson (1929), who showed that 10-day-old larvae mostly died within 4 h in seawater. Bordage (1908) also reared *A. serrata* Spence Bate (*A. pilipes* Newport?) of Reunion in freshwater and there is evidence that *A. innocous* can also breed successfully in this medium. I was informed that in the ornamental pool in Dominica in which certain observations were made numbers had increased since the original introduction. On the other hand Johnson (1967), speaking apparently from personal experience of *A. spinipes* Newport in Malaya, says that 'post larvae have been collected in marine habitats', and Hunte (1975) noted that larvae of *A. lanipes* Holthuis were not apparently harmed when the salinity was gradually increased to 20‰ over a 3 h period. This, however, is still less than 60 ‰ seawater.

Ecological evidence suggests reproduction in freshwater by at least one of the smaller Dominican atyids. Eggs of *Micratya poeyi* hatch as zoea larvae. Although Chace & Hobbs (1969) remark, doubtless correctly, that some of these are unlikely to avoid being swept into the sea, I am more impressed by the occurrence of adults in the upper reaches of streams several miles from the sea and at over 1300 ft in altitude. Often such streams are torrential and present many obstacles to upstream migration by small prawns. The distribution of juveniles along the length of a suitable stream would throw light on this. Certainly small juveniles occur in streams (Chace & Hobbs record individuals with a carapace length of only 1.1 mm) though precise records of their altitude and distance from the sea are not recorded. Even if these small individuals occurred near the sea the chances of them having dispersed there are remote.

*Xiphocaris*, a larger prawn – but one less adapted to rapid flow – evidently undertakes such upstream movements for juveniles occur in large numbers in slow-flowing water near the sea and can tolerate at least some increase in salinity. It does not, however, ascend higher than 900 ft (Chace & Hobbs 1969). More significantly, very small individuals – carapace length 2.0–2.2 mm – were found in freshwater near the mouth of the Layou River by Chace & Hobbs, where I also found many juveniles (carapace lengths 3.0–5.5 mm in a small sample). If these had been in the sea, of which there is no proof, their stay must have been brief and opportunities for dispersal scant. Thus, although larval forms may play a part in dispersal via the sea and would appear to be the only agents capable of explaining the wide distribution of certain Indo-Pacific species – and on the face of it the obvious one – this is far from conclusively demonstrated. Furthermore, available evidence suggests that such dispersal is prohibited on physiological grounds in certain cases where it would appear to be the only means available.

Hawaii is a striking example. These islands are less than 5 million years old and the main island less than 1 million, but have been colonized by the specialized *Atya bisulcata* which could scarcely have done so as an adult. Even if its larvae showed perfect physiological adaptation to seawater – and Edmondson's work showed they do not – the crossing of large tracts of open ocean is not easy to conceive. The relative youthfulness of Hawaii militates against colonization at a time when larvae were better suited to dispersal by sea, and the specializations of the adults testify to a long sojourn in freshwater. Further, the occurrence of this species on several islands of the group suggests dispersal since its differentiation as a distinct species.

Of the 13 West Indian atyids 3 are subterranean species which are confined to the islands and are of restricted distribution. *Xiphocaris elongata*, the most primitive living atyid, is also confined to these islands, throughout which it is widely dispersed. *Atya lanipes* and *Potimirim americana* (Guérin-Ménéville) are also known only from the West Indies, each being reported from three islands of which Jamaica is common to both. The remaining seven epigeal species are all known from mainland areas in Central or South America or both though their range is imperfectly known.

TABLE 1. THE EPIGEAN ATYID AND FRESHWATER PALAEMONID FAUNAS OF CERTAIN WEST INDIAN ISLANDS

	area/miles <sup>2</sup>	Atyidae	Palae- monidae	total epigeal Caridea
Cuba	44 164	7	4	11
Jamaica	4 411	8	4	12
Puerto Rico	3 423	7	5	12
Guadeloupe	583	7	6	13
Dominica	305	6	5	11

Recently much interest has been directed to the question of what determines the number of species of a given taxonomic group on islands, and attempts have been made to relate numbers to island size, distance from the mainland, from nearest neighbour and so on. A relevant example is the exercise of Terborgh (1973), who compared the number of species of birds on West Indian islands with island size, altitude and inter-island distance. The number of species increases with area. This is in keeping with the situation in terrestrial animals generally, for which, in a given region of relatively uniform climate, there is an orderly relation between island size and number of species (MacArthur & Wilson 1967). No such relation holds good for the atyids of the five adequately surveyed West Indian islands, which embrace a wide size range. Cuba, much the largest island, has most species – nine – but of these two are subterranean and their presence is related to geology and its ecological consequences rather than to size. If the comparison is confined to epigeal species then size clearly bears little relation to species diversity (table 1). Although almost ten times as big as Jamaica, Cuba has one species fewer, and although almost 150 times as big as Dominica, has only one species more. Nor does proximity to the nearest land mass have much predictive value – but for biological rather than statistical reasons. Although Cuba is the most favourably located island in this respect (though it has probably never been united to the mainland) the mainland distribution of atyids is such that no advantages accrue. The same sort of picture emerges from a comparison of the freshwater representatives of the other local family of carideans, the Palaemonidae, again excluding cavernicolous forms of which there are four species of *Troglocubanus* in Cuba and one in Jamaica. From the point of view of atyids (and palaemonids) a small island such as Dominica



evidently offers almost as many ecological opportunities as does an island as large as Cuba. Each island is to an atyid (or palaemonid) the same as many islands to a bird. Each stream is the analogue of an island. This helps to explain the difference between the ratio, island size: number of species in groups such as birds and atyid prawns. If even a small island, such as Dominica, has many streams, then the range of available habitats is probably not very different from that presented by the much larger Cuba. Half a dozen streams may present the full spectrum of habitats available in the climatic region in which they occur. Thus an increase in the number of streams may not materially increase the number of habitats. As in the case of West Indian humming-birds (Lack 1973) the number of species on each island has been determined primarily by ecological factors, in particular the availability of habitats, and not by the difficulties of dispersal. When the diversity of habitats increases – the availability of caves in Cuba and Jamaica is an excellent example – these opportunities are exploited and the number of species increases. The riddle posed by the atyids is that, although the problems of dispersal appear to have been easily surmounted – as shown by the occurrence of the same species in many streams and on several apparently well isolated islands – we have little idea of how this was done.

In the West Indies and surrounding continental regions differentiation of the atyid stock has led to the formation of several species and even genera. At the generic level *Xiphocaris* is endemic to the West Indies while *Micratya*, *Potimirim* and *Jonga* are all confined to the West Indies and adjacent land masses. Some occur on several islands. If dispersal was an event of the distant past one would expect more evidence in the form of geographical speciation. The lack of such suggests at least intermittent gene exchange between the populations involved. Furthermore, the pattern of distribution of such animals is more complex than that of such mobile terrestrial creatures as birds where, in spite of ecological obstacles, an island, once reached, offers relatively few barriers to exploration, if not colonization. Atyid prawns, however, occur in many isolated streams, each the equivalent of an island to a bird, so differentiation within an island would appear feasible. Of this there is little evidence.

Within Dominican streams some ecological separation between species is clearly apparent. *Xiphocaris* and *Jonga* differ from the other species, and between themselves, in habitat preferences and feeding mechanisms. Differences between the remaining species, while clear, are not yet fully explained. *Atya innocous* (common) and *A. scabra* (rare) may compete. Here, *A. innocous*, which scrapes and filters, may have an advantage over *A. scabra* which is specialized for filtering and, perhaps because of this or perhaps because forced there by *A. innocous*, appears to be restricted to regions of fast-flowing water. *Micratya* is smaller than either and can therefore frequent smaller crevices, whether among stones or piles or drifted leaves, but may compete with young *Atya*. *Potimirim* is also rare and apparently confined to fast flowing water, but whether by preference or because forced there by competition remains unknown.

Before I visited Dominica, Dr H. H. Hobbs Jr kindly provided background information and also gave me preserved specimens of all its atyid species which not only facilitated recognition in the field but gave me hints of what to observe there. For these kindnesses I am most grateful. I also thank Miss Olive Forshaw for much practical help and in particular for her care in printing the photographs used in the plates, Dr L. B. Holthius who provided a xerocopy of an otherwise virtually unobtainable paper, and Dr K. E. Banister who identified the fishes mentioned.

## REFERENCES

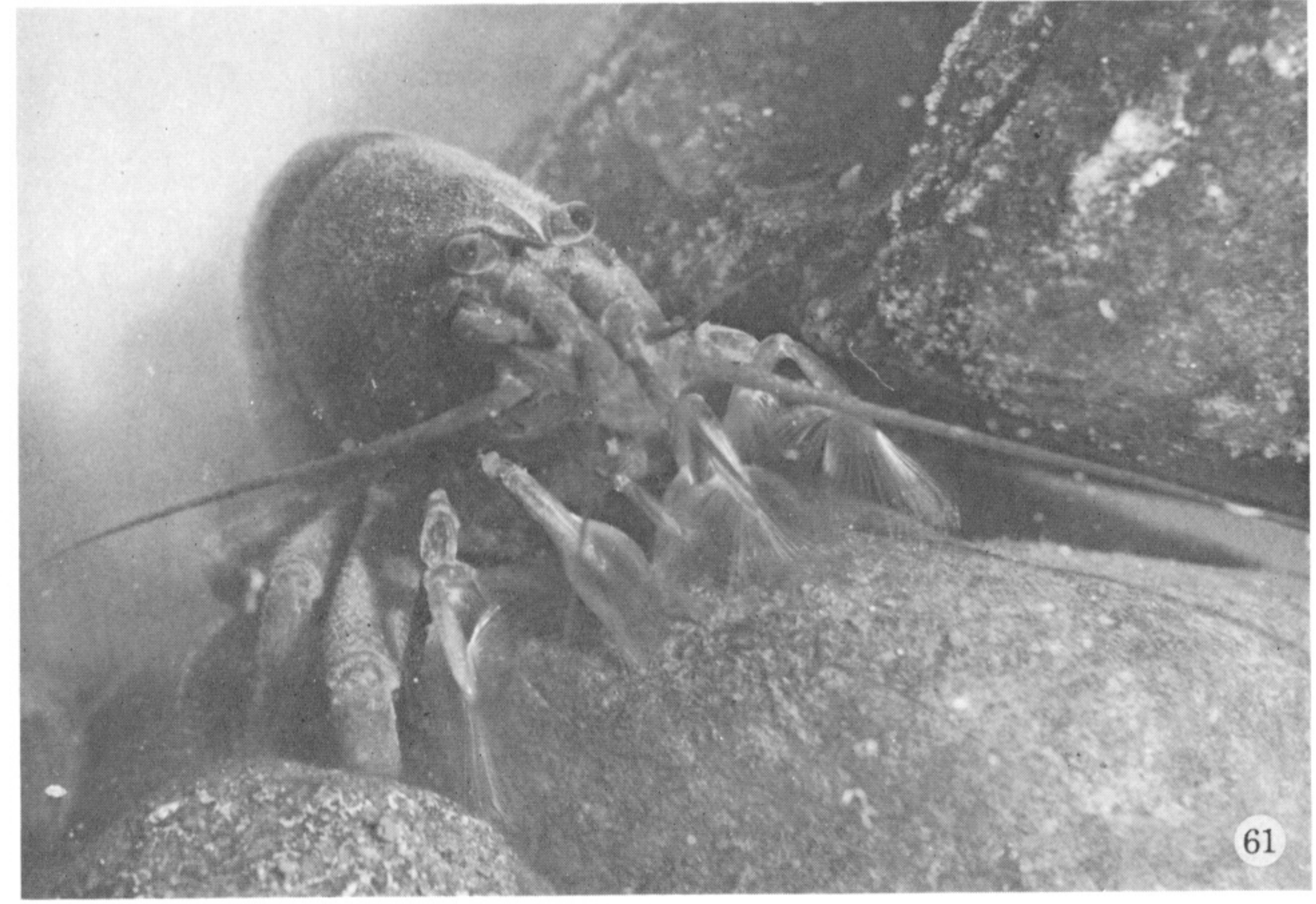
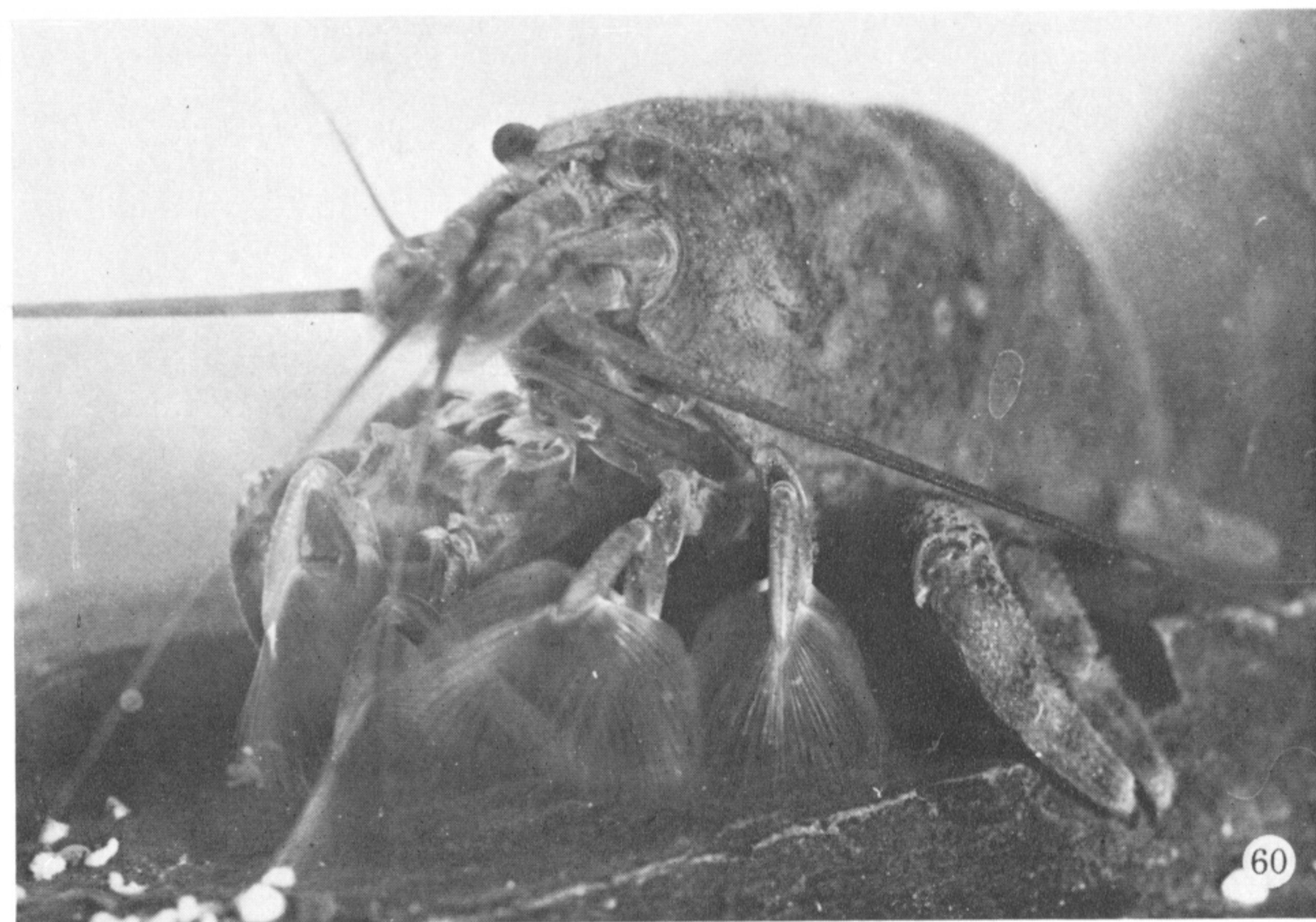
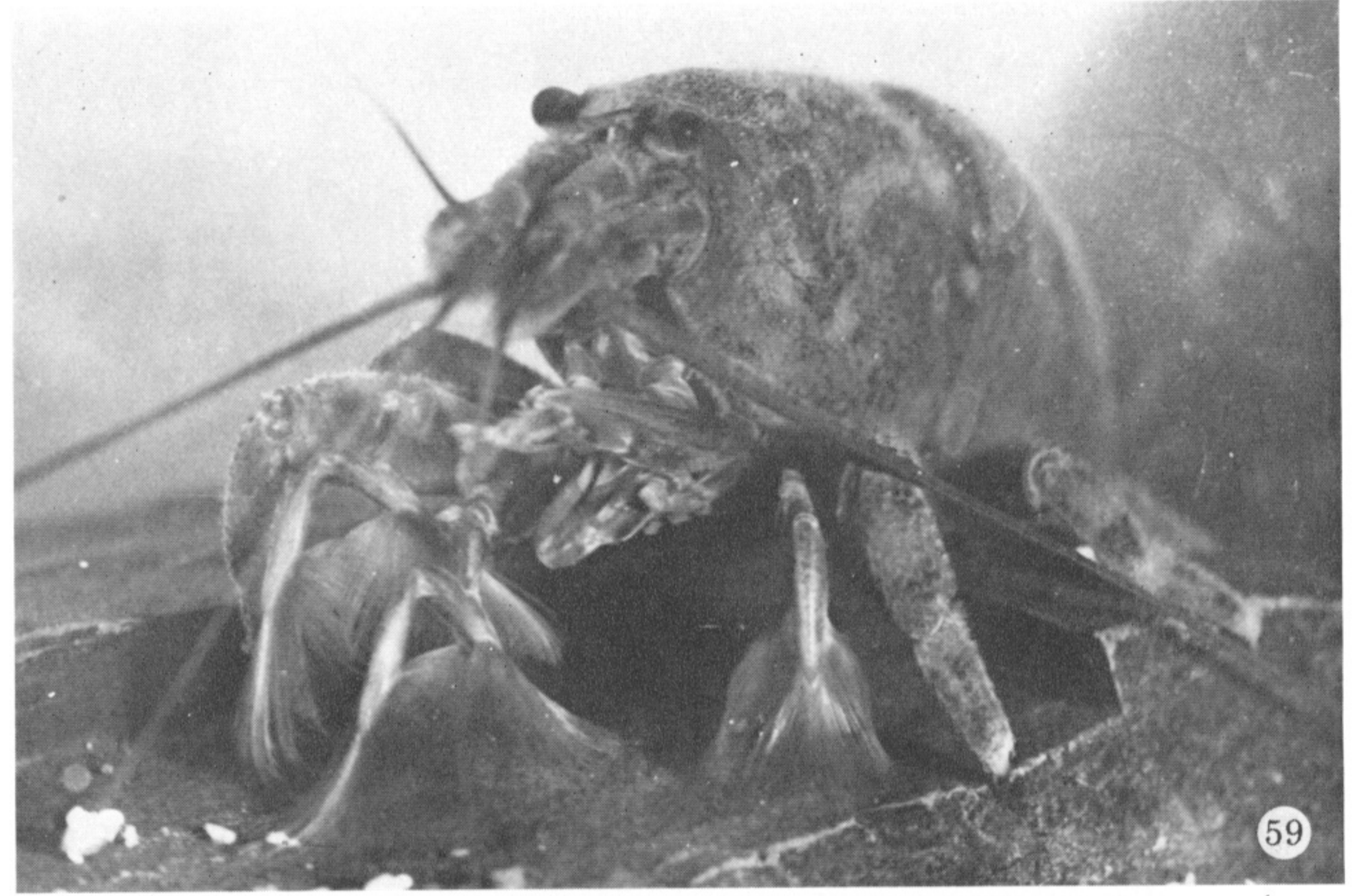
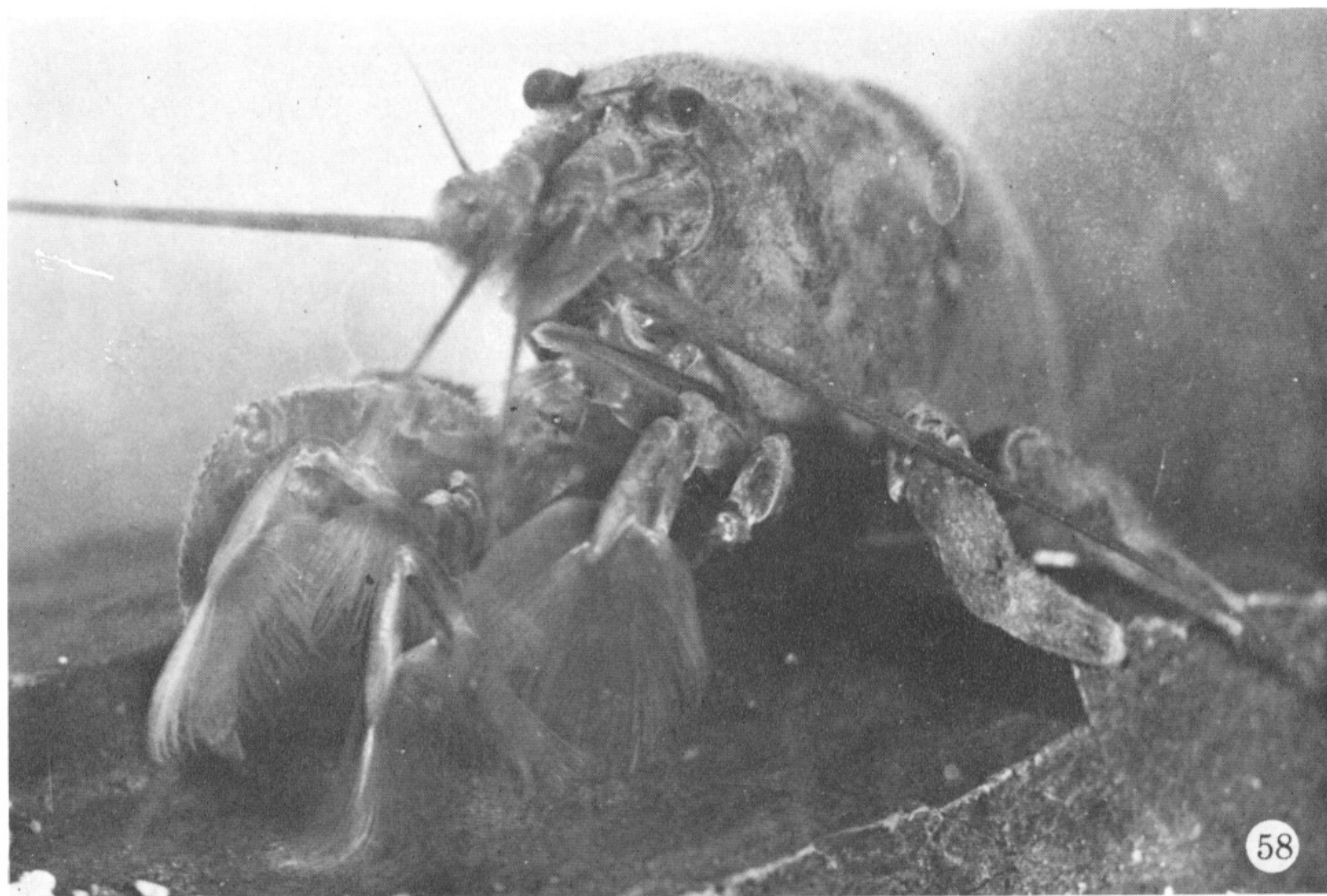
- Amans, P. 1881 Recherches anatomiques et physiologiques sur la larve de l'*Aeschna grandis*. *Lab. Zool. Fac. Sci. Montpellier* (sér. 3) **1**, 63–74. (Original not seen.)
- Berkeley, A. A. 1928 The musculature of *Pandalus danae* Stimpson. *Trans. R. Can. Inst.* **16**, 181–231.
- Beurlen, K. 1950 Alguns restos de crustáceos decápodes d'água doce fósseis no Brasil. *Anais Acad. bras. Cienc.* **22**, 453–459.
- Bonnier, J. 1899 Sur les pénéides du genre *Cerataspis*. *Trav. stn Zool. Wimereux* **7**, 27–49.
- Bordage, E. 1908 Recherches expérimentales sur les mutations évolutives de certains Crustacés de la famille des Atyidae. *C. r. hebd. Séanc. Acad. Sci., Paris* **147**, 1418–1420.
- Bouvier, E. L. 1925 *Recherches sur la morphologie, les variations, et la distribution géographique des crevettes d'eau douce de la famille des atyidés*. *Encycl. ent.* **4**, 370 pp.
- Cannon, H. G. 1947 On the anatomy of the pedunculate barnacle *Lithotrya*. *Phil. Trans. R. Soc. Lond. B* **233**, 89–136.
- Cannon, H. G. & Manton, S. M. 1927 On the feeding mechanism of a mysid crustacean, *Hemimysis lamornae*. *Trans. R. Soc. Edinb.* **55**, 219–253.
- Chace, F. A. Jr & Hobbs, H. H. Jr 1969 The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. *Bull. U.S. natn. Mus.* **292**, 258 pp.
- Chace, F. A. Jr & Manning, R. B. 1972 Two new caridean shrimps, one representing a new family, from marine pools on Ascension Island (Crustacea: Decapoda: Natantia). *Smithson. Contr. Zool.* no. 131, 1–18.
- Cowles, R. P. 1915 The habits of some tropical Crustacea: II Feeding habits of *Atya molluccensis* and *Caridina* species. *Philipp. J. Sci.* **10**, 11–18.
- Darnell, R. M. 1956 Analysis of a population of the tropical freshwater shrimp *Atya scabra* (Leach). *Am. Midl. Nat.* **55**, 131–138.
- Davies, L. 1974 Evolution of larval head-fans in Simuliidae (Diptera) as inferred from the structure and biology of *Crozetia crozetensis* (Womersley) compared with other genera. *Zool. J. Linn. Soc.* **55**, 193–224.
- Davis, C. C. 1964 A study of the hatching process in aquatic invertebrates. IX: Hatching within the brood sac of the ovoviviparous isopod, *Cirolana* sp. (Isopoda, Cirolanidae). X: Hatching in the freshwater shrimp *Potimirim glabra* (Kingsley) (Macrura, Atyidae). *Pacif. Sci.* **18**, 378–384.
- Edmondson, D. H. 1929 Hawaiian Atyidae. *Bull. Bernice P. Bishop Mus.* no. 66, 3–36.
- Ellis, C. H. 1944 The mechanism of extension in the legs of spiders. *Biol. Bull. mar. biol. Lab., Woods Hole* **86**, 41–50.
- Flint, O. S. Jr 1968 Bredin–Archbold–Smithsonian biological survey of Dominica. 9. The Trichoptera (Caddis flies) of the Lesser Antilles. *Proc. U.S. natn. Mus.* **125**, 1–86.
- Fryer, G. 1960 The feeding mechanism of some atyid prawns of the genus *Caridina*. *Trans. R. Soc. Edinb.* **64**, 217–244.
- Fryer, G. 1963 The functional morphology and feeding mechanism of the chydorid cladoceran *Eurycerus lamellatus* (O. F. Müller). *Trans. R. Soc. Edinb.* **65**, 335–381.
- Fryer, G. 1965 Studies on the functional morphology and feeding mechanism of *Monodella argentarii* Stella (Crustacea: Thermosbaenacea). *Trans. R. Soc. Edinb.* **66**, 49–90.
- Fryer, G. 1966 *Branchinecta gigas* Lynch, a non-filter-feeding, raptatory anostracan, with notes on the feeding habits of certain other anostracans. *Proc. Linn. Soc. Lond.* **177**, 19–34.
- Fryer, G. 1968 Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): a study in comparative functional morphology and ecology. *Phil. Trans. R. Soc. Lond. B* **254**, 221–385.
- Fryer, G. 1974 Evolution and adaptive radiation in the Macrothricidae (Crustacea: Cladocera): a study in comparative functional morphology and ecology. *Phil. Trans. R. Soc. Lond. B* **269**, 137–274.
- Harrison, A. D. & Rankin, J. J. 1975 Forest litter and stream fauna on a tropical island, St Vincent, West Indies. *Verh. int. Verein. theor. angew. Limnol.* **19**, 1736–1745.
- Hart, C. W. 1961 The freshwater shrimps (Atyidae and Palaemonidae) of Jamaica, W.I.; with a discussion of their relation to the ancient geography of the Western Caribbean area. *Proc. Acad. nat. Sci. Philad.* **113**, 61–80.
- Hart, C. W. Jr & Hart, D. G. 1969 A contribution to the limnology of Dominica, West Indies. *Proc. Acad. nat. Sci. Philad.* **121**, 109–126.
- Hedgepeth, J. W. 1968 The atyid shrimp of the genus *Syncaris* in California. *Int. Revue ges. Hydrobiol. Hydrogr.* **53**, 511–524.
- Holthuis, L. B. 1954 On a collection of decapod Crustacea from the Republic of El Salvador. *Zool. Verh., Leiden*, no. 23, 1–43.
- Holthuis, L. B. 1963 On red coloured shrimps (Decapoda, Caridea) from tropical land-locked saltwater pools. *Zool. Meded., Leiden* **38**, 261–279.
- Holthuis, L. B. 1973 Caridean shrimps found in land-locked saltwater pools at four Indo-West Pacific localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaiian Islands), with the description of one new genus and four new species. *Zool. Verh., Leiden*, no. 128, 1–48.
- Hunte, W. 1975 *Atya lanipes* Holthuis 1963, in Jamaica, including taxonomic notes and description of the first larval stage (Decapoda, Atyidae). *Crustaceana* **28**, 66–72.

- Huxley, T. H. 1880 *The crayfish. An introduction to the study of zoology*. New York: Appleton. (xiv + 371 pp.)
- Hynes, H. B. N. 1970 *The ecology of running waters*. Liverpool University Press (xxiv + 555 pp.).
- Johnson, D. S. 1967 Some factors influencing the distribution of freshwater prawns in Malaya. *Proc. Symp. Crustacea, Ernakulam*, part 1, 418–433.
- Lack, D. 1973 The number of species of hummingbirds in the West Indies. *Evolution, Lancaster, Pa.* **27**, 326–337.
- Lévêque, C. 1974 Crevettes d'eau douce de la Guadeloupe (Atyidae et Palaemonidae). *Cah. O.R.S.T.O.M. (sér. Hydrobiol.)* **8**, 41–49.
- Macarthur R. H. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton University Press (xi + 203).
- Manton, S. M. 1928 On some points in the anatomy and habits of the lophogastrid Crustacea. *Trans. R. Soc. Edinb.* **56**, 103–119.
- Manton, S. M. 1958 The evolution of arthropodan locomotory mechanisms. 6. Habits and evolution of the Lysioptaloidea (Diplopoda), some principles of leg design in Diplopoda and Chilopoda, and limb structure of Diplopoda. *J. Limn. Soc. (Zool)* **43**, 487–556.
- Manton, S. M. 1958a Hydrostatic pressure and leg extension in arthropods, with special reference to arachnids. *Ann. Mag. nat. Hist.* (13) **1**, 161–182.
- Manton, S. M. 1964 Mandibular mechanisms and the evolution of arthropods. *Phil. Trans. R. Soc. Lond. B* **247**, 1–183.
- Manton, S. M. 1973 Arthropod phylogeny – a modern synthesis. *J. zool. Lond.* **171**, 111–130.
- Maynard, D. M. & Dando, M. R. 1974 The structure of the stomatogastric neuromuscular system in *Callinectes sapidus*, *Homarus americanus* and *Panulirus argus* (Decapoda Crustacea). *Phil. Trans. R. Soc. Lond. B* **268**, 161–220.
- Mocquard, F. 1883 Recherches anatomiques sur l'estomac des crustacés podophtalmiques. *Anals Sci. nat. (Zool.)* **16**, 1–311.
- Müller, F. 1881 *Atyoida potimirim*, eine schlammfressende Süßwassergarneele. *Kosmos* **9**, 117–124.
- Müller, F. 1892 O camarão miudo do Itajahy, *Atyoida potimirim*. *Archos. Mus. nac., Rio de J.* **8**, 155–178.
- Ortmann, A. E. 1894 A study of the systematic and geographical distribution of the decapod family Atyidae. *Kingsley. Proc. Acad. nat. Sci. Philad.* **1894**, 397–416.
- Parry, D. A. 1957 Spider leg-muscles and the autotomy mechanism. *Q. Jl microsc. Sci.* **98**, 331–340.
- Parry, D. A. & Brown, R. H. J. 1959 The hydraulic mechanism of the spider leg. *J. exp. Biol.* **36**, 423–433.
- Parry, D. A. & Brown, R. H. J. 1959a The jumping mechanism of salticid spiders. *J. exp. Biol.* **36**, 654–664.
- Patwardhan, S. S. 1934 On the structure and mechanism of the gastric mill in Decapoda. I. The structure of the gastric mill in *Paratelphusa guerini* (M. Edw.). *Proc. Indian Acad. Sci. B* **1**, 183–196.
- Patwardhan, S. S. 1935 On the structure and mechanism of the gastric mill in Decapoda. II. A comparative account of the gastric mill in Brachyura. *Proc. Indian Acad. Sci. B* **1**, 359–375.
- Patwardhan, S. S. 1935a On the structure and mechanism of the gastric mill in Decapoda. III. Structure of the gastric mill in Anomura. *Proc. Indian Acad. Sci. B* **1**, 405–413.
- Patwardhan, S. S. 1935b On the structure and mechanism of the gastric mill in Decapoda. VI. The structure of the gastric mill in raptantous Macrura. *Proc. Indian Acad. Sci. B* **1**, 414–422.
- Patwardhan, S. S. 1935c On the structure and mechanism of the gastric mill in Decapoda. V. The structure of the gastric mill in natantous Macrura–Caridea. *Proc. Indian Acad. Sci. B* **1**, 693–704.
- Patwardhan, S. S. 1935d On the structure and mechanism of the gastric mill in Decapoda. VI. The structure of the gastric mill in natantous Macrura–Peneidea and Stenopidea; conclusion. *Proc. Indian Acad. Sci. B* **2**, 155–174.
- Reddy, A. R. 1935 The structure, mechanism and development of the gastric armature in Stomatopoda with a discussion as to its evolution in Decapoda. *Proc. Indian Acad. Sci. B* **1**, 650–675.
- Roxo, M. G. de O. 1940 Preliminary note on fossil Crustacea from Bahia, Brazil. *Anais Acad. bras. Cienc.* **12**, 279–280.
- Schminke, H. K. 1972 *Hexabathynella halophila* gen.n., sp.n. und die Frage nach der marinen Abkunft der Bathynellacea (Crustacea: Malacostraca). *Mar Biol.* **15**, 282–287.
- Schminke, H. K. 1973 Evolution, System und Verbreitungsgeschichte der Familie Parabathynellidae (Bathynellacea, Malacostraca). *Mikrofauna Meeres.* **24**, 1–192.
- Schminke, H. K. 1974 Mesozoic intercontinental relationships as evidenced by bathynellid Crustacea (Syn-carida: Malacostraca). *Syst. Zool.* **23**, 157–164.
- Schminke, H. K. 1975 Phylogenie und Verbreitungsgeschichte der Syncarida (Crustacea, Malacostraca). *Verh. dt. zool. Ges.* **1974**, 384–388.
- Snodgrass, R. E. 1938 Evolution of the Annelida, Onychophora, and Arthropoda. *Smithson. misc. Collns* **97** (6), 1–159.
- Snodgrass, R. E. 1950 Comparative studies on the jaws of mandibulate arthropods. *Smithson. misc. Collns* **116** (1), 1–85.
- Terborgh, J. 1973 Chance, habitat and dispersal in the distribution of birds in the West Indies. *Evolution, Lancaster, Pa.* **27**, 338–349.
- Thomas, W. J. 1970 The setae of *Austropotamobius pallipes* (Crustacea: Astacidae). *J. zool. Lond.* **160**, 91–142.
- Van Weel, P. B. 1955 Processes of secretion, restitution, and resorption in gland of mid-gut (glandula media intestini) of *Atya spinipes* Newport (Decapoda-Brachyura). *Physiol. Zool.* **28**, 40–54.

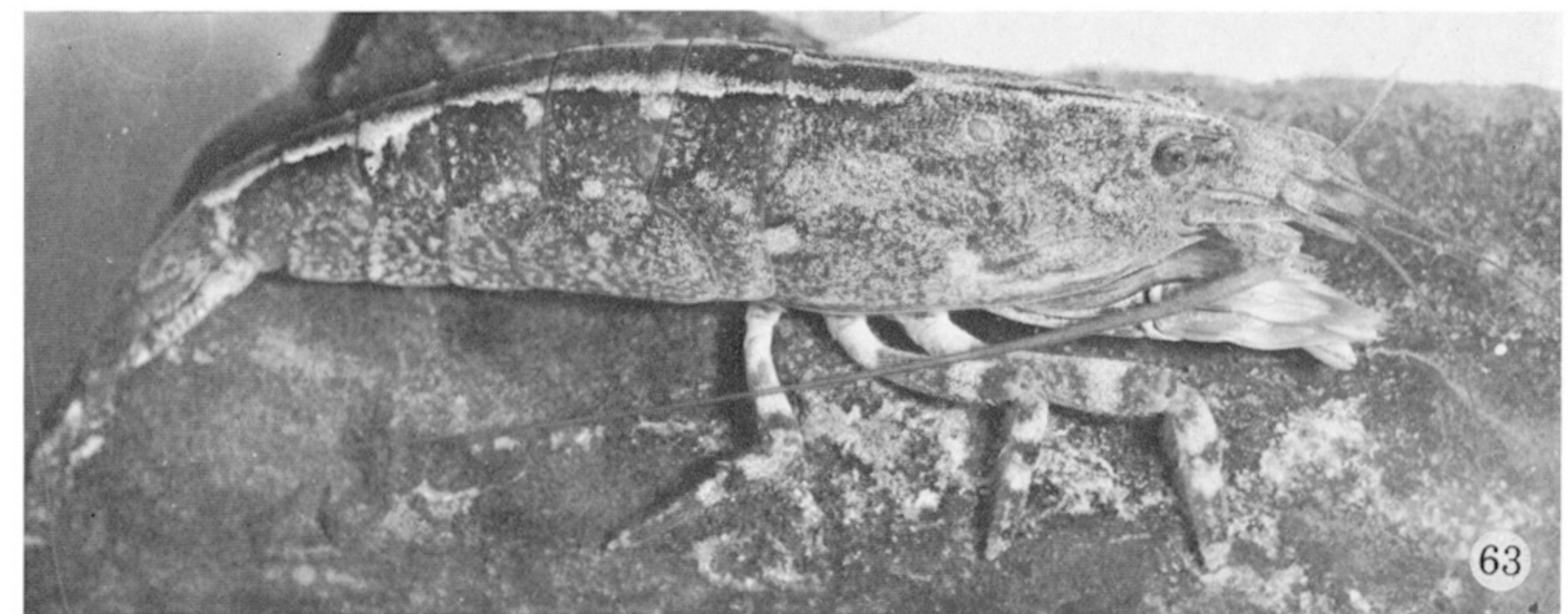
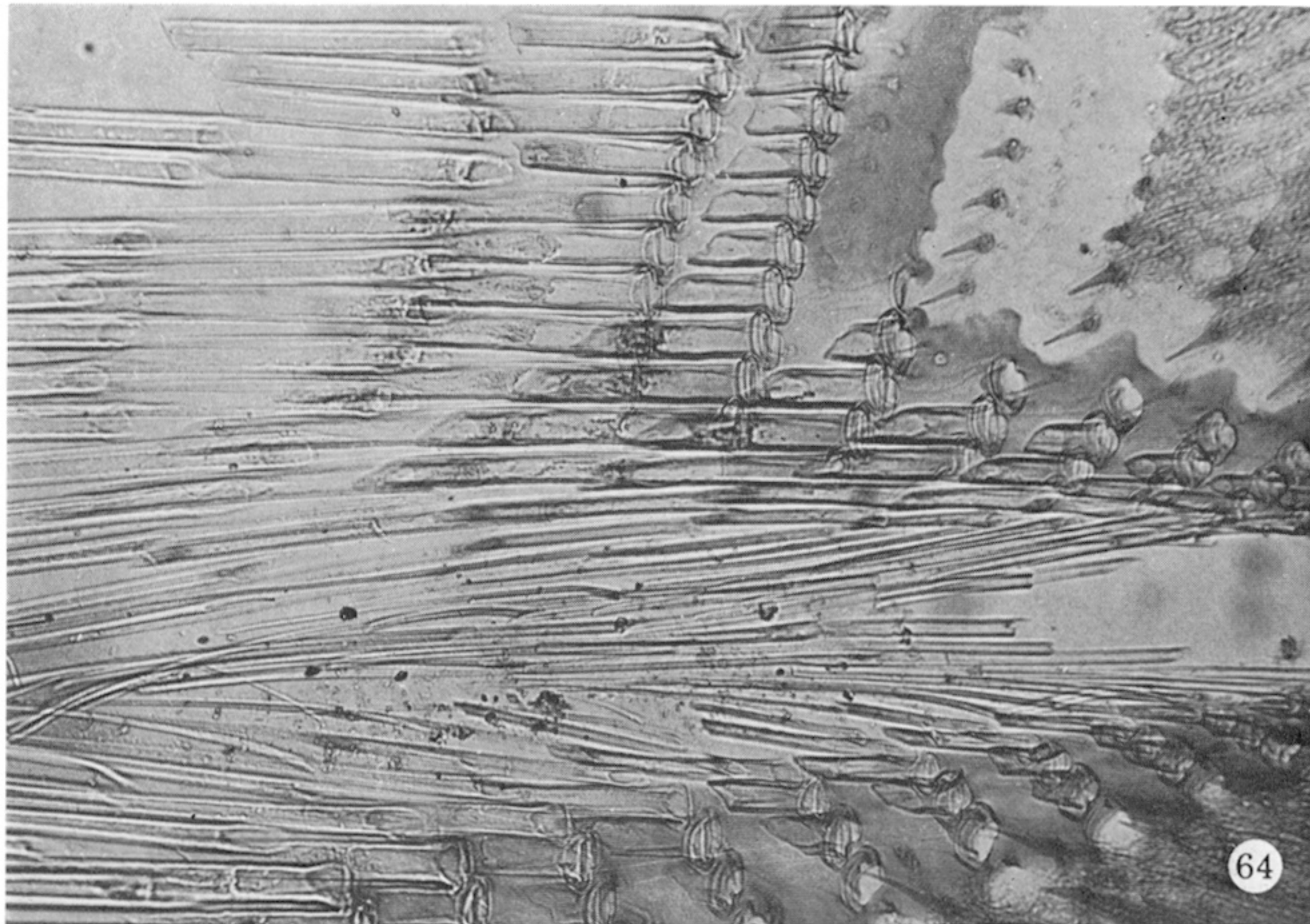
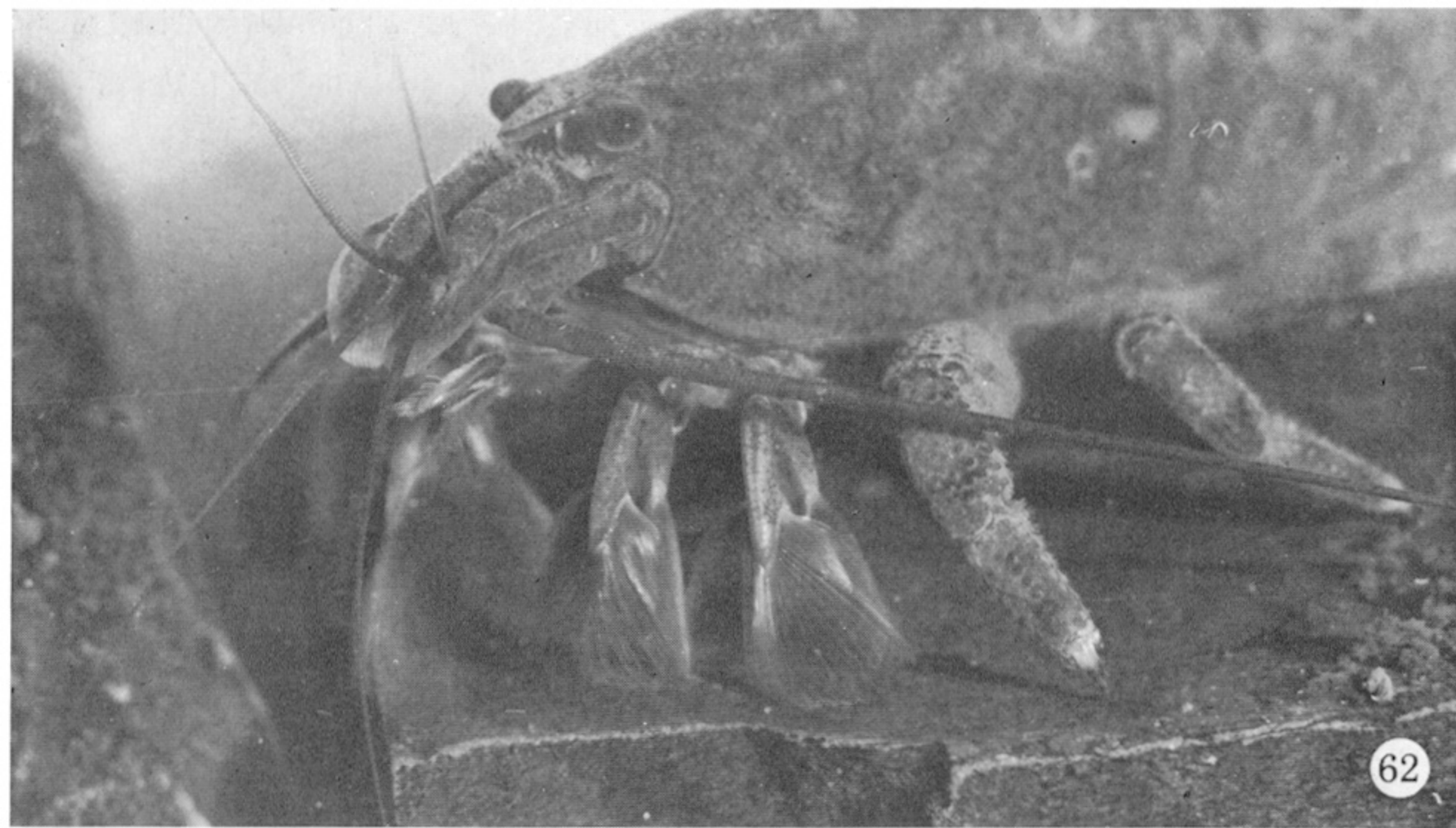
- Villalobos, A. 1943 Estudio morfologico de la *Atya scabra* (Crust. Decap.). Thesis, Univ. Nac. Autonoma de Mexico. 70 pp.
- Villalobos, A. 1959 Contribucion al conocimiento de los Atyidae de Mexico. II. (Crustacea, Decapoda). Estudio de algunas especies del genero *Potimirim* (= *Ortmannia*), con descripcion de una especie nueva en Brasil. *An. Inst. Biol. Univ. Méx.* **30**, 269-330.
- Yonge, C. M. 1924 Studies on the comparative physiology of digestion. II. The mechanism of feeding, digestion and assimilation in *Nephrops norvegicus*. *J. exp. Biol.* **1**, 343-389.

LIST OF ABBREVIATIONS USED ON FIGURES

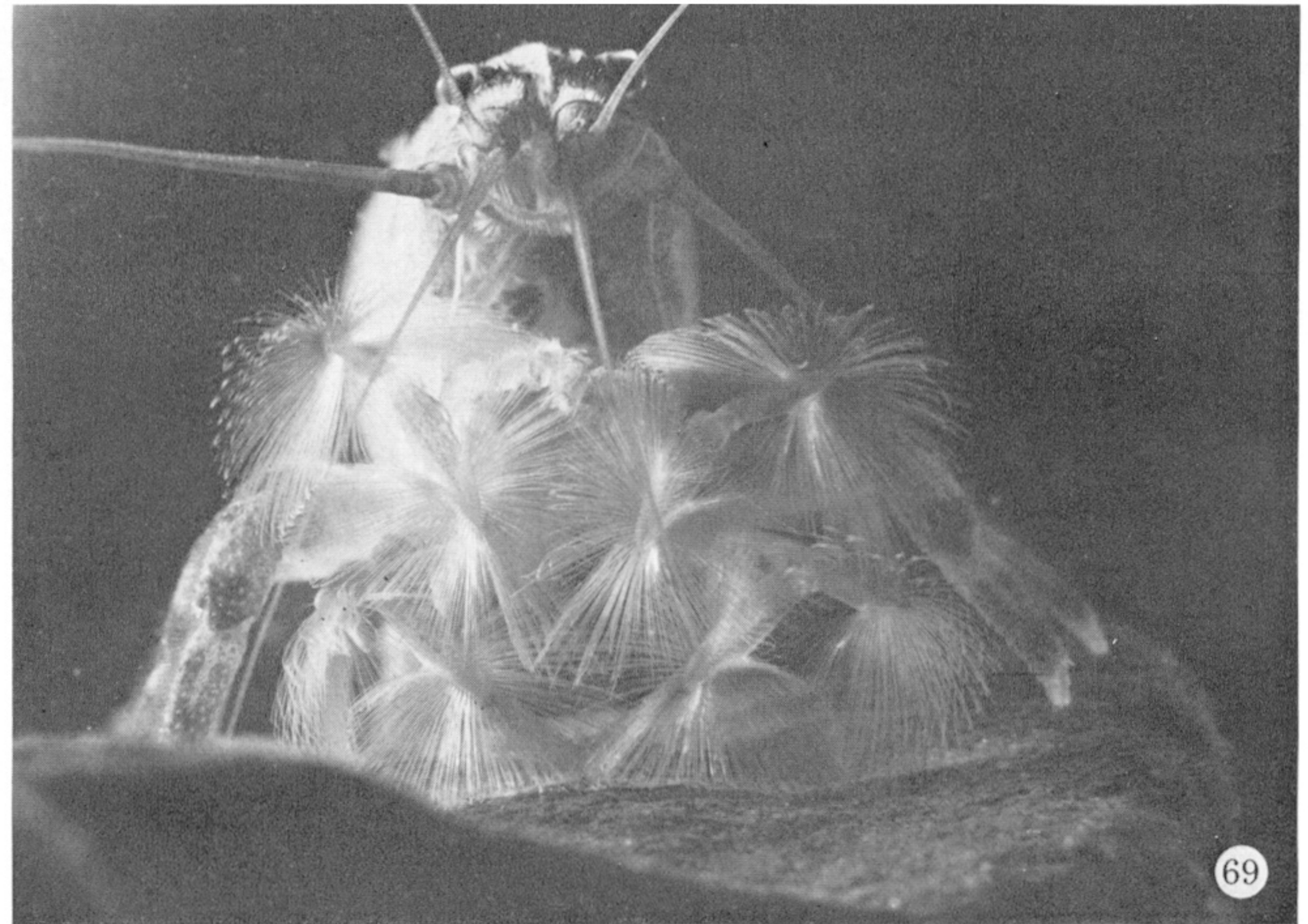
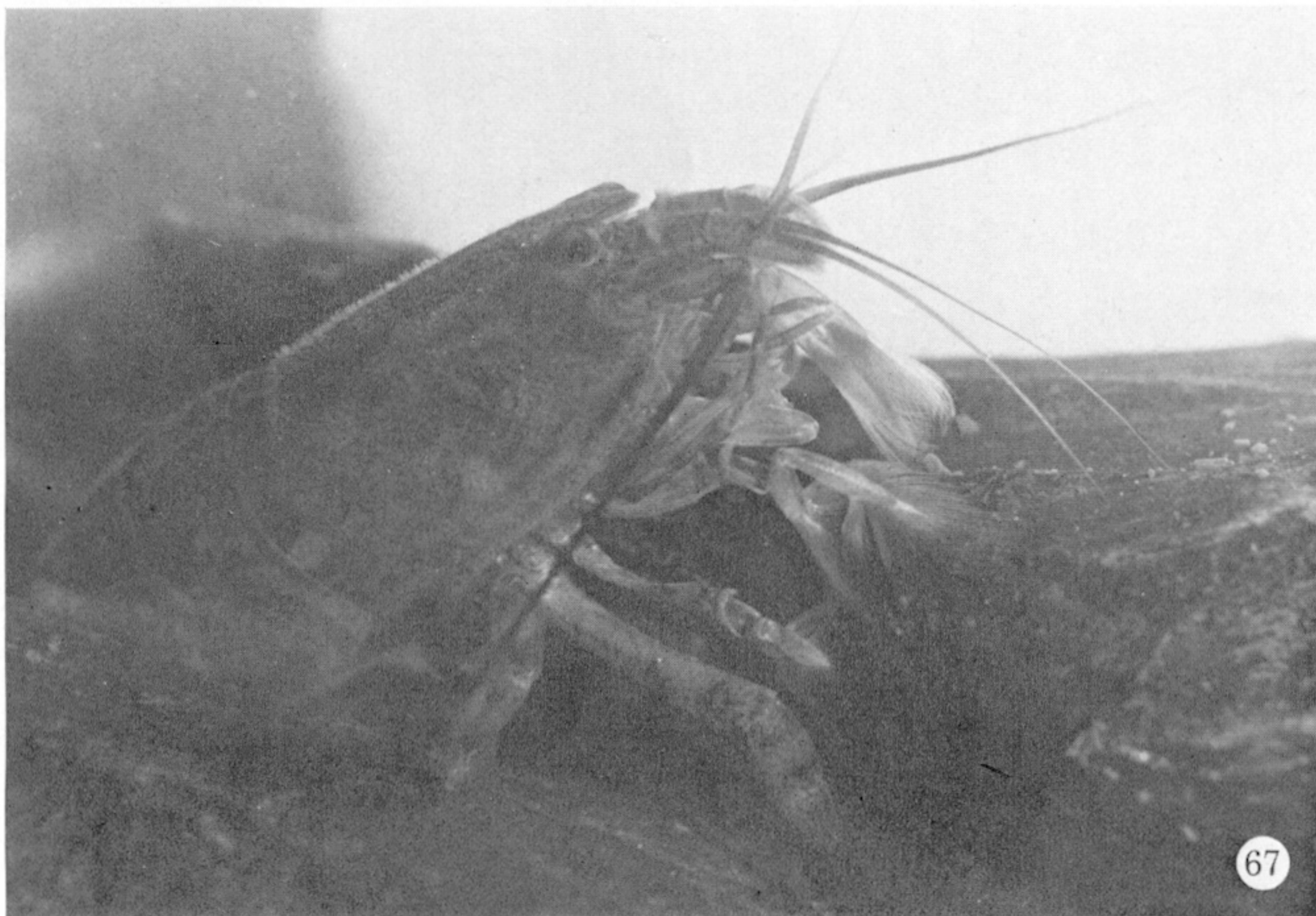
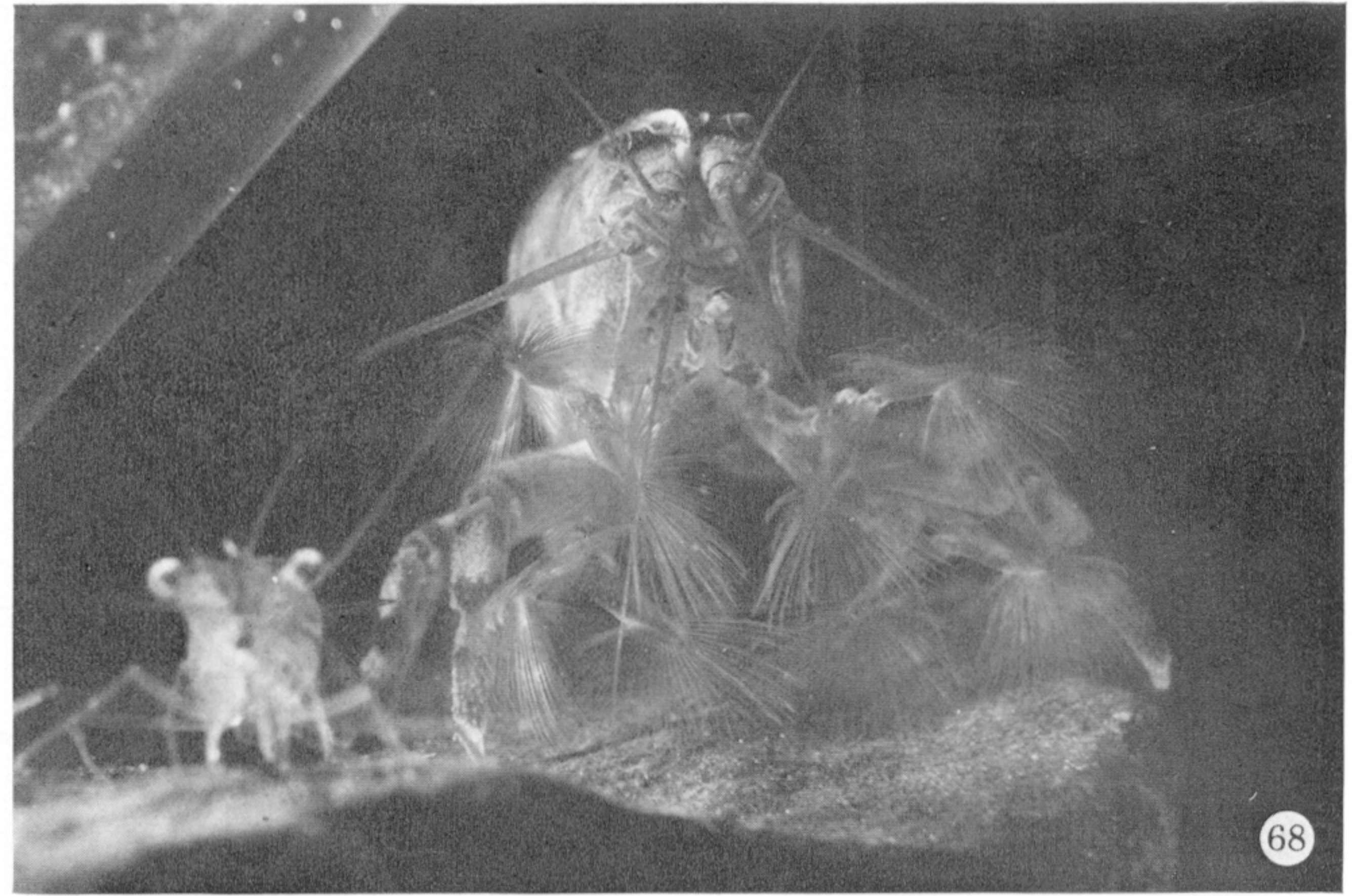
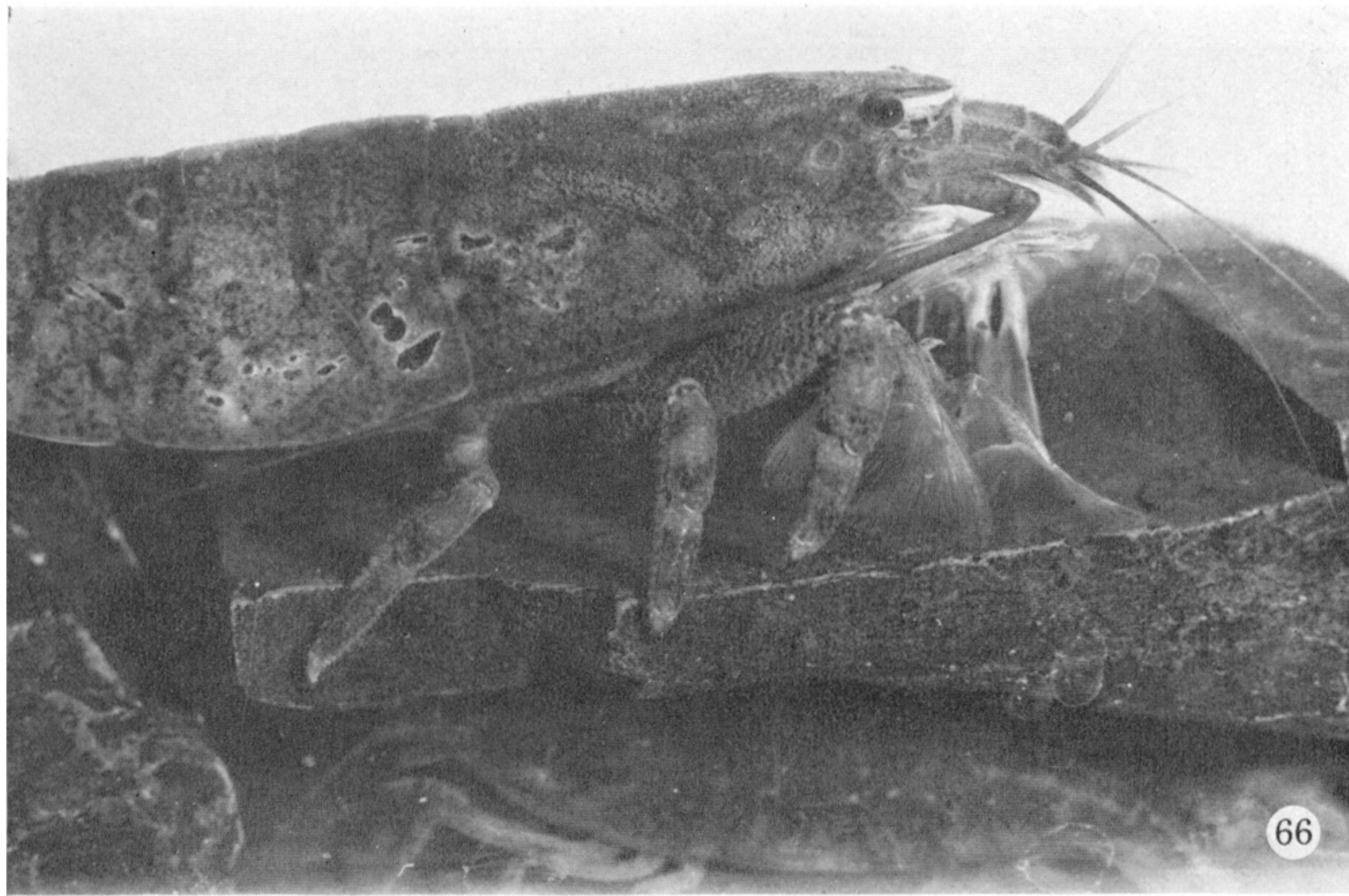
A	apodeme	LS Mxlle	lifting spines of proximal endite of maxillule
AC	aperture in cuticle	LT	lateral teeth
ACP	anterior comb plate	M	muscle
ACS	spines of anterior comb plate	Mand	mandible
AM	arthrodial membrane	MG	mid gut
APL	anterior portion of pleuropyloric ossicle	MO	mesocardiac ossicle
B	binding tendinous layer	MP	spinous median projection
BR	basal ring	MT	median tooth
BS	blade-like spines of dactylus	MX	maxilla
C	carpus	Mxlle	maxillule
CB	cutting blade of mandible	Mxp 1, 2, 3	maxillipeds 1, 2, 3
CBP	chitinous blade of propus	O	occluded region
CC	carpal cup	OE	outer excavation
CCH	cardiac chamber	Oes	oesophagus
CHC	cheliped cuticle	P	propus
CLS	cleaning spine of maxilliped 2	PCH	pyloric chamber
CM	convoluted membrane	PCP	posterior comb plate
CPV	cardio-pyloric valve	PCS	spines of posterior comb plate
CS	cavity of seta	PE Mx	proximal endite of maxilla
CSC	cleaning setae of lateral channel	PE Mxlle	proximal endite of maxillule
CU	cuticle	PE Mxp1	proximal endite of maxilliped 1
D	dactylus	PF	posterior face of mandible
DE	denticles of gland filter	PG	paragnath
DE Mx	distal endite of maxilla	PGC	paragnath, cut away
DE Mxlle	distal endite of maxillule	PL	pleuropyloric ossicle
DP	denticles of median projection of gland filter	P Mxp 1, 3	palp of maxillipeds 1, 3
DR	distal row of spines	PO	ptero-cardiac ossicle
FD	flattened denticle	PPO	posterior setae of pterocardiac ossicle
FL	flanking lips of gland filter	PS Mxlle	posterior spines of proximal endite of maxillule
F Mx	fence of setae of proximal endite of maxilla	PV	pivot
F Mxlle	fine funnelling setae of proximal endite of maxillule	PY	pyloric ossicle
GF	gland filter	R Mand	right mandible
G Mxp1	grid of distal endite of maxilliped 1	RPG	right paragnath
GS	guarding spines of channel between pyloric and cardiac chambers	S	spring
GS Mxp 1, 2, 3	guarding spines/setae of proximal endite of maxillipeds 1, 2, 3	SCP	spinules of posterior comb plate
GSS	guarding spinules of channel between pyloric and cardiac chambers	S Mxlle	short setae of dorsal edge of proximal endite of maxillule
GU	groove of uropyloric ossicle	S Mxp2	setae of maxilliped 2
HC	hinging cuticle	S1 Mxp2	distal segment of maxilliped 2
ILC	infero-lateral cardiac ossicle	S2 Mxp2	penultimate segment of maxilliped 2
IP	incisor process of mandible	SN	safety net of maxilliped 1
J	joint between distal and penultimate segment of maxilliped 2	SP	spinous projection of mandible
L	ligament	SPC	spinules of dorso-lateral wall of pyloric chamber
LA	labrum	SPL	spines of pleuropyloric ossicle
LC	lateral channel between pyloric and cardiac chambers	SR	supporting ring
LD	lateral denticle	SSCP	spinules of posterior comb plate
LL	lateral lobe of urocardiac ossicle	S Mxlle	stem of distal endite of maxillule
L Mand	left mandible	SS Mxlle	stout spines of proximal endite of maxillule
L Mxp1	long setae of proximal endite of maxilliped 1	SZO	spines of zygo-cardiac ossicle
LPO	outer lateral setae of pterocardiac ossicle	T	tendon
LR	lateral ridge	TL	teaselling lobe of maxilla
		TR	thickened rim
		UO	urocardiac ossicle
		UPO	uropyloric ossicle
		W	wall of cardiac chamber
		ZO	zygo-cardiac ossicle



FIGURES 58-61. For description see opposite.

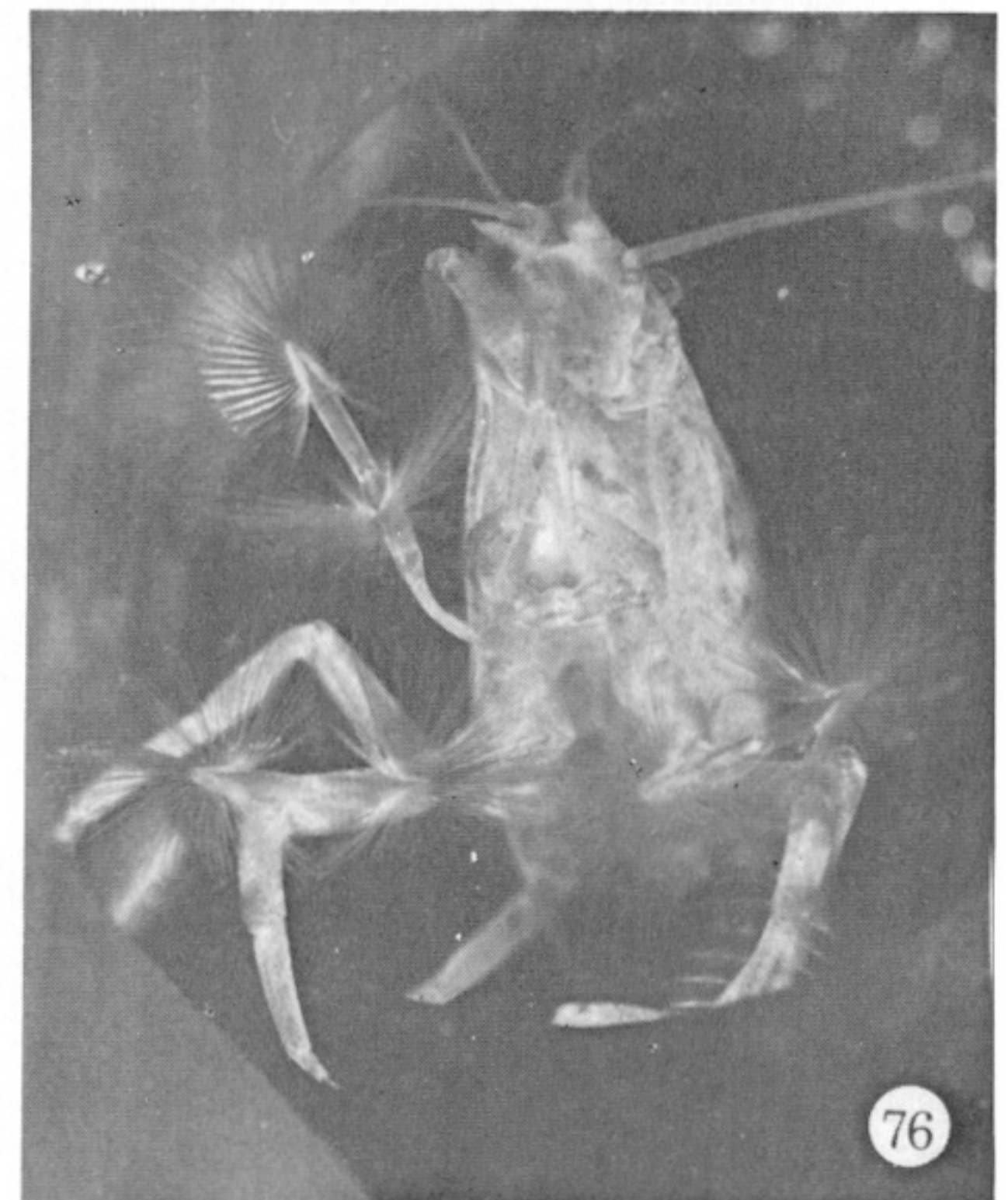
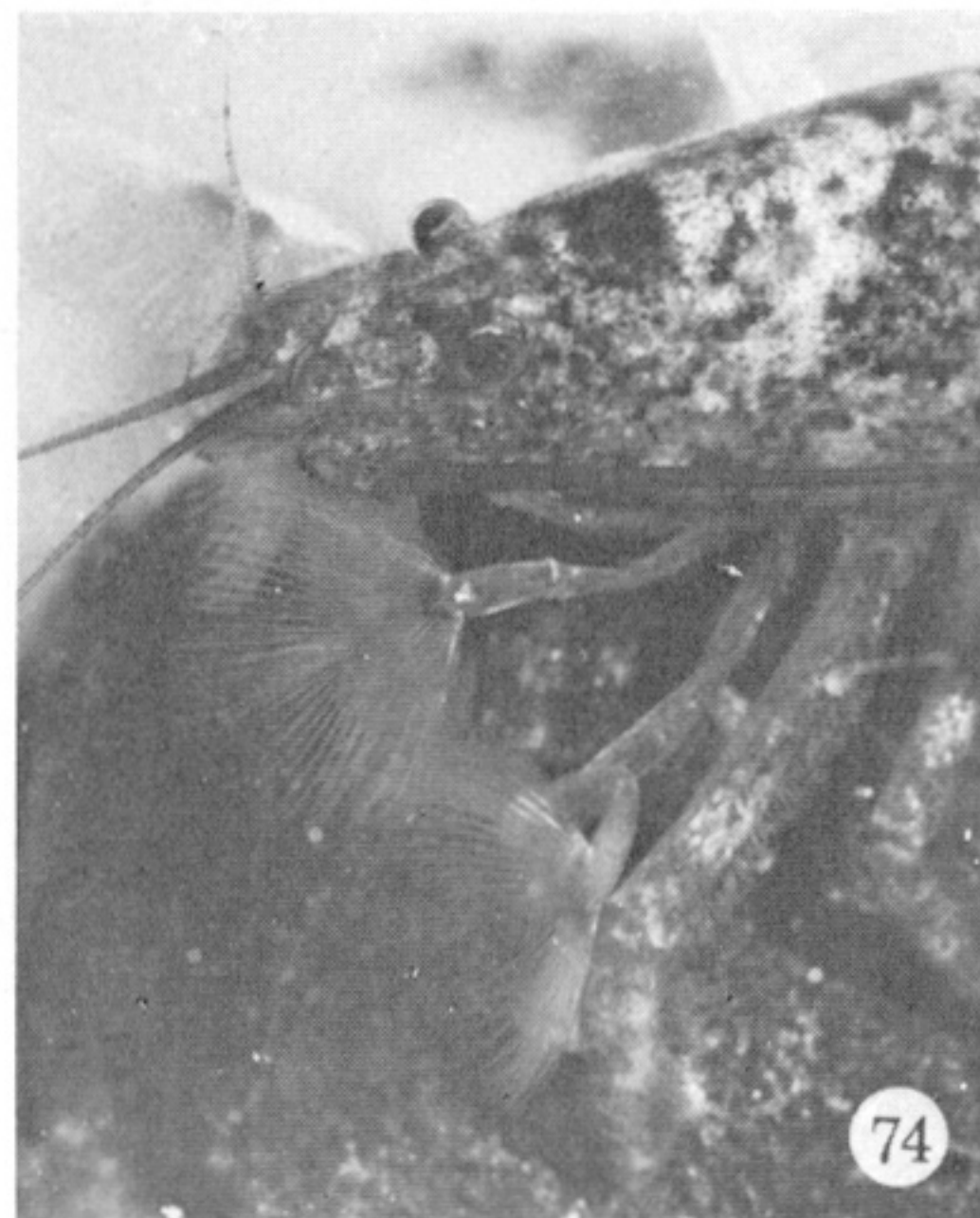
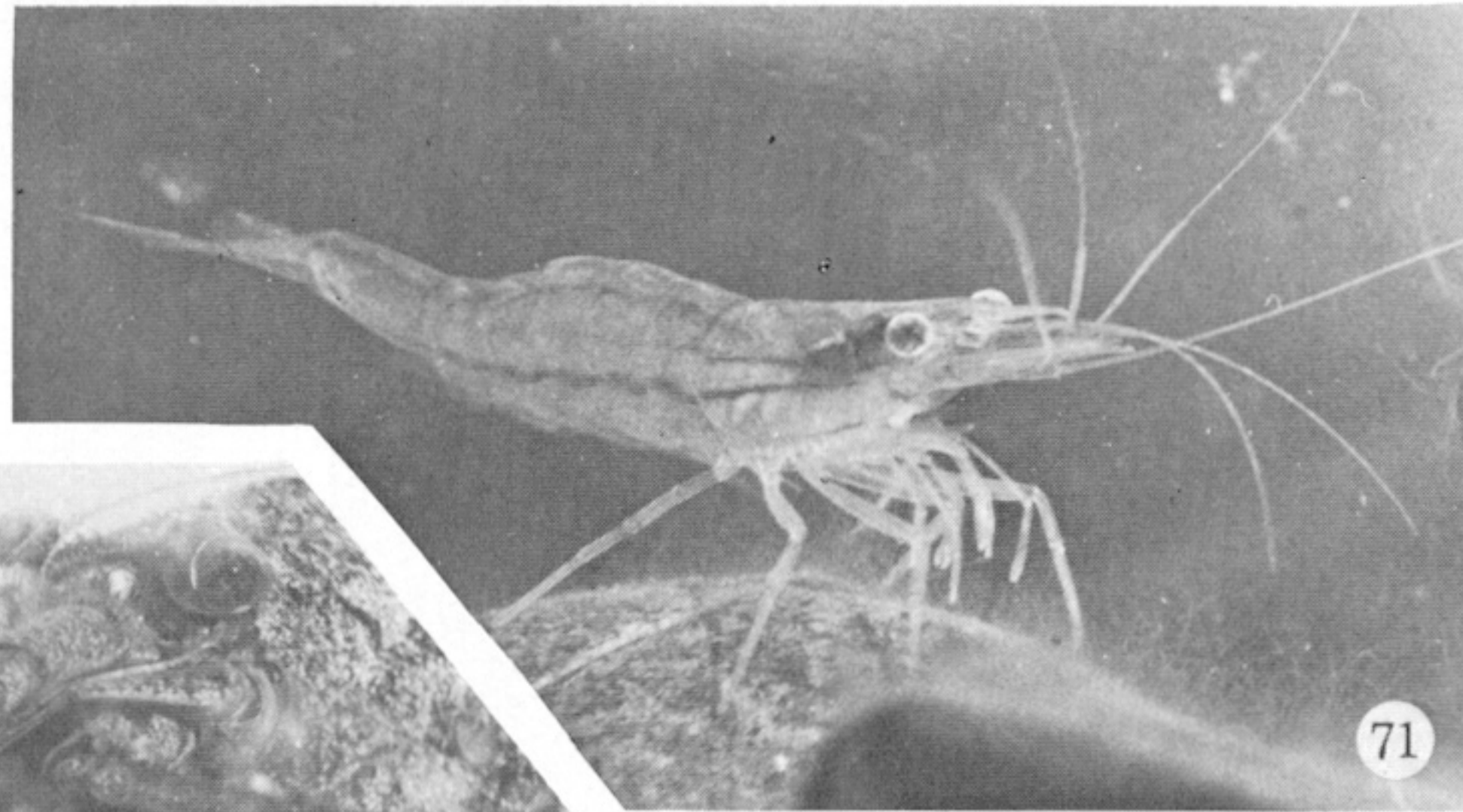
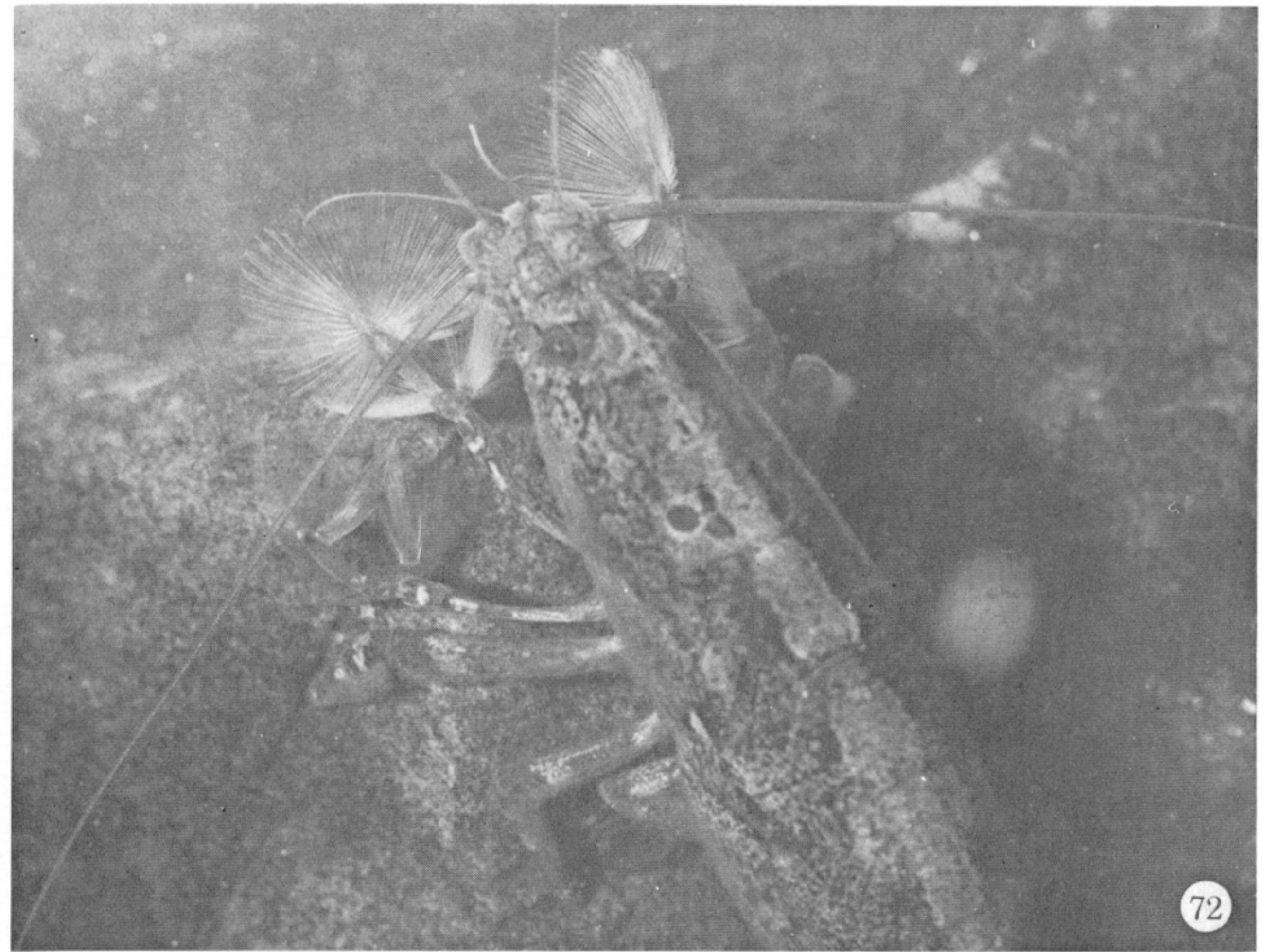
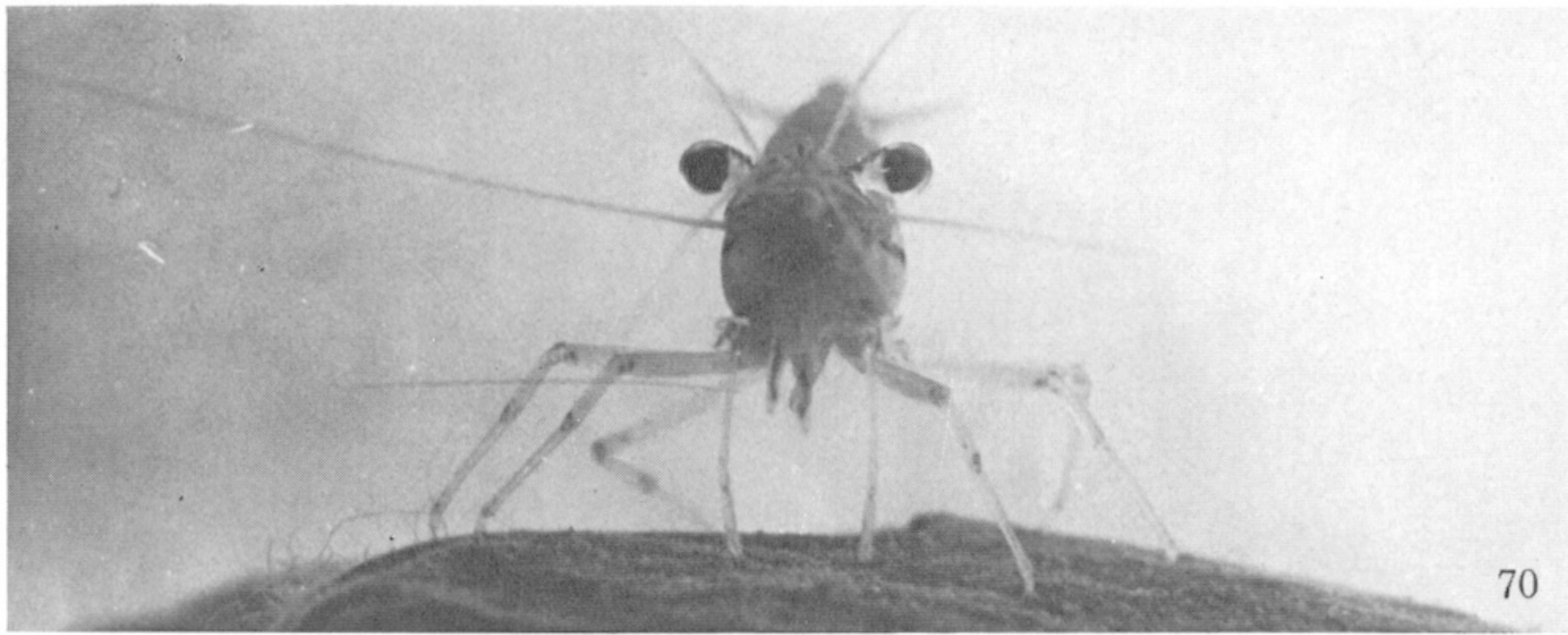


FIGURES 62-65. For description see opposite.

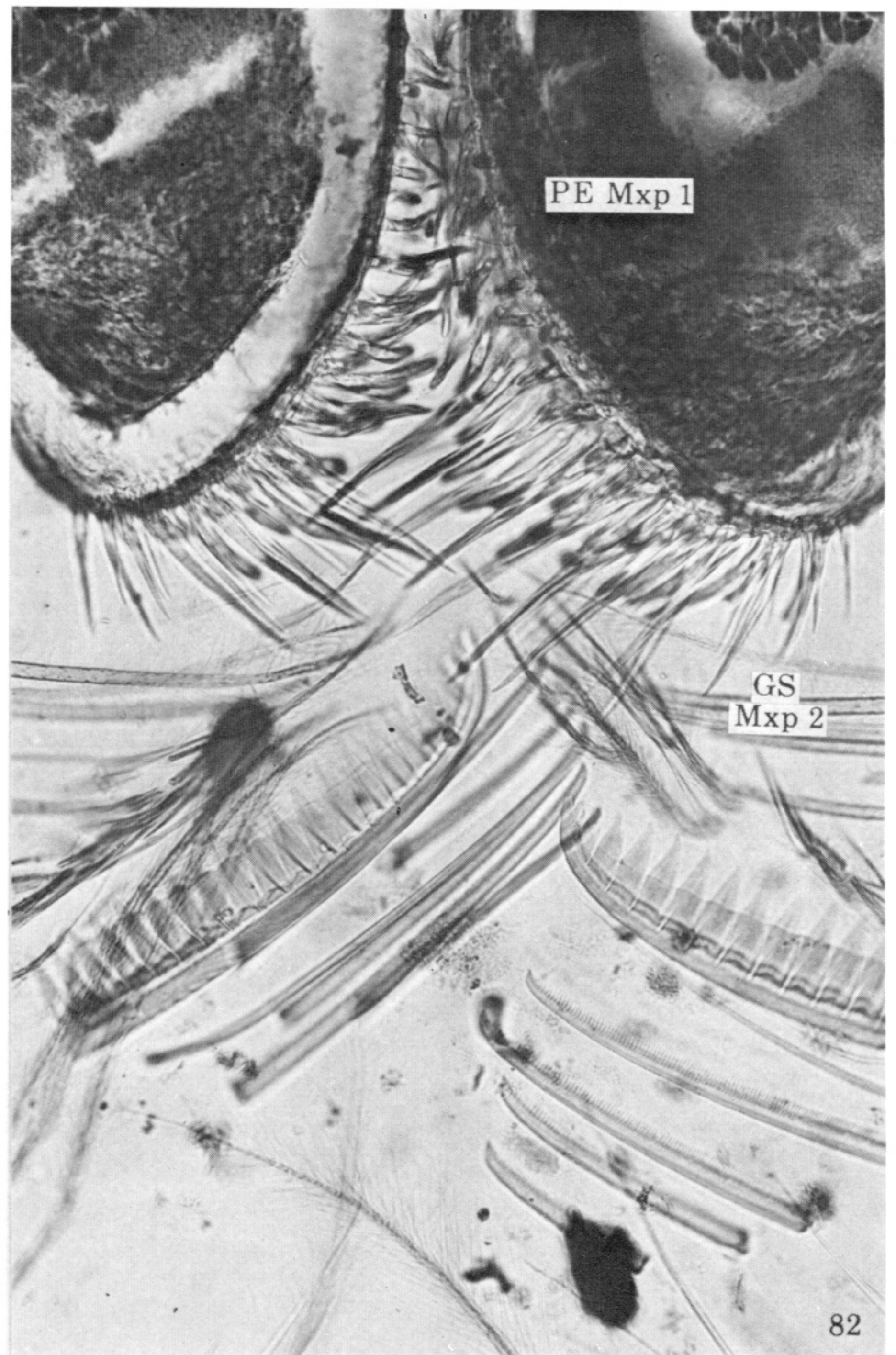
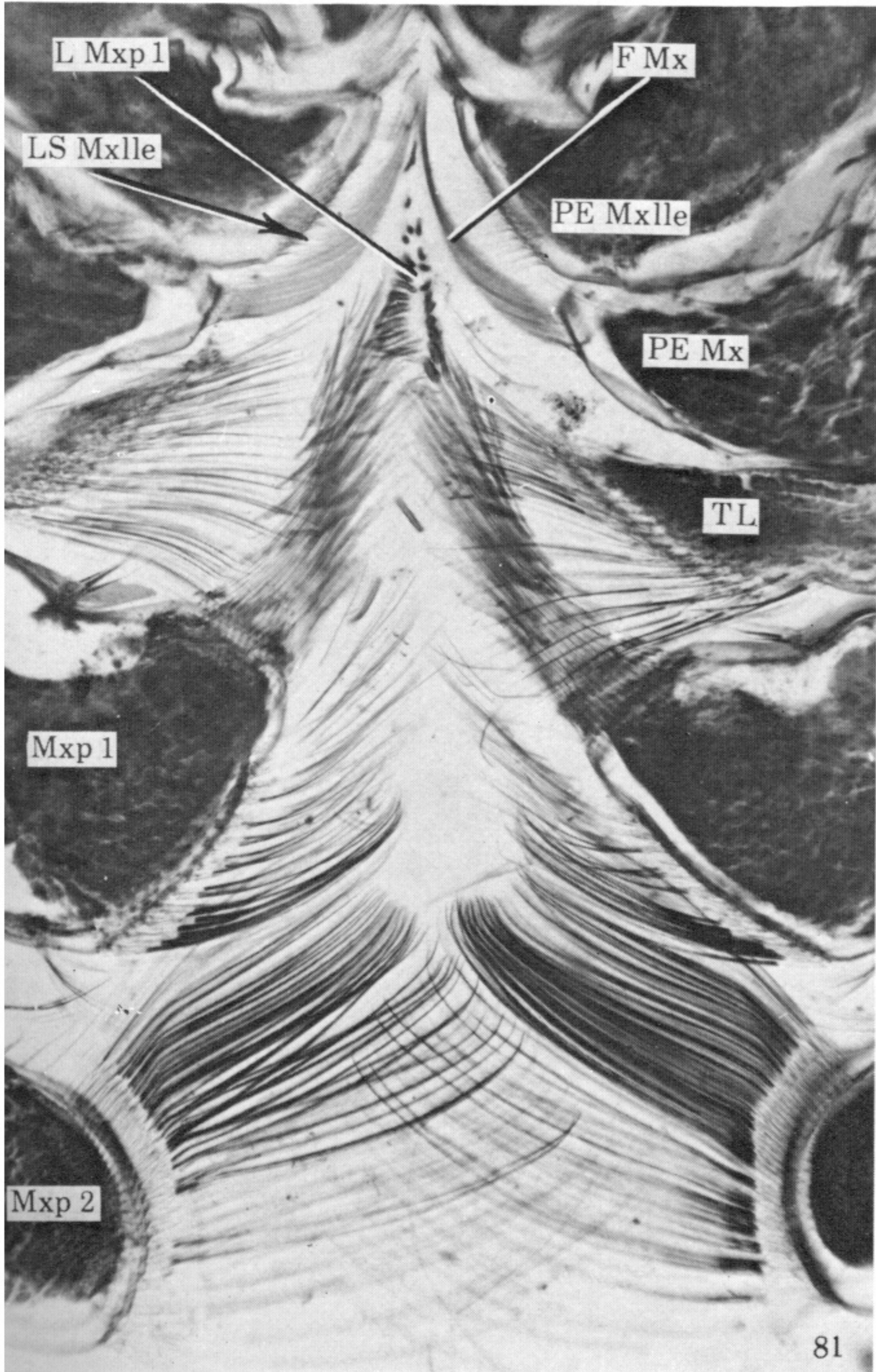
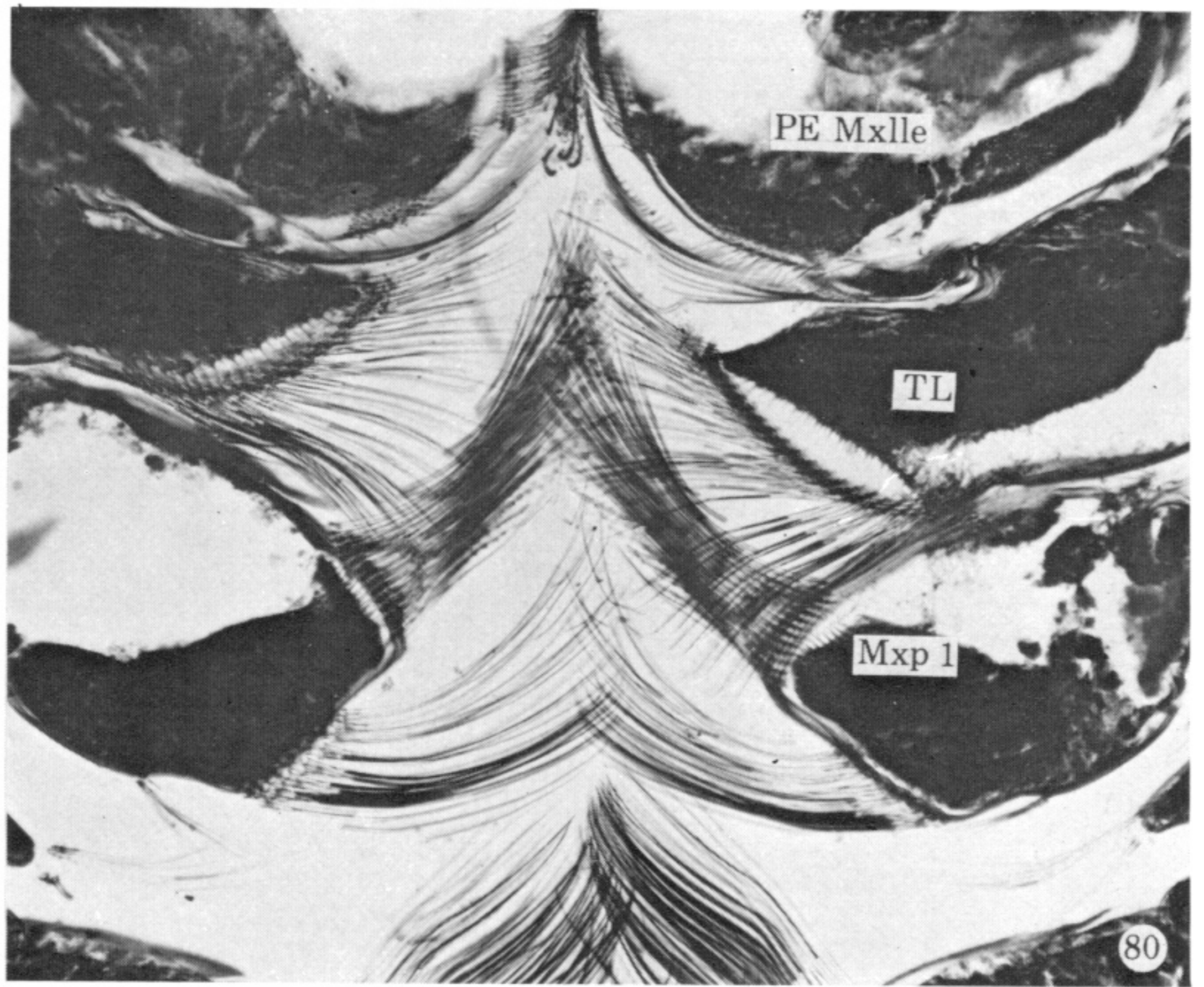
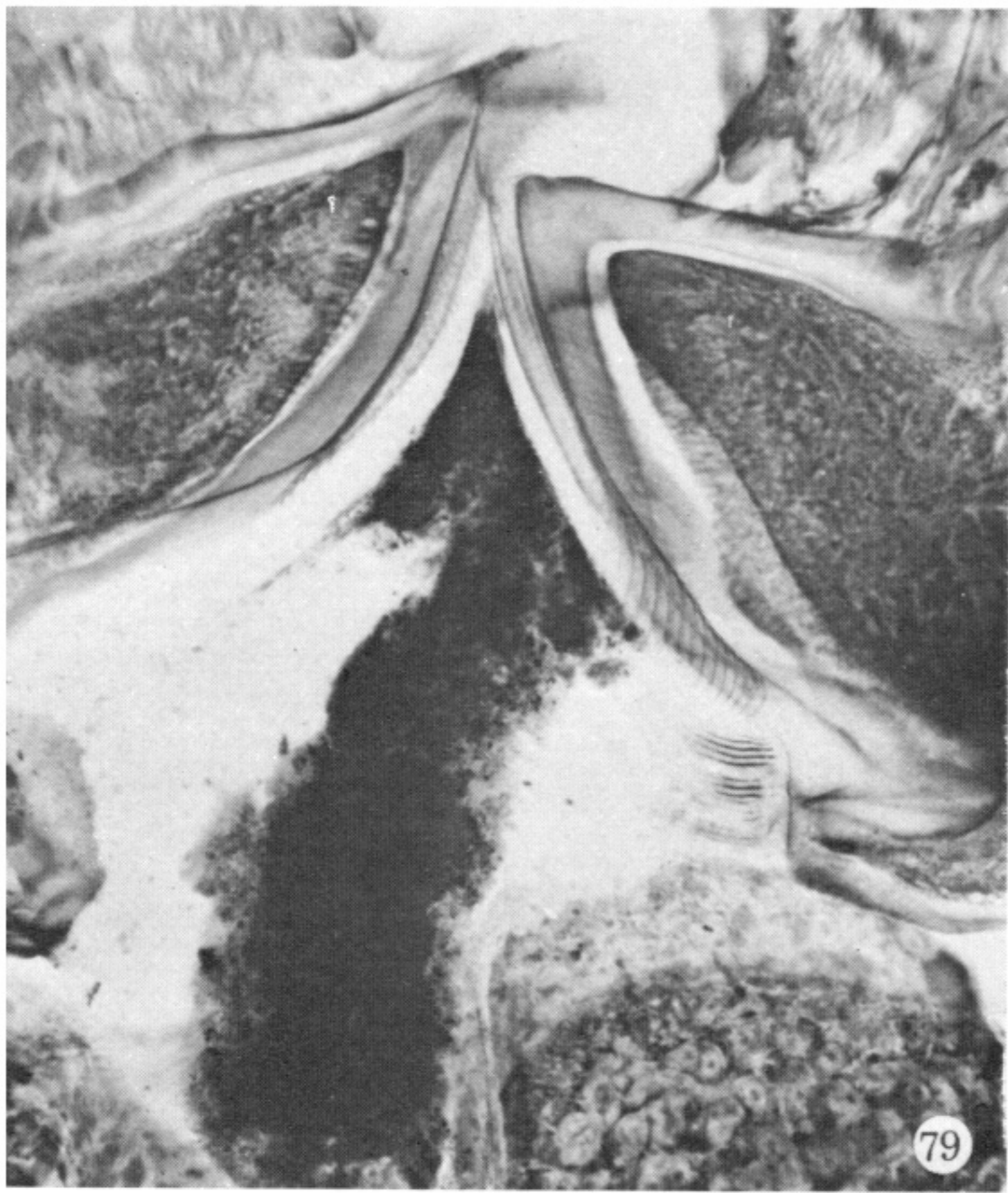


FIGURES 66-69. For description see opposite.

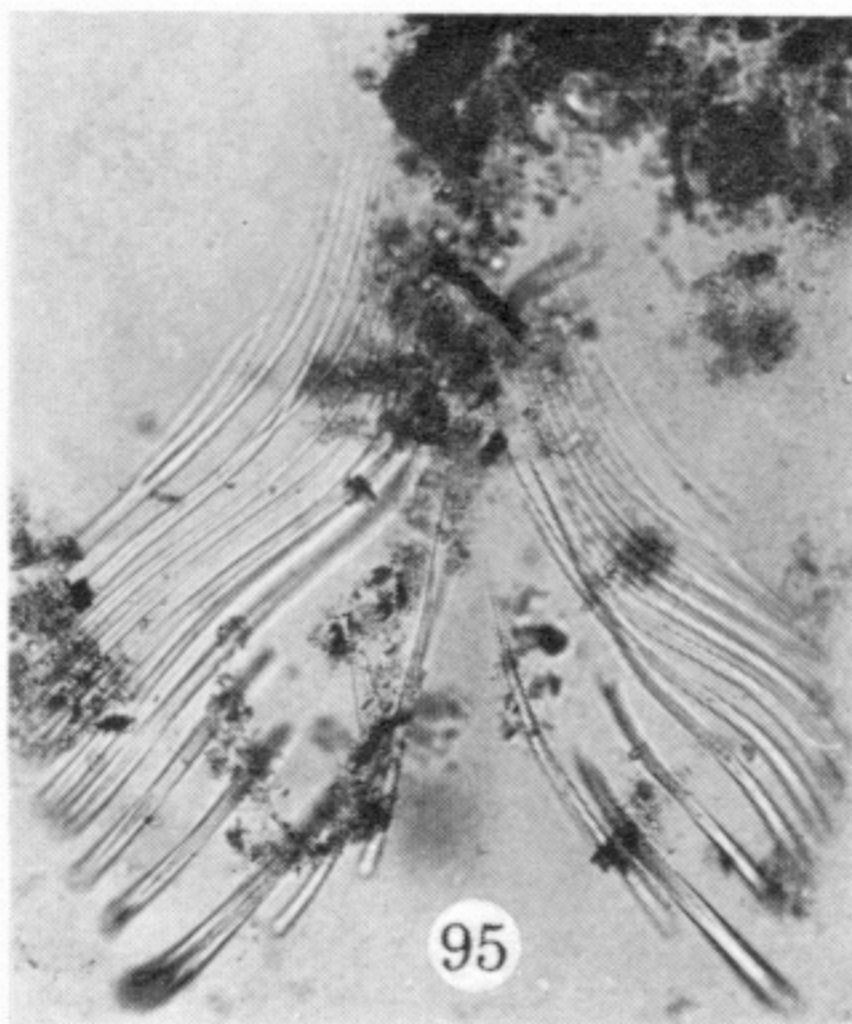
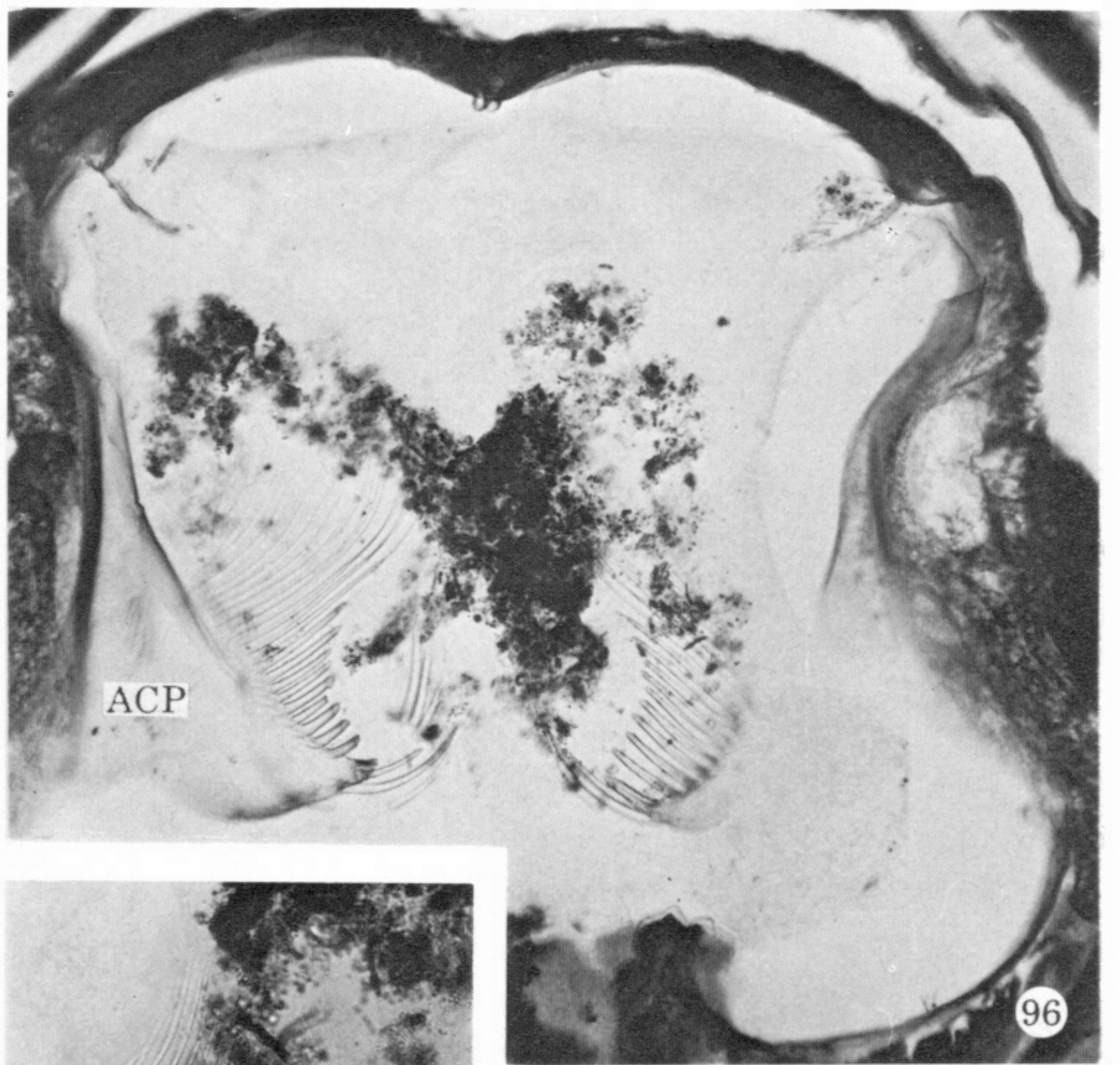
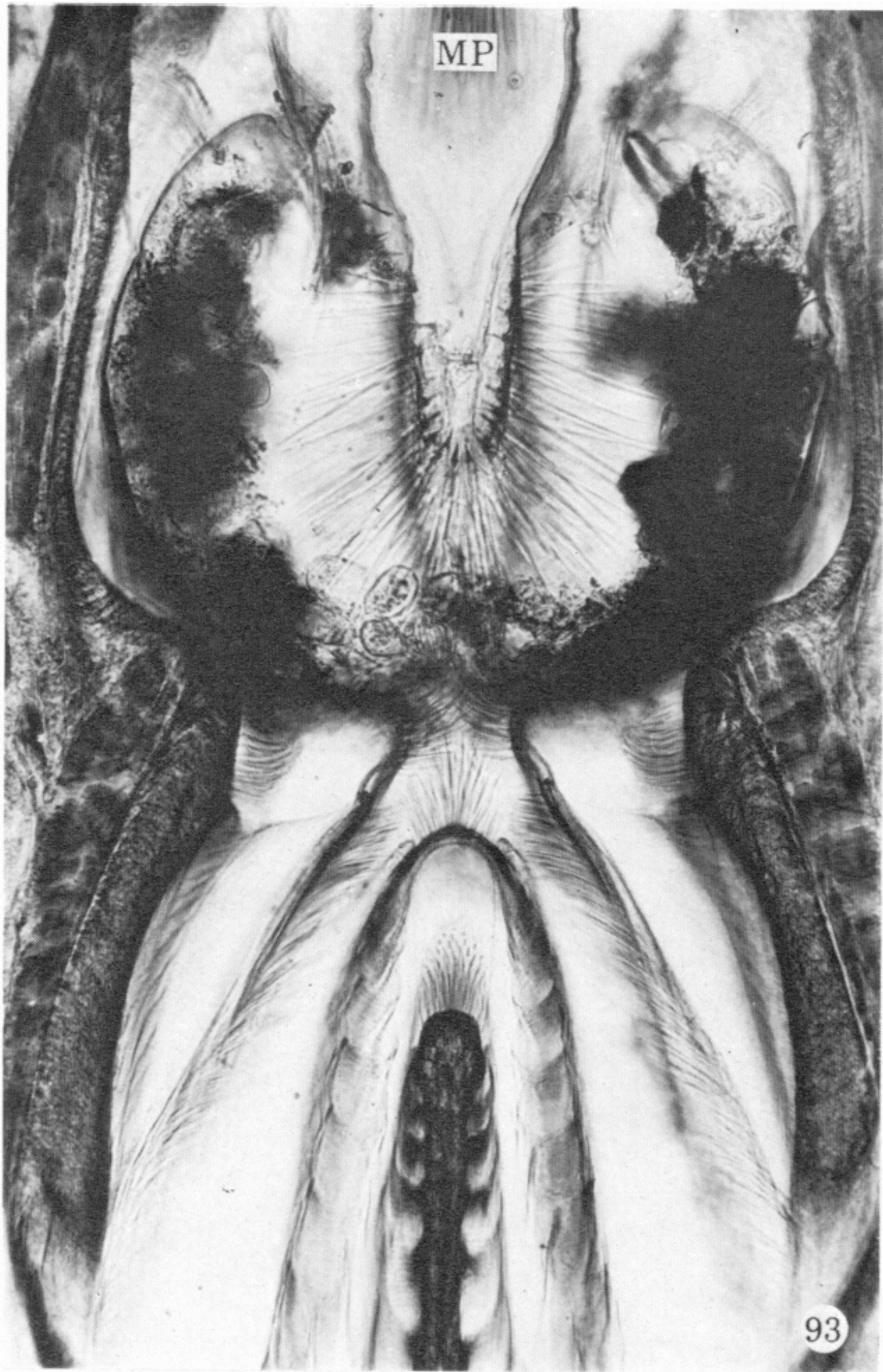




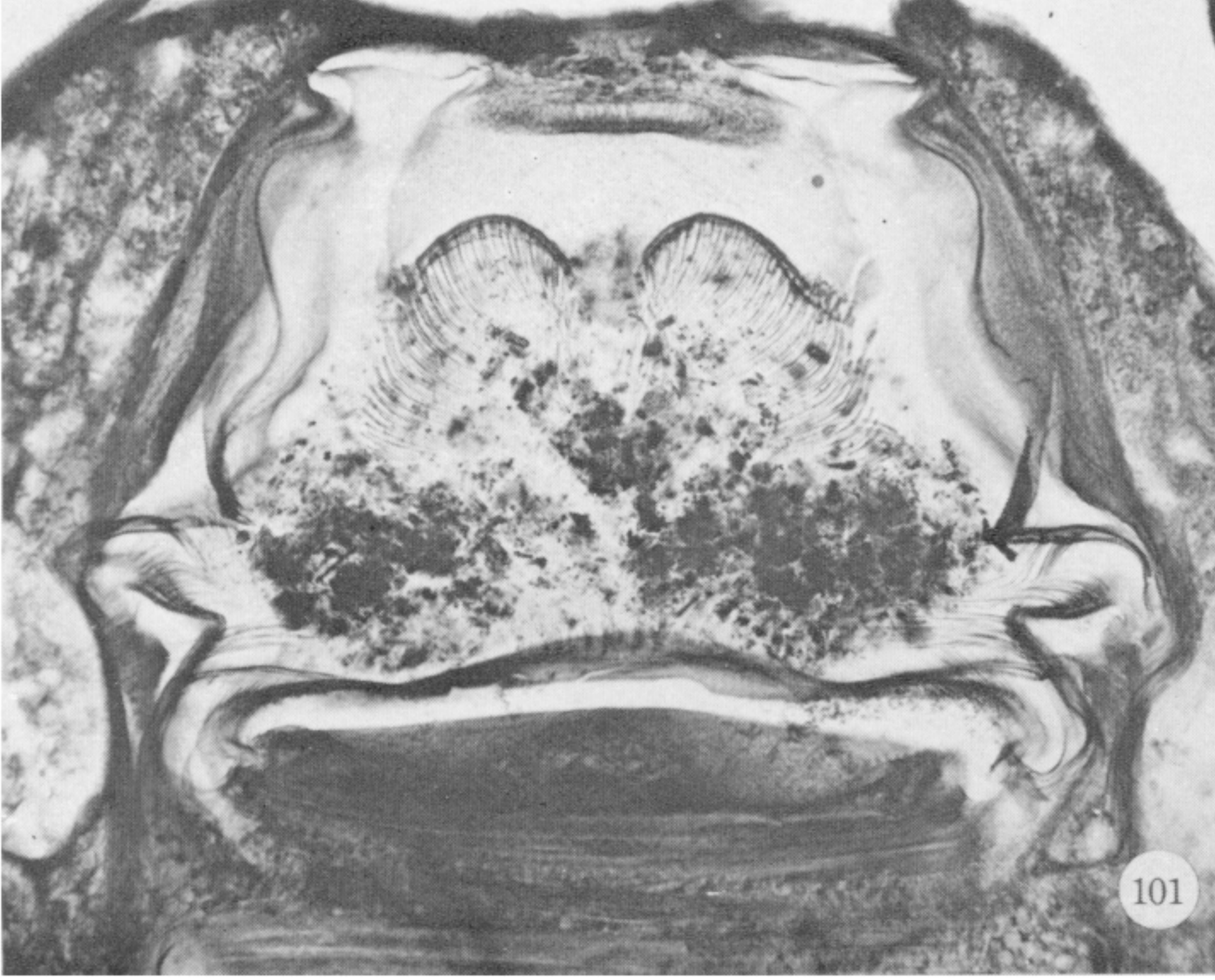
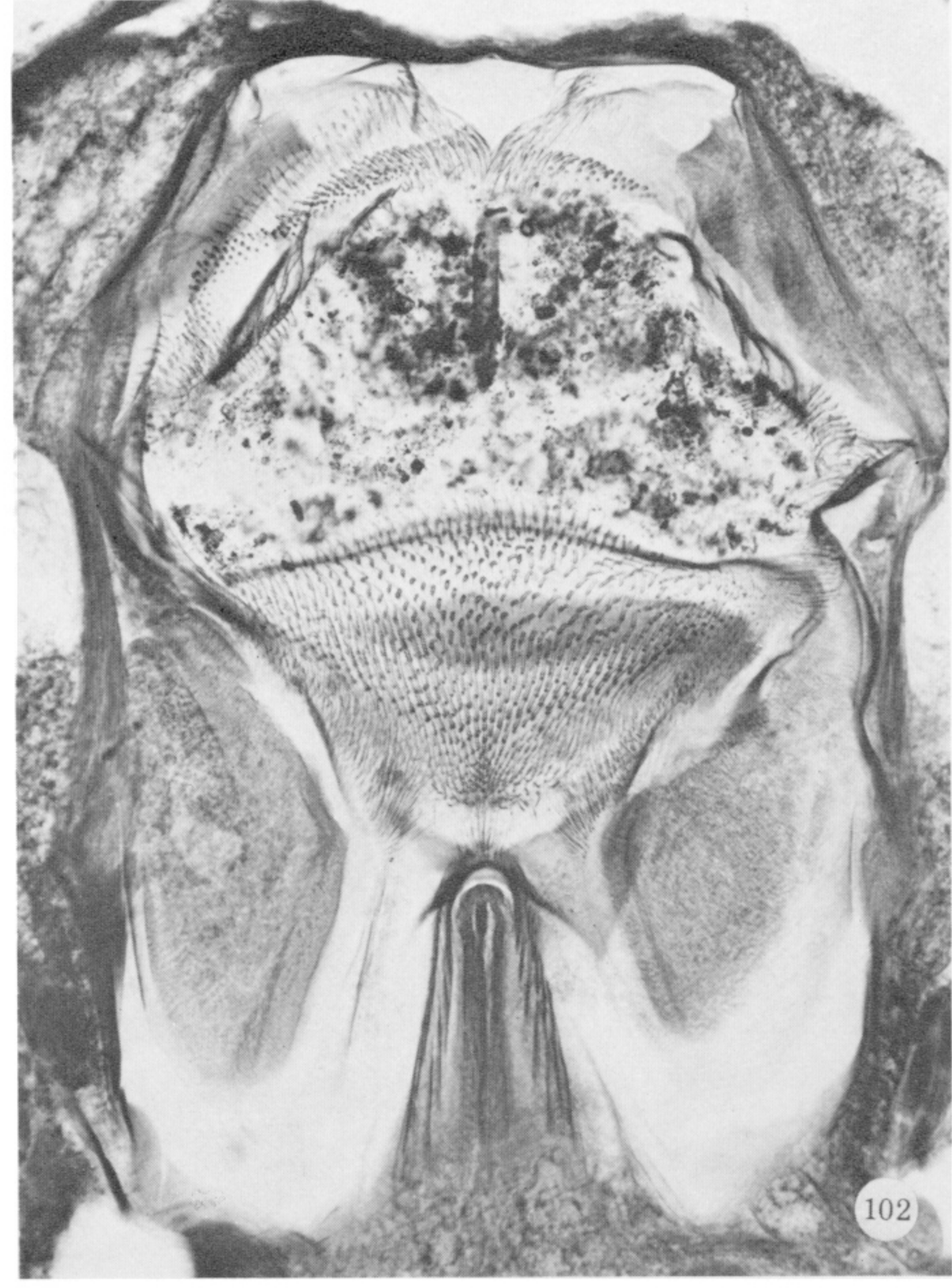
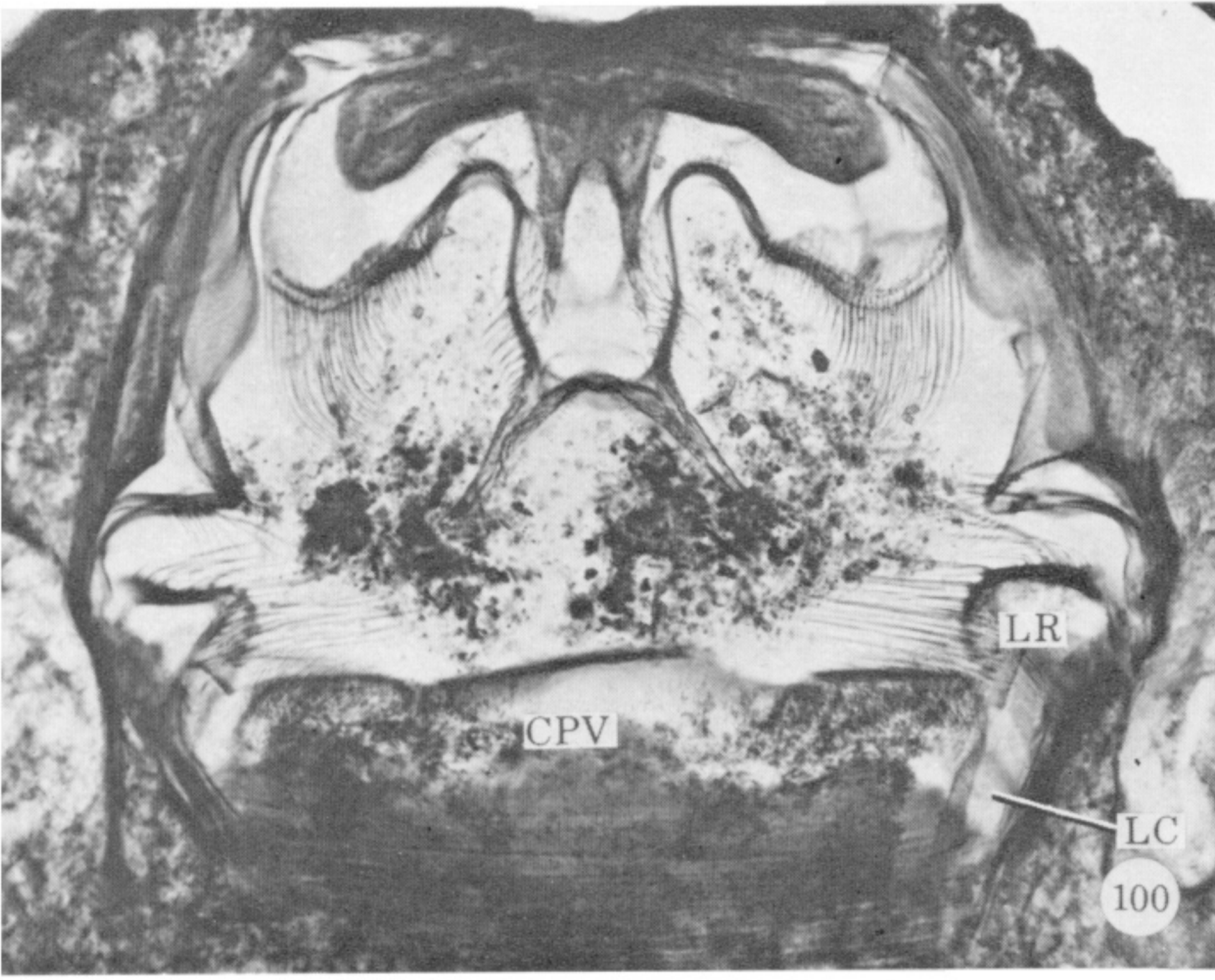
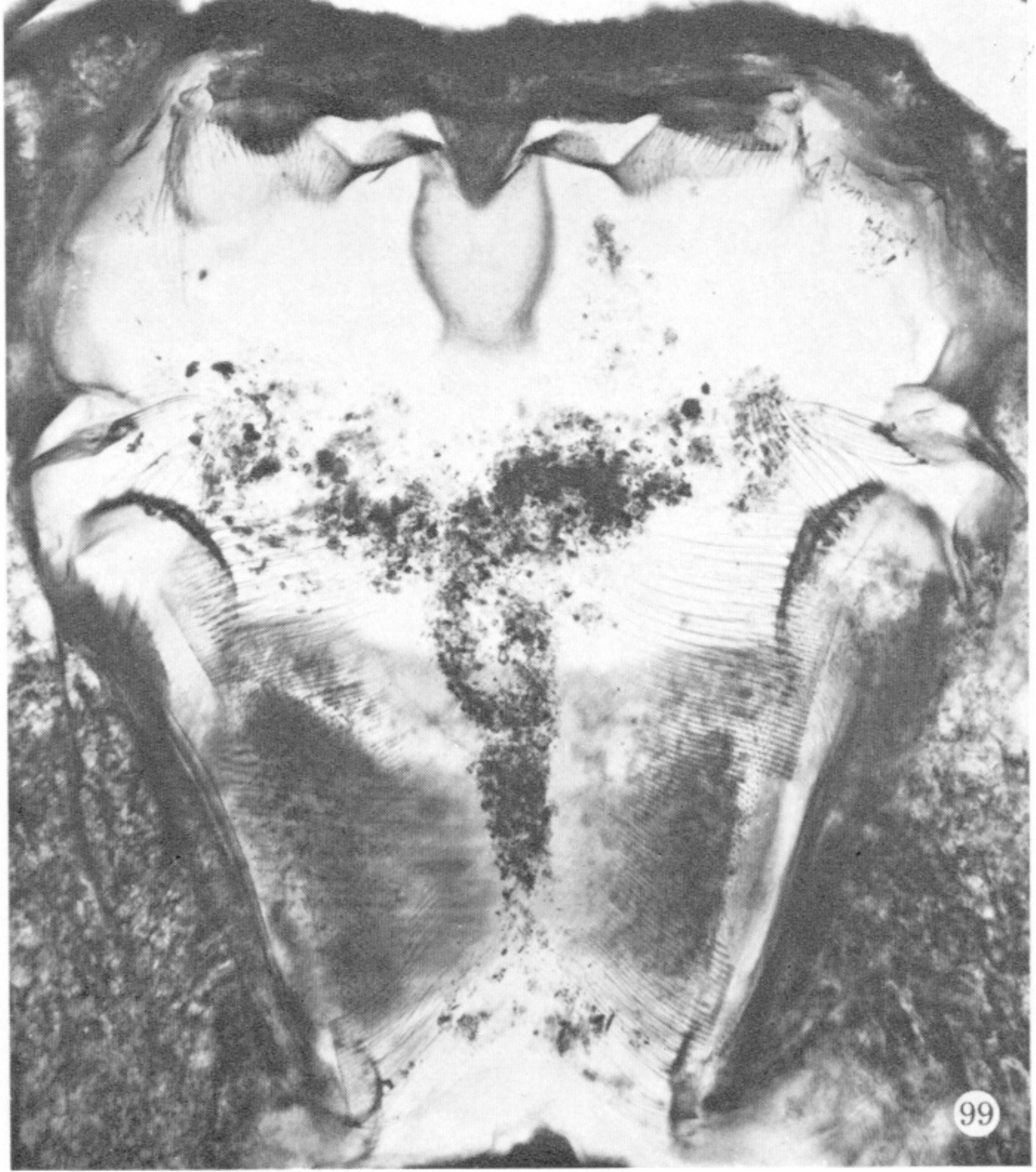
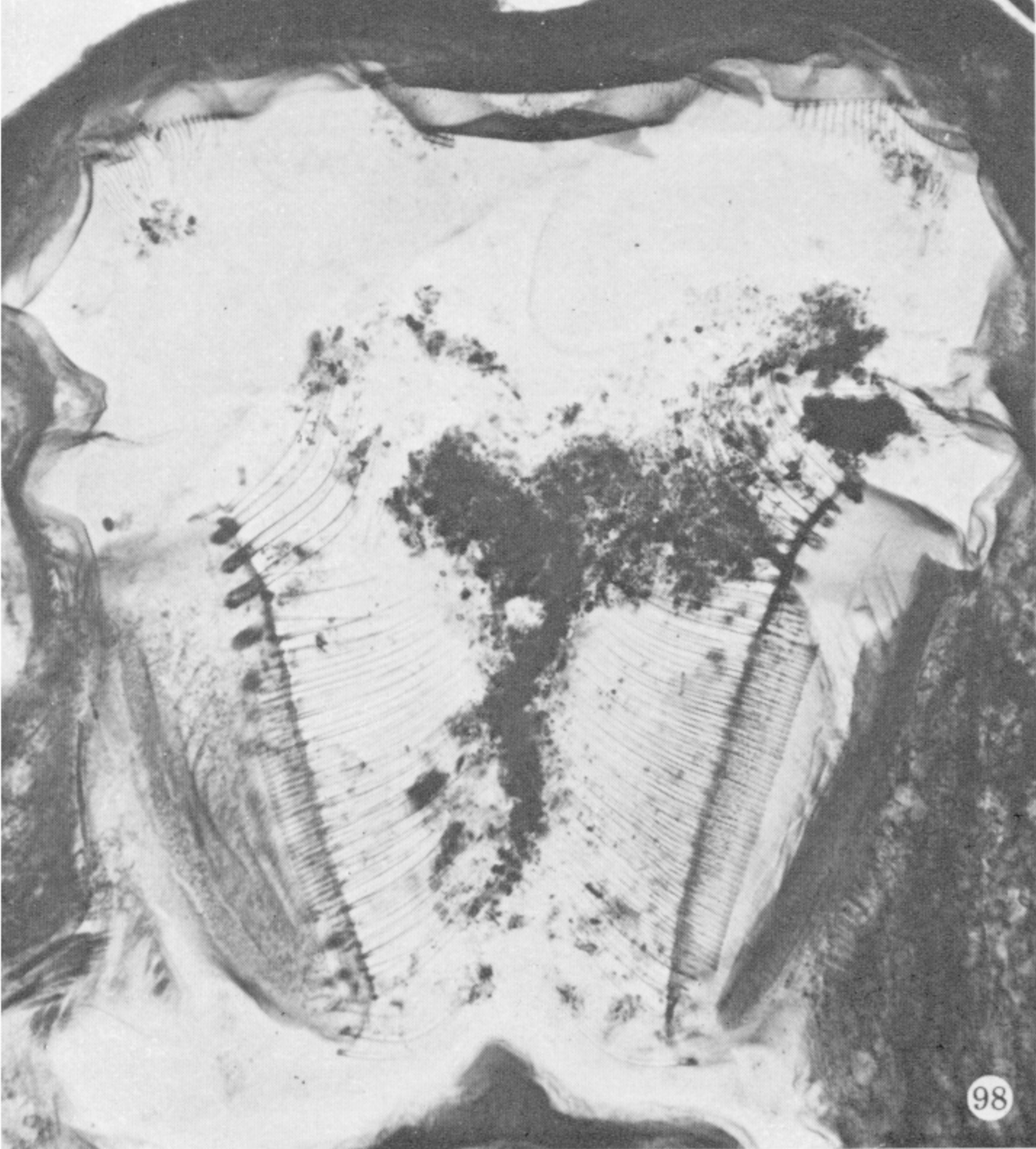
FIGURES 70-76. For description see opposite.



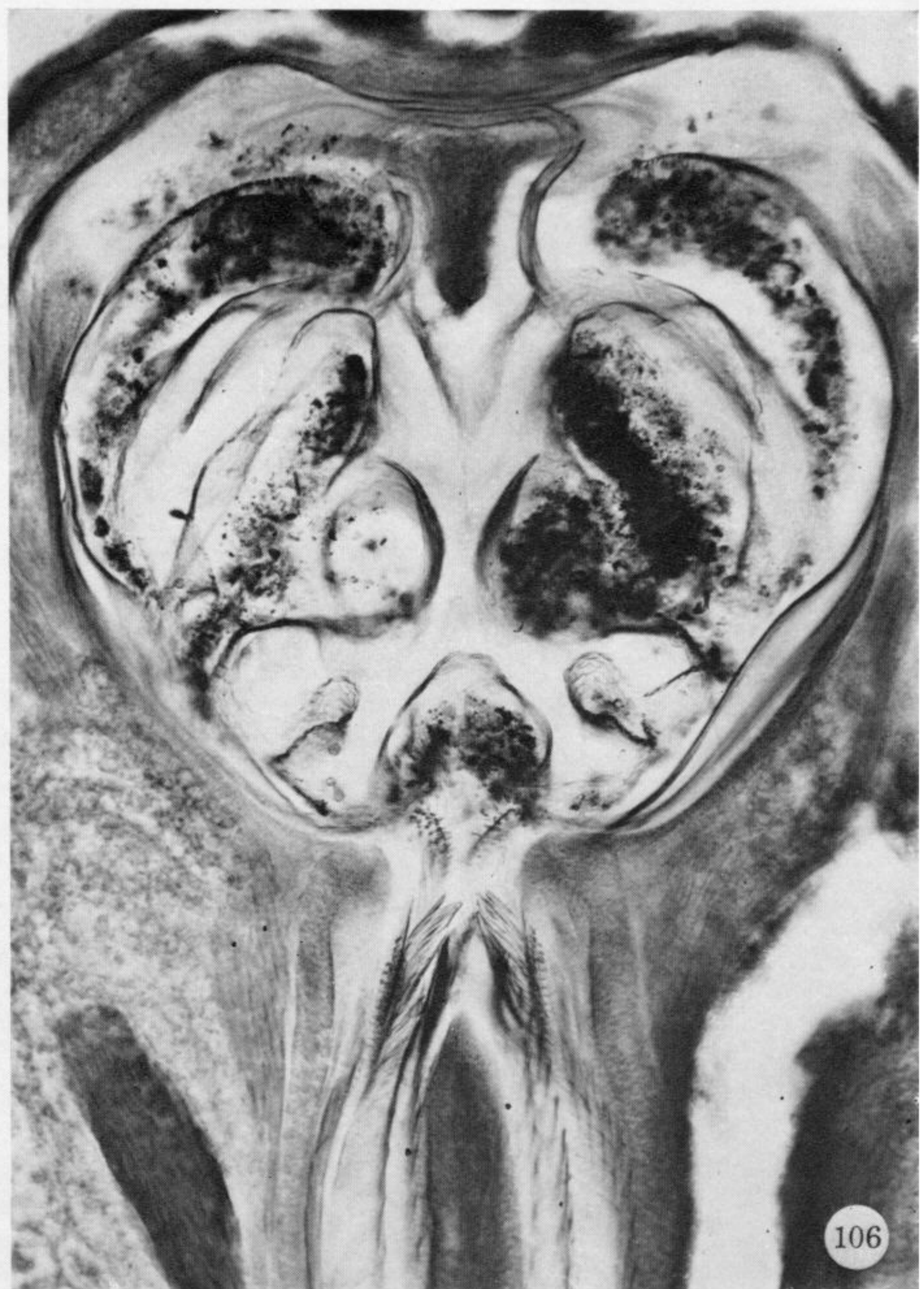
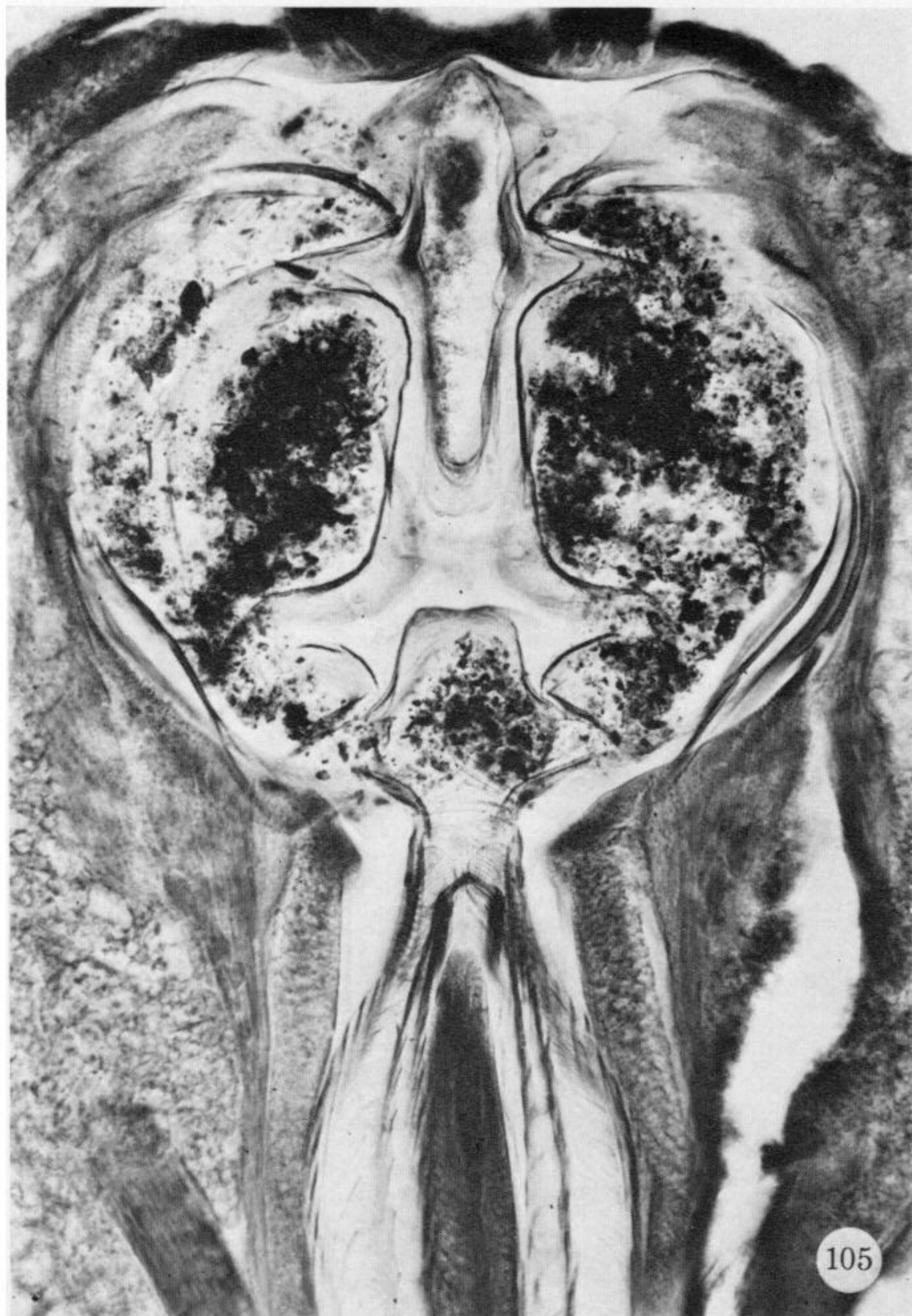
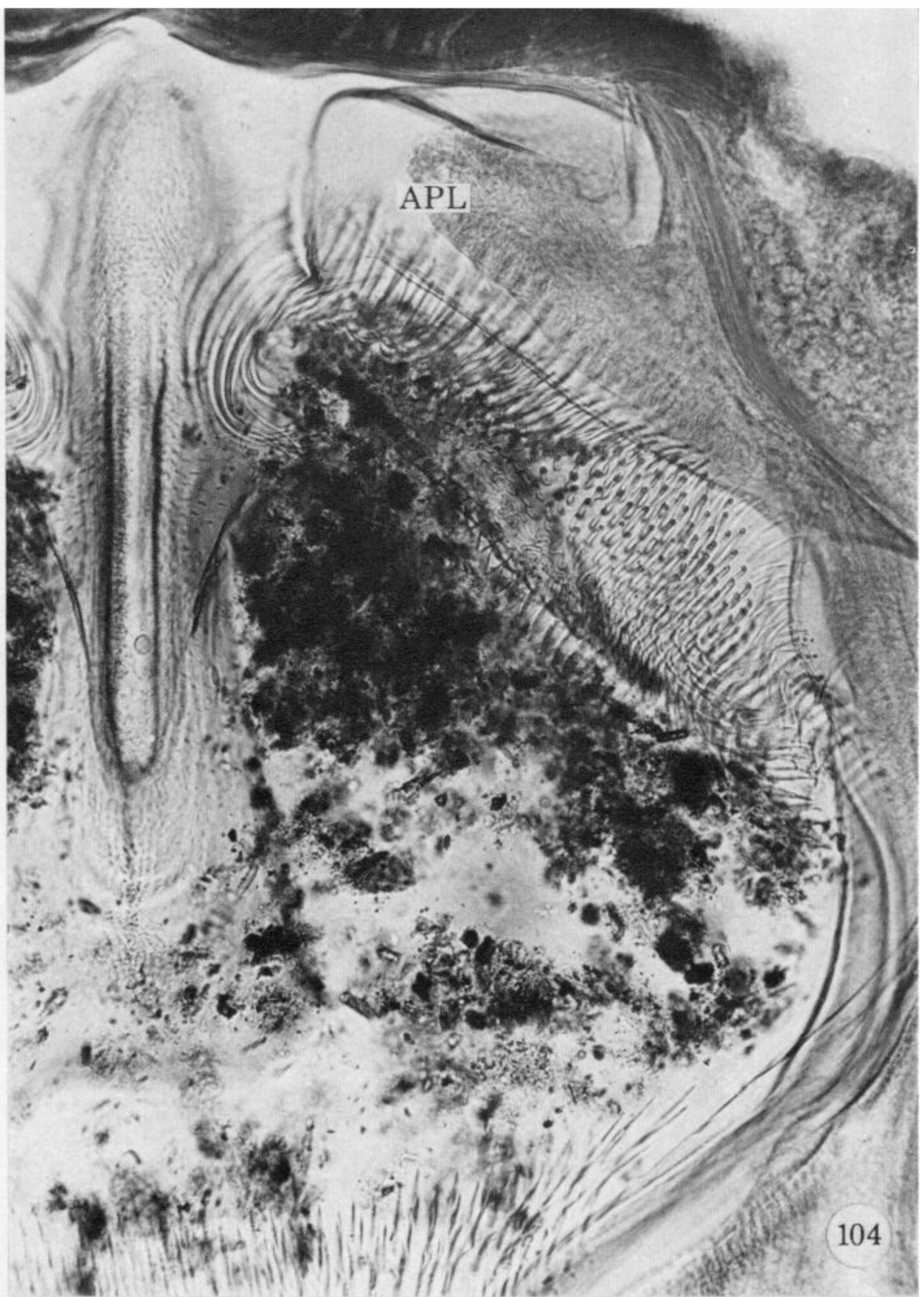
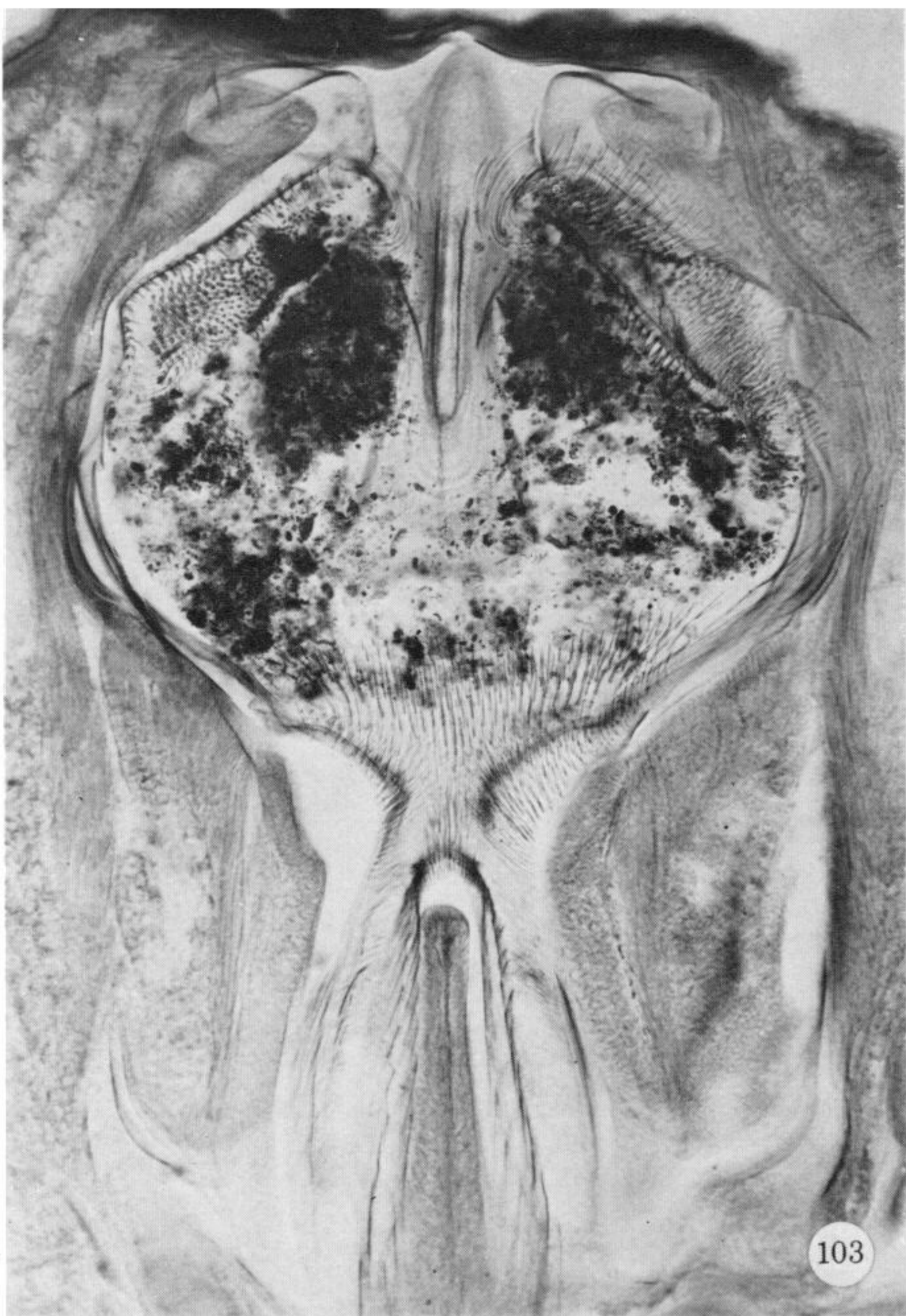
FIGURES 79-82. For description see opposite.



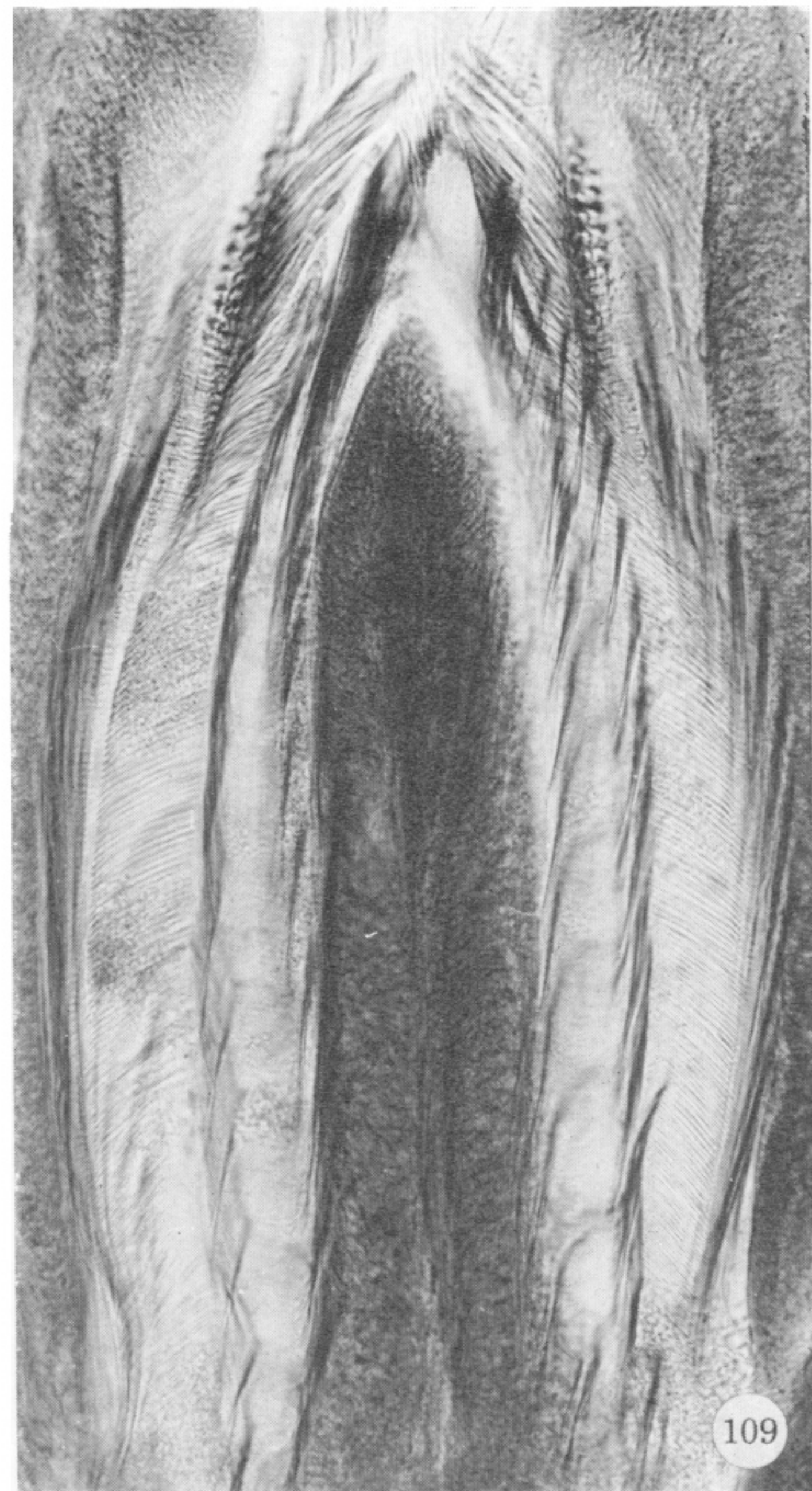
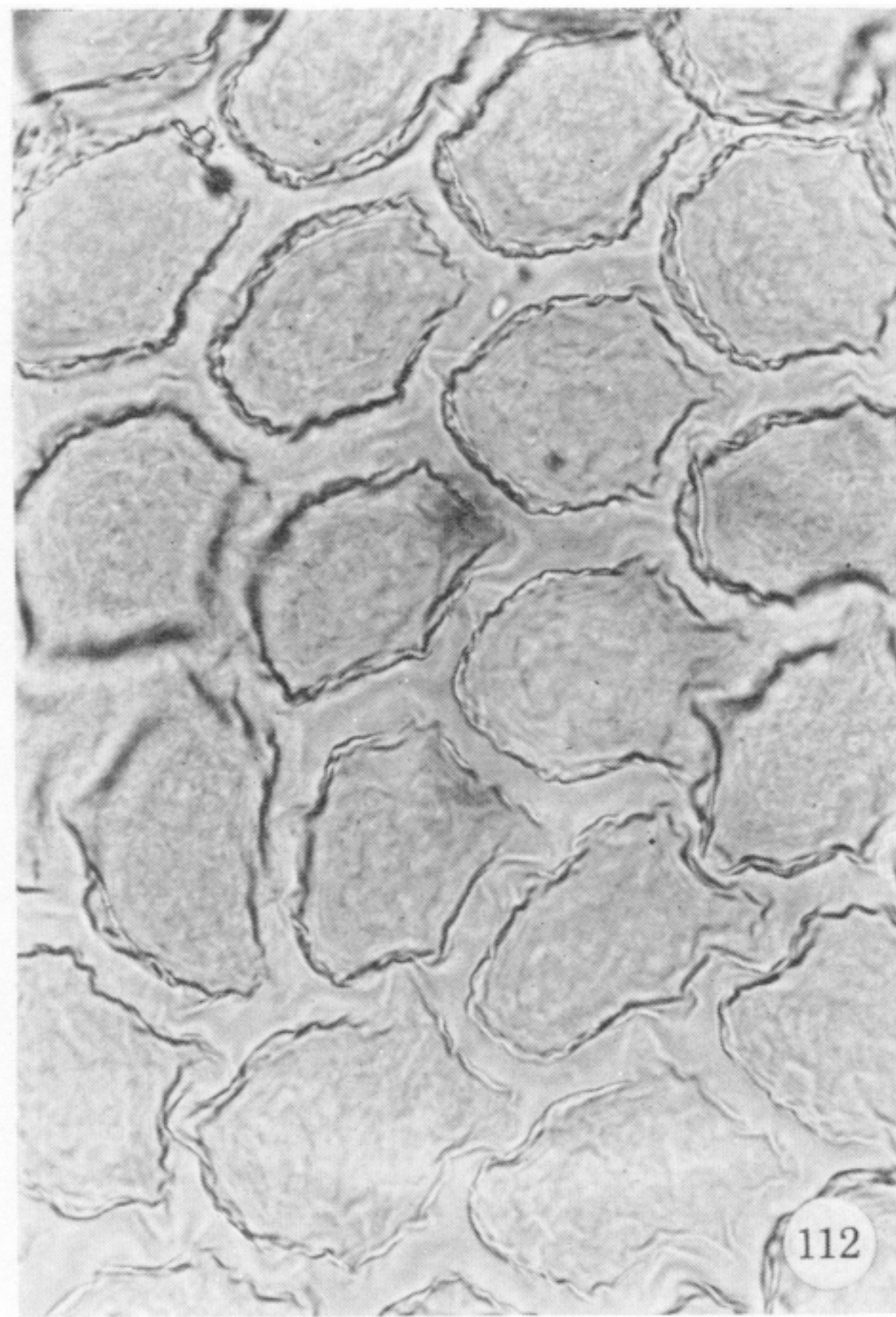
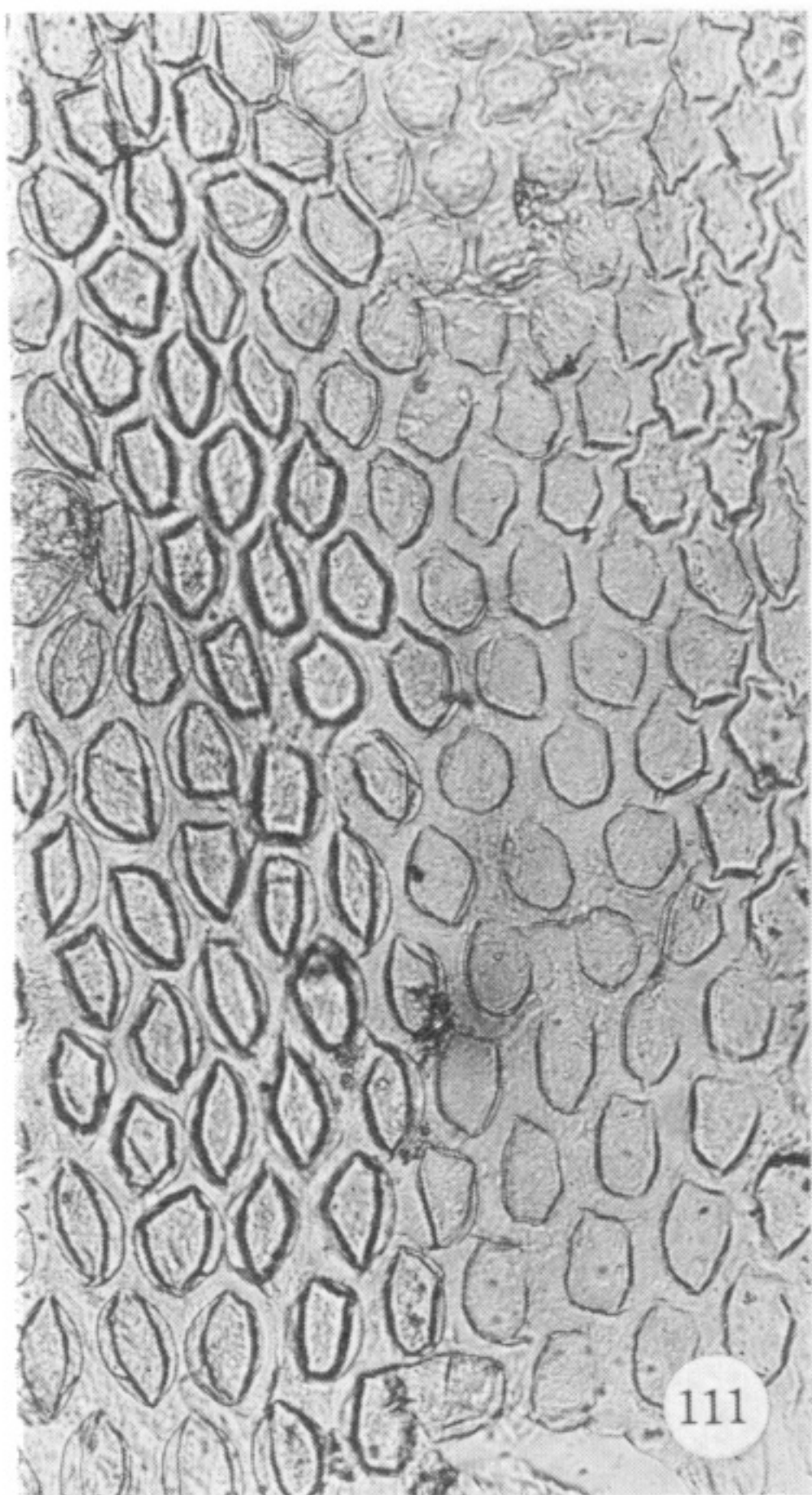
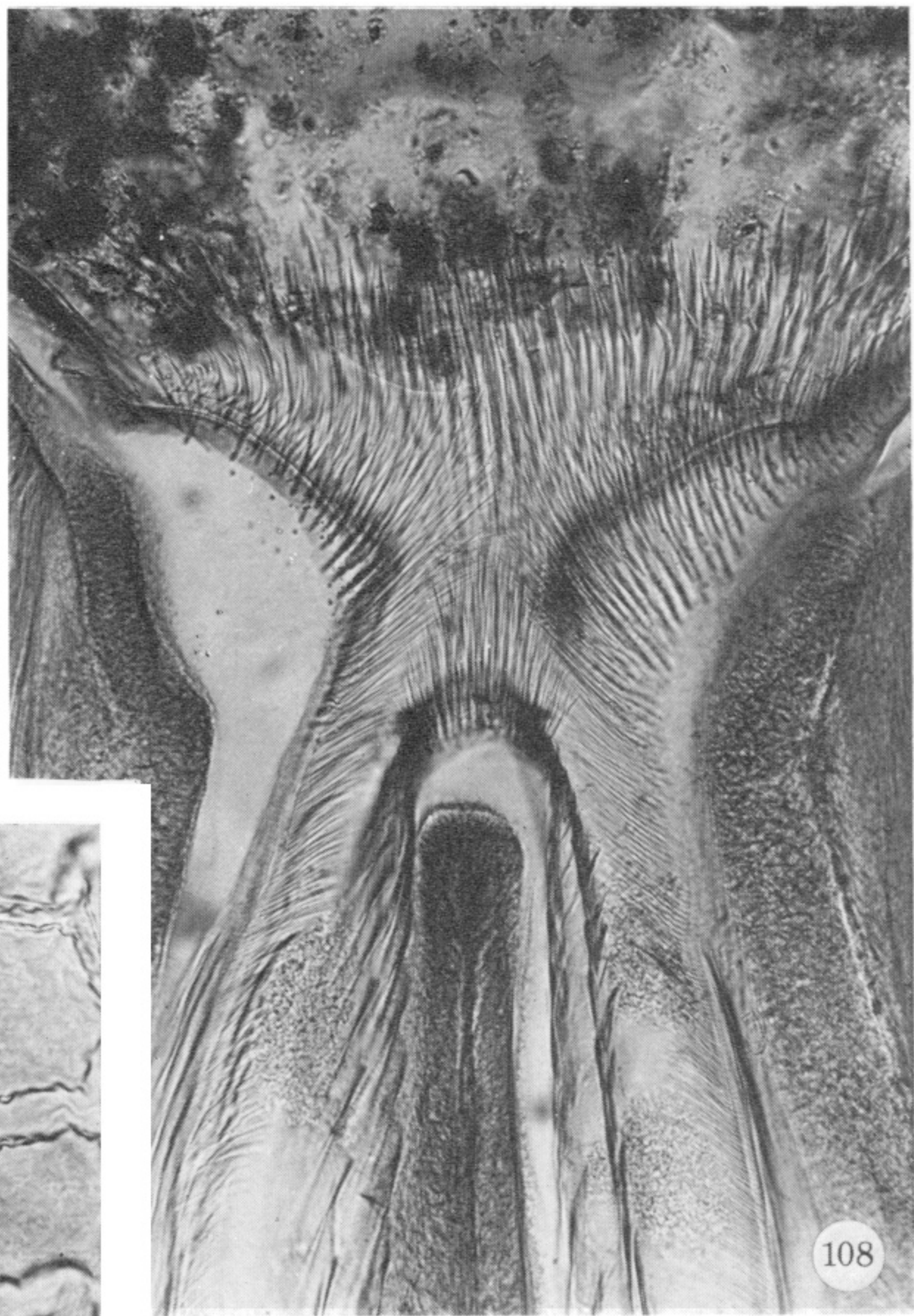
FIGURES 93-97. For description see opposite.



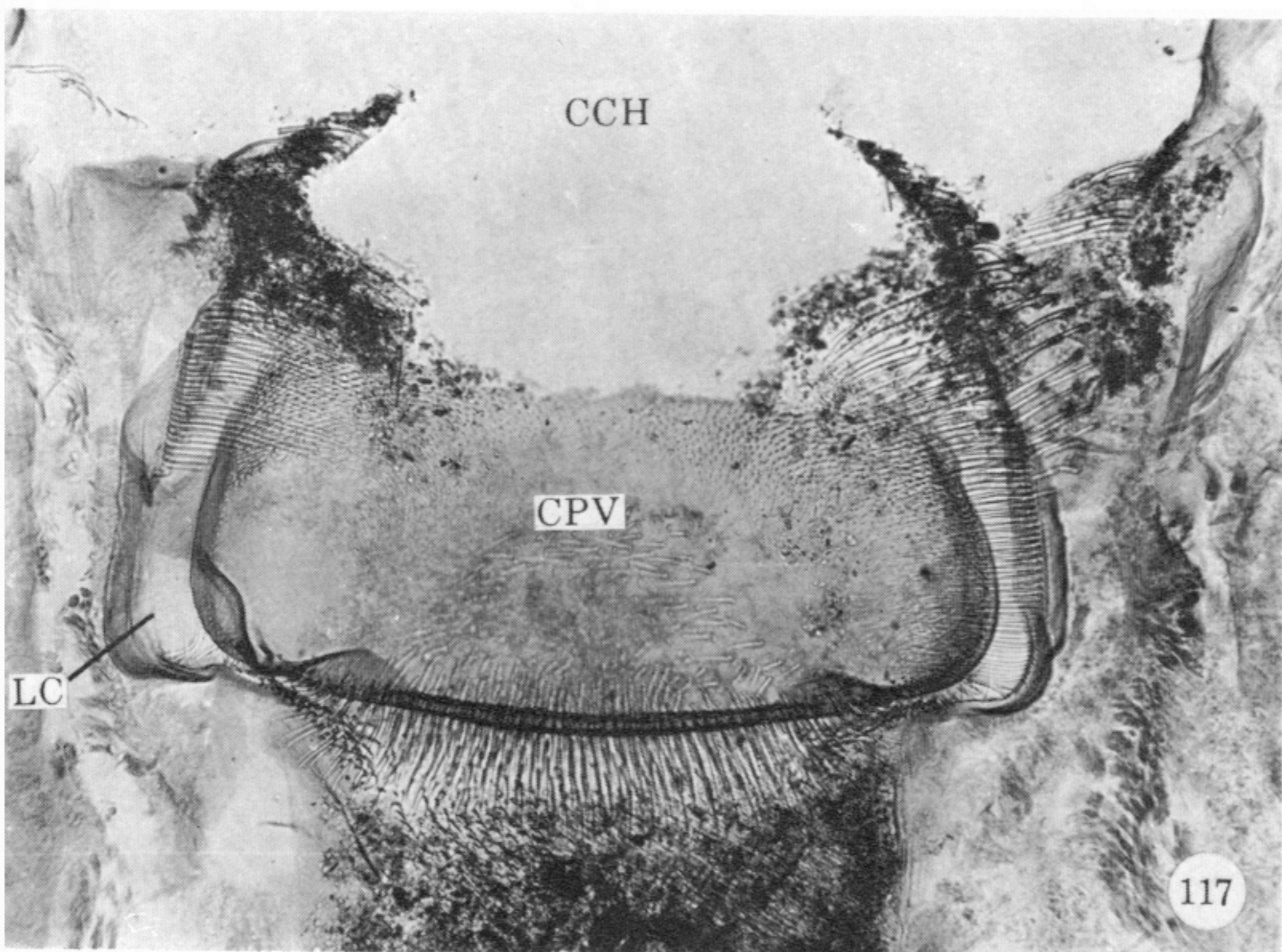
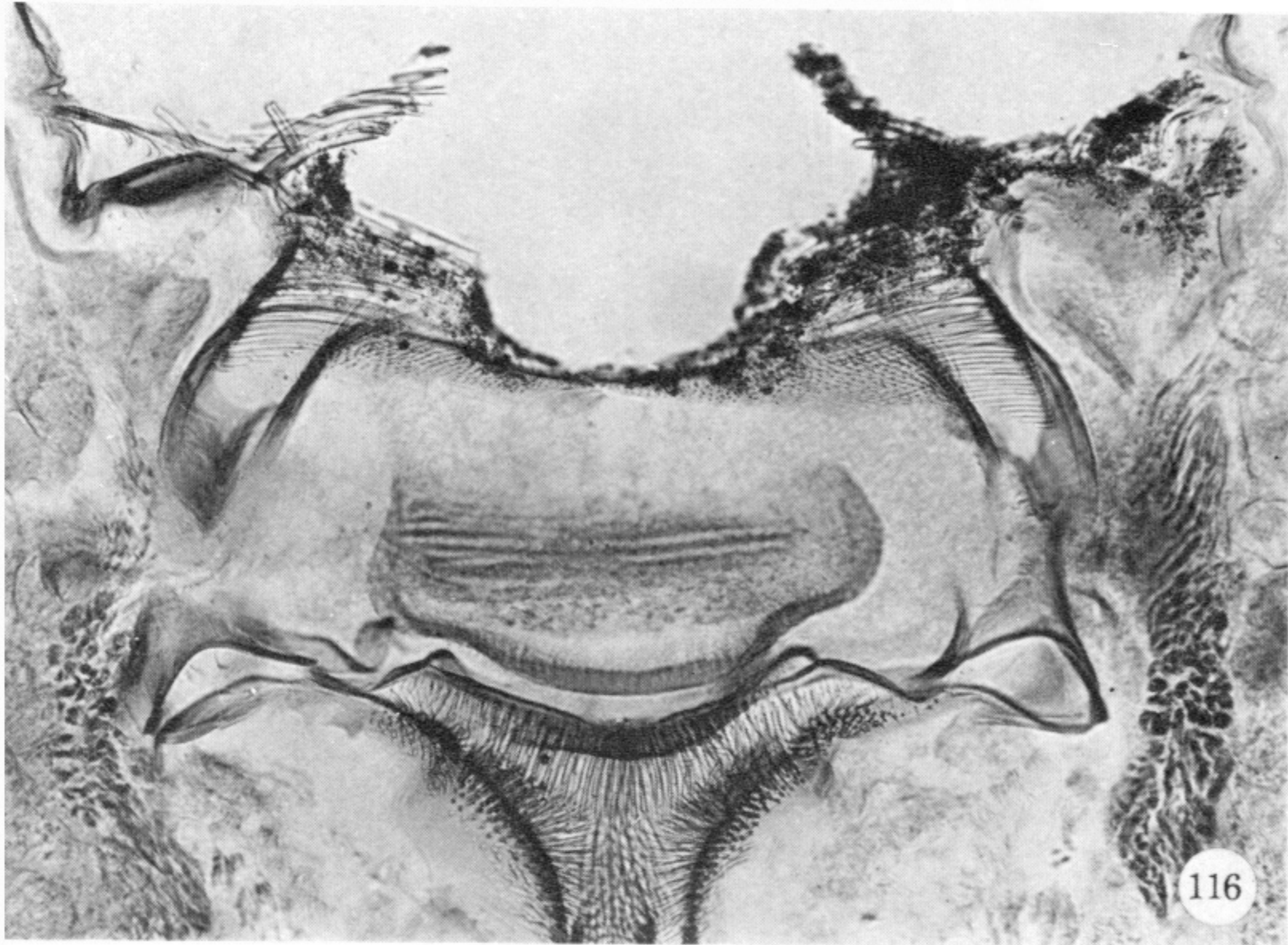
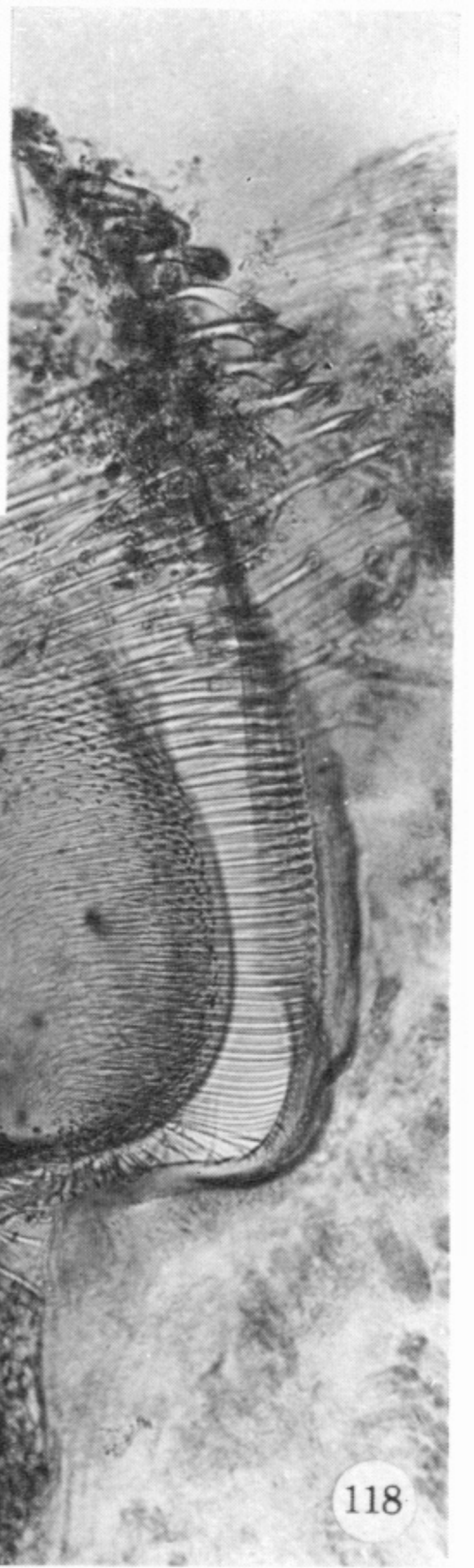
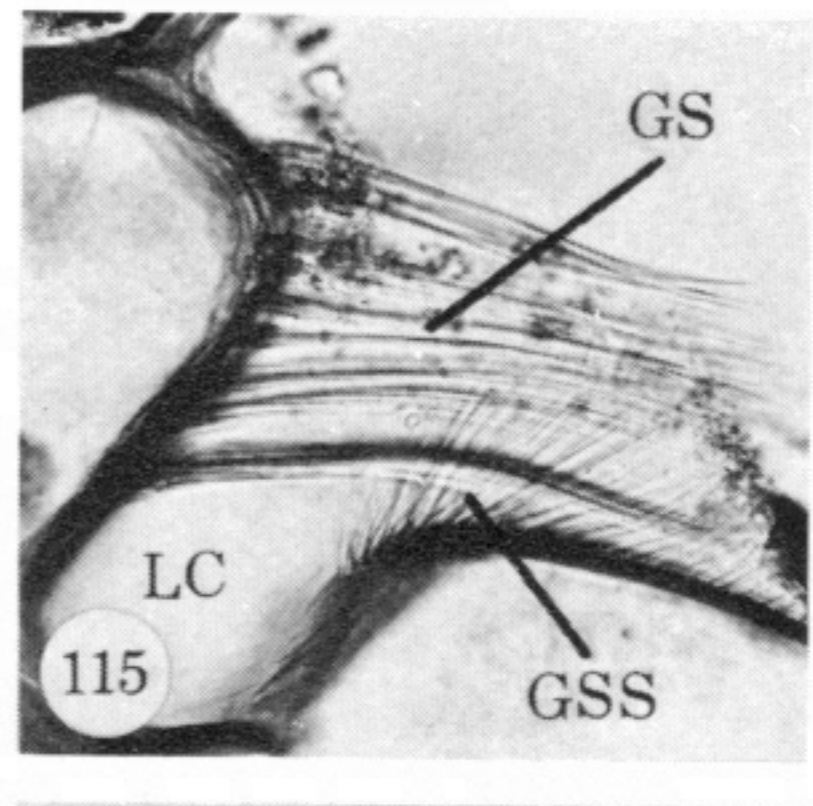
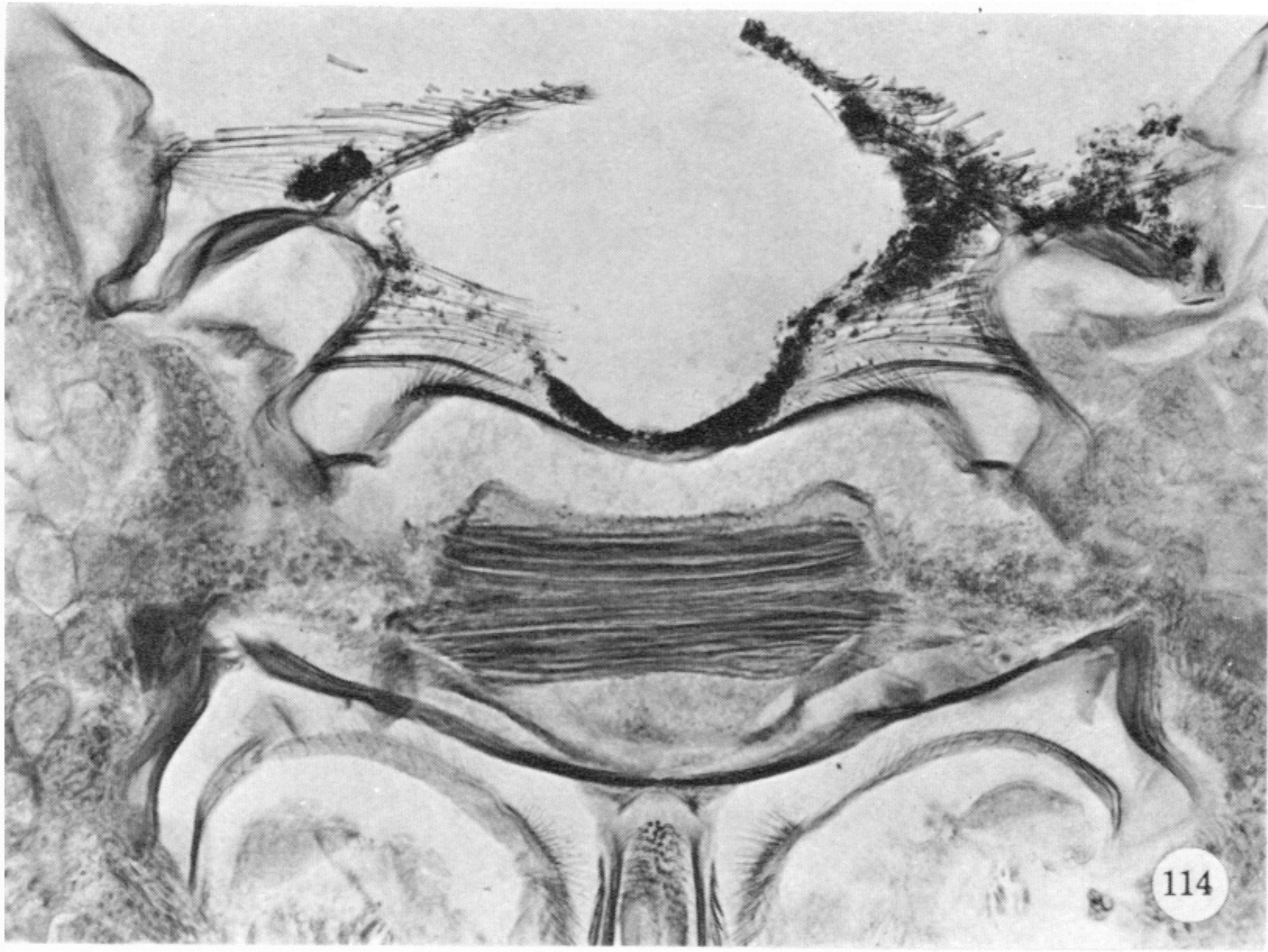
FIGURES 98-102. For description see opposite.



FIGURES 103-106. For description see opposite.



FIGURES 107-113. For description see opposite.



FIGURES 114-119. For description see opposite.