THE ATYID PRAWNS OF DOMINICA

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That the fauna of Europe in general, and of Britain in particular, gives a very imperfect idea of the importance of several groups of freshwater animals is perhaps insufficiently appreciated by European workers. An excellent example of such faunal poverty is provided by the decapod crustaceans – the group that includes crabs, crayfishes and prawns. Of this group there is only one truly native British species, the common crayfish *(Austropotamobius pallipes)*. In warmer regions, and especially in the tropics, the situation is often different. Here prawns and crabs are sometimes important constituents of the freshwater fauna. In few places can this be more clearly seen than in the West Indian island of Dominica. Here, where a copious rainfall is reflected by much rich forest and many perennial streams, the number of species of prawns greatly outnumbers that of fishes, which they replace as the dominant large animals of flowing water. The streams also harbour aquatic and semi-aquatic crabs thus emphasizing crustacean dominance. Of the prawns six species belong to the family Atyidae (Fig. 1) and five to the Palaemonidae. It is the former family that concerns us here.

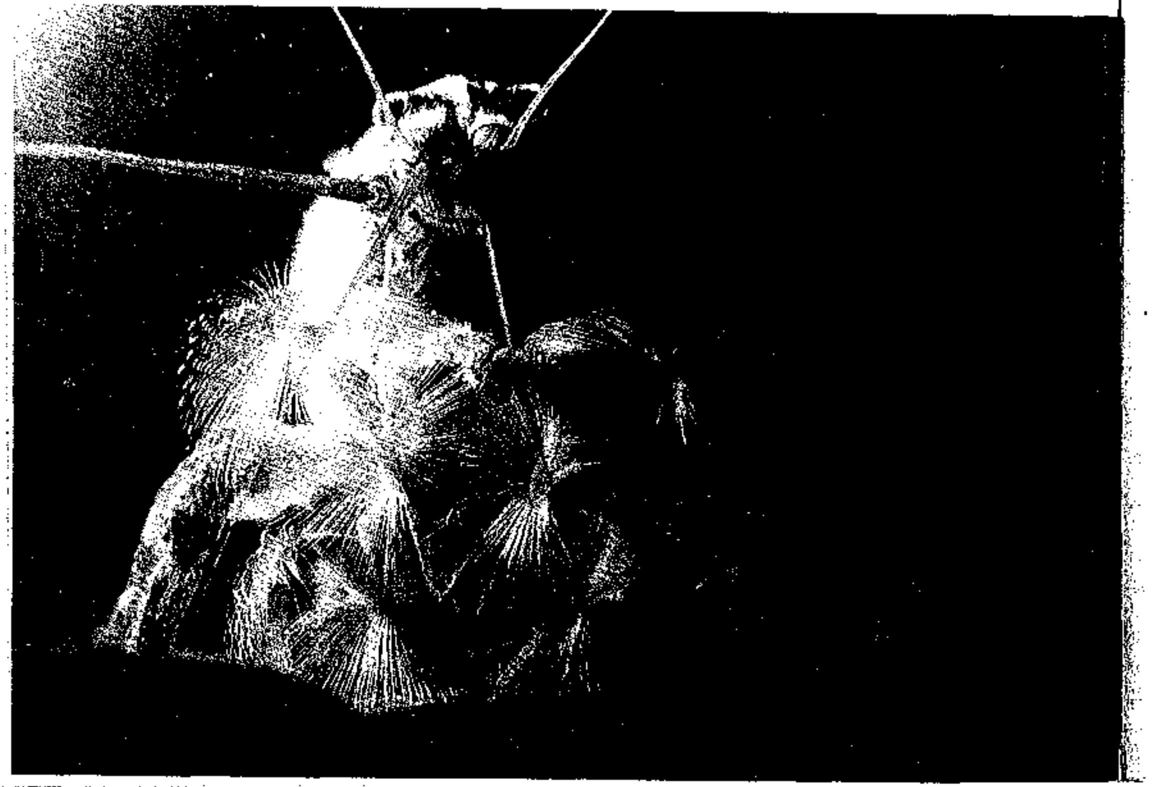
Atyids, which students of the Crustacea regard as primitive prawns, have a circumtropical distribution but additionally some have penetrated into temperate regions, sometimes in surface waters, sometimes as cavernicolous forms. An intriguing aspect of their distribution is that, although they are, and have long been, freshwater animals – fossils are known from freshwater deposits of Cretaceous age, and they have produced endemic genera in Lake Tanganyika – they have succeeded in colonizing many oceanic islands. The West Indies is an area of particular interest to the student of the family as representatives of several genera sometimes occur on one island. For its size Dominica is particularly rich in this respect. Especially interesting is the fact that its fauna includes not only the most primitive living atyid (a West Indian endemic, *Xiphocaris elongata*) but also two representatives of what is almost certainly the most advanced genus, *Atya*. Each of the other three species belongs to a separate genus.

All Dominican atyids are detritus feeders. Their food comes from the forest, leaves from which fall continuously into the streams and there break down into particles sufficiently small to be collected by the specialized food-gathering devices which they employ. If the forest is destroyed the atyids will disappear, either as a result of the lack of food or by scouring and drying up of the streams.

The primitive *Xiphocaris*, which reaches a length of 7 cm if one includes the long rostrum, is a lightly-built, transparent prawn with a well-defined ecological niche. It frequents quiet pools in streams over whose bottoms it tiptoes delicately, picking up individual small particles of detritus with its two pairs of chelipeds ('nippers') that are specialized for this purpose. It is

PLATE 3 *Atya innocous* advancing over a stone and collecting food by sweeping as it does so. The white particles are a proprietary breakfast food laid as bait. (See Plate 4.)

PLATE 4 (above) As Plate 3. The animal has advanced further and its chelipeds are shown at different phases of the cycle of movement. (below) *Atya innocous* facing a current with all its cheliped bristles spread to form four contiguous filtering baskets that passively collect suspended food particles.



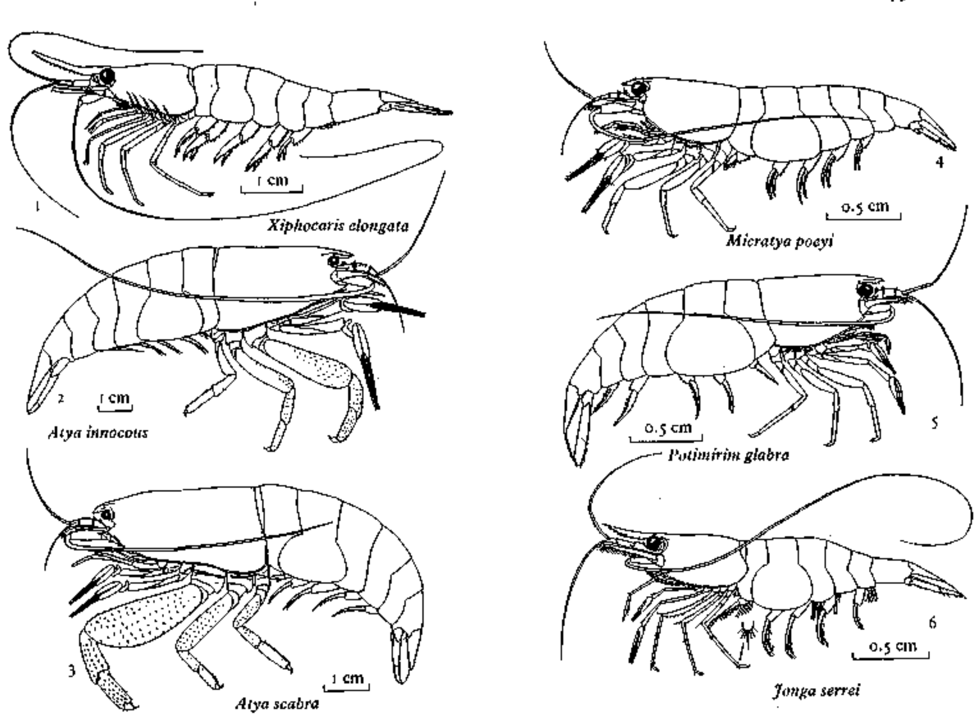


FIG. 1. The atyid prawns of Dominica.

also an efficient swimmer, and employs a very spectacular escape mechanism. When approached it leaps backwards by flexing its abdomen with such force as to propel it out of the water and through the air for considerable distances. On alighting it may make one or more additional leaps, presumably by further flexions of the abdomen, before disappearing beneath the surface.

In its method of food collection it differs from all other atyids in that its chelipeds are used directly for seizing food particles, as in the familiar crabs and crayfishes, whereas its relatives employ rows of highly specialized cheliped bristles. Although primitive, *Xiphocaris* employs complex machinery for dealing with the collected food in its passage from the chelipeds, via the mouthparts, to the mouth. A second complicated mass of apparatus located in the fore-gut is then used for sorting and processing the collected material.

All other Dominican atyids are crawlers rather than swimmers, and all have an elaborate method of food collection, again employing the chelipeds, but in a different way from *Xiphocaris*. In these species each 'finger' of the pincer of the cheliped, itself highly modified, is fringed by rows of elaborate bristles whose form, number and arrangement differ from species to species. In all cases these bristles are expanded into an opposing pair of fans as the cheliped is extended, and can then be placed against a stone or other object and brought together. In so doing each fan sweeps up small particles and when the two come together, closing as they do so, they enclose an accumulation of such material. This can then be passed to the mouthparts.

Such is the basic outline of the process. Many refinements are possible and have been exploited. The way in which the fans are expanded and closed also demands attention. Clearly, simple bristles will be less effective at sweeping than those which are modified by the development of ridges or side bristles so it is not surprising to find many such modifications nor to find that different species have specialized in different ways to enable them to exploit different habitats and niches. For example, the small *Jonga serrei* (generally less than 2·5 cm in length) habitually lives in slow-flowing water, usually near stream mouths, not because it needs brackish water but because in the mountainous Dominica it is only here that such slow flow is to be found. Here it scrapes both hard objects on the bottom and marginal vegetation and its bristles have become highly specialized as scrapers and brushes. Furthermore they are arranged in arcs so that, as the pincers close and the two fans sweep towards each other, the inner arcs of beautifully formed scrapers pass over the substratum first. These are followed by larger brushes that sweep up any material that is dislodged but not passed on directly by the scrapers. Thus are surfaces efficiently swept.

Specialized in a different way but employing similar principles are the two species of *Atya* – *A. innocous* (to 12 cm+) which is very common, and *A. scabra* (to at least 10 cm) which is much rarer. Both have extremely long cheliped bristles, so much so that the tip of a closed cheliped resembles the business end of an artist's paint brush. In order to permit this bunching together of the bristles there have had to be fundamental changes in the organization of the distal segments of the cheliped such as are not to be found in other decapods but which need not concern us here. When these bristles are expanded they make very large fans which can be used to collect material from stones in a similar manner to the shorter scrapers and brushes of *Jonga* (Plates 3, 4 above). They can, however, be used in another and even more remarkable way. The fans can be expanded and kept in this position as long as required. If expanded fans are turned to face the oncoming current they form a passive filter (Plate 4 below) whose 'pores' are reduced because the spaces between adjoining bristles are spanned by fine setules. Thus a fan can act as a filtering basket and catch drifting particles. The efficiency of this device is further enhanced by placing the four pairs of fans together, thus making up a large, continuous filtering surface. In the Malacostraca such a device is unique to *Atya* and its relatives. It bears remarkable convergent similarity to that employed by larvae of simuliid flies but the origin and anatomy of the various components is, of course, very different.

Both the Dominican species of *Atya* frequently filter in this way, often for many hours at a time, but aquarium observations suggest that *A. scabra* does so more persistently than *A. innocous* and that, while the latter regularly sweeps up particles, the former seldom does so. This difference is reflected in slight differences in the nature of the bristles. A few of those of *A. innocous* have fine teeth, detectable only under the microscope, which will help it to sweep up particles, but such are lacking in *A. scabra*. This difference helps us to understand the ecological preferences of the two species and may go some way to explaining why *A. innocous* is much more common than *A. scabra*. Its greater efficiency as a scraper may give it an advantage.

Another Dominican atyid is *Micratya poeyi* which, with a maximum length of only about 2·3 cm, is in many respects a miniature version of *Atya*. This is an extremely abundant species and, like *Atya*, can both scrape and filter passively. The least known species is *Potimirim glabra* whose cheliped bristles are specialized for sweeping and show few signs of being used for passive filtration.

The food collecting mechanism thus briefly described presents many problems to the zoologist. Particularly intriguing is the way in which the fans of bristles are expanded. Examination of the way in which the bristles are inserted on the cheliped segments reveals that no muscles whatsoever are attached to any of them – yet they are clearly under the precise control of the animal. The secret is revealed by the way in which they are attached to the hollow cheliped segments. Each bristle is tubular and sits over a hole in the cheliped cuticle (Fig. 2). Thus its cavity is in direct continuity with the fluid-filled cavity of the cheliped, itself continuous with the haemocoele of the trunk. Further, each bristle is beautifully pivoted so that it can swing freely, but only in one direction. Apart from the pivot the gap between the bristle and the cheliped cuticle is spanned by cuticle, thin in part but, opposite the pivot, thrown into a fold. Now, if haemocoelic pressure is locally increased, pressure in each bristle increases and, because it is pivoted, it swings in a predetermined direction until it can go no further. Thus is the fan expanded. At this point the convoluted cuticle is straightened out and is under tension. When the pressure is reduced this bit of cuticle acts as a spring, returning to its previously convoluted form and, in so doing, pulls the bristle back to its 'closed' position. Extension of the bristles is thus effected by a hydraulic mechanism, closure by the utilization of energy stored in a spring. It is easy to see that the fan will remain expanded so long as pressure is maintained. It is also easy to see that, by employing such a mechanism, all the bristles of a cheliped extend simultaneously and at the same rate. Each cheliped can, however, operate independently of its fellows.

Notwithstanding the fact that these prawns take great care of their long and slender bristles there is always a risk that one may be broken. Should this be so leakage of body fluids would be a potentially serious hazard were it not for the fact that a simple but effective safety device prevents such a

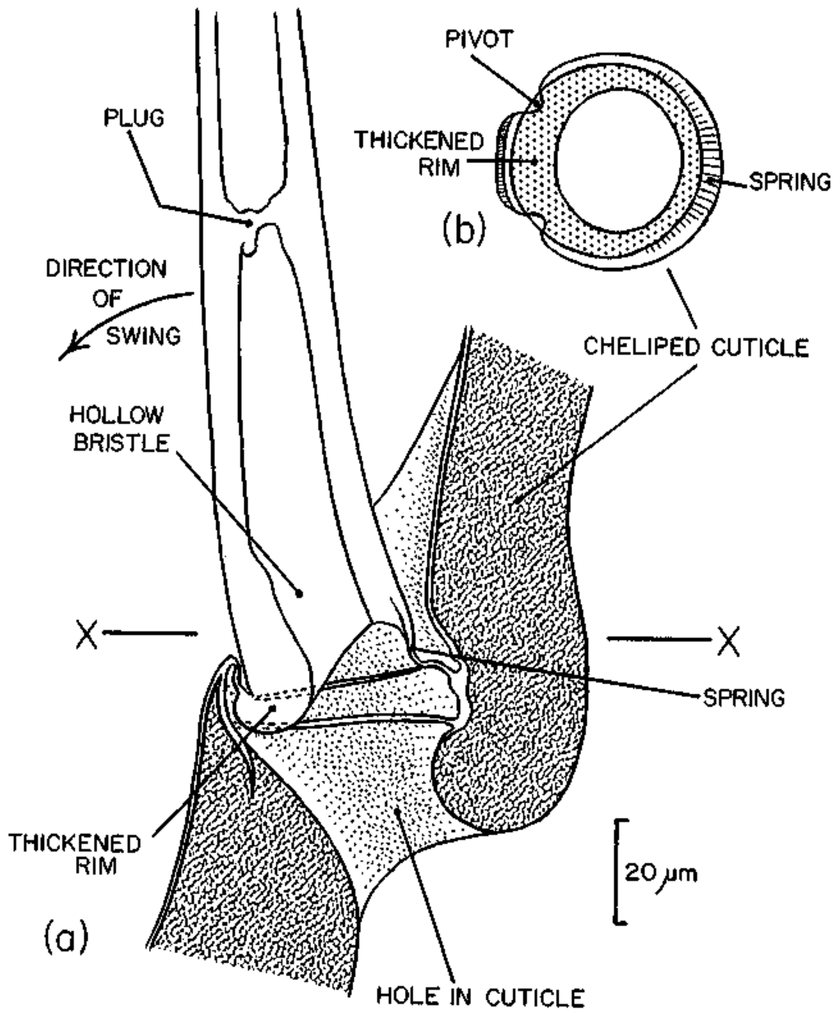


FIG. 2. (a) Longitudinal section through the base of a cheliped bristle of *Atya scabra*. (b) Semi-diagrammatic transverse section of such a bristle at the level x—x of figure 2(a).

tragedy. Not far from its base the lumen of the bristle is occluded by a chitinous plug (Fig. 2) so that the long distal portion, while hollow, is completely cut off from a shorter basal region. Thus, if broken anywhere in the most vulnerable region beyond the plug, no loss of fluid ensues. The plug is sufficiently far from the base not to interfere with the mechanism for extending the bristle.

Food collected by *Atya* and its relatives, whether by sweeping or by passive filtration, is passed by the chelipeds to the mouthparts which are exceedingly complex. Even minute particles can be swiftly and efficiently removed from the chelipeds. These are then manipulated by various processes, including one akin to teaselling, and transferred to mandibles that display a curious blend of primitive and specialized attributes in both anatomy and musculature. Of them it is possible to say that they retain features to be seen in some of the most primitive crustaceans on which have been superimposed specializations as remarkable as any to be seen in the Malacostraca.

Many large decapods, such as crabs and crayfishes, seize large masses of food which are sheared into manageable lumps by the mandibles – used in atyids for sweeping fine particles into the oesophagus and scarcely at all for grinding – and store them in the fore-gut. Here they can be masticated at leisure by stout 'teeth' (ossicles) developed in its walls which are pulled together by powerful muscles. Being feeders on fine particles *Atya* and its relatives have no need of such a device but face different problems, namely those that involve the manipulation, sorting and posterior transfer of these particles. Here therefore the ossicles are elaborated as complex combs and sweeping devices. Further, like other decapods, atyids have, as an integral part of the fore-gut, a complicated structure called a gland filter which allows the entry of only exceedingly fine particles and material in solution which passes ultimately to the hepatopancreas – here an organ of both secretion and absorption.

Study of these animals in both field and laboratory has not only thrown light on the way in which they are constructed and how they utilize the complex structures that they have evolved, but has given a glimmer of understanding of the way in which they manage to live together. All eat basically the same kind of food – detritus derived from leaf litter – but the various species collect it in different ways and from different habitats within the streams. They also manipulate it in different ways though this may be irrelevant from the ecological standpoint.

Life histories are inadequately known. In *A. innocous* at least, mating is successfully accomplished in aquaria and fertile eggs are then carried by the females. These produce zooea larvae that have never been reared beyond the age of 10 days, but given spacious conditions this should be possible. Their fate in nature is not known but one doubts whether a period of marine life is necessary, as evidence of successful reproduction in an ornamental pond was obtained in Dominica.

The two species of *Atya* are eaten in large numbers by the people of Dominica, as are the local palaemonids, and are an excellent source of very palatable protein. Basketfuls of such prawns are sometimes collected from suitable reaches, or pools on streams that can be dammed and drained to facilitate this, and casual collection is practised elsewhere. A possible role for these prawns elsewhere is the utilization of detritus in heated power-station waters. In themselves they are innocuous, pacific animals and the only safeguard necessary before introducing them to such waters would be to ensure that they did not serve as hosts to pathogenic micro-organisms. They are incapable of surviving an English winter in unheated waters.

A more detailed account of these prawns, with 121 illustrations, is given in a paper published in *Phil. Trans. R. Soc. (B)*, **277**, 57–129 (1977). Thanks are given to The Royal Society for permission to use, sometimes in a modified form, illustrations from this paper.

VARIATION IN BACTERIAL POPULATIONS IN TIME AND SPACE

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Among the many problems which beset the bacterial ecologist, one of the most intractable, and unfortunately the most basic, is that of obtaining a reliable estimate of the bacterial population. At any given time this population will consist of a mixture of autotrophs (organisms deriving carbon from inorganic sources and energy either from inorganic oxidation reactions or sunlight) and heterotrophs (deriving carbon and energy from organic compounds). This nutritional diversity is a major contributing factor to the problem. The bacteriologist may obtain estimates of the 'total' or the 'viable' population in any given sample. The former usually represents the number of particles of bacterial shape and size which have been concentrated on a membrane filter. There are several microscopical techniques for counting these particles but those which have received most attention in recent years are epifluorescence and scanning electron microscopy. The fluorescence technique involves addition to the sample of a dye which reacts with living cell constituents (e.g. acridine-based fluorochromes which are thought to react with DNA and RNA, the nucleic acids which control cell reproduction and growth). The sample is then drawn through a black membrane filter and the particles, including the bacteria, which are trapped on the membrane surface are counted by incident light fluorescence (epifluorescence) microscopy. The light for excitation is directed down through the objective on to the membrane surface. If this light is of a suitable wavelength the particles are excited and emit light of a lower energy (longer wavelength) which passes back up through the objective and via a series of selective filters and mirrors to the eyepiece. There are many variants on this method (Jones 1974; Jones & Simon 1975) but they, like the scanning electron microscope procedure, suffer from the disadvantage that no reliable information is provided on whether the bacteria counted are active or capable of growth and division. To obtain this information we must turn to one of the so-called 'viable counting procedures'. The sample is incubated in the presence of a nutrient medium until visible bacterial growth occurs. This is usually done in this laboratory by spreading known volumes of water on the surface of CPS agar (Taylor 1940; Collins & Willoughby 1962), and counting the colonies which develop after a suitable incubation period. The CPS agar has been thoroughly tested in a number of laboratories and appears to yield higher counts of viable freshwater heterotrophs than other media available at present. We cannot, however, assume that all heterotrophic bacteria produce visible colonies, nor that the medium will support the autotrophic organisms mentioned above. Lake waters in this district yield direct counts which vary between 1×10^6 and 10×10^6 bacteria ml^{-1}, whereas counts of viable organisms are two to three orders of magnitude lower than this at 1×10^3 to 20×10^3 bacteria ml^{-1}. Clearly we are not culturing all the bacteria that are capable of growth, but on the other hand we may be