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ON THE ORIGIN OF CRUSTACEA

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SUMMARY

Crustaceans are predominantly aquatic arthropods with a characteristic naupliar stage. Their known evolutionary history extends at least from the Early Cambrian. They display many features convergent with the chelicerates, uniramians and trilobites and formerly were classified with these groups in Arthropoda.

It seems more appropriate to study the origins of Crustacea by reference to their Cambrian representatives than by seeking to establish particular intuitions concerning early crustaceans based on a knowledge of living forms only.

Among Cambrian fossils, the lobopod *Aysheaia* is irrelevant to crustacean origins. Similarly, the living Tardigrada are best consigned to a separate phylum although they seem to be a related group with several primitive characters and are likely, on zoogeographic grounds, to have had a long evolutionary history.

Assuming that Crustacea are monophyletic, the existing fossil record dictates that the ancestral taxon possessed a complex of characters out of which evolved (during Cambrian times) at least: bradoriids and other primitive ostracode-like animals; *Canadaspis* and other phyllocarid-like forms; *Branchiocaris* and similar notostracan-like forms. Several other Cambrian taxa may be either true crustaceans or examples of convergence. Some show similarities to anostracans and conchostracans.

The diversity and complexity of the Cambrian fossils suggest that a basic crustacean facies was already established by the Late Precambrian (Ediacaran).

Introduction

Most crustaceans are aquatic invertebrates, inhabiting marine or continental athalassic and freshwater environments, although many terrestrial-adapted species are known. The total of crustacean species is not known definitively but has been conservatively reported at 40,000 (Gruner and Holthuis, 1967, cited in Moore, 1969, p. R59). This number is near the known species of Ostracoda alone (McKenzie, 1973). Probably, the total number of described crustacean species is nearer 100,000. This larger figure takes into account the rich fossil record of Crustacea which extends from the Early Cambrian to Recent, i.e. spans over 550 million years.

It is scarcely surprising that such a large pool of species embraces a remarkable diversity of forms. Nevertheless, the homogeneity of Crustaceans as a group has rarely been questioned. A particularly powerful argument in favour of the unity of Crustacea is adduced from embryology. Thus, ". . . the mode of development in Crustacea is based on spiral cleavage and a configuration of presumptive areas whose subsequent development is as a nauplius . . ." (Anderson, 1973, p. 471). The typical crustacean nauplius (metanauplius) is an ontogenetic stage which, embryologically at least, may be considered to possess a basic segmentation that includes antennular, antennal and mandibular segments (McKenzie, 1972, p. 172).

With some major exceptions (e.g. Ostracoda), most mature crustaceans possess three more or less well-defined tagmata—cephalon, thorax and abdomen—analogously with the non-related Trilobita. In general, cephalic features tend to be conservative among the several crustacean groups and typically include two pairs of antennary appendages. Behind these are segments which carry gnathobasic mandibles and up to two pairs of maxillae (in some groups one pair is interpreted as having been lost during evolution). The total possible number of cephalic segments is thus six but some or all may be fused.

On the other hand, the crustacean thorax is rather variable both in its segmentation and appendages but usually displays metamery. Some conception of its variability may be gained by study of Table 1, which lists the number of serially homologous thoracic limb pairs in carapace-bearing crustaceans and in some Burgess Shale (Middle Cambrian) arthropods with affinities to Crustacea. Likewise, the abdomen is variable and terminates either in an anal segment plus uropods or in a telson with or without uropods (Bowman, 1971).

Crustaceans often possess a carapace, although many groups lack one. It may be bivalved and enclose all or most of the body (Ostracoda, Conchostraca, Cladocera and cirripede cyprid larvae), or be a simple head-shield (Notostraca), or be bivalved and cover only the anterior part of the body (Phyllocarida). When bivalved it articulates either along a ligament or through hinge structures (Ostracoda). It seems best to consider the carapace as representing a grade of evolution (Manton, 1969)* rather than as indicating relative ancestry between groups being compared, although the fossil record clearly indicates that the most ancient preserved crustaceans all had carapaces (Table 1).

Table 1. Numbers of serially homologous paired thoracic appendages and segments in carapace-bearing crustaceans (modified from Jones and McKenzie, 1980).

Anderson (personal communication, June 1980) has noted that in all Malacostraca the number is 8, even though some of the anterior segments may have their limbs modified as maxillipeds.

Other ancient crustacean groups, e.g. Anostraca/Lipostraca (Devonian–Recent) and Syncarida (Carboniferous–Recent) lack a carapace.

Group	Serially homologous paired thoracic appendages and segments	Geologic range
Bradoriida	4	Cambrian–Ordovician
Ostracoda	3	Cambrian–Recent
Phyllocarida	8	(?) Cambrian–Recent
Branchiocaris	12–13	Middle Cambrian
Burgessia	3 + 7	Middle Cambrian
Waptia	10	Middle Cambrian
Cirripedia	6	(?)Cambrian–Recent
Eocarida	6–8	Devonian–Permian
Conchostraca	10–30	Devonian–Recent
Notostraca	11	Devonian–Recent
Hoplocarida	4 + 4	Devonian–Recent
Decapoda	5	Devonian–Recent
Peracarida	5–7	Carboniferous–Recent
Cladocera	6	Permian–Recent
Argulidae	4	Mesozoic–Recent
Euphausiacea	8	(?)–Recent

* This concept apparently is confusing for some workers who correlate functional morphologic equivalence with taxonomic hierarchies. Such correlations may occur but are not necessarily a corollary of the concept, which holds that functional equivalence (grade) may be attained in different lines at about the same or at different times depending on their several evolutionary rates.

Summarising, crustaceans have in common a characteristic embryology and naupliar stage (sometimes as a metanauplius: Sanders, 1963, p. 14); characteristic cephalic features which include biramous antennae, biramous gnathobasic mandibles and a more or less common number of partially or wholly fused head segments; and, often, a carapace.

Early crustaceans or pre-crustaceans

All discussions on origins have a common problem: whether to concentrate on the conditions leading up to a particular event or on the earliest expressions of that event. This problem is well expressed in current research on the origin of life where two distinct schools have arisen: one prebiological, represented by the work of chemists such as Ponnamperuma and Fox; the other early organic, and represented by the work of biologists such as Margulis and Schopf. Both groups use the uniformitarian approach of comparisons with modern phenomena and living organisms (Margulis, 1970).

With respect to the origins of Crustacea, such a problem is resolved by the fact that virtually nothing is known of a crustacean record prior to the Early Cambrian although the complex organisations of Cambrian Crustacea suggest that there must have been one. *Parvancorina*, a carapace-bearing (?) taxon in the famous Ediacaran fauna of South Australia, is the only conceivable Precambrian candidate—its age is about 680×10^6 years—but Delle Cave and Simonetta (1975) compare it with *Skania* and argue against it being a crustacean.

Skania is a member of the later, equally famous, Middle Cambrian Burgess Shale fauna of western Canada which has a highly diverse arthropodan assemblage that includes several distinct stocks of carapace-bearing crustaceans; and there are numerous other Cambrian crustacean records. Most notable of these latter is the recent description of phosphatocopine ostracodes from the Late Cambrian of Sweden and from Late Cambrian rocks which have been re-sorted into Pleistocene drift deposits of northern Germany (Müller, 1979). The apatite preservation of the appendages of these ancient ostracodes is excellent.

Thus there are a number of well-preserved early crustaceans. This paper will consider some of them. It will also use an uniformitarian approach and study their living descendants, the objective being to develop ideas on the likely characteristics of the early Crustacea.

En route to my conclusions, it will be necessary to deal in a definitive manner with the relevance or otherwise for crustacean evolution of the bilaterally symmetrical lobopodial coelomate *Aysheaia*, another of the exotic suite of animals from the Burgess Shale.

Homeomorphy with other arthropodans

In 1973, Sidnie Milana Manton formalised taxonomically the concepts which she had pursued vigorously over five decades (Manton, 1973). In consequence, the phylum Crustacea is nomenclaturally available and, more importantly, its relationships with other arthropodans are better understood. These relationships were elaborated in greater detail by Manton in her classic book "The Arthropoda" published shortly before her untimely death (Manton, 1977).

The concept of polyphyly in arthropodans depends upon the elucidation of numerous homeomorphic characters. This fact remains not widely appreciated so that some workers persist in proposing a monophyletic origin for Arthropoda (Simonetta and Delle Cave, 1978). Presumably, such workers regard these characters as homologous rather than homeomorphic. Quoting Simonetta and Delle Cave (op. cit., p. 88), ". . . gli Artropodi paleozoici mostrano possedere una base morfologica comune che depone per l'essenziale monofiletismo del phylum . . ."

The difference between homology and homeomorphy can be demonstrated by considering in some detail the crustacean mandible and by contrasting this type with the homeomorphic mandibles of other arthropodans. That these basically different structures can have the same function, i.e. can operate as one or another kind of jaws to bite, triturate or pierce food, demonstrates a generally similar grade of evolution, but this is not homology.

Crustacean mandibles

In a major paper, Hessler (1964) discussed the comparative skeleto-musculature of Crustacea in support of the thesis that Cephalocarida are the most primitive living members of the phylum. I later applied Hessler's results to a comparison between the extrinsic musculature of Ostracoda and Cephalocarida (McKenzie, 1972) with the assistance of two recently published studies (Kesling, 1965; Smith, 1965). It seems fruitful to review the topic as an example of homology between groups of Crustacea.

Crustacean mandibles are the third pair of adult appendages from the front. It is important to understand this homology of position for two reasons. First, in some early well-preserved crustaceans (ostracodes) the third pair of appendages is not yet adapted for specialised functions with regard to feeding (Müller, 1979). Secondly, even in modern crustaceans the mandibles may not be so adapted. This is the case, for example, with the mandibles, maxillae and fifth limbs of adult males in the ostracode family Sarsiellidae; when examined the guts of these males were found to be empty, i.e. adult sarsiellid males do not feed. On the other hand, mature sarsiellid females have limbs adapted for food-gathering and examination of gut contents has indicated that they and juveniles of both sexes feed voraciously (Kornicker, 1969).

Crustacean ontogeny indicates that the mandible retains the classic grundplan of a crustacean biramous limb: it comprises a protopod, endopod and exopod. This is well illustrated by Sanders (1963, Figs 14, 16, 28–30) for the nauplii of several groups and has been documented for ostracodes by several authors (Kesling, 1951; Tseng, 1976). Note that for Ostracoda, even in some ancient groups, the exopod is usually reduced or lacking—except in Bradoriida (Müller, 1979).

Although crustacean mandibles are homologous and conform to the common scheme for a crustacean appendage they can differ considerably, their morphologic variety representing the grade of evolution reached by each group in terms of its feeding pattern. Some idea of how these patterns can differ is given by the résumé below with respect to Ostracoda.

For Bradoriida, Müller (1979, p. 23) has suggested that the animals were nectobenthic and fed on plankton which they filtered through bristles on their cephalic limbs. Podocopida are usually benthic or epibenthic omnivorous detrital scavengers, carnivores (I have observed them prey on a weakened anostracan), suctorial feeders by special adaptations of the mouthparts associated with mandible coxales having the form of piercing stylets (McKenzie, 1969) or filter feeders. The latter adaptation, involving a previously undescribed organ (filter fan) on the hypostome, ". . . may be taken for the initial stage of development of a new large group with a new adaptational level . . ." (Schornikov, 1976). Myodocopida are benthic, epibenthic and pelagic detrital scavengers, mud ingesters, filter feeders, predators and collectors (Kornicker, 1975, pp. 39-42). Platycopida are filter feeders with different adaptations for this mode from cylindroleberidid myodocopids and the specialised podocopids mentioned above, as Schornikov illustrates (op. cit., pp. 248-249). In terms of the fossil record, the most ancient surviving ostracode stock is Podocopida.

Figure 1 illustrates the mandibles of the podocopids *Renaudcypris* (Cypridacea) and *Paralimnocythere* (Cytheracea), representing the two most numerous groups of living Podocopida adapted to marine and freshwater aquatic environments respectively—probably interstitial in the case of *Renaudcypris*. *

The general morphology of the mandible is illustrated for *Paralimnocythere*. The protopod, as usual, is 2-segmented, with a powerful gnathobasic coxale oriented vertically against the body; the basale is attached to it medially and dorsally bears a setose vibratory epipod; the palp (endopod) is 2-segmented (3-segmented in many other podocopids); and the exopod is interpreted as either absent or reduced to a powerful plumose annulated dorsal bristle (illustrated). The extrinsic musculature of this limb is shown for *Renaudcypris* (McKenzie, in press) and conforms to that described for other podocopids (Kesling, 1965, etc.). This musculature attaches the limb to the endoskeleton, the dorsal internal surface of a carapace valve and the anteromedial mandibular scars; additionally, the rounded top edge of the coxale is rotated against the internal cuticular lining of the valve as the limb works and develops a mandibular fulcral callus which can be seen on well-preserved material. The most powerful muscles are those to the endoskeleton and two of the dorsally attached muscles. This muscular array allows both backward–forward and outward–inward movement of the coxale. Since *Renaudcypris* is a scavenger/browser among the relatively large interstices of a coarse coralline littoral sand, the mandibles function to gather (grasp) bits of foodstuff and proffer them to the mouth. The food current is ventral and moves from the posterior forwards.

Unlike Ostracoda, which is the largest group in Crustacea, the Cephalocarida comprises only eight known species in four genera. The tagmata are clearly defined: cephalon; thorax of 7-8 segments; abdomen of 11-12 segments, plus an anal somite with long uropods. The mandible is not described

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* Usually, cypridaceans are athalassic or freshwater-adapted and cytheraceans are marine (both groups are marine *in origin*). Nevertheless, the examples illustrated here display the typical mandibular morphology among Podocopida. Even Schornikov's newly described abyssal filter feeding podocopid has a mandible of this type (1976, p. 253) as does the most ancient surviving podocopid stock, *Bairdia* (Maddocks, 1969). So too does the metacopine 'living fossil' *Saipanetta* (McKenzie, 1967).
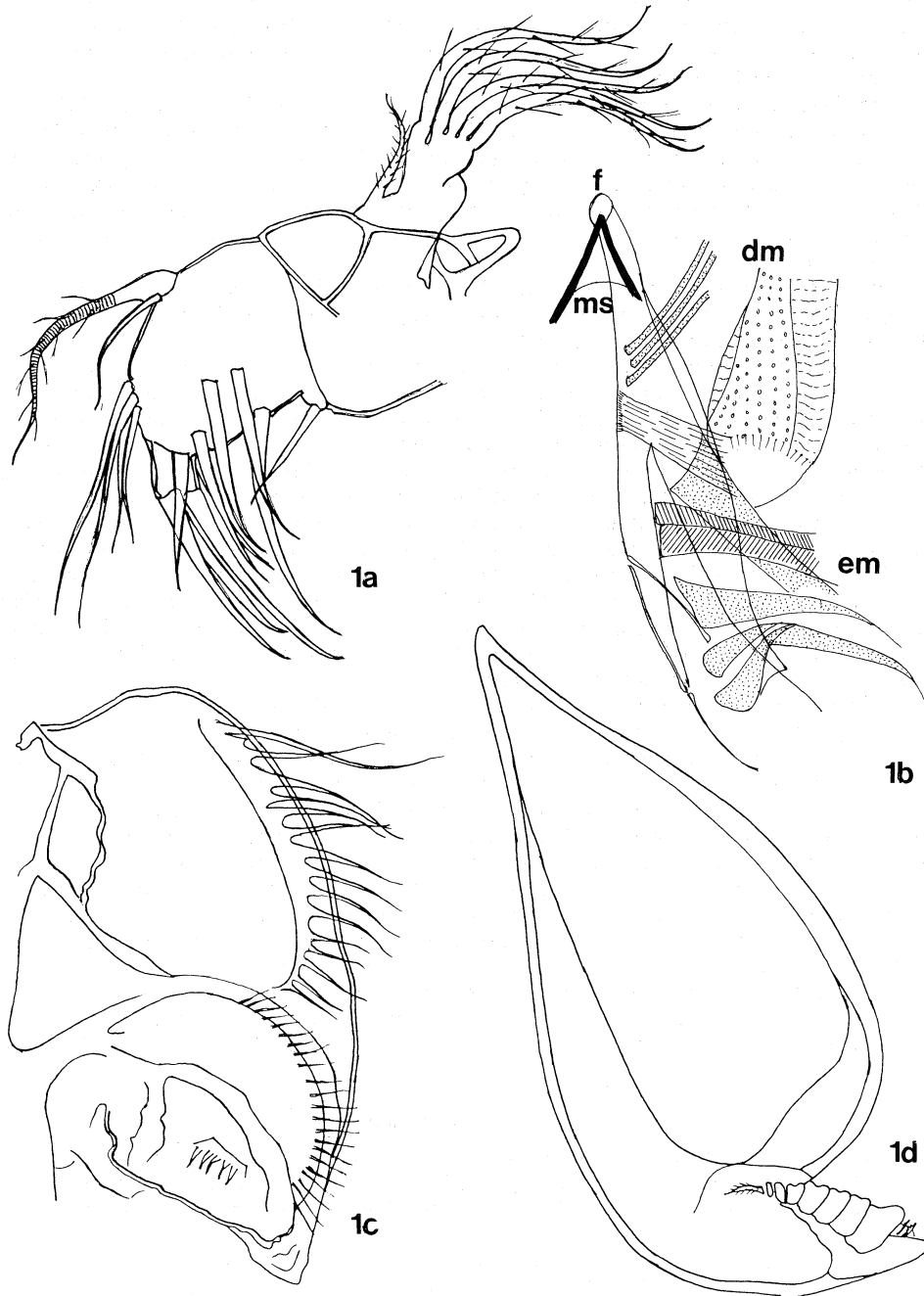
Fig. 1. Feeding apparatus of *Paralimnocythere* sp. and of *Renaudcypris gorongae* McKenzie. 1a, mandible basis, epipod and endopod of *Paralimnocythere*. 1b, part of mandible coxale of *Renaudcypris*: dm, muscles to the dorsal scar field of the carapace; em, muscles to the endoskeleton (= endosternite, = ventral cephalic tendon); ms, chitinous mandible supports to the mandibular scars in front of and below the central rosette of adductor scars; f, fulcral point. One slender front edge muscle to the dorsal scar field is not illustrated. With this array, the coxale is capable of both adductor-abductor and promotor-remotor, i.e. of slightly rotary, movement. 1c, labrum of *Paralimnocythere*. 1d, mandible coxale of *Paralimnocythere*.

or referred to in the latest genus to be erected, *Chiltoniella* (Knox and Fenwick, 1977), but its extrinsic musculature has been carefully illustrated by Hessler (1964, Fig. 12). Comparison with the extrinsic musculature of *Candona suburbana* Hoff 1942 made earlier (McKenzie, 1972, pp. 173-175) clearly sustains the conclusion that there are numerous and important correspondences between the extrinsic muscles of ostracodan and cephalocarid mandibles.

Functionally too the cephalocarid mandible is similar to its podocopid counterpart. Of the known cephalocarids, *Hutchinsoniella* at least is a non-selective deposit feeder, ingesting diatom frustules, sand, silt and detritus. Its food comes from the flocculent zone of subtidal muds. When feeding, the mandibles present to the mouth detritus captured on the gnathobases which has been passed forward to them by the posterior limbs along a ventral food groove. The movement of the gnathobases during feeding is both backward–forward and outward–inward, i.e. slightly rotary; again similar to *Renaudcypris* (Sanders, 1963), pp. 9, 12, 13).

Other detailed studies of crustacean mandibular musculature have been made by Manton (1964, Figs 3, 7–9, 11) for the animals *Chirocephalus*, (Anostraca), *Anaspides* and *Paranaspides* (Syncarida), *Ligia* (Isopoda) and *Calanus* (Copepoda); and *Nebalia* (Phyllocarida) (op. cit., p. 22).

All these mandibular musculatures display the following common features: a powerful set of muscles uniting the inner face of the coxa above the gnathobase with the endoskeleton; at least two powerful muscles, one of them often divided, which join the central-upper inner face of the coxa with the dorsal surface of the valve, cephalon, head capsule or head-shield; a fulcral point at the rounded upper edge of the coxa allowing backward–forward and outward–inward, slightly rotary, movements (Fig. 2).

This basically similar musculature can serve different functions in different animals. As indicated, it enables "secondary transverse biting" (grasping) of foodstuff in Cephalocarida and Ostracoda; a similar function characterises its operation in syncarids, isopods and copepods. But in Anostraca and Phyllocarida the functional effect is a grinding-rolling movement achieved mainly by promotor-remotor movements which are derived, according to Manton, from ancestral locomotory movements. Manton suggests that the grinding-rolling mandible is primitive but there is no explanation for this preference in her papers (e.g. Manton, 1963, p. 113). I repeat, the extrinsic musculature is similar for both types of movement—transverse biting and grinding-rolling.*

What differs is the gnathobase. Plate 1 shows that anostracan and notostracan mandibles are superbly adapted for a grinding-rolling function. But they may take other roles.

Observations of the feeding behaviour of the notostracan *Triops* indicate that it can be a savage carnivore.† I once collected *Triops granarius* (Lucas, 1864) and the anostracan *Streptocephalus dregei* Sars 1899 in the same sample jar from a pond on the Dwyka Tillite, near Grahamstown, South Africa. The *Streptocephalus*, unable to take avoiding action in the confined space and weakened by reduced oxygenation, proved no match for the *Triops* and were unrecognisable within half an hour. Thus, these broad corrugated, mandibular coxal gnathobases can hold and assist to rip soft animal tissue as well as grind and squeeze soft food (such as the green algae favoured by many anostracans). In their predatory role, notostracans also employ maxillary gnathobases which resemble (are homeomorphic with) the mandibular gnathobases of other crustaceans and make efficient grasping appendages (Plate 1).

Summarising, this brief review suggests that grinding-rolling and transverse biting are equally primitive adaptations of the third pair of appendages for feeding and require essentially the same extrinsic musculature. In every case the gnathobase is coxal, near the body, part of the protopod of a biramous limb.

Other arthropodan mandibles

Considering the other arthropodan groups, it is apparent that different feeding habits are involved.

Among chelicerates, the longest surviving group is the Merostomata (Silurian–Recent, a span of over 400 million years), represented in modern seas by the limulid horseshoe crabs. These marine and

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*"The explanation, I think, is that the promotor-remotor rolling action is assumed to be primitive because it is derived from a prior (hypothetical) condition in which the limbs of the 'mandibular' segment were walking limbs. The transverse biting action, on this view, is emphasised secondarily in association with the modification of these limbs as mandibles, though it probably had its origins in the transverse movements of the limb bases of walking limbs." (Anderson, personal communication, June, 1980.)

† Elsewhere (California, China) *Triops* is feared as a major ricefield pest because it tears at the young plants during the aquatic cycle of the crop. Probably, it is best thought of as a predatory omnivore.
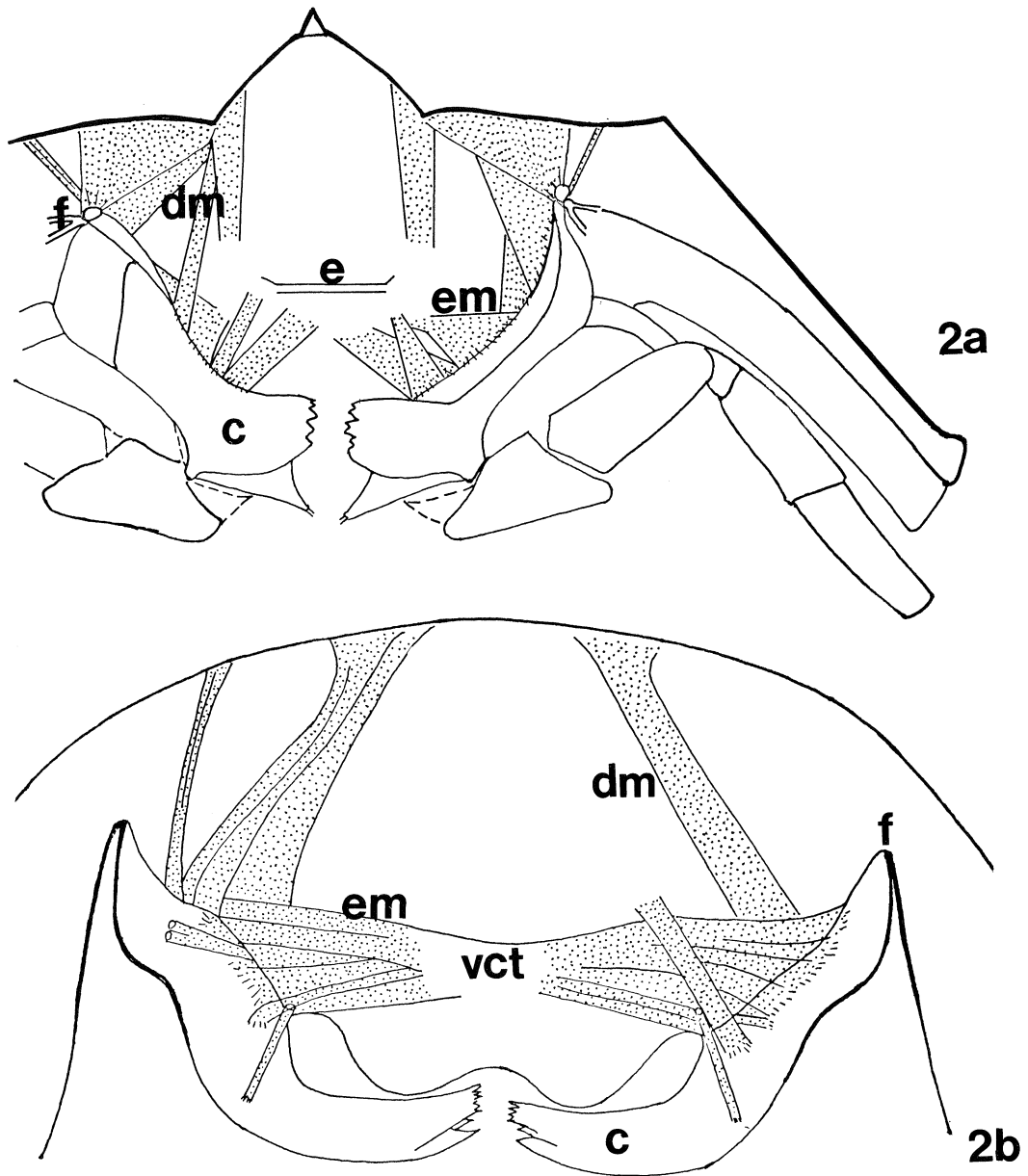
Fig. 2. Feeding apparatus of chelicerates (*Tachypleus tridentatus* Leach) and cephalocarids (*Hutchinsoniella macrocantha* Sanders) after Manton (1964, 1977) and Hessler (1964) respectively. c, coxale; dm, dorsal muscles; em, muscles to the endosternite (*Tachypleus*) or ventral cephalic tendon (*Hutchinsoniella*); e, endosternite; vct, ventral cephalic tendon; f, fulcral point. In *Tachypleus*, Y-shaped pleurite and large fan-shaped dorsal muscles both articulate at the fulcral point region. 2a, *Tachypleus*. 2b, *Hutchinsoniella*.

nearshore adapted animals represent more nearly the ancestral chelicerate stock than any order of the other major branch, Arachnida, including the scorpions which were about to embark upon the transition to a terrestrial environment when they first appear in the fossil record—somewhat later than the

xiphosurids. Störmer (1970) notes, ". . . Characteristic of the scorpions is the external digestion of prey." None of the adaptations of either fossil or living scorpions to achieve this (suctorial) feeding mode have any similarities with the structures or musculature described for Crustaces (Störmer, op. cit., pp. 345-348).

The feeding pattern of horseshoe crabs is grossly similar to that of some crustacean predators such as the decapod crabs but, as pointed out by Manton (1964, pp. 34-37), differs in details. It consists of the provision of food via chelipeds to gnathobases which then push it into an oval food basin where they shred and chew it before it is ingested. There is no ventral food current carrying food forwards to these coxae. The chelipeds take up food directly below themselves as the animals burrow and grub in the substrate. The gnathobases of horseshoe crabs are homeomorphic with crustacean coxal gnathobases, not homologous. The extrinsic musculature of limulid coxae includes a large fan-shaped dorsal coxal muscle which is not present in crustaceans (Manton, op. cit., Fig. 15). This and other dorsal muscles articulate via characteristic Y-shaped pleurites with the under surface of the carapace where it joins the pleural arthrodial membrane (Manton, op. cit., fig. 17); see also Fig. 2 this paper). This differs from the crustacean musculature described above as one would expect from the basically different feeding habits.

As far as the other living arthropodan groups are concerned—Onychophora, Myriapoda and Insecta—their evolution is inextricably linked to the invasion of the land and a subsequent radiation into the extensive newly available soil and vegetative niches. Not only can we not identify the immediate ancestors of these early uniramians, we have similar difficulties with the immediate ancestors of some crustacean geoups which made the same transition, e.g. Lipostraca/Anostraca, Notostraca and Conchostraca. This chorologic criterion has rarely been given its full weight (McKenzie, 1970; Simonetta and Delle Cave, 1975; McKenzie, 1977). As I concluded earlier, ". . . considerations pertaining to the evolution of the predominantly terrestrial uniramians, therefore, need not cloud the perceptions of workers interested in the older predominantly aquatic crustaceans" (McKenzie, 1977, p. 269).

Manton, without reference to any chorologic principle, has dissected the detailed skeletomusculature and evaluated the form and habits of all orders of Myriapoda, of Onychophora and of a sufficient number of the insect (hexapod) groups to satisfy the most persistent advocate of detail. With respect to mandibular mechanisms her classic paper for the Royal Society makes clear that, ". . . since the crustacean mandible is primarily a gnathobase and the hexapod mandible a whole limb it would be surprising to find more than convergent resemblances between them . . ." Manton, 1964, p. 101). In her summation, Manton extends this conclusion to the Myriapoda and Onychophora (p. 106).

Aysheaia

Unless one has seen fossils of *Aysheaia* from the celebrated Middle Cambrian Burgess Shale of western Canada and has some knowledge of living Onychophora it is difficult to appreciate the long enduring supposition that *Aysheaia* represents an ancestral onychophoran stock. Indeed, this remains a common textbook dogma and at one time or another Calman, Cannon and Manton all subscribed to it.

However, there are several objections to such an hypothesis. As already mentioned, Onychophora are terrestrial and thus could not antedate the first life on land (Latte Silurian-Early Devonian). Next, unlike some other groups with similar characters, e.g. Tardigrada, which are adapted for respiration in aquatic and semi-aquatic environments, Onychophora are physiologically incapable of life in water. They breathe in air with the assistance of tracheae and in a marine environment would quickly drown. The fantasy of a horde of land-dwelling *Aysheaia* crawling across the littoral to their certain doom in a Mid-Cambrian Canadian sea, like lemmings, is exciting but is dissipated by the abundant evidence that *Aysheaia* was part of a rich sublittoral biocoenose engulfed by a catastrophic submarine mudflow (Briggs, 1976 and references cited therein). No trace of jaws or jaw-like structures has ever been found in the *Aysheaia* fossils and the latest interpretation of their feeding habits is that they may have preyed on sponges, using their spinose antennae to lacerate these organisms and then feeding suctorially (Whittington, 1978); i.e. the position of the mouth is terminal in *Aysheaia* not ventral as in Onychophora. Finally, the movement of *Aysheaia* must have been dissimilar in detail to that of Onychophora. About these latter animals, Manton (1977, p. 284) has written ". . . the use of exploratory sensory antennae to find narrow crevices or paths of least resistance may have led to the extreme powers of the Onychophora to distort their bodies, without pushing, so penetrating through narrow channels leading to more commodious spaces where larger predators could not follow . . ." As pointed out by Della Cave and Simonetta (1975, p. 76), the Burgess Shale substratum was a fine mud—its texture suggests the flocculent

Table 2. Comparative morphology and habits of *Aysheaia* (A), Onychophora (O), Tardigrada (T), Elasipoda (E): an example of common evolutionary grades leading to (convergent) common characters. X = present; — = absent.

Characters	A	O	T	E
marine habitat	X	—	X[1]	X
bilateral symmetry	X	X	X	X
terminal mouth	X	—	X	X
posterior anus	X	X	X	X
gut, a simple straight tube	X	X	X	X[2]
jaw apparatus	—	X	—	—
oral papillae	X	X	X	X
eyes	—	X	X	—
annulated body	X	X	X	X[3]
annulated limbs	X	X	X	X[4]
dorsal spines, tubercles, etc.	X	X	X	X
frontal structure[5]	X	X	X	X
pairs of lobopodial feet	10	14–43	4	4–5
terminal or near terminal claws	X	X	X	—
posterior of body projecting	—	X	—	X
longitudinal, transverse and dorsal-ventral musculature[6]	X	X	X	X
slow, non-pushing gait[7]	X	X	X	X
feeding habits[8]	suct.	pred.	suct.	suct.
moulting (vs continuous growth)	—	—	X	—
metameric characters	X	X	X	X
size (mm)	10–60	14–150	0.01–1.2	5–50
distribution[9]	rest.	rest.	cosmop.	cosmop.
Cambrian fossils	X	—	?	X

1. Terrestrial aquatic and semi-aquatic tardigrades are also known.
2. cf. discussion in text (*Aysheaia*).
3, 4. The elasipodid *Scotoplanes* has a pseudosegmented body; several elasipodid genera have annulated lobopodial limbs.
5. Interpreted as anterior appendage in *Aysheaia* (Whittington, 1978); an antenna in Onychophora; tardigrades have antero-lateral cirri, some complex, e.g. in *Parastygarctus*; in Elasipoda, complex frontal structures are known in e.g. *Periamma, Periagone*.
6 cf. discussion in text (Tardigrada).
7. Implies a capacity to vary limb length when walking and to allow promotor-remotor swing.
8. *Aysheaia* has been interpreted as preying on glass sponges suctorially (Whittington, 1978); most onychophorans prey on small invertebrates, using jaw blades (see Manton, 1977, pp. 97-99 for discussion and illustrations) and a labral 'sucking tube'; tardigrades use their stylets to pierce plant tissue and extract the juices; elasipodids are suctorial deposit feeders and mud ingesters.
9. cf. discussions in text (*Aysheaia*).

zone of sublittoral ooze—and the associated organisms were often sponges (Whittington, 1978, pp. 192-194, fig. 90); there was no need for *Aysheaia* to negotiate narrow passages.

These important differences suggest to me that any apparent resemblances between *Aysheaia* and Onychophora are instances of convergence between stocks far removed in time and phylogeny and all subsequent research has sustained this opinion.

This objection to any close relationship between *Aysheaia* and Onychophora is reinforced by the fact that *Aysheaia* also has many characters in common with other lobopodial animals which, unlike Onychophora, are known to inhabit marine environments similar to that in which *Aysheaia* lived before it was catastrophically buried. Previously, a possible affinity with Tardigrada has been discussed (Delle

Cave and Simonetta, 1975; Whittington, 1978), a possibility which I had suggested independently in correspondence with Whittington. I shall discuss this in more detail in the next section. But the resemblances between *Aysheaia* and yet another group of little known marine animals, the echinoderm Elasipoda, have hitherto been ignored (McKenzie, in correspondence with Whittington and Belyaev, 1975).

Table 2 compares about twenty characters of *Aysheaia*, Onychophora, Tardigrada and Elasipoda and indicates that the latter have many features in common with the other three taxa, including a comparable size range to *Aysheaia*—the minute size of Tardigrada has been cited as an objection to *Aysheaia* having tardigradan affinities.

The great variety of living Elasipoda is such that it does not require an extraordinary stretch of the imagination to place *Aysheaia* among them although some objections to such a conclusion will be discussed. What may not be widely appreciated, however, is that the holothuroid Elasipoda are considered to be one of the most ancient echinoderm stocks.

While other Cambrian echinozoan fossils, such as *Helicoplacus* and *Eothuria* exhibit a distinct anti-clockwise torsion in their preserved tests, no traces of such torsion exist in restorations of ancient holothuroid echinozoans such as *Protocaudina*, a Carboniferous elasipodid-like animal in which the bilateral symmetry remains undistorted. Earlier fossils, such as *Laggania* and *Mackenzia* (like *Aysheaia* components of the Burgess Shale fauna) once thought to be holothuroids, are now classified elsewhere (Croneis and McCormack, 1932); but *Louisella*, a bilaterally symmetrical lobopod also from the Burgess Shale, seems clearly an elasipodid (Durham, 1974).

The evidence from biogeography indicates that both marine Tardigrada and the exclusively marine Elasipoda are cosmopolitan—unlike *Aysheaia* and Onychophora. While many gaps remain in our understanding of their dispersal patterns, it is already clear that several tardigrade marine genera have Tethyan affinities (Renaud-Mornant, 1979), i.e. they are distributed from the Central Pacific coasts to Indonesia and Australia; and that Elpidiidae, the largest of the elasipodid families, probably dispersed from a parental stock in the southern Indian Ocean (Belyaev, 1974). These patterns suggest a Palaeozoic origin for both groups with dispersive radiations during the Mesozoic—early Tertiary when Tethys was a major seaway, the Gondwana continents were drifting apart and the southern Atlantic and Indian Ocean had their origins. The best current interpretations of distributions of land and sea in the Palaeozoic (Smith, Briden and Drewry, 1973; Scotese, Bambach, Barton, van der Voo and Ziegler, 1979) suggest that the most favourable period for dispersive radiations between the southern and northern hemispheres was during the Middle Ordovician (about 450 million years ago).

While such an analysis is hypothetical it is at least anchored plausibly in time and space and environment. The dogma which relates *Aysheaia* and Onychophora is founded only on a morphological resemblance.

Considering life habits and morphologic characters, a principal objection to the possibility that *Aysheaia* could have been an echinoderm stock related to Elasipoda is that, although both have terminal mouths (unlike Onychophora), living elasipodids are deposit feeders and mud ingesters with a long coiled alimentary canal whereas the fossils of *Aysheaia* clearly show a short straight food tract free of mud.* But early echinoderms probably had simpler alimentary systems and this hypothesis, that all echinoderms arose from a bilaterally symmetrical ancestor with a short straight food tract and a dipleurule larva stage, is still favoured in the literature (e.g. Fell, in Marshall and Williams, 1974). The most recent analysis of *Aysheaia*'s feeding habit suggests that it preyed on sponges (Whittington, 1978) but nowhere in the detailed descriptions of the remarkably preserved *Aysheaia* fossils is there any reference to the contents of the animals' alimentary canals although it is hypothesised that these were not mud-filled (Whittington, 1978, p. 192).

Of the remaining distinctions between *Aysheaia* and elasipoda listed in Table 2, the numbers of pairs of lobopodial feet does not seem of great significance since *Aysheaia* is midway between the other taxa in this respect. The posterior projection of the body in Elasipoda is a common character with Onychophora hence should not make the possibility of an elasipodid affinity any less likely than that of an onychophoran one. This leaves the absence of terminal claws on the lobopodial limbs as the sole important distinguishing character.

On balance, it seems that a possible affinity between *Aysheaia* and elasopodid echinoderms is worthy of more detailed study. On the other hand, no firm new evidence can be adduced for a link between *Aysheaia* and the Crustacea.

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* Further with respect to elasipodid feeding, it has been suggested that their highly aqueous tissue and the low ambient (deep sea) temperatures probably enable them to live without much food.

Tardigrada

As noted in the previous section, Delle Cave and Simonetta (1975) first drew attention to the similarities between Tardigrada and *Aysheaia* which were later discussed by Whittington (1978). The discussion by these authors was relatively superficial, however, and this section intends to treat the possible relationships in greater detail, drawing on recently published work and personal confirmatory research.

Tardigrada are a phylum of minute aquatic and semi-aquatic animals which formerly were considered to be mostly terrestrial but are now known to include numerous marine species, mainly from nearshore and interstitial environments. They have been recorded on every continent but are well-known only from northern hemisphere terrestrial ecosystems. Southern hemisphere terrestrial species have been neglected. Marine taxa, although long passed over, are now being carefully studied and it is already clear from their morphology, diversity and widespread distribution that the primitive tardigrades were marine. This being so, the phylum must antedate the Cretaceous, from which the first fossil tardigrade, a terrestrial species trapped in amber, was described (Cooper, 1964).

Living descendants of the ancestral stock belong in the wholly marine suborder Arthrotardigrada of the order Heterotardigrada. Some general information on the embryonal ontogeny of tardigrades is provided in Cuenot (1932, pp. 12-13) and the moult ontogeny of heterotardigrades has been studied for the genera *Batillipes* and *Stygarctus* (McGinty and Higgins, 1968; Renaud-Mornant and Anselme-Moizan, 1969).

By embryonal stage V, several tardigradan characteristics are already present, namely: the buccal region and stylets; the pharyngeal bulb; and the four trunk segments. Developed embryos use their stylets to hatch. The earliest larval stage of *Stygarctus*, however, shows no segmentation and (although all four pairs are developed) the lobopodial limbs have only two terminal claws each. Complete segmentation in *Stygarctus* is attained by the third larval stage and the four pairs of feet now have the adult number of claws (four each) but the adult size and reproductive capability are not acquired until the next (fourth) stage (Renaud-Mornant and Anselme-Moizan op. cit., pp. 885-887). *Batillipes* also reaches adulthood in the fourth larval stage then undergoes a fifth (adult) developmental stage (McGinty and Higgins, 1968). The number of moults to adulthood in these taxa is rather fewer than for most crustaceans (Sanders, 1963, p. 69; McKenzie, 1972, pp. 182-183).

Tardigrade have a terminal or ventroterminal mouth (Table 2) and feed suctorially via protrusible stylets powered by specialised muscles in the body (Fig. 3). This buccal apparatus is clearly visible through the transparent body in many tardigrades but may be obscured by the exoskeletal segmental armour (cuirass) of others, such as *Stygarctus*. The whole structure is cast off in an initial phase of moulting but the musculature remains behind with the body and attaches itself to the newly formed buccal apparatus of the next stage. Once the buccal apparatus has reformed, the rest of the body cuticle moults. This two-phase moulting pattern is unknown in Crustacea.

Tardigrade excretion is incompletely understood. It includes defecation into an old moult as the new moult casts it off, and excretion via the epidermis where the excretory products accumulate as granules (Ramazotti, 1972). Such habits are not known in Crustacea.

All tardigrades have a slow non-pushing gait (Table 2) which facilitates their identification under the microscope when examining mosses and fine marine detritus for living specimens. Indeed, it is responsible for their common name: water bears. There is no basic difference between this gait and that of the Onychophora or that hypothesised for *Aysheaia* (Whittington, 1978, p. 192) or that of the echinozoan elasipodid *Scotoplanes* as recently photographed at 1060 m depth in the San Diego Trough, off California (Hansen, 1972).

But crustaceans move differently although retaining the basic metachronal rhythm, promotor-remotor swing and more or less well developed adductor-abductor movements. In the simplest case—walking/swimming—the coxa of a segmented crustacean limb swings transversely through a narrow arc against flexible cuticle around the body joint. A pivot joint at the distal end of the next segment (basis) favours limited adductor-abductor movements of the endopod and/or exopod (in modern crustaceans, usually one branch of the standard biramous limb is precociously adapted for locomotion and the other branch is adapted for a different function). Further small movements in the vertical plane are accomplished via intersegmental hinge joints of the endopod/exopod. All these movements are implemented by the limb's extrinsic and intrinsic flexor and extensor muscles (Manton, 1977, pp. 39-48).

The mechanisms which power such gaits are hydrostatic for all the groups cited but in the case of Tardigrada there is a basic difference in the intrinsic musculature of the locomotory lobopods. As first illustrated by Renaud-Mornant (1965) and confirmed in her laboratory by this author working
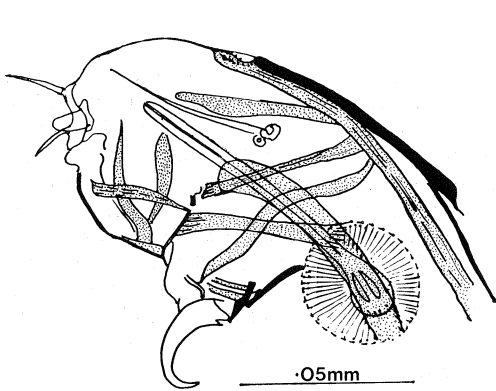
·05mm

Fig. 3 (above). Feeding apparatus of a tardigrade, *Echiniscus* sp., drawn in the retracted position. When feeding, the muscles illustrated power the protrusion of the stylet from the head.

Fig. 4 (right). Telescopic limbs of a tardigrade, *Florarctus hulingsi* Renaud-Mornant. Both protruded and retracted states are shown. Note also the powerful transverse muscles. (The anterior leg pair and the terminal claws of some legs not illustrated.)

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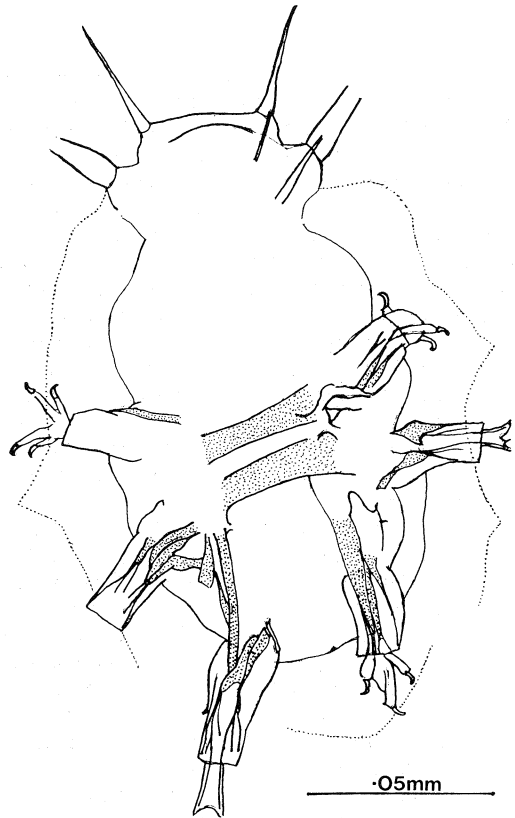
on a different specimen, the limbs of Tardigrada are telescopic. Thus, they shorten and extend in a manner basically unlike the lobopods of Onychophora because the muscles are differently disposed (Fig. 4)—I cannot comment on the comparison with Elasipoda due to a lack of reference material and no musculature is preserved for *Aysheaia*. On the other hand, the extrinsic musculature of these limbs in Tardigrada is similar to that for many arthropodans (Fig. 5).

Body turgor in tardigrades is maintained by several groups of muscles: dorsolateral and ventrolateral; transverse, dorsoventral. The musculature of the tardigrades was first figured (diagrammatically) by Marcus (1929) for several taxa and Fig. 6 is my confirmatory, more explicit drawing of part of the musculature of *Batillipes pennaki* Marcus 1947. Although several muscles are not illustrated in this drawing (particularly some transverse muscles), it is sufficiently clear that the muscular organisation is similar in pattern to that of many arthropods (cf. Hessler, 1964)—again I cannot comment with respect to Elasipoda and *Aysheaia*, for the same reasons as cited earlier.

As regards the types of muscles involved, the (more primitive) marine heterotardigrades have cross-striated muscles like many arthropodans, including Pentastomida, but unlike Onychophora which have obliquely striated muscles (Kristensen, 1978). Eutardigrades, however, have smooth or obliquely-striated muscles, except for the pharyngeal bulb and stylet muscles which are cross-striated (Walz, 1975). In explication, Kristensen (p. 182) suggests, ". . . the ancestral tardigrades had arthropod cross-striated muscles, these were transformed (by functional requirements), when tardigrades adapted to the terrestrial biota . . ." Thus, muscle types may fail to substantiate oft-stated claims on the primitiveness of onychophoran organisation vis-a-vis primitive tardigrades and the early marine crustaceans which will be considered later.

Some other characteristics of Tardigrada can be considered more briefly. They serve either to separate tardigrades from Crustacea or to suggest further possible links with *Aysheaia*, sometimes both at once.

Returning to ontogeny, a feature of tardigrade larval development is that all four pairs of limbs are present in the first stage and there is no subsequent addition of limbs during the larval ontogeny.
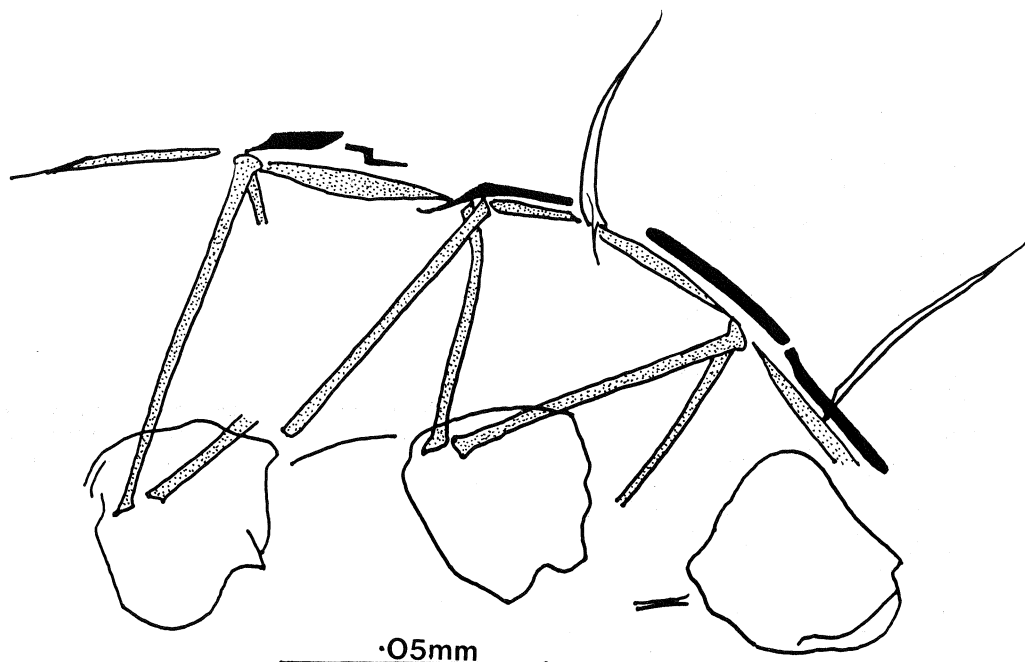
Fig. 5. Extrinsic leg muscles of a tardigrade, *Echiniscus* sp. (see also Marcus 1929), anterior to the left.

This is unlike the situation in Crustacea but is comparable with the fossil record of *Aysheaia*. A second point is that larval size increases in Tardigrada are not consistent with the crustacean Law of Growth, originally proposed by Brooks (1886) as ". . . the length of the larvae increases uniformly at each moult by one-fourth of its length before the moult . . ." Subsequent research (Skogsberg, 1920, pp. 123-147) has shown that hardly any taxa develop with such regular size increments throughout their larval ontogeny but nonetheless the Law is approximately correct. The growth factor in Tardigrada does not conform to this crustacean pattern (Renaud-Mornant and Anselme-Moizan, 1969).

An important factor of similarity between Tardigrada and *Aysheaia* (and one which distinguishes between Tardigrada and Crustacea) is the disposition of their posterior pair of limbs. In *Aysheaia* and Tardigrada these are terminal; In Crustacea, the body terminates in a telson, anal segment, posterior lobe, furca, uropods, but never in a pair of locomotory limbs. Earlier authors have given due weight to this factor (Delle Cave and Simonetta, 1975).

These authors have also drawn attention to the common possession of oral papillae in *Aysheaia* and Tardigrada. The observation can be extended also to Onychophora and to Elasipoda (Table 2.)

A final brief comment on sight. While Tardigrades are commonly thought to possess eyes, many interstitial species lack them, including *Stygarctus* and many other arthrotardigradan heterotardigrades. While *Aysheaia* is illustrated as blind (Whittington, 1978, pp. 187, 192, 193) the evidence is insufficient to support such an interpretation. The flocculent texture of the Burgess Shale sediment is such that if small eyes were present in *Aysheaia* they would not necessarily be preserved. This factor, therefore, cannot be considered to contribute either way—for or against a possible relationship between Tardigrada and *Aysheaia* or Crustacea.

Conclusions about *Aysheaia*

The extended and relatively detailed discussion of *Aysheaia* and some taxa homeomorphic with it has shown that the similarities of this celebrated Burgess Shale animal to such phyla as Echinodermata and Tardigrada are at least as worthy of attention as its much touted relationships with arthropodans, especially Uniramia but including also the Crustacea.
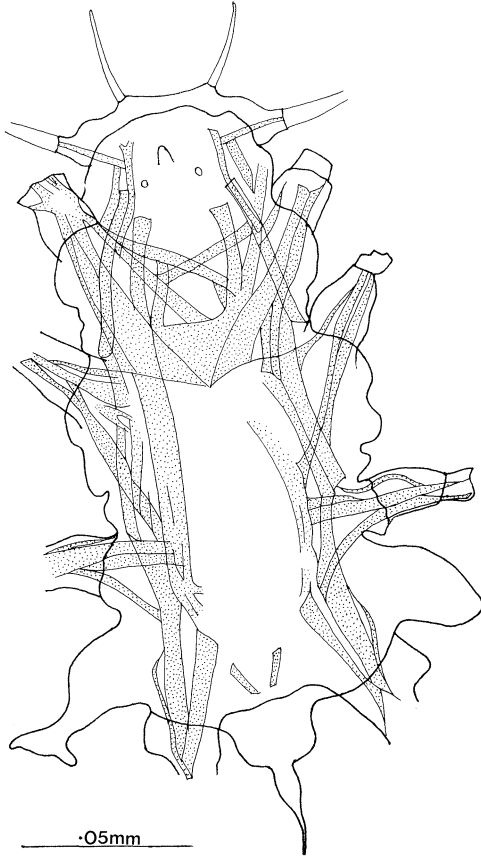
Fig. 6. Musculature of a tardigrade, *Batillipes pennaki* Marcus, posterior transverse muscles not shown. The general organisation is rather similar to that of many arthropodans.

In respect of some fundamental habits of life, the similarities are obviously due to convergence. Thus, in considering locomotion, the intrinsic musculature of a tardigrade lobopod is shown to differ basically from that of the uniramian Onychophora, i.e. the lobopods in these two groups are homeomorphic not homologous (Fig. 4). Further, the musculature which powers the feeding stylets of Tardigrada is not recapitulated in that which activates elasipodid ingestion or the ventroterminal jaw blades of onychophorans. Again, each of the three groups with which *Aysheaia* has been compared respires differently, with the most specialised adaptation among them being the air-breathing tracheae if onychophorans.

In the light of such data (cf. also Table 2), the relevance of *Aysheaia* to the evolution of any of the arthropod phyla can be considered minimal. Few crustacean workers should quarrel with such a conclusion.

Early crustaceans

The irrelevance of *Aysheaia* to the origins of Crustacea does not mean that there is now a lack of material on which to base some ideas on the topic. On the contrary, the marine Cambrian sediments of the world hold a rich diversity of early crustaceans and there are many other early fossils which can be considered as crustacean in their affinities rather than, say, trilobitan or cheliceratan.

Considering true Crustacea first, the major early fossil group is undoubtedly the bivalved ostracodan Bradoriida. Once considered to be conchostracans (Ulrich and Bassler, 1931), these animals are now generally confirmed as phosphatocopid ostracodes (Müller, 1964) although Jones and McKenzie (1980) warn that, as presently understood, bradoriids are probably polyphyletic and include phyllocarid-like or branchiopod-like species.
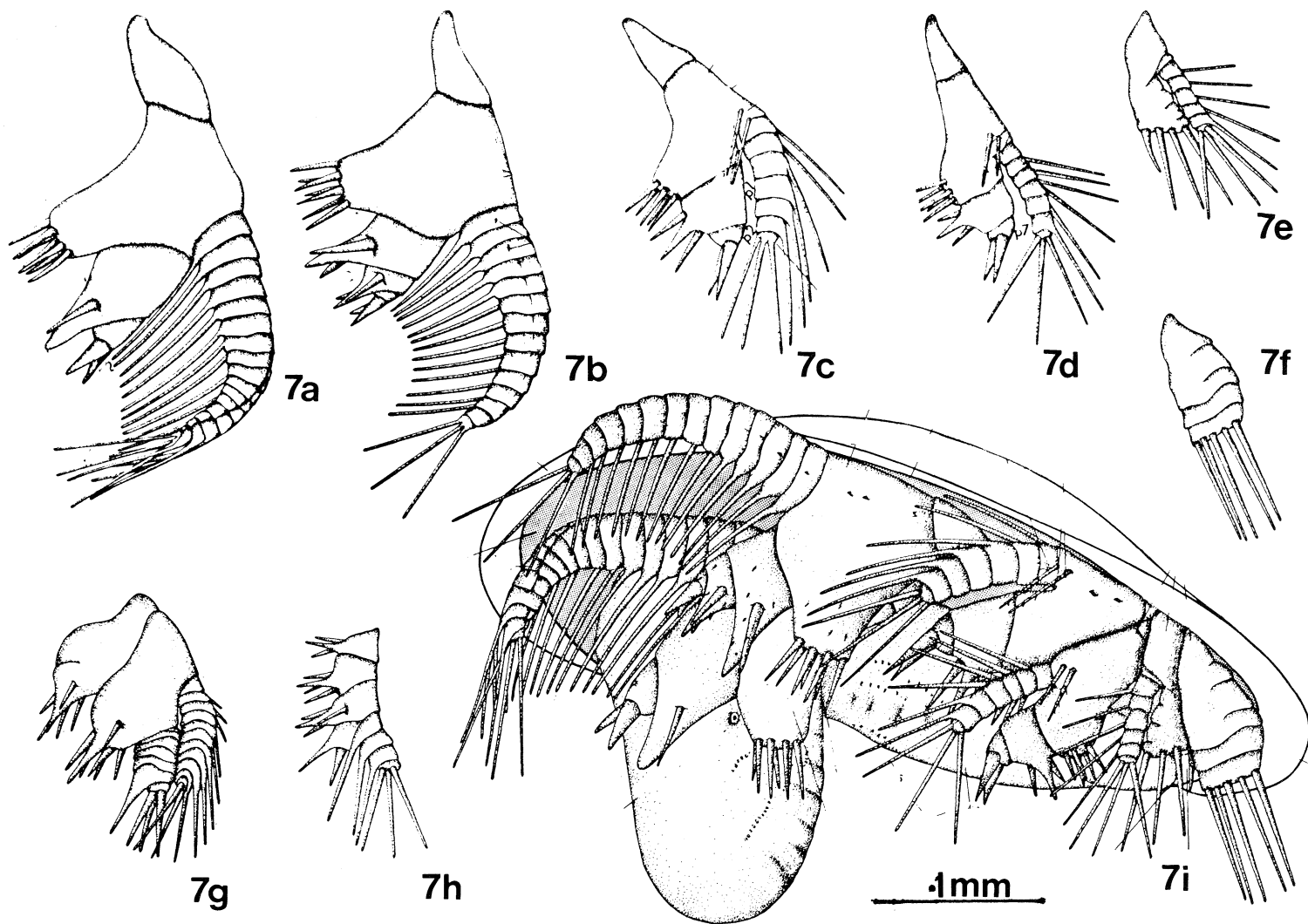
Fig. 7. Anatomy of a Cambrian bradoriid ostracode, *Vestrogothia spinata* Müller (after Müller 1979). 7a, first appendage; 7b, second appendage; 7c, third appendage; 7d, fourth appendage; 7e, fifth appendage; 7f, sixth appendage, (all the same specimen); 7g, fourth appendage; 7h, fifth appendage (both from another specimen of *Vestrogothia* sp.). 7i, reconstruction of the animal. Note that the first appendage of *Vestrogothia* is the antenna. This animal lacks an antennule. However, a uniramous antennule is present in *Hesslandona unisulcata* Müller, another Cambrian bradoriid (Müller, 1982).

This notwithstanding, over 260 species in about 60 genera have been described as bradoriids from Cambrian and Early Ordovician sequences (Jones and McKenzie, op. cit.). The group is cosmopolitan and its environmental associations include nearshore phosphorites as well as sublittoral mudstones and shales, indicating an adaptive range from the shoreline to well offshore. The taxonomy appears to be plagued by over-zealous splitting but it is nevertheless true that bradoriid assemblages commonly comprise a diversity of species and genera. Obviously, they were as well adapted for life in the Cambrian as the more widely known Trilobita.

Knowledge about the habits of life of Bradoriida remained sketchy until the recent publication of high quality micrographs of entire animals including their soft anatomy (Müller, 1979). Müller's rich collections of over 400 specimens with preserved soft parts and several thousands of empty carapaces came from four different localities in Sweden and northern Germany. Subsequently, further bradoriid material with traces of the soft anatomy preserved has been discovered in Australia (McKenzie and Jones, 1979) and has added significantly to our understanding of the group.

Morphologically, the major new data are that ostracodan phosphatocopine bradoriida had uniramous antennules, biramous antennae and mandibles plus at least four other pairs of appendages behind these (Müller, 1982), and that the thorax was probably four-segmented (McKenzie and Jones, op. cit.). The multi-segmented limbs were not modified for specialised functions except that the segments bore numerous long setae (Müller, 1979, pp. 21-23). As Müller expresses it (p. 1), the animals were ". . . nectobenthic filtering plankton feeders." These features are illustrated in Fig. 7.

Additionally, there are occasional records from the Cambrian of ostracodes belonging to groups other than Bradoriida. Possibly, these were benthic detrital scavengers.

At least two other crustacean groups are represented in the Cambrian faunas of the world but specimens with well-preserved appendages are practically confined to the Middle Cambrian Burgess Shale of Canada.

The richest material is of the phyllocarid-like *Canadaspis perfecta* (Walcott, 1912) of which some 5000 specimens have been collected (Briggs, 1978). *Canadaspis* and *Perspicaris*, the latter represented by about a dozen specimens also from the Burgess Shale, are the best authenticated possible Cambrian phyllocarids, since the assignments of other taxa, such as, *Isoxys, Odaraia, Plenocaris, Saccocaris, Tuzoia*, to this group are all more uncertain (Rolfe, in Moore, 1969; Whittington, 1974; Briggs, 1977; Glaessner, 1979).

Of the two supposed Cambrian phyllocarids, *Perspicaris* may have been nectobenthic (Briggs, 1977) while *Canadaspis* probably lived benthically (Briggs, 1978). Both animals were part of the rich arthropodan biocoenose of a flocculent sublittoral mud and ooze which owes its exceptional preservation to a fortunate accident of burial. The feeding mode of *Perspicaris* is unknown, but the sclerotised gnathobasic mandible coxae of *Canadaspis* and its spinose thoracic appendages suggest that it was a detrital scavenger over the substrate mud and that food particles were directed forwards to the mouth via a ventral feeding current generated by epipodial fans.

The remaining crustacean group, of branchiopod-like animals, is represented in the Burgess Shale by the genera *Protocaris* and *Branchiocaris*, but the appendages are preserved only in *Branchiocaris* (Briggs, 1976). This animal is considered to have been benthic and to have fed on substrate detritus by using antennary appendages; apparently it lacked gnathobasic mandible coxae (Briggs, op. cit., pp. 11-12).

Other Burgess Shale taxa may show affinities to Crustacea but their precise relationships are obscure and, since their redescription is in train, analyses based on the old literature are premature. They include the genera *Waptia* and *Burgessia* of which *Waptia* appears to be bivalved (Whittington, 1974, pl. 18, fig. 5) and *Burgessia* univalved (Simonetta and Delle Cave, 1975, pl. 5, fig. 5). Simonetta (personal communication, April 1980) links *Burgessia* with Notostraca, and *Waptia* with the evolution of Cirripedia, especially Ascothoracica. Having dissected both notostracans and ascothoracic cirripedes (McKenzie, 1972, fig. 3 which is diagrammatic only), I do not subscribe to either of these interpretations. Among other discrepancies, *Waptia* lacks the large, flexed and forwardly pointing antennules with terminal adhesive organs which are characteristic of Ascothoracica (Tessmann, 1904, pp. 1, 2, fig. 11); and *Burgessia* differs so widely from Notostraca in antennules, labrum, headshield, number of segments, telson, etc., that I do not consider them even remotely connected. *Waptia* may well be a crustacean but *Burgessia* appears to be cheliceratan and too clumsy to have had the life habits of Notostraca (cf. Fox, 1949). The difficulties of assigning any of these arthropodans to the major modern groups are also discussed by Manton and Anderson (1979).

Of the numerous genera assigned uncertainly to Phyllocarida, one at least may belong elsewhere;

this is the genus *Isoxys* Walcott 1890. Glaessner (1979) places it tentatively with phyllocaridans but Simonetta and Delle Cave (1975) give it separate ordinal status,* and Simonetta (pers. comm., April 1980) now wonders if in fact it is arthropodan. Of living crustaceans, *Isoxys* most nearly resembles the pelagic halocyprid Ostracoda, especially the genera *Euconchoecia* Müller 1980 and *Conchoecia* Dana 1849 (cf. Müller, 1906). However, the fossil record of halocyprids only goes back to the Cretaceous; and as *Isoxys* can be an order of magnitude larger than both *Euconchoecia* and *Conchoecia* its similarity to these taxa is probably due to convergence.

As new Cambrian faunas are studied, many other taxa with affinities to Crustacea undoubtedly will be described. In particular, the faunas of Cambrian phosphorites should prove rewarding because of the astonishing detail of apatite preservation. Figure 8 indicates that one such study is already under way. It includes the first record of a presumably telescopic limb for the Cambrian, plus assorted appendages, limb segments and abdominal segments all of which appear to be arthropodan. The preservation is so faithful that some pieces retain traces of musculature, and others may preserve muscle attachment sites. When the host rock is sectioned, parts of setiferous limbs and bivalves with an indistinct internal soft anatomy can be identified on slides viewed by transmitted light. This rich material comes from the Middle Cambrian Duchess Phosphorite of Queensland, but almost 100 other localities are recorded by Notholt, in Cook and Shergold (1979, pp. 71-86, fig. 13) who lists all known early phosphorites for the world. A further factor in favour of more detailed work on phosphorite faunas is that this rock type extends into the Precambrian so it may well yield well-preserved Crustacea and other arthropodans which are more primitive than any hitherto known.

The origin of crustacea

We know that Cambrian fossil Crustacea are abundant and may expect to find new, well-preserved Late Precambrian taxa. Unfortunately, the best known Precambrian material, South Australia's notable Ediacaran fauna, does not include Crustacea, with the possible exception of *Parvancorina* (Glaessner, 1962), although other arthropodans are present.

We can, however, make some reasonable assumptions concerning the characteristics of the primitive crustaceans.

Firstly, Manton (1977) has demonstrated the unity of crustaceans as a major group of invertebrate animals. Her conslusions have been underlined by the work of Anderson (1973, p. 467): ". . . the basic theme of crustacean embryonic development is seen to differ fundamentally, not only from the clitellate-like mode of development underlying the development of onychophoran embryos, but also from the basic annelid mode of development itself. The interpolation of a nauplius stage in the developmental sequence itself is fundamentally different and could not posssibly be a modification of any annelid mode of development."

Apart from their embryology, the later development of crustaceans has some common characteristics. Anderson (1973, pp. 290-308) notes that after the nauplius hatches all post-mandibular segments are developed from the short post-naupliar region. He did not discuss Ostracoda in this context, but ostracodes have a mode of post-naupliar segment development similar to that of other generalised Crustacea, though the bivalve carapace, antennules, antennae and mandibles are developed precociously in the embryo to yield a distinctive nauplius. Taking absolute body length as the criterion, proportionate development of ostracode cephalic limbs (antennule, antennae and mandibles) is complete even at this naupliar stage (McKenzie, 1973, p. 184, Table III), after which Ostracoda add appendages more regularly than any other crustacean group until adulthood is reached (McKenzie, 1972, pp. 182-183, Tables I, II). Although Ostracoda are regarded as non-segmented and highly cephalised—both interpreted as specialisations— the Bradoriida clearly have at lease four thoracic segments (McKenzie and Jones, 1979) and the posterior chitinoskeletons of several living taxa suggest that ostracodes had abdominal segmentation also earlier in their phylogeny (Schulz, 1976). There is no reason to doubt that this thoracic and abdominal development took place from the post-naupliar region as for other Crustacea.

Anderson (1973, p. 301) goes on to hypothesise six pairs of trunk (thoracic) limbs as the basic adult number, the argument being based on metamorphosis in cephalocarids where all limbs are involved in all functions. Functionally, these limbs are thought of as responsible for swimming, crawling and feeding movements and their rhythm is metachronal. Mechanically, the lowest number of limb pairs

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* Specimen 189301 from the Walcott collection in the Smithsonian Institute, Washington D.C., does not seem an *Isoxys* in my opinion although recorded as such by Simonetta and Delle Cave (1975, pl. 54), but I have not checked the original material.
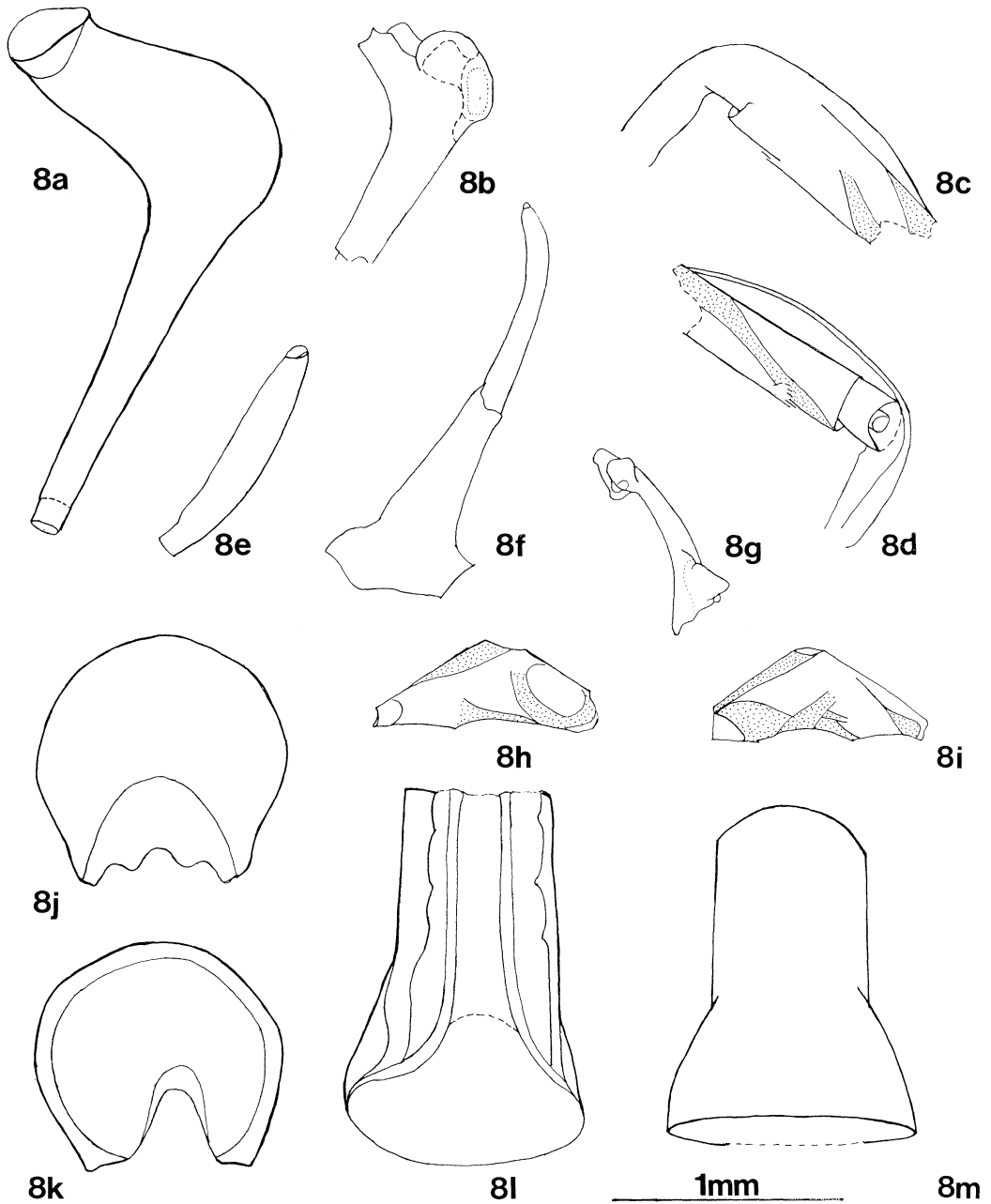
Fig. 8. Bits of arthropodans from the Cambrian phosphorites near Duchess, Queensland. 8a, movable, pleural(?) spine; 8b, ball-headed joint of movable spine; 8c, part of thoracic limb; 8d, other side of 8c, showing probably telescopic limb segments; 8e, segment of walking leg, with hinge joints at each end; 8f, sensory spine; 8g, "rib", with pivot joints at each end; 8h, "trochanter", showing supposed muscles (transmitted light); 8i, other side of 8h, showing other supposed muscles; 8j, posterior(?) face of abdominal segment; 8k, anterior(?) face of abdominal segment; 8l, ventral view of same segment as 8j, 8k; 8m, dorsal view of same segment. Published with the permission of the Director, Bureau of Mineral Resources, Geology and Geophysics, Canberra.

which can work metachronally is three, and as Table 1 indicates this is the number of serially homologous thoracic limb pairs in modern Ostracoda (Podocopa). Bradoriida have at least four such limb pairs behind the cephalic limbs but as only juveniles with well-preserved appendages have been recovered so far the adult number is possibly greater (Muller, 1979). The difference between podocopid Ostracoda and other crustaceans may be due to a reduction to the lowest mechanically possible number of metachronal, locomotory thoracic limb pairs, imposed by the necessity to maintain a capacity for all functions within the relatively restricting valves of the carapace.

Very many ostracodes display adaptations of the thoracic region for other purposes than locomotion. These include: adaptation to interstitial environments, e.g. Cladocopa, Parvocytheridae; clasping during copulation and cleaning, e.g. Cypridacea; food forwarding of filtered or grasped substrate detritus, e.g. Platycopa, Myodocopa. The latter adaptations are particularly pertinent since it is debatable whether locomotion is a more primitive necessity than feeding. Rather, both functions are equally vital and in many ostracodes the antennae bear the burden of swimming, e.g. Myodocopa, or crawling, e.g. Platycopa.

A further criterion is adult size. Here the primitive fossil crustaceans differ markedly. The hypothesised phyllocaridans *Canadaspis* and *Perspicaris* range from about 10 mm to more than 50 mm (Briggs, 1977, 1978) and the branchiopod-like taxa *Protocaris* and *Branchiocaris* from 43 mm to 87 mm (Briggs, 1976). The Cambrian ostracodes, however, are all much smaller, ranging from less than 1 mm to about 2 mm. Presumably, all three groups and the numerous other early arthropodans which have been described meet the biochemical criteria imposed by Towe (1970) for the synthesis of collagen and cuticle and fall within his definition of small and simply structured metazoans. The size of the only possible Precambrian crustacean, *Parvancorina*, is about 3 cm but no appendages of this taxon are preserved to link it with any of the three Cambrian groups.

Considering these three groups, only the Bradoriida juveniles had a biramous antennule; and only in the Bradoriida was the third appendage from the front a generalised biramous limb rather than a specialised mandible (Fig. 7). In fact, all the first three limb pairs were very similar in their organisation. It is difficult to explain away such general characters as indicating an embryonisation of development, or specialisation, or oligomerisation from some earlier more complex condition. The bradoriid thorax had at least four segments. The bradoriid abdomen is unknown but by analogy with modern ostracodes may have had a chitinous exoskeleton indicating at least six segments, followed by a telson and laminate uropods (Schulz, 1976, figs 2, 12, 13, 17-20). The entire soft anatomy was fully enclosed within a bivalved chitinophosphatic carapace. If an eye was present, it was naupliar.

In the branchiopod-like *Branchiocaris*, the first two limbs of a mature specimen were uniramous but the remainder of the soft anatomy was biramous and serially homologous and the body ended in a telson plus uropods. The division between the cephalon and thorax is unknown and that between the thorax and abdomen poorly defined, but probably it lies at about the 12th or 13th segment. The combined thorax-abdomen had 46 segments. A bivalved carapace covered the anterior of the body. If eyes were present they were located beneath the carapace.

In the mature *Canadaspis*, the first two limbs were likewise uniramous and the mandible had a sclerotised gnathobase of the transverse-biting type. There were two postmandibular maxillae and eight serially homologous thoracic limb pairs. The abdomen had seven segments and the body ended in a telson with uropods. A bivalved carapace covered the cephalothorax. There were two simple stalked eyes.

These groups form the basis for an interpretation of the origin of Crustacea. It may well be, as Anderson concludes (1973, p. 471) that ". . . the metamerically segmented coelomates which gave rise to the Crustacea cannot be identified . . .", but these groups afford the most secure basis for any such attempt.

Manton (1973, p. 128) states ". . . we can do no fossil embryology . . ."; nevertheless, of the three groups both phyllocaridans and ostracodes are known to hatch as young adults, and the Cambrian Bradoriida at least followed such a developmental scheme. Because we are less sure of the relationship betweeen *Branchiocaris* and modern branchiopods it is not possible to extend this suggestion with confidence to *Branchiocaris*. Clearly, however, even in the Early Cambrian crustaceans exhibited some embryonisation of development. The adults were specialised in relation to active swimming and plankton filter-feeding in the case of bradoriids and for benthic grubbing and detrital scavenging in the case of the phyllocaridan-like taxa. *Brachiocaris*, with its small mouth and lack of mandibles, presumably used its large antennary appendages to grasp and gather food. Both sexes were probably present in all three groups although we can only be sure of this in the case of the ostracodes (Müller, 1964).

Extrapolating from these data, the ancestral types probably exhibited the following common features: a bilateral symmetry; uniramous antennules; biramous antennae and mandibles, developed as generalised

biramous limbs in the adult form; some embryonisation of naupliar development, possibly including the early secretion of a carapace; thoracic and abdominal development from the post-naupliar region; more or less well-expressed sex dimorphism; discontinuous growth by moulting. The habits of life of these small earliest crustaceans would have been appropriate to marine epibenthic or nektobenthic niches, adapting them for bottom scavenging, predation or filtatory feeding, in the main via generalised limbs and a ventroterminal mouth. Their basic movements were promotor-remotor and adductor-abductor and were accomplished via serially similar cross-striated muscles. Turgor was maintained hydrostatically and by longitudinal and transverse muscle bundles. They had naupliar eyes.

Such ancestral animals should be looked for in deposits no older than the Ediacaran (680 m.y. BP) in which as we have observed there is yet no obvious crustacean taxon. The reason for such a choice is geochemical not biological. Holser (1974), in a paper culminating two decades of painstaking research, has established the occurrence of a major catastrophic event in the history of the world ocean between about 650 to 550 m.y. BP (op. cit., fig. 1). Towards the end of this period, abundant fossil evidence has convinced us of an explosive radiation in many groups of invertebrates, notably trilobitans, cheliceratans and carapace-bearing crustaceans. It seems plausible that the beginning of this catastrophic period was the era during which Crustacea commenced their evolution towards dominance among invertebrate metazoans of the world's aquatic environments.

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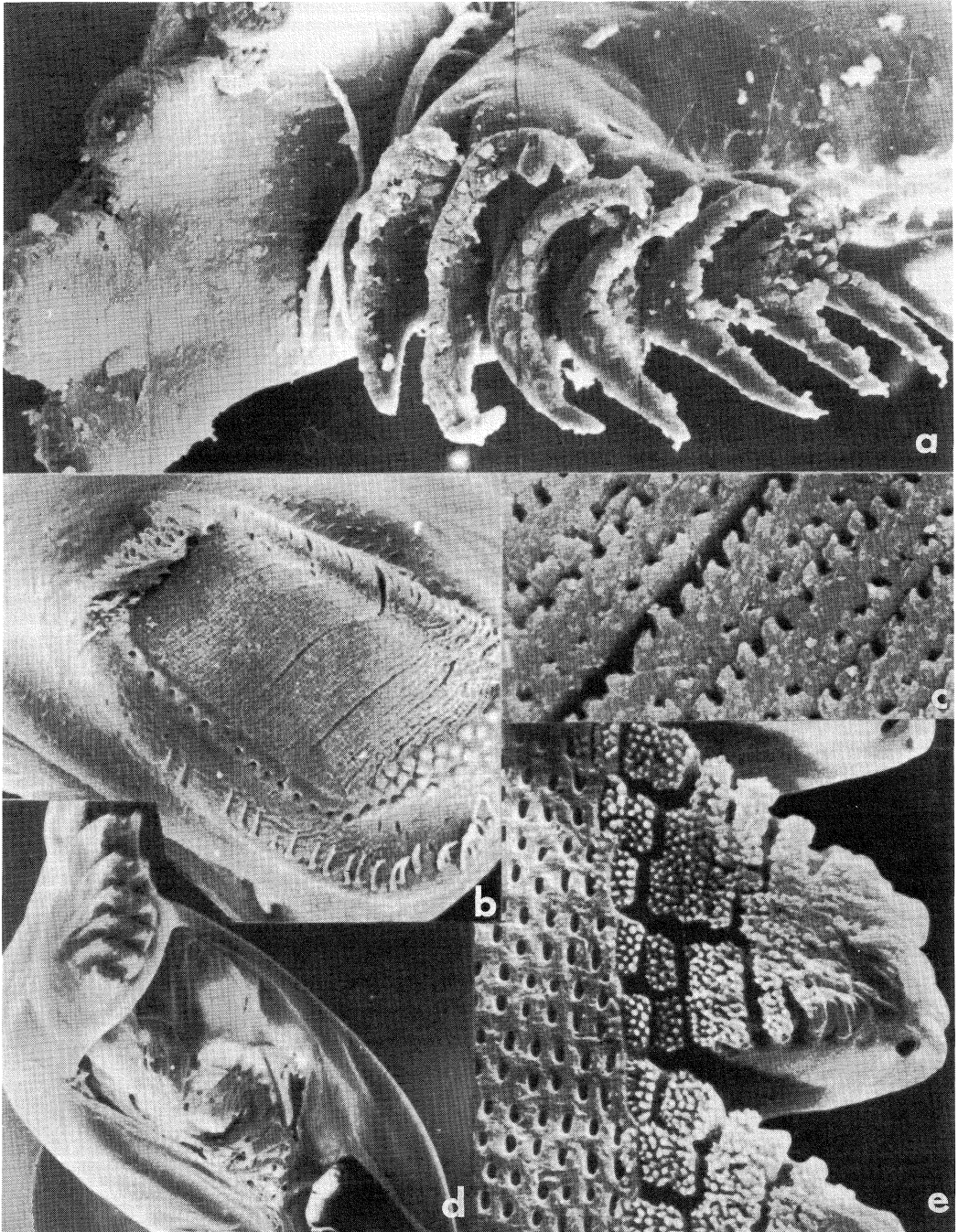
Plate 1. Feeding in Recent Notostraca and Anostraca. **A-C**, *Lepidurus* (Notostraca) gnathobases; **A**, biting gnathobase × 440; **B**, grinding-rolling gnathobase × 180; **C**, detail of grinding-rolling gnathobase × 1800; **D**, *Triops* (Notostraca), biting gnathobase × 28; **E**, *Dendrocephalus* (Anostraca), detail of grinding-rolling gnathobase × 1800.

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