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Fryer, plate 7
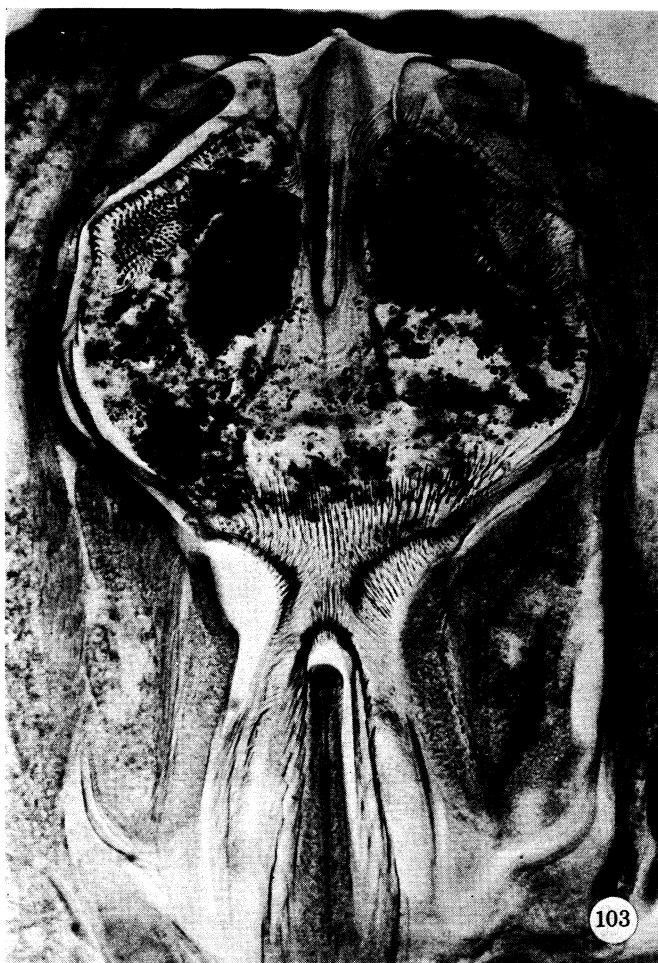

FIGURES 98–102. For description see opposite.

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 zygocardiac 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

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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 pleuropyloric 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 pleuropyloric 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 zygocardiac 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 pleuropyloric 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 pleuropyloric 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.
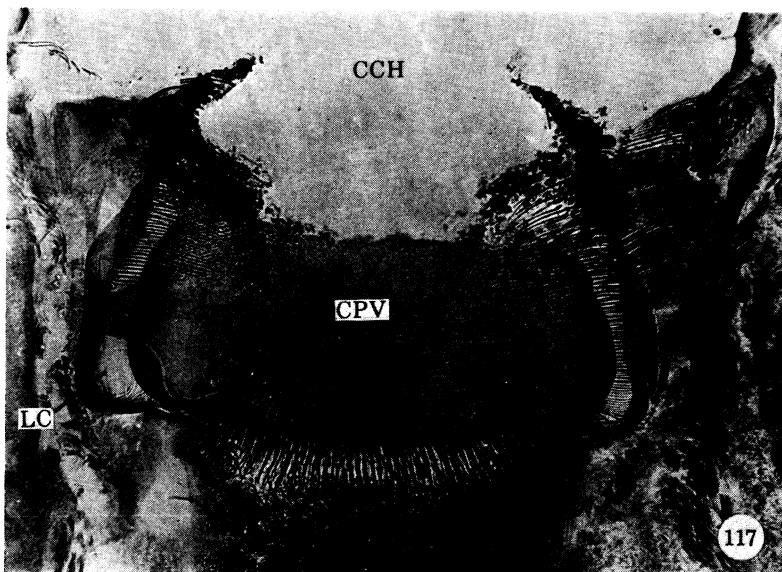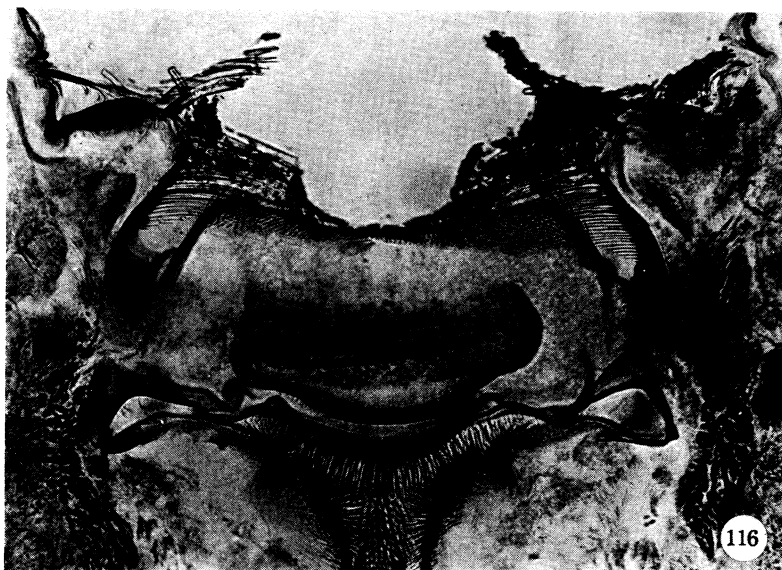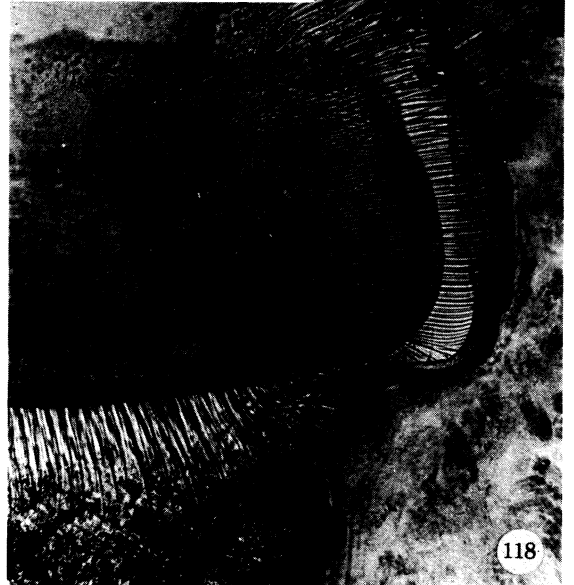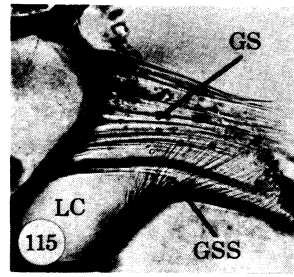
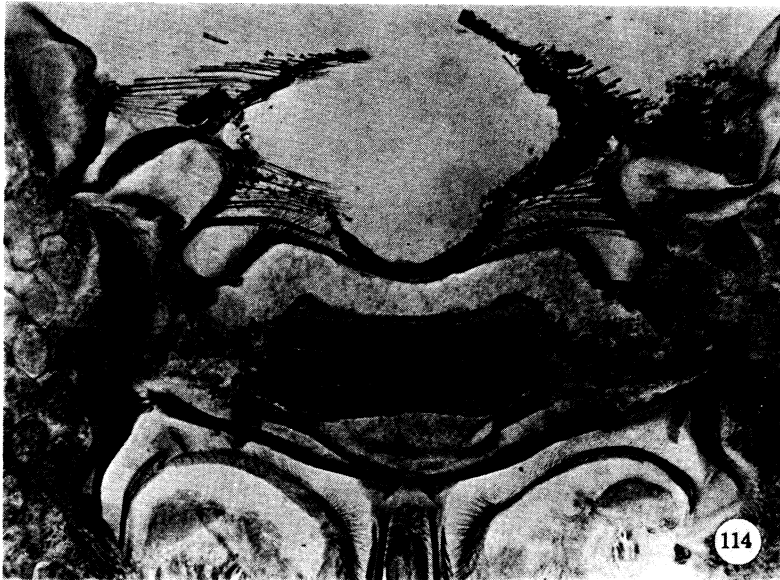FIGURE 112. Details of the convoluted membrane.

FIGURE 113. *Xiphocaris elongata.* Transverse section through the gastric chamber of the fore-gut showing the posterior comb plates.
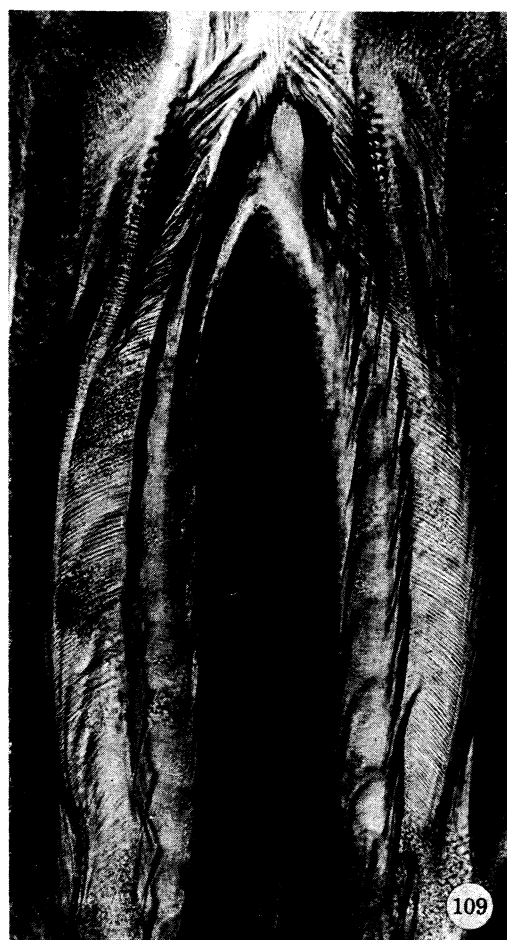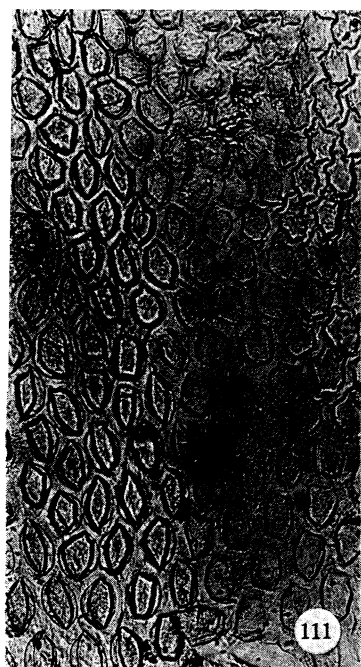
FIGURES 107–113. For description see opposite.

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Fryer, plate 10

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

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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
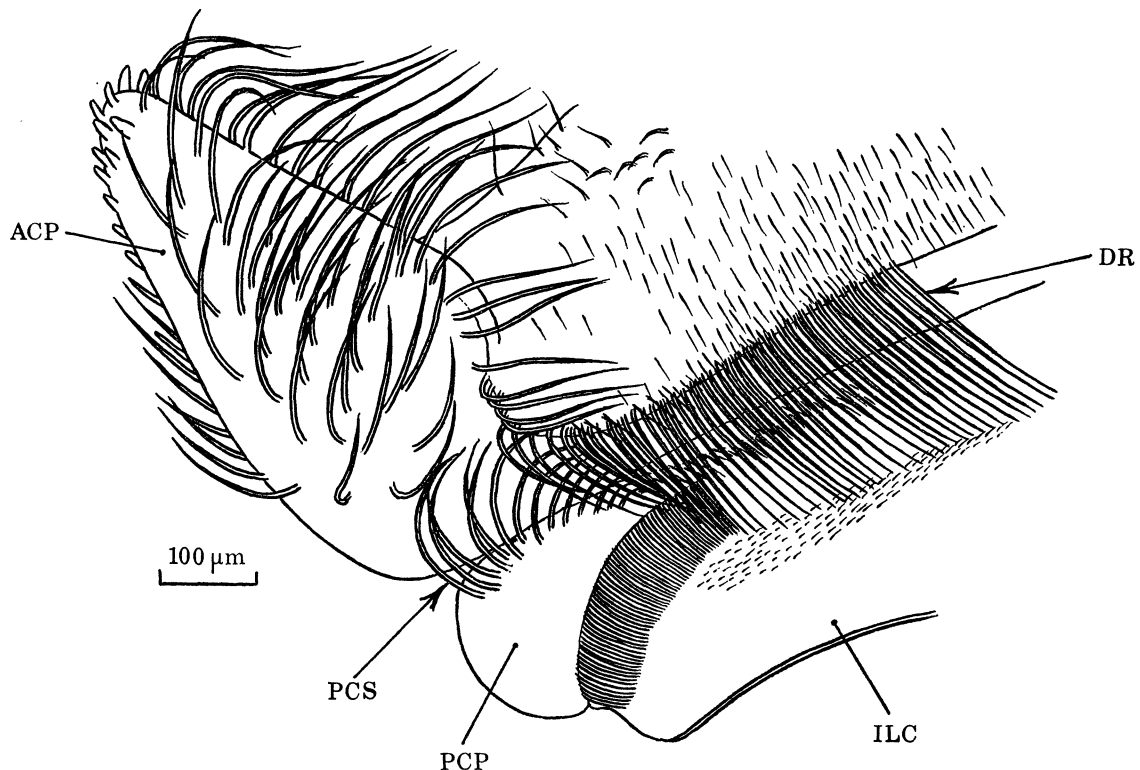

FIGURE 120. *Xiphocaris elongata.* The anterior comb plate (ACP) and the anterior part of the posterior comb plate (PCP) of the cardiac chamber of the fore-gut as revealed by dissection.

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*.
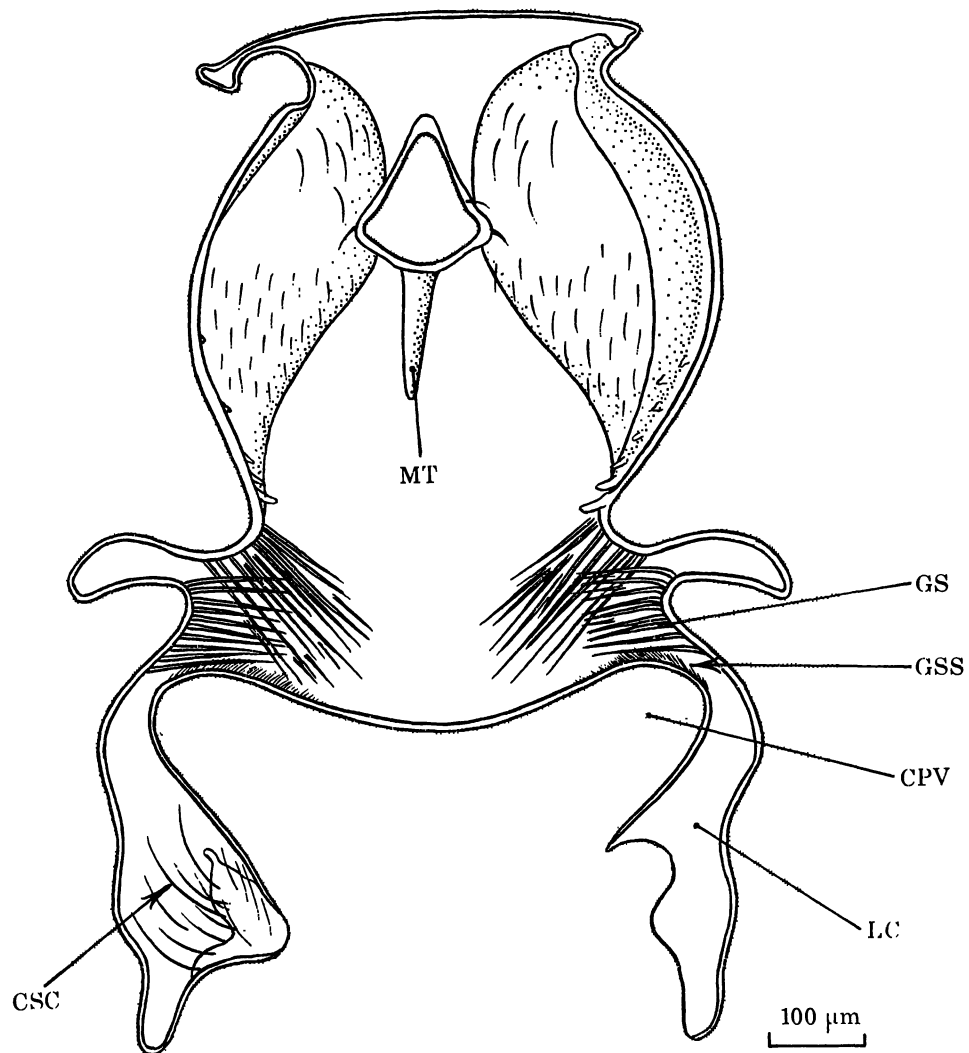

FIGURE 121. *Xiphocaris elongata*. Transverse section through the fore-gut at the level of the median tooth, to show especially the channels (LC) at each side of the cardio-pyloric valve (CPV) which unite the pyloric and cardiac chambers, and the spines (GS) and spinules (GSS) that exclude food particles 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-Acanthophyroid 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. Athough 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-Menéville) are also known only from the West Indies, each being reported from three islands of which Jamaica is common to both. The remaining seven epigean 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^2	Atyidae	Palae-monidae	total epigean Caridea
Cuba	44164	7	4	11
Jamaica	4411	8	4	12
Puerto Rico	3423	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 sub-terranean and their presence is related to geology and its ecological consequences rather than to size. If the comparison is confined to epigean 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 fresh-water 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.

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 *Eurycercus 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. *Zoöl. 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 Lysiopetaloidea (Diplopoda), some principles of leg design in Diplopoda and Chilopoda, and limb structure of Diplopoda. *J. Linn. 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 podophthalmaires. *Annls 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 (Syncarida: Malacostraca). *Syst. Zool.* **23**, 157–164.

Schminke, H. K. 1975 Phylogenie und Verbreitungsgeshichte 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. Zoöl.* **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
AC   aperture in cuticle
ACP   anterior comb plate
ACS   spines of anterior comb plate
AM   arthrodial membrane
APL   anterior portion of pleuropyloric ossicle

B   binding tendinous layer
BR   basal ring
BS   blade-like spines of dactylus

C   carpus
CB   cutting blade of mandible
CBP   chitinous blade of propus
CC   carpal cup
CCH   cardiac chamber
CHC   cheliped cuticle
CLS   cleaning spine of maxilliped 2
CM   convoluted membrane
CPV   cardio-pyloric valve
CS   cavity of seta
CSC   cleaning setae of lateral channel
CU   cuticle

D   dactylus
DE   denticles of gland filter
DE Mx   distal endite of maxilla
DE Mxlle   distal endite of maxillule
DP   denticles of median projection of gland
           filter
DR   distal row of spines

FD   flattened denticle
FL   flanking lips of gland filter
F Mx   fence of setae of proximal endite of
           maxilla
F Mxlle   fine funnelling setae of proximal endite of
           maxillule

GF   gland filter
G Mxp1   grid of distal endite of maxilliped 1
GS   guarding spines of channel between
           pyloric and cardiac chambers
GS Mxp 1, 2, 3   guarding spines/setae of proximal
           endite of maxillipeds 1, 2, 3
GSS   guarding spinules of channel between
           pyloric and cardiac chambers
GU   groove of uropyloric ossicle

HC   hinging cuticle

ILC   infero-lateral cardiac ossicle
IP   incisor process of mandible

J   joint between distal and penultimate seg-
           ment of maxilliped 2

L   ligament
LA   labrum
LC   lateral channel between pyloric and
           cardiac chambers
LD   lateral denticle
LL   lateral lobe of urocardiac ossicle
L Mand   left mandible
L Mxp1   long setae of proximal endite of maxilli-
           ped 1
LPO   outer lateral setae of pterocardiac ossicle
LR   lateral ridge

LS Mxlle   lifting spines of proximal endite of
           maxillule
LT   lateral teeth

M   muscle
Mand   mandible
MG   mid gut
MO   mesocardiac ossicle
MP   spinous median projection
MT   median tooth
MX   maxilla
Mxlle   maxillule
Mxp 1, 2, 3   maxillipeds 1, 2, 3

O   occluded region
OE   outer excavation
Oes   oesophagus

P   propus
PCH   pyloric chamber
PCP   posterior comb plate
PCS   spines of posterior comb plate
PE Mx   proximal endite of maxilla
PE Mxlle   proximal endite of maxillule
PE Mxp1   proximal endite of maxilliped 1
PF   posterior face of mandible
PG   paragnath
PGC   paragnath, cut away
PL   pleuropyloric ossicle
P Mxp 1, 3 palp of maxillipeds 1, 3
PO   pterocardiac ossicle
PPO   posterior setae of pterocardiac ossicle
PS Mxlle   posterior spines of proximal endite of
           maxillule
PV   pivot
PY   pyloric ossicle

R Mand   right mandible
RPG   right paragnath

S   spring
SCP   spinules of posterior comb plate
S Mxlle   short setae of dorsal edge of proximal
           endite of maxillule
S Mxp2   setae of maxilliped 2
S1 Mxp2   distal segment of maxilliped 2
S2 Mxp2   penultimate segment of maxilliped 2
SN   safety net of maxilliped 1
SP   spinous projection of mandible
SPC   spinules of dorso-lateral wall of pyloric
           chamber
SPL   spines of pleuropyloric ossicle
SR   supporting ring
SSCP   spinules of posterior comb plate
S Mxlle   stem of distal endite of maxillule
SS Mxlle   stout spines of proximal endite of
           maxillule
SZO   spines of zygocardiac ossicle

T   tendon
TL   teaselling lobe of maxilla
TR   thickened rim

UO   urocardiac ossicle
UPO   uropyloric ossicle

W   wall of cardiac chamber

ZO   zygocardiac ossicle