

Functional Morphology and Diversity

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COMMENTS ON CRUSTACEAN BIODIVERSITY AND DISPARITY OF BODY PLANS

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Abstract

The science of natural history is built on twin pillars: cataloging the species found in nature, and reflecting on the variety and function of body plans into which these species fit. We often use two terms, *diversity* and *disparity*, in this connection, but these terms are frequently used interchangeably and thus repeatedly confused in contemporary discourse about issues of function and form. Nevertheless, *diversity* and *disparity* are distinct issues and must be treated as such; each influences our views of the evolution and morphology of crustaceans.

CRUSTACEAN DIVERSITY

Crustaceans exhibit great disparity in basic body plans (I return to this subject below), but disparity of crustacean form is different from crustacean biodiversity, that is, the number of species we have within any particular group. No one knows for certain the exact number of species within any group of organisms, although the situation might improve with the appearance of online catalogs for particular groups. The people who set up these databases and maintain them as new species are added and old species are placed in synonymy provide a much-needed service toward adequately cataloging the tree of life. Nevertheless, as humans we like numbers—they are easily understood. So I have made my own tally (Table 1.1) and present a summary of estimates compiled from various authorities as to the total number of crustacean species.

There is clearly no agreement on numbers among the authors listed in Table 1.1, although the estimates have gone up through time. With the exception of Minelli (1993) and Brusca and

Table 1.1. Various estimates of global numbers of species of crustaceans.

| Estimated number of species | Source |
|-----------------------------|--------------------------------|
| 44,950 | Bouchet (2006) |
| 32,000 | Brusca and Brusca (1990) |
| 68,171 | Brusca and Brusca (2003) |
| 40,000 | Groombridge and Jenkins (2000) |
| 39,000 | May (1988) |
| 75,000 | Meglitsch and Schram (1991) |
| 55,364 | Minelli (1993) |
| 38,000 | Ruppert and Barnes (1994) |
| 49,658 | This chapter |

Brusca (2003), who appear to have attempted a real count, the other authors obviously provided rounded off and rough estimates. For example, the number provided by Meglitsch and Schram (1991) was an estimate of what the highest number might be at some point in time when knowledge of the number of species will have reached a plateau.

Although we know a great deal about groups of invertebrates, our knowledge is not very good and rather incomplete. I examined the patterns through time in documenting animal taxon diversity (Schram 2003) and noted several periods during which plateaus of relative inaction followed bursts in activity. It seems clear from these charted patterns that we are currently in one of those periods of increased activity, but whether we will soon reach a new plateau, or whether increased use of molecular techniques to identify monophyletic groups might continue to add new taxa at all levels—from phylum down to species—I cannot say. However, increasing application of molecular techniques does seem to indicate that we have underestimated the degree of cryptic speciation in nature.

Having stated this, I feel honor bound by the charge given to me by the editors to provide my own numbers, so I tally here the currently known crustacean species. Table 1.2 is based on a census of relevant websites, currently available monographic literature, and the best estimates of authorities active in one or more of these groups. The reader should keep in mind that this is a tally of species numbers at this point in time, and these figures can only increase as our knowledge of these taxa evolves. In fact, the survey made by Martin and Davis (2006) seems to indicate that no asymptotes are yet emerging in the pace at which new species are being described.

First, the total number of species obtained by this survey, 49,658, is not too far off from the estimates of Bouchet (2006) and Minelli (1993). Within that number, some things deserve special notice. Of the two largest groups on this list, Maxillopoda and Malacostraca, the numbers are of similar magnitude—almost 19,000 and something more than 29,000, respectively. The number of maxillopodans can only increase. The 9,500 copepods is only an estimate, although it may stand close to the actual numbers of currently described species. Nevertheless, copepod taxonomy is an active discipline, and increasingly sophisticated techniques of study will help isolate cryptic species. The 8,008 species of ostracodes is only an estimate, and if we factor in fossil species, we would more than double that number. Furthermore, the application of molecular methods in Crustacea will likely affect our understanding of species level biodiversity. For example, I am surprised at the relatively low number for the thecostracans, but parasitism is rampant in the group, and underestimates of species diversity would prevail in taxa with such

Table 1.2. Census of species numbers in various crustacean groups.

| Taxon | Number of species |
|---------------------------|------------------------|
| Branchiura (Argulida) | 175 |
| Branchiura (Pentastomida) | 100 |
| Mystacocarida | 13 |
| Branchiopoda | 509 |
| Anostraca | 307 |
| Cyclestherida | 1 |
| Laevicaudata | 36 |
| Notostraca | 15 |
| Spinicaudata | ≈150 |
| Cladocera | 450 |
| Maxillopoda | 18,911 |
| Copepoda | 9,500 |
| Ostracoda | ≈8,008 |
| Myodocopida | 1,608 (+500 fossils) |
| Podocopida | 6,400 (+9,500 fossils) |
| Thecostraca | 1,403 |
| Ascothoracica | >99 |
| Cirripedia | 1,304 |
| Acrothoracica | >61 |
| Rhizocephala | >355 |
| Thoracica | 948 |
| Facetotecta | 12 |
| Tantulocarida | 28 |
| Remipedia | 19 |
| Cephalocarida | 10 |
| Malacostraca | 29,471 |
| Phyllocarida | 39 |
| Stomatopoda | 456 |
| Eumalacostraca | 28,976 |
| Syncarida | >187 |
| Bathynellacea | >170 |
| Anaspidacea | 17 |
| Peracarida | 15,686 |
| Amphipoda | 6,950 |
| Cumacea | 1,342 |
| Isopoda | 5,270 |
| Lophogastrida | 56 |
| Mictacea | 5 |
| Mysida sensu lato | 1,085 |
| Mysida sensu stricto | 1,075 |
| Stygiomysida | 10 |
| Spelaeogriphacea | 4 |
| Tanaidacea | 940 |

Table 1.2. (Continued)

| Taxon | Number of species |
|------------------|-------------------|
| Thermosbaenacea | 34 |
| Eucarida | 13,103 |
| Amphionidacea | 1 |
| Decapoda | 13,016 |
| Dendrobranchiata | 522 |
| Caridea | 2730 |
| Stenopodidea | 57 |
| Reptantia | 9,707 |
| Euphausiacea | 86 |
| Total | 49,658 |

The higher taxonomic grouping of this table accords with the conclusions derived from the discussion of disparity of form given later in this chapter. Classes are shown in boldface.

highly reduced body forms. For example, rhizocephalans seem poised on the edge of a renaissance in interest, and the number of species anticipated will increase.

Malacostraca constitutes a large number of species, but the species distribution is uneven because some subgroups are very large (amphipods, isopods, reptant decapods), while others are small (mictaceans, spelaeogriphaceans, and the amphionidacean). In fact, any group associated with cave or groundwater habitats appears likely at the lower end of species number estimates, but these habitats are difficult to study, and every attempt to sample these communities turns up new and interesting species, which can only continue into the future. (In this connection, one need only consider the work on crayfish in North America to see what happens when intensive systematic interest is focused on a group.)

Some major class- and order-level taxa presently have low species numbers (remipedes and cephalocarids), but here, too, we have animals living in habitats that are difficult to sample (anchialine caves and the deep sea). Other groups contain very cryptic creatures living in places that, although well studied, nevertheless are often overlooked (mystacocarids in interstitial beaches).

Because of the great disparity of body plans exhibited by crustaceans, we have a problem in comparing the species numbers in one group with another. The taxa in Table 1.2 are organized around the currently recognized class and order levels, but how does one compare ordinal differences seen in malacostracans with what are called orders within the maxillopodans? Recognizing a decapod from an amphipod is quite easy (both are orders of Eumalacostraca), but not many people could easily distinguish a cyclopoid from a calanoid (they are both orders of Copepoda) without being carefully schooled in the differences. Hence, trying to compare numbers of species within groups across the major taxonomic (class-level) units of crustaceans is truly like comparing apples to oranges or, in this case, lobsters to zooplankton.

Nevertheless, strange patterns arise when we look within groups. Consider the peracaridans, for example. Why are there so many species of amphipods (6,900) compared to thermosbaenaceans (34) or mictaceans (5)—approximately two and three orders of magnitude difference? Are amphipods truly that much better adapted to their environments, an explanation often assumed to be true? If so, how and why? Or, are some other factors at play that might augment or possibly even ignore issues of adaptation? Some of these factors might be

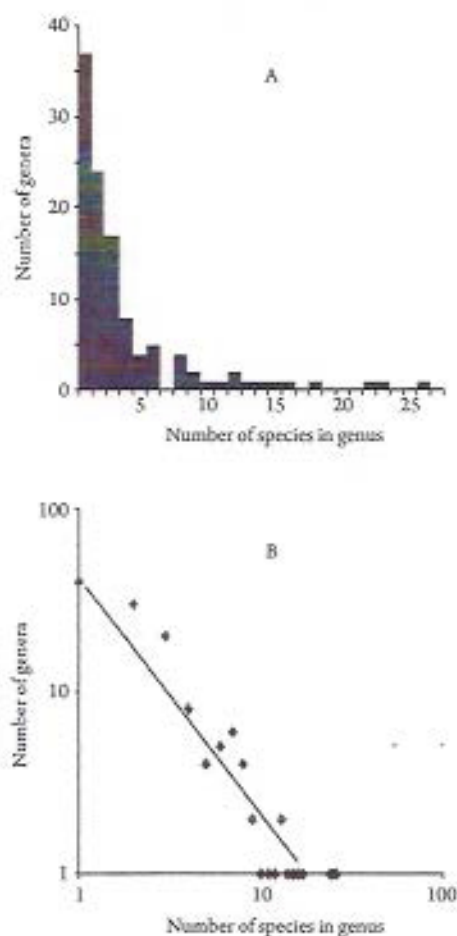


Fig. 1.1.

Arithmetic hollow curve (A) and log-log (B) plots of size distributions of genera of Stomatopoda (as number of included species) roughly conforming to power law $N(x) = ax^{-k}$. For details about the method, see Minelli et al. (1991).

difficulty of habitat access for study (mentioned above), age of a clade, habitat heterogeneity, and expressions of chance in nature. The various authors of other volumes in this series will explore many of these issues.

The element of chance plays an important role in classification. Willis and Yule (1922) and Minelli et al. (1991) observed that the size of supraspecific taxa as related to the included sub-taxa (species in genera, genera in families, etc.) follows a power law. They concluded that the structure of biological classification is naturally fractal. This structure can be expressed as a hollow curve that, if plotted on a log-log scale, would conform to $N(x) = ax^{-k}$.

We can illustrate this with one example from Malacostraca, the unipeltate stomatopods (mantis shrimp). As of this writing, we recognize 456 species in 112 genera of mantis shrimp, with an additional 123 nominal species currently in synonymy. If we consider only the 456 recognized species, distribution numbers range from one of the largest genera, *Nannosquilla*, with some 26 species, down to 36 genera with but a single species each. Graphing this diversity, we can see that on an arithmetic scale it forms a hollow curve (Fig. 1.1A), and on a log-log plot a

straight line emerges (Fig. 1.1B). The fractal pattern becomes apparent when examining genera within families (data not shown), where we would again see a log-log plot that roughly matches that of species in genera. Whether this pattern appears in other groups of crustaceans remains to be tested, but I have no doubt that it will hold as it has in other groups of animals and plants.

As humans, we are naturally inclined to seek causative explanations for patterns of biodiversity. However, I believe we do not necessarily need to explain why one particular genus, such as *Nannosquilla* with 26 species, is somehow better adapted than its confamilial sister genera, in this case *Mexisquilla* and *Keppelius*, each with only a single species. As we chart species biodiversity, we should be open to the possibility that the relative number of taxa within any particular group may represent nothing other than the manifestation of the operations of a stochastic, fractal universe, to say nothing of the vagaries of individual taxonomic decisions. Many authorities might reject my pessimism here, but at the very least, a stochastic, fractal biodiversity has to be one of several alternative hypotheses to consider.

CRUSTACEAN DISPARITY OF BODY PLANS

The crustaceans are the most variable of all the arthropod groups; that is, there is a great disparity of body plans throughout their ranks (Fig. 1.2). If we are to assume that Crustacea is a monophyletic group, then they are not like any other arthropods. This high degree of variability is a very real problem with some serious implications, because if we take this disparity of form at face value, then we should seriously question whether all these various groups can constitute a single monophylum.

When one looks at other major arthropod groups outside of Crustacea, there appears to be no great disparity of plan within these taxa (see Meglitsch and Schram 1991); members of each group fit a concise definition. For example, members of Insecta (Hexapoda) have a body divided into a five-segment head with the first postantennal segment bearing appendages modified as a labrum, a three-segment thorax with two sets of wings in the pterygote insects borne on the second and third segments, and an abdomen of 10–12 somites. All insects conform to this definition with some exceptions, for example, allowing for fusion of segments at the terminus of the abdomen or modification of wing arrangements. Insects have a unified body plan.

Myriapoda as a whole do vary in some features such as body length but have in common that their trunk is not divided into a thorax and abdomen and that their gonopores are generally located on the anterior aspect of the trunk. The individual groups of myriapods conform to common plans: Symphyla have 12 trunk segments with the gonopores on the fourth somite; Pauropoda bear 12 trunk segments with the gonopore on the second somite; and Diplopoda, with several very distinct orders, all exhibit well-developed diplosomites, that is, pairs of segments fused dorsally but distinct ventrally, and their gonopores are located on the second trunk segment. The individual orders of diplopods vary only regarding the total number of trunk somites: pselaphognaths have at least 10–12, but colobognaths can exceed 30. Chilopoda have variable trunk segment numbers, extending from 15 to more than 180 pairs of legs, depending on group, but all chilopods without exception have long antennae and modify the first trunk limb as a fang equipped with a poison gland to facilitate their carnivory. Centipedes also uniquely bear gonopores on the posterior aspect of the trunk.

The subphylum Cheliceriformes exhibits only a few "head" segments, essentially two, and these are fused with the anterior, or locomotory, part of the trunk to form a prosoma. The anteriormost somite (the one just posterior to the asegmental acron), the homolog of the antennal segment in other arthropods, does not carry antennae but rather is equipped with a pair of chelicerae. The second segment, what in other arthropods is referred to as the first postantennal



Fig. 1.1.
Disparate body types among crustaceans.

segment, typically bears a well-developed set of limbs, albeit variously developed. There are no exceptions to this basic format.

Within the cheliceriforms, the highly distinctive Pycnogonida appear to be all legs, their prosoma reduced to a thin cylinder. The mouth is located terminally on a long proboscis. The small turreted "head" bears chelicerae, a second set of limbs called *palps*, and a third set of limbs modified as *ovigers* in the males. Posterior to these limbs, most pycnogonids utilize four pairs of legs for locomotion (a few forms with five or six pairs are known). All sea spiders conform to this body plan.

Arachnida have a six-segment *prosoma*, with chelicerae, pedipalps, and four pairs of walking legs. The trunk bears an additional *opisthosoma* of diverse form but composed of some 13 somites, with the first segment greatly reduced as a narrow pedicel and the second bearing the gonopores. Opisthosomal limbs are missing or greatly reduced. Despite a great variety of body profiles, especially regarding the *opisthosoma*, all arachnids conform to this single plan.

Merostomata, a small group today, was more extensive (and diverse) in the past. The *prosoma* bears six pairs of limbs. The chelicerae are followed by four sets of modest-sized walking limbs with specialized *gnathobases*, the first of which in the males is modified for

grasping the female during copulation, and a somewhat larger fifth set effective in grooming the underside of the prosoma. The next somite, the pregenital segment, is reduced but bears modified limbs, the chilidia. Unique among living cheliceriforms, the opisthosome of the merostomes bears six pairs of limbs posterior to the genital segment. All merostomes conform to this plan.

From this short review, we can see that all these groups of arthropods have concise diagnoses, with distinct sets of apomorphies that characterize all members of the group. Crustacea, if viewed as a single group, simply does not have this.

CAN WE DIAGNOSE A MONOPHYLETIC CRUSTACEA?

Any invertebrate zoology textbook can provide a set of characters for Crustacea. When I was asked to provide such a diagnosis 25–30 years ago (Schram 1979, 1982), I certainly did not hesitate. However, we now realize it is not sufficient to simply string together any list of characters. Ideally, as in the arthropod examples cited above, these characters should be unique derived features that diagnose all members of the group. To rephrase this in contemporary terms, a diagnosis should offer synapomorphies that together uniquely delineate a monophyletic group. We strive for *natural taxonomies*, classifications that reflect evolution. It is critical to determine if this is possible for Crustacea.

A commonly accepted diagnosis of Crustacea consists of the following: (1) head of five somites, each bearing a set of appendages consisting of two pairs of antennae, a pair of mandibles, and two pairs of maxillae; (2) body consisting of three regions: head, thorax, and "abdomen"; (3) trunk appendages primitively multiramous; and (4) development consisting of a series of discrete larval and/or juvenile stages, initiated by a stage termed a *nauplius*.

Let us inspect these features one by one in order to determine if these characters provide that unique set of descriptors we require for a diagnosis of Crustacea. In the discussion below, I restrict the term *Crustacea* to mean a monophyletic group and the term *crustaceomorph* to connote the amalgam of arthropod types that we generally and broadly refer to as "crustaceans" (fossil and recent) but that may or may not be monophyletic. Table 1.3 will assist the reader in following along the taxa and many of the relevant features discussed below.

"Head of five somites, each bearing a set of appendages consisting of two pairs of antennae, a pair of mandibles, and two pairs of maxillae"

These are not a unique set of features. A head consisting of five somites is shared with insects and the myriapods (see above; Meglitsch and Schram 1991), and, as would follow, most of the head appendages of these somites are shared among the three groups, namely, the first set of antennae, mandibles, and two sets of maxillae. It is only regarding the so-called second set of antennae that we might have a distinctive crustaceomorph feature since myriapods and insects lack a limb in this position.

The second antennae are generally perceived as *specialized* sensory limbs and as such could serve as a defining apomorphy. This descriptor arises from the mental image of Crustacea conjured up by thinking of a shrimp or a lobster (a malacostracan), and this image without a doubt presents us with an icon of an arthropod with a set of sensory limbs at this position, albeit with slight anatomical variations, depending on group (Fig. 1.3A).

Nevertheless, sensory second antennae are *not* characteristic of all groups of crustaceomorphs. Chapter 7 provides additional details concerning antennae, but a short overview will suffice here to make a point. Remipedes have quite distinctive limbs in this position (Fig. 1.3B) that I suspect serve equally as a hydrofoils to direct currents of water that flow

Table 1.3. Comparative morphology of various aspects that define body plans among various groups of crustaceomorphs.

| Taxa | Head (no. somites) | Trunk regions | Postthorax | Thorax length (no. somites) | Segment no. of gonopore position | | Trunk limb rami | First larval segments |
|------------------------|-----------------------|------------------|------------|--------------------------------|-------------------------------------|--------|--------------------|--------------------------|
| | | | | | Male | Female | | |
| Oligo-crustacea | | | | | | | | |
| Branchiura | 5 | 2 | - | 4 | 4 | 4 | 2 | ? |
| Mystacocarida | 5 | 2 | 3 | 5 | 4 | 4 | 1 | 4 |
| Skara | 5 | 2 | 2 | 1 | ? | ? | 2 | ? |
| Martiniisoria | 4 | 2 | 2 | 3 | ? | ? | 2 | 4 |
| Branchiopoda | | | | | | | | |
| Laevicaudata | 5 | 1 | - | 10-11 | 11 | 11 | M | 3 |
| Notostraca | 5 | ?2 | ?p | 11 | 11 | 11 | M | 3 |
| Spinicaudata | 5 | 1 | - | 16-32 | 11 | 11 | M | 3 |
| Cyclotheria | 5 | 1 | - | 16-32 | 11 | 11 | M | 3 |
| Cladocera | 5 | 2 | - | 4-6 | | | | 3 |
| Anostraca | 5 | 2 | 2 | | 12 | 12 | M | 3 |
| Lepidocaris | 5 | 2 | 2 | | ? | | 2, M | |
| Rehbachella | 5 | 2 | 2 | 12 | ? | | 1 | 3 |
| Waptia | 5 | 2 | 2 | 11-? | ? | | | ? |
| Eucrustacea | | | | | | | | |
| Cephalocarida | 4 | 2 | 2 | 8 | 6 | 6 | M | 5 |
| Maxillopoda | | | | | | | | |
| Copepoda | 5 | 2 | 2 | 7 | 7 | 7 | 2 | 3 |
| Cirripedia | 5 | 1 | 2 | 7 | 7 | 1 | 2 | 3 |
| Ostracoda | | | | | ?7 | ?7 | | 3 |
| Braconaris | 5 | 2 | 2 | 7 | ? | | 2 | 4 |
| Malacostraca | | | | | | | | |
| Eumalacostraca | 5(+) | 2 | p | 8 | 8 | 6 | 2 | 3 |
| Hoplocarida | 5(+) | 2 | p | 8 | 8 | 6 | 2 | 3 |
| Phyllocarida | 5 | 2 | p | 8 | 8 | 6 | M | 3 |
| Remipedia | 6 | 1 | - | - | 15 | 8 | 2 | 3 |

Abbreviations: a, abdomen; M, multiramous; p, pleon. Neither the list of taxa nor the features are exhaustive of all possibilities but cover the major elements discussed in the text.

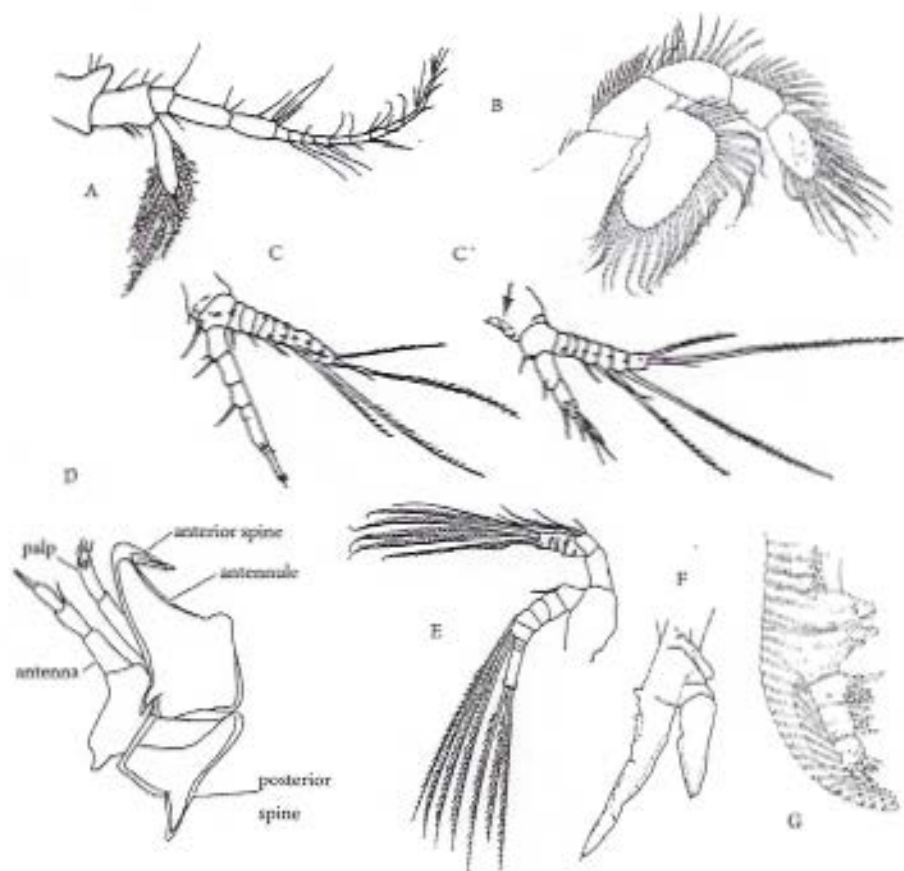


Fig. 1.3.

Various functional types of "antennal" limbs found in crustaceans. (A) Sensory: *Apsudes hermaphroditicus*, tanaid (from Lang 1953). (B) Swimming hydrodynamic plane: *Lasionectes entrichoma*, a remipede (from Schram et al. 1986). (C and C') Locomotory/feeding: *Derocheilocaris ingens*, a mystacocarid (from Hessler 1969), antenna (C) and mandible (C'). The arrow indicates gnathal lobes. (D) Part of an attachment complex: *Argulus foliaceus*, a branchiuran (from Martin 1932). (E) Swimming: *Archimimaphria discoveryi*, a copepod (from Boxshall 1983). (F) Host penetration: *Gorgonolaureus mazikae*, an ascothoracidan (from Grygier 1982). (G) Swimming/feeding: *Bredocaris admirabilis*, a Cambrian maxillopodan (from Müller and Walossek 1988).

around the head and perhaps also to aid in creating some of those currents by flapping the hydroplane-like exopods. Although no work has yet been done on functional morphology of this limb, I believe it safe to say that the remipede antenna is not a purely sensory appendage. Mystacocarids have a pair of limbs behind the first antennae that are virtually identical in form to the mandibles (Fig. 1.3C,C'), except these so-called second antennae lack the gnathal armament at the base of the limb that occurs on the mandibles. The mystacocarid "antennae" are locomotory limbs. Branchiurans possess broad plates in this position with basal hooks and terminal, recurved spines—nothing sensory at all but rather serving to assist with attachment (Fig. 1.3D). Tantulocarids lack head appendages altogether. Copepods have well-developed limbs in this position that serve for the most part as the primary organs of swimming (Fig. 1.3E). It is difficult to specify what this limb does in ascothoracicans, where

all head limbs are highly modified to achieve attachment to a host or to penetrate host tissues (Fig. 1.3F). In cirripedes, the adults lack the antennae, but the nauplius and cypris larvae have limbs in this position to assist in swimming; the second antennae disappear at the time of attachment prior to metamorphosis to the adult cirripede. Finally, within the wide array of Cambrian microarthropods that are considered to bear some relationships to modern groups (see chapter 2), such as *Bredocaris* (Fig. 1.3G), *Martinsonia*, *Rehbachella*, *Skara*, and *Walassekia*, the so-called second antennae are more often than not locomotory limbs, similar in structure to the mandibles and maxillae of these fossils.

We can conclude from this brief survey that the only character that Crustacea share at this position, that is, the first segment posterior to the true antennae, is simply the presence of a pair of limbs. However, this is to say nothing—the mere presence of limbs on the first postantennal segment, or any postantennal segment for that matter, is a generalized, primitive, or plesiomorphic feature.

As noted above, merostomes, pycnogonids, and arachnids also have a limb in this position, but that does not make them crustaceomorphs. In arthropods, all segments generally carry limbs, at least on the head and thorax; it is only when limbs are particularly specialized, or even missing, that things become more interesting and can serve to help diagnose a group. For example, the presence of a limb on this first somite posterior to the antennae in crustaceomorphs stands in contrast to what occurs in myriapods and insects. In these latter groups, the limb buds on the first postantennal somite are diverted from forming a limb into producing the special labrum seen in these groups. We know this is so because, at least for insects, developmental gene expression studies reveal that the labrum is the “appendage” of the so-called intercalary (first postantennal) segment (Boyan et al. 2002). This diversion of the first postantennal anlagen into forming the upper lip rather than a set of limbs clearly is a derived feature. It is the lack of limbs on the first postantennal segment of insects and myriapods that is a noteworthy and significant apomorphy, not the mere presence of a limb on that segment as occurs in crustaceomorphs, cheliceriforms, and many fossil groups such as trilobites.

Crustacea are generally said to have a five-segment head. However, many crustaceomorph groups include at least one pair of maxillipeds and the associated “thoracic” somite into the head, and we thus speak of a *cephalothorax*. Most of the time, it is clear that these maxillipeds are obviously modified anterior thoracic limbs. Development in the many crustaceomorph groups that have maxillipeds allows us to document successive stages wherein the maxillipeds become specialized and their associated somites through successive molts become incorporated into the cephalon during ontogeny. However, at least one group of crustaceomorphs, the remipedes, does not exhibit such a transition. Koenemann et al. (2007, 2009) observed no biramous precursor state to the uniramous maxilliped in the earliest larval stages—the remipede maxilliped and its segment are part of the head in the earliest recognized ontogenetic stages. Consequently, we could say that the remipedes, for all intents and purposes, have a six-segment head (Koenemann et al. 2009).

In summary, this first part of the diagnosis of Crustacea (head of five somites, each bearing a set of appendages consisting of two pairs of antennae, a pair of mandibles, and two pairs of maxillae) is not informative.

“Body consisting of three regions: head, thorax, and ‘abdomen’”

Body tagmosis is often an important component of defining an arthropod body plan. For example, as noted above, among the chelicerates a discrete head is lacking because the anterior segments associated with feeding and sensation are fused with the segments bearing the walking limbs to form a solid unit, the prosoma, a very distinctive feature.

The possession of a head, thorax, and abdomen is certainly distinctive, but it is also a feature shared with insects. Hence, while we might appear to have, with tagmosis, another argument for seeking some kind of relationship between crustaceomorphs and insects, that is, within a monophylum Pancrustacea or Tetraconata (Wheeler et al. 2004, Giribet et al. 2005), we do not have an effective component for a definition that seeks to uniquely define Crustacea.

Furthermore, crustaceomorphs themselves vary considerably in this regard, as we will pursue in more detail below. The number of thoracic segments can be characteristic, but only for individual crustaceomorphs and not for Crustacea as a whole. Remipedes have a long, homonomously developed trunk with no differentiation between anterior and posterior sectors. Mystacocarids have five and branchiurans have four thoracomeres. Large-bodied branchiopods often have 11 or 12 thoracomeres. Many maxillopodans and the malacostracans have seven or eight thoracomeres: maxillopodans *sensu stricto* have seven, while cephalocarids and malacostracans have eight.

Moreover, the possession of an abdomen is not a uniting feature. This variability is true not only regarding external, gross anatomical features such as total numbers of segments and those with and without paired limbs on the segments, but also for the underlying expression of *Hox* (homeobox) family genes as well (Fig. 1.4). In connection with the latter, Abzhanov and Kaufman (2004) and Schram and Koenemann (2004a) surveyed the available information concerning *Hox* gene expression in crustaceans. There are two fundamentally different types of posterior tagmata: the abdomen, a region without expression of the *abd-A* (abdominal A) *Hox* gene; and the pleon, a region with the expression of *abd-A*. Species with the latter type, the malacostracans, possess appendages on the segments and also display a well-differentiated central nervous system in that body region, whereas species with the former type, which lack *abd-A* expression in that body region (branchiopods and maxillopodans), lack appendages on these segments and do not have a well-differentiated central nervous system in these segments. It is for this reason that Schram and Koenemann (2004a) concluded that the old term *pleon*, as applied to the posterior region of the trunk of malacostracans, is not just an equal and interchangeable alternative for the term *abdomen*; the use of *pleon* as a descriptor is an absolute necessity. *Hox* gene expression indicates that the pleon of malacostracans and the abdomen of other crustaceans exhibit fundamentally different developmental pathways.

Admittedly, the amount of available data is limited. As is the case with developmental work, researchers focus on the study and manipulation of model organisms. Among malacostracans, *Porcellio scaber* and *Procambarus clarkii* provided the model systems of preference for studies of *Hox* patterning, and among entomostracans, *Artemia franciscana* and *Mesocyclops edax* have served as the models, and the latter has been only incompletely investigated. The determination of *Hox* gene expression in diverse arthropods was a leading line of research in arthropod evo-devo studies in the late 1990s and early 2000s, but such investigations have waned, at least for now. In light of the above phylogenetic usefulness of this line of research, we should look forward to more animals being investigated in this regard.

Nevertheless, this part of the definition of crustaceans (body consisting of three regions: head, thorax, and "abdomen") is not a particularly informative statement.

"Trunk appendages primitively multiramous"

This descriptor is also not very informative. The presence of bi- and/or multiramous limbs is widely accepted to be a primitive condition in Arthropoda; most authorities would concede that uniramy is derived. However, here, too, the devil is in the details. Schram and Koenemann (2001) reviewed the information available concerning early development of crustacean limbs, and Williams (see chapter 3) delves into this subject more deeply.

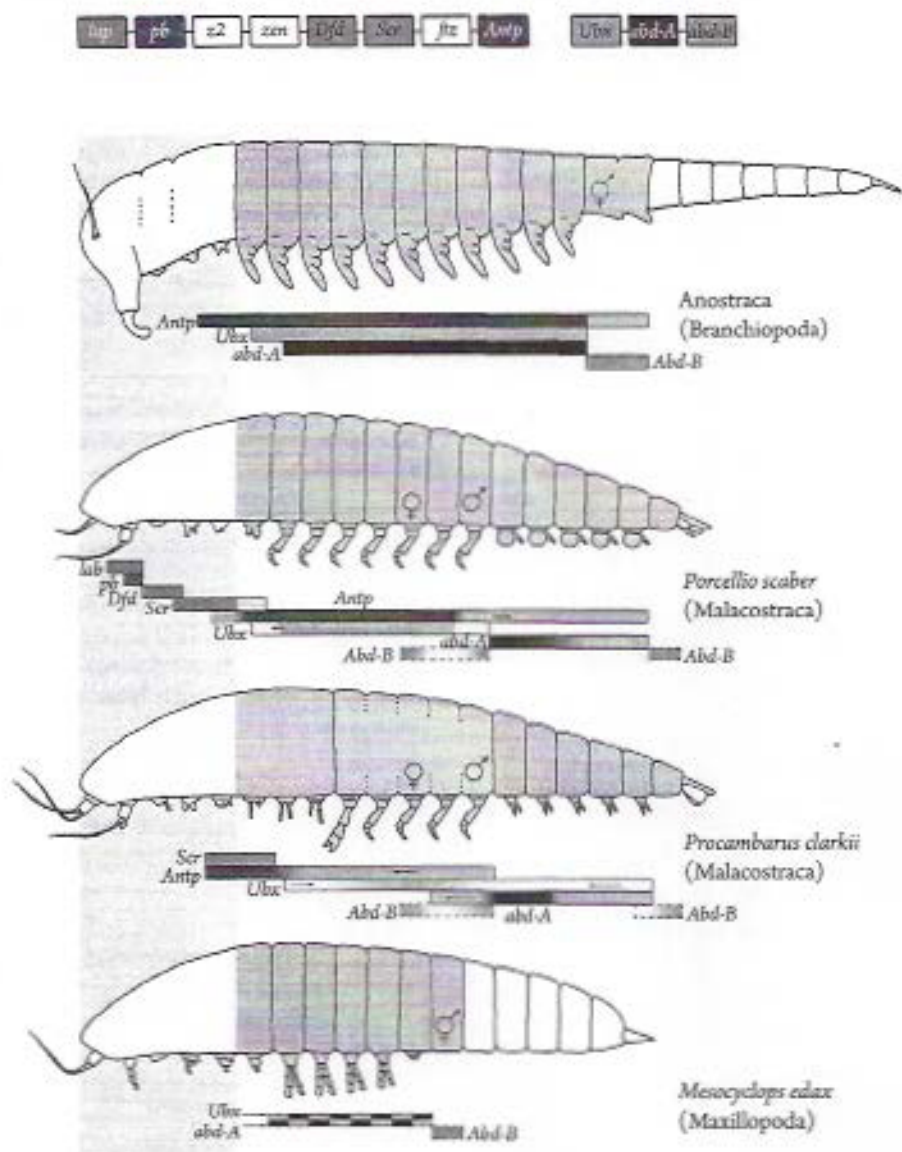


Fig. 1.4.

Hox gene expression pattern for various crustaceans. Shaded areas denote thorax or thorax/pleon. Note the different patterns from an abdomen (no Hox) and a pleon (with *abd-A*). Modified from Schram and Koenemann (2004a).

We can summarize here, nevertheless, a few basic patterns of limb development. One, in which the proximal pedestal of the limb carries distally a tubular, segmented telopod, is sometimes referred to as the *Drosophila* model because it was first recognized and studied in detail using the fruit fly *Drosophila* (Cohen 1990). It is the most common pattern of limb development seen in all biramous crustacean limbs that have been examined, particularly using *Mysidopsis bahia* (Panganiban et al. 1995). The limb anlage becomes forked, leading

eventually to the exopodal and endopodal rami. The gene *distalless* (*dll*) is expressed at the tips of the developing rami. A rather different pattern, however, prevails in Branchiopoda, often referred to as the *Artemia* model and documented with studies on *Artemia* and *Triops* (Williams and Müller 1996, Williams 1998). Rather than a uni- or biramous limb anlage, limb development begins with a mediolaterally directed ridge upon which eight lobes subsequently appear. The expression of *dll* occurs in varying patterns on these eight lobes, which proceed to form the unarticulated, leaflike limb, or corm, characteristic of the branchiopods. Similar gross anatomical sequences of limb development (though without the related gene expression patterns) have been documented for *Cyclostheria* (Olesen 1999) and the cladocerans (Olesen 1998). Hence, the multiramous limb of branchiopods has a fundamentally different mode of development from that seen in the crustaceans bearing biramous or uniramous limbs.

Thus, this part of the definition of Crustacea (trunk appendages primitively multiramous) is not an informative statement. The statement equates all crustaceomorph limbs and ignores widely divergent, perhaps incompatible, modes of development.

"Development consisting of a series of discrete larval and/or juvenile stages, initiated by a stage termed a *nauplius*"

In examining this characteristic sequence, we possibly come upon firmer ground in seeking a unique set of features to define Crustacea. Many living groups of arthropods exhibit epimorphic development. The animals essentially hatch with the complete set of segments characteristic of the adult; the individuals increase in size only with each molt.

Other groups of arthropods (some of the myriapods), although they resemble the adults in general form, hatch with fewer segments than the adults and add segments with each molt. Some Crustacea do this; for example, peracarids brood their young, and some of these are expelled from the marsupium as little "juvenile" forms, called *mancas*, which eventually molt and add a segment to achieve the adult condition.

Many crustaceomorphs, however, hatch as larvae, and these larvae not only possess fewer segments than the adults but also exhibit a distinctive larval form. Successive molts then not only add segments but also metamorphose the form. Does this constitute an apomorphy for Crustacea? Other arthropods have larvae. Extensive larval stages are known for the trilobites, and pycnogonids have a larva; many larvae, both nauplii and other intriguing forms, are known from the fossil record (see Müller and Walossek 1986). However, there are distinctive patterns of molting and metamorphosis that serve to absolutely unite some crustaceomorphs. Taxa within Cirripedia are clearly united by the presence of a distinctive nauplius with frontolateral horns and a postnaupliar cypris larva in the life cycle. Branchiopods have a characteristic nauplius with a naupliar process on the antennae. Zoeae are diagnostic larvae of decapod malacostracans.

The nauplius stage is often said to represent a phylotypic stage through which in theory all Crustacea passed in the course of the evolution of the group. We need to express some caution here—not all crustaceomorphs begin independent life as a nauplius larva, that is, exhibiting a larva characterized by possession of only three sets of limbs: the first and second antennae and the mandibles. There are crustaceomorphs that do (or did) not begin life as a nauplius but rather have as the initial stage a metanauplius, that is, a stage with more than just the three sets of naupliar limbs and/or more than the three naupliar segments. The issue is confused in the literature with the almost completely interchangeable use of the terms *nauplius* and *metanauplius*. This interchangeability implies that it is almost irrelevant as to what the basic structure of the first larva is—if it is tiny, possesses only a small number of limbs and segments, is given to swimming, and may or may not be filter feeding,

then it is a "nauplius." We see here the differences between a structural and a functional definition.

Which groups have an *orthonauplius*—a larva with only three pairs of appendages as seen in Branchiopoda, Maxillopoda, Remipedia, and euphausiacean and dendrobranchiate Malacostraca? Each of these *orthonauplii* bears a distinctive form. As noted above, branchiopod nauplii possess a naupliar process on the second antenna designed to facilitate feeding. Variations occur within the Maxillopoda. Among the most distinctive of nauplii, those of cirripedes bear anterolateral horns, frontal filaments anterior to the first antennae, and a long caudal process. There are four to six naupliar stages, depending on the group. Copepod nauplii exhibit a nauplius in almost its complete and pristine state, although the two *orthonaupliar* stages are nonfeeding because the gut is not developed until the metanaupliar phase. Ostracodes pass through a single nauplius stage, but the limbs are not completely developed, and in some species the early developmental stages (nauplius and the metanauplii) are retained within the mother's shell until they are shed near the end of their development. The Cambrian fossil *Rehbachella* had an *orthonauplius*. Finally, the free nauplii of the euphausiaceans (two) and dendrobranchiates (one) are very simple in form and do not feed, and even the succeeding metanauplii can be nonfeeding, also true of remipedes. Most of the other eumalacostracans pass through a clear egg-nauplius phase within the egg (Schram 1986).

The diversity of naupliar form and function led Scholtz (2000) to suggest that we should distinguish between primary and secondary nauplii, that is, between nauplii that are indeed primitive and an original part of the life cycle, and nauplii that are secondarily reevolved. Scholtz believes that the primitive stage for malacostracans is the embryonized egg-nauplius and that the nonfeeding, free nauplii of euphausiaceans and dendrobranchiates actually evolved from ontogenetic sequences without a free nauplius. One consequence of Scholtz's observations is that the nauplius larva would not be a phylotypic stage for all crustaceomorphs.

Other groups of crustaceomorphs exhibit a variety of first stages in their development. Cephalocarida begin as a metanauplius, the first stage of which has five limbs and a variable number of limbless segments. Mystacocarida hatch as metanauplii with four sets of limbs and five additional limbless segments.

The significance of these metanaupliar stages becomes evident when we consider the larval development in certain of the Cambrian Orsten microarthropods. The larval sequences for many of the Cambrian Orsten taxa are known; *Bredocaris*, *Martinsonia*, and *Phosphatocopina* all had four sets of limbs in the earliest phases, what Walossek has referred to as a "head larva" (Walossek and Müller 1990). *Agnostus* and the other trilobites in their earliest stages also bear four. There seems to be a basis for concluding that the naupliar stage, with its three sets of limbs, is derived from forms with four (possibly five) sets of limbs.

Larvae are features of aquatic arthropods, but the nauplius larva is undoubtedly a derived form. Unfortunately, not all crustaceomorphs have a nauplius, which is perhaps a problem whose full implication remains to be determined; some groups may have lost it, but other groups probably never had it.

At the beginning of this section I asked the question, What is Crustacea? It appears that we cannot use an unambiguous set of apomorphic descriptors to diagnose a monophyletic Crustacea. Developmental patterns and the nauplius larva appear to offer the best chance of doing so. However, since we have crustaceomorphs that do not exhibit the naupliar stage, we might conclude that the nauplius has evolved independently several times in the evolution of crustaceomorphs or has been lost several times; otherwise, if one demands that the nauplius be treated as diagnostic, Crustacea is not a monophyletic group.

It would appear from the above discussion that we must conclude that crustaceomorphs are whatever is left over among the arthropods after we have assigned everything else to other clearly defined monophyletic groups.

WHAT ARE THE CRUSTACEOMORPH BODY PLANS THAT MIGHT BE MONOPHYLETIC?

We now have a conundrum. If we cannot define a monophyletic Crustacea with a single, consistent set of derived characters, can we perhaps diagnose smaller monophyletic groups within the current array of crustaceomorphs? I do believe that there are groups within this assemblage that are monophyletic (Schram and Koenemann 2004a).

Short-Bodied Forms (Oligo-Crustacea)

Branchiura

Two groups of short-bodied forms at first glance would not appear to be at all alike (Fig. 1.5) but share a similarity regarding gonopore location. The living branchiurans are parasites of fish with highly modified mouthparts, but their gonopores open on the fourth thoracic somite. While there appears to be an abdomen, it is not differentiated into segments and is little more than a single or bilobed sac (Fig. 1.5A–C). Of special note is Pentastomida, the sister group of the branchiurans. Comparative sperm ultrastructure (Wingstrand 1972) and molecular sequence studies (Abele et al. 1989) revealed a close link of Branchiura with Pentastomida, odd wormlike parasites of the respiratory system in higher vertebrates (Fig. 1.5E).

This pairing of branchiurans and pentastomids might appear peculiar, but it is a group of great age; pentastomid fossils exist from the early Paleozoic Orsten faunas (Walossek and Müller 1994, Walossek et al. 1994). The several species of Cambrian/Ordovician pentastomids (Fig. 1.5D) can convincingly be compared to living pentastomids (see Walossek and Müller 1994, their fig. 21), although the fossils have trunk limbs but lack the proboscis bearing the mouth. Walossek and colleagues interpret these fossils as parasites, but there is no direct evidence of this. These fossils could have been ordinary free-living members of the infauna. Nevertheless, what the fossils do show without any debate is that, in combination with the sperm and sequence data above, the ancestry of branchiurans is very ancient.

Mystacocarida

In contrast to the branchiurans, the mystacocarids are microscopic members of the beach meiofauna, almost wormlike in form, with a well-developed set of mouthparts, including maxillipeds, but with four pairs of rudimentary thoracic limbs (Fig. 1.5F). The gonopores are located on the fourth thoracic somite. Mystacocarids, too, may be of great age because, in some respects, they are not unlike Skaracarida, the Cambrian fossil group from the Orsten of Sweden (Müller and Walossek 1985) (Fig. 1.5G).

Schram and Koenemann (2004a), using morphologic analysis tempered by Hox gene expression, found mystacocarids and branchiurans to be sister taxa. The results of molecular studies for both of these groups are confusing because long-branch attraction has been a persistent problem in these analyses; for example, Spears and Abele (1997) encountered this phenomenon when their results placed mystacocarids, remipedes, and cephalocarids together and in some proximity to chelicerates (a strange array), and the branchiurans emerged in a clade with podocopan ostracodes. Giribet et al. (2005) increased both the number of taxa sampled and genes sequenced but obtained a confusing collection of results depending on variant runs of taxa sampled (with and without fossils): mystacocarids and branchiurans sometimes appear alongside copepods and ostracodes; under other circumstances, branchiurans emerge elsewhere. Although the taxon sampling of Giribet et al. (2005) is impressive for all arthropods (and especially for hexapods), it is not particularly broad within crustaceomorphs. More recently, Regier et al. (2008) using nuclear

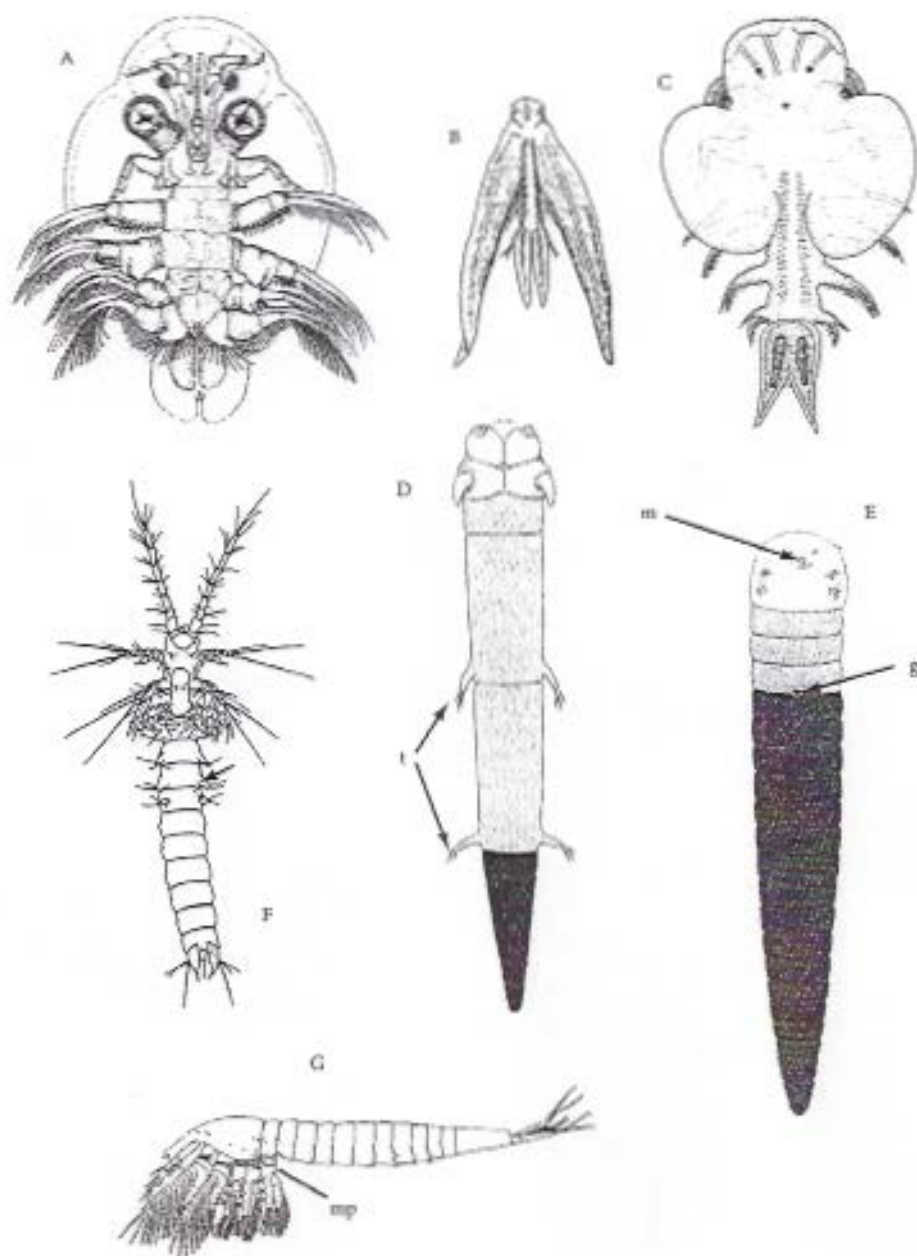


Fig. 1.5.

Body types of "short-bodied" crustaceans. (A-C) Diverse types of Branchiura (from Schram 1986). (A) *Argulus*. Note the highly modified mouthparts for attachment. (B) *Dipteropeltis*, with highly reduced body and winglike carapace. (C) *Chensopeltis*, displaying weak trunk and limb segmentation. (D and E) Diagrammatic Pentastomida (modified from Walossek and Müller 1994, their fig. 11). (D) Diagram similar to the Cambrian genus *Heymonsicambria*. Note the reduced trunk limbs (l). (E) Diagram of a generalized living pentastomid. m, mouth; g, gonopore; light gray, anterior trunk; dark gray, posterior trunk or abdomen. (F) *Derocheilocaris*, a mystacocarid. The arrow indicates approximate location of gonopore on fourth trunk limb. (G) *Skars minuta* Müller and Walossek, 1985, a Cambrian fossil crustacean that might represent a mystacocarid stem form. mp, maxilliped.

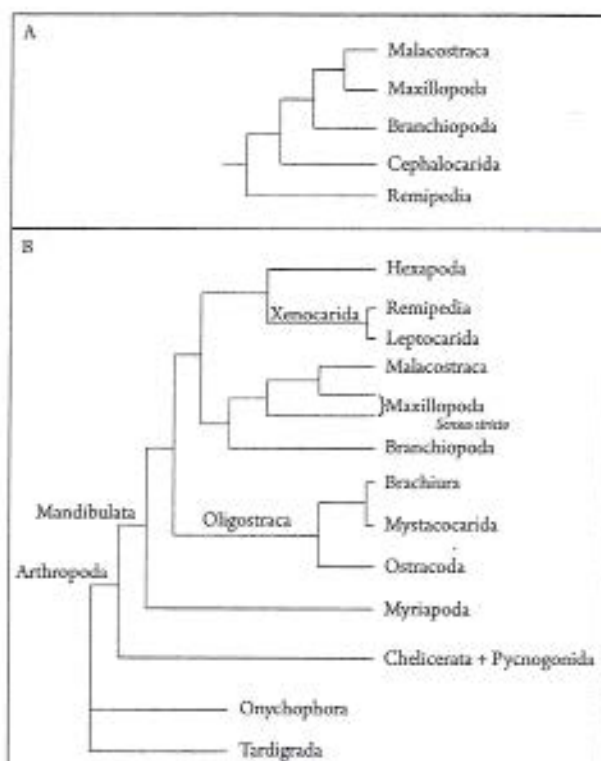


Fig. 1.6.

(A) A classic understanding of crustacean phylogenetic relationships, based on morphology. (B) A summary version of one of the more recent molecular phylogenies. Modified after Regier et al. (2010).

protein coding genes also found branchiurans as a sister taxon to podocopan ostracodes. While the breadth of their molecular sample was impressive, the taxon sample was again selective; for example, no mystacocarid was included. To remedy the situation, Regier et al. (2010) have expanded the taxon base and increased the number of genes sequenced; their results identified a clear clade with Mystacocarida, Branchiura, and Pentastomida within a group they termed "Oligostraca" (Fig. 1.6). The analysis by Koenemann et al. (2010) also placed these short-bodied groups together with these short-bodied groups. Oddly, these clades also contained Ostracoda (see below).

The shortness of the body in these orders imposes definite constraints. The lack of an elaborated abdomen in branchiurans and pentastomids undoubtedly limits their ability to move around. One could speculate whether this lack was a factor in both groups adapting parasitic lifestyles. So, too, with mystacocarids: the lack of a well-developed abdomen could have constrained adapting a vermiform, interstitial existence where abilities to swim or otherwise move around are minimized.

Branchiopoda

Living Branchiopoda

This large and fascinating group is almost exclusively restricted to freshwater, with a few exceptional cladocerans that are marine. One is tempted to speculate that they might have been

marine to begin with and then shifted to fresh waters. However, the evidence for that is not robust, and even most of the fossils, such as they are (mostly conchostracans), are preserved in freshwater to brackish water situations.

The branchiopods do exhibit a distinctive set of features that outline a body plan for the group. We have noted above in passing the distinctive mode of limb formation—from horizontal ridges that subsequently become multilobed, rather than uni- or biramous limb bud anlagen—and the nauplius larva. Consideration of the large-bodied branchiopods adds some further depth to our knowledge of the branchiopod bauplan, of which Anostraca serves as a model.

Traditionally (see Calman 1909, Schram 1986), anostracans were conceived as having an 11-segment thorax and a 9-segment abdomen. The first two legless, abdominal segments formed a fused genital complex. However, Hox gene expression studies reveal that the genes *Antennapedia* (*Antp*), *Ultrabithorax* (*Ubx*), and *abd-A* all are expressed in the thorax of *Artemia*, with a residual expression of *Antp* in the genital segments (Fig. 1.4). Abdominal B (*abd-B*), a marker for “end of thorax” and the genital segments, occurs in the genital segments (Abzhanov and Kaufman 2004, Schram and Koenemann 2004a). Hence, the genital segments are better considered thoracic, rather than abdominal, with the gonopores being carried on the twelfth segment of the thorax. The abdominal segments posterior to the genital complex do not exhibit Hox gene expression.

Notostraca and the conchostracans have the gonopores opening on the eleventh or between the eleventh and twelfth trunk segments. Notostraca (Fig. 1.7A,B) carry a well-developed pair of limbs on each of the “thoracic” segments (the first two being somewhat modified from that seen on the others), but posterior to this region the limbs become increasingly smaller as one moves posterior in the sequence of somites, and there is little correspondence between the number of limbs and the segment boundaries—there are many more limbs than apparent segments. Regrettably, as yet no Hox gene expression studies have been performed on notostracans.

The conchostracans are now generally divided into three monophyletic groups: Laevicaudata (Fig. 1.7C), Spinicaudata (Fig. 1.7D), and Cyclestherida (Fig. 1.7E) (Martin and Davis 2001), but they, too, appear to carry the gonopore in a position similar to that of Notostraca. The first of these, the laevicaudatans, or Lynceidae, have fewer trunk segments than the other two, but at least the female gonopore opens near the base of the eleventh, or penultimate, appendage (Linder 1945). The location of the male pore still must be confirmed (Martin et al. 1986). The other conchostracan groups have many more trunk segments, up to 32, with no differentiation between segments and limbs posterior to the genital openings, which are said to occur on the eleventh somite.

Thus, most Branchiopoda feature thin, foliaceous, unjointed limbs, with trunks divided into an anterior section with well-developed limbs and good Hox expression, and with gonopores at or near the eleventh or twelfth trunk somite. The four groups of Cladocera (Fig. 1.7F-I), while they are clearly branchiopods, exhibit extreme forms of body reduction, or oligomery. All these branchiopods bear either a well-developed carapace or a derivative thereof. Only the anostracans (Fig. 1.7J) lack a carapace, and most authorities place the fairy shrimp as a sister group to all other branchiopods (Richter et al. 2007).

The restriction of branchiopods to freshwater habitats entices one to wonder why these groups have become so limited. The unique mode of limb development perhaps precludes the development of anything other than thin, foliaceous, cormlike appendages. This in turn might have engendered an overall body habitus that lacks well-sclerotized and/or calcified body somites. Under these constraints, freshwater habitats, especially transient ones, provide satisfactory refugia.

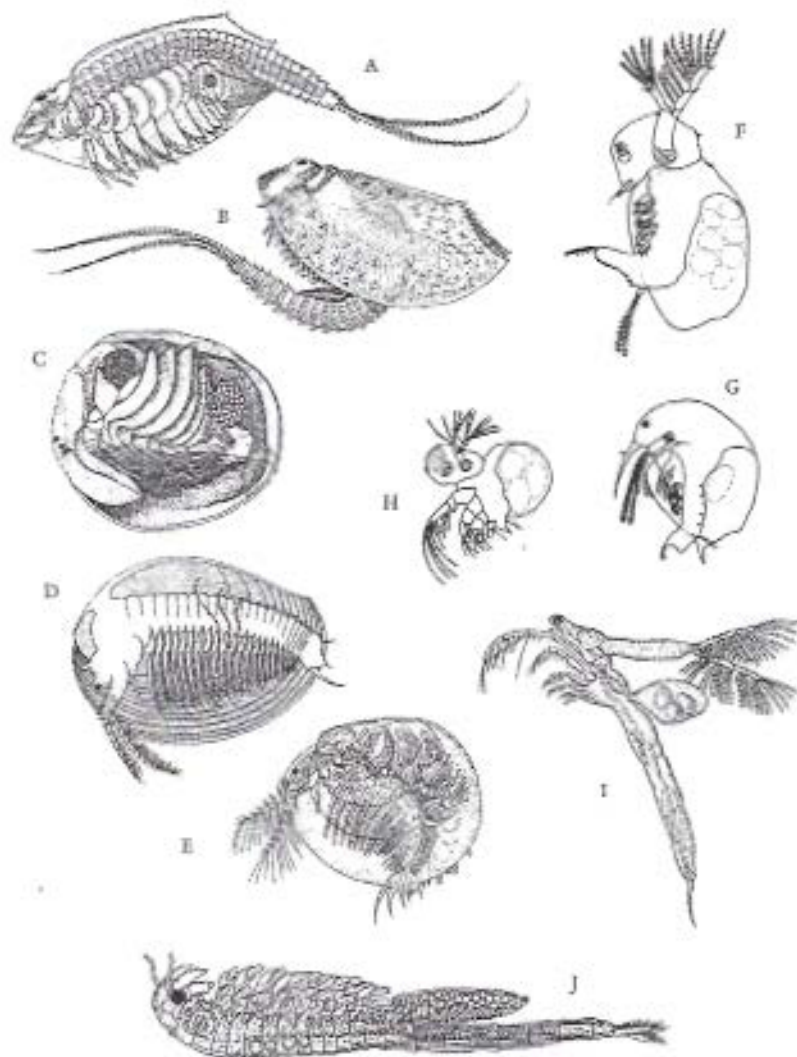


Fig. 1.7.

Body types of Branchiopoda. (A and B) *Lepidurus arcticus*, Notostraca (after Sars 1896): with carapace removed (A) and with carapace intact (B). (C–E) Various conchostracans. (C) *Lynceus gracilicornis*, Laevicaudata (modified from Martin et al. 1986). (D) *Limnadia lenticularis*, Spinicaudata (after Sars 1896). (E) *Cycletheria hislopi*, Cycletherida (after Sars 1887). (F–I) Various infraorders of Cladocera (after Lilljeborg 1901, Birge 1918). (F) *Sida crystallina*, Ctenopoda. (G) *Bosmina longispina*, Anomopoda. (H) *Podon intermedius*, Onychopoda. (I) *Leptodora kindtii*, Hoplopoda. (J) *Branchinecta limnabli*, Anostraca (after Lynch 1964).

Fossil Stem-Branchiopods

All authorities accept crown group Branchiopoda as a monophyletic group, based on the distinctive nauplius larva and the form and ontogeny of the trunk limbs. However, the branchiopods are also noteworthy in that a number of fossil forms are known that either occupy a stem position to the branchiopod clade or in some instances actually stand within the group.

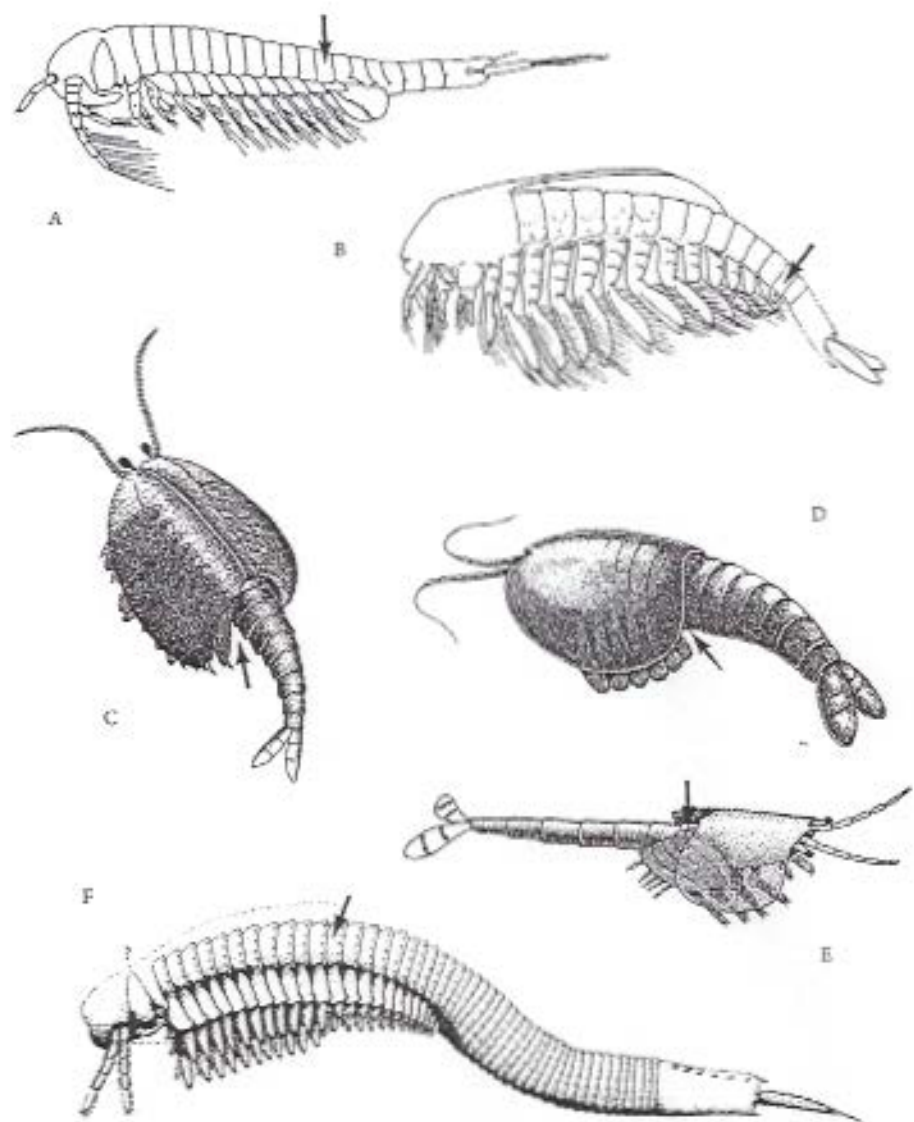


Fig. 1.8.

Fossil species that might have some relationship to Branchiopoda, either near the base of that group or as stem forms. Arrows indicate the twelfth thoracomere, the segment at or just posterior to the end of the thoracic limb series, which might bear the gonopores. (A) *Lepidocaris rhyniensis*, Devonian (from Scourfield 1926). (B) *Rehbuchiella kinsekulensis*, Upper Cambrian (from Walossek 1993). (C–E) various Cambrian waptiids. (C) *Chuandianella ovata* (from Chen and Zhou 1997). (D) *Pauloterminus spinodorsalis* (from Taylor 2002). (E) *Waptia fieldensis* (from Briggs et al. 1994). (F) *Castracollis wilsonae* (from Fayers and Trewin 2003).

The lipostracan *Lepidocaris rhyniensis*, a unique Devonian fossil (Fig. 1.8A), is preserved in great detail within nodules of chert. The thoracic limbs are both multiramous (thoracopods 1 and 2) and biramous (thoracopods 3–5). However, the presence of fully developed maxillae (Schram 1984), rather than the vestigial form characteristic of true branchiopods, indicates possibly only a sister-group relationship with crown Branchiopoda.

Rehbachella (Fig. 1.8B) has figured prominently in discussions of branchiopod origins (Walossek 1993). However, Schram and Koenemann (2001) took exception with this and concluded that *Rehbachella*, while possibly a stem form, was not a branchiopod *sensu stricto* since not only do they possess biramous thoracopods, but also these limbs arise from biramous anlagen and not the multilobed ridge of true branchiopods. Hence, I believe *Rehbachella*, at best, is a stem form.

Another fossil group from the Cambrian could be relevant to understanding stem evolution of branchiopods, the waptiids (Fig. 1.8C–E). The genus *Waptia* from the Burgess Shale of Canada is probably the most famous. However, several genera are known (Briggs et al. 1994, Chen, and Zhou 1997, Taylor 2002) and all appear to have a subdivided thorax with apparently four anterior telopodous limbs and six posterior foliaceous limbs. The gonopores have yet to be identified for waptiids, but I would venture a guess that they probably occurred on the eleventh trunk segment.

Although the recent large-scale molecular analyses of Giribet et al. (2005) and Wheeler et al. (2004) typically find Hexapoda as a sister group to all crustaceomorphs, there is an alternative hypothesis. Schram and Koenemann (2004b), VanHook and Patel (2008), Lartillot and Philippe (2008), and Dell’Ampio et al. (2009) obtained trees with insects and Branchiopoda as sister groups. These results were based on developmental gene expression patterns and molecule sequences, and these trees serve to propose alternative hypotheses concerning branchiopod relationships.

Finally, there are fossils such as *Castracollis wilsonae* (Fig. 1.8F) that exhibit body plans that are complex but nevertheless place them within branchiopods, in this case 11 large, foliaceous, cormlike limbs on the anterior thorax followed by another series of similar limbs but much reduced in size (Fayers and Trewin 2003). *Castracollis* might or might not have had a carapace.

E crustacea

What remains of the crustaceomorph taxa after clades of short-bodied and branchiopodan types are isolated is a confederation of diverse forms: Cephalocarida, Malacostraca, Remipedia, and Maxillopoda. When viewed as a whole, these taxa are divergent in terms of both habitus and habitat; nevertheless, all these groups bear gonopores on the sixth through eighth thoracic somites. There are a couple of interesting exceptions to this rule, which I note below.

Cephalocarida

This group of hermaphrodites is small both in size and in species numbers. It has a thorax of eight segments and a limbless abdomen of 12 segments (Fig. 1.9A). The form of the maxillae is very similar to that seen for the thoracopods. The gonopores are located on the sixth thoracomeere. Nothing is known of Hox gene expression in cephalocarids.

The body plan of cephalocarids might exhibit the results of the same sorts of constraints we saw above with mystacocarids. In this case, the elongate, limbless abdomen with extended terminal caudal rami at best probably functions like the tail on a kite: a stabilizer to minimize drag and the effect of turbulence as the animals swim. The long series of thoracic limbs developed as swimming paddles provide more locomotory abilities than that seen in the tiny thoracopods of mystacocarids, but nonetheless, competition from larger and more mobile forms probably forced the cephalocarids to retreat to flocculent bottom sediments in order to make a living.

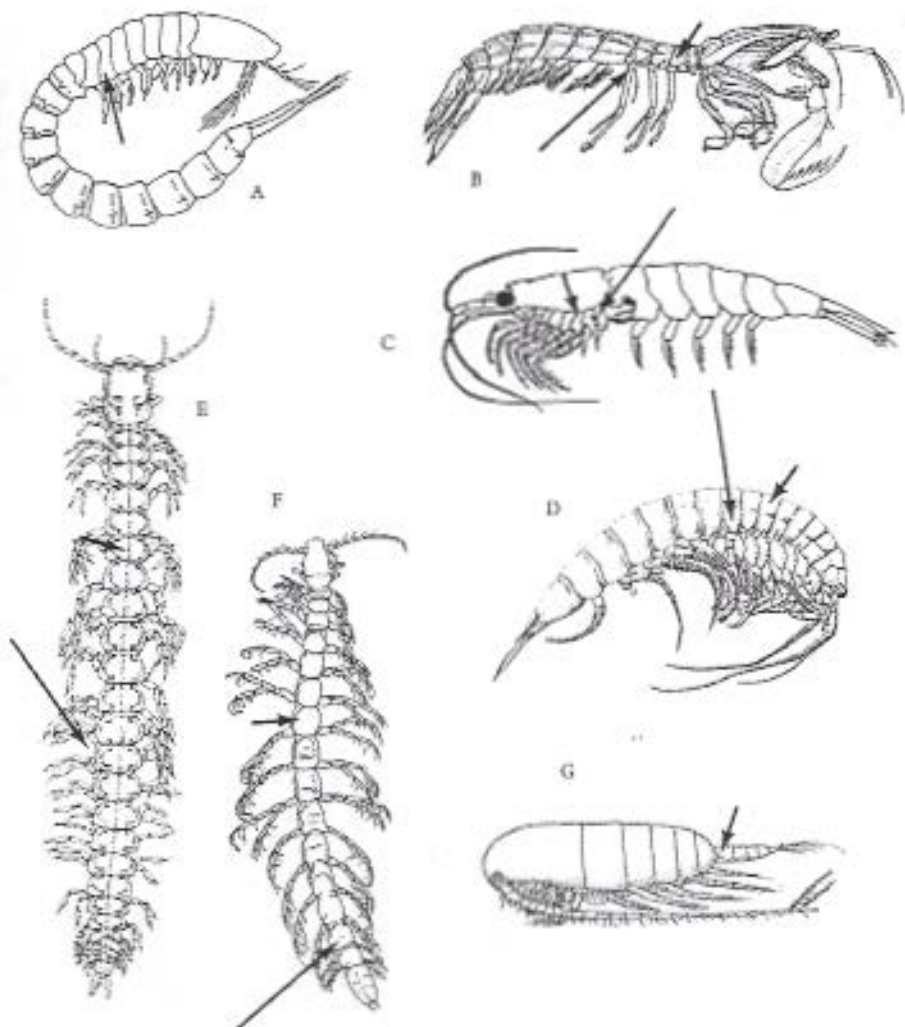


Fig. 1.9.

The four major groups among the core bauplan of Crustacea, with gonopore-bearing segments indicated by arrows. (A) A cephalocarid, *Hutchinsoniella macracantha*, a hermaphrodite with pores on the sixth thoracomere (modified from Schram 1986). (B) A hoplocarid Malacostraca, a male *Squilla mantis*. The male pore (long arrow) would be on the eighth thoracomere; the female pore (short arrow) would be on the sixth thoracomere (modified from Calman 1909). (C and D) Two types of eumalacostracan Malacostraca: with (C) and without (D) a carapace. (C) A euphausiid, *Meganyctiphanes norvegica*. The male pore is on the eighth thoracomere (long arrow); the female pore, on sixth thoracomere (short arrow) (modified from Mauchline and Fisher 1969). (D) The syncarid *Anaspides tasmanica*. The male pore is on the eighth thoracomere (long arrow); the female pore, on sixth thoracomere (short arrow) (modified from Schminke 1978). (E and F) Two types of remipede, hermaphrodites with the male pore on the eighth thoracomere (long arrow) and the female pore on the fifteenth thoracomere (short arrow). (E) Medium-length body, *Speleonectes girouensis* (modified from Yager 1994). (F) Short-length body, *Micropacter yagerae* (modified from Emerson and Schram 1991). (G) A typical maxillopodan, *Calanus finmarchicus*. Male and female pores open on seventh thoracomere (modified from Calman 1909).

Malacostraca

This most variable of crustacean groups nevertheless has a fundamentally uniform structural plan. The trunk is divided into an anterior thorax of eight segments and a posterior pleon of six or seven segments, sometimes fewer. All trunk somites generally bear appendages, but noteworthy variations can occur, such as one or more thoracopods serving as maxillipeds or posterior thoracopods and/or pleopods being greatly reduced or absent. Hox genes are expressed throughout the body (Abzhanov and Kaufman 2004, Schram and Koenemann 2004a) with *Ubx* characteristic of the thorax and *abd-A* of the pleon (Fig. 1.4). The female gonopores occur in association with the sixth thoracic segment, while the male pores are on the eighth.

The malacostracans are typically said to contain three groups: the small nectobenthic leptostracans (not illustrated), the obligate carnivorous hoplocaridans (Fig. 1.9B), and the extremely diverse caridoid eumalacostracans that have forms both with a carapace (Fig. 1.9C) and without (Fig. 1.9D). The diversity of this group is examined in greater detail in other chapters in this volume.

We might say that the great versatility imparted by the malacostracan body plan is responsible for its success. The long series of limbs, extending through both the thorax and pleon, allows a great degree of variation and specialization that undoubtedly has allowed the group to radiate to the extent it has, with great numbers of species and remarkable variations in structure.

Maxillopoda

With the problematic *Mystacocarida* and *Branchiura* removed from the maxillopodans, where textbooks often place them, there remains a core set of taxa that appear to conform to a single body plan. The old formula of 5-6-5 or the newer viewpoint of 5-7-4—five cephalic, seven thoracic, and four abdominal somites (see Newman 1987)—has great consistency throughout the group. The old interpretation was of a thorax with six limb-bearing segments and an abdomen of five segments always lacking limbs. An alternative interpretation of the gonopore-bearing segment as actually part of the thorax (Newman 1987) leaves only four abdominal somites; this interpretation makes more sense not only in terms of what we can see in other groups, for example, the free gonopore-bearing segment of the anostracans that occurs just posterior to a set of trunk limbs mentioned above, but also in terms of what limited information we have concerning Hox gene expression, with *Ubx* and *Abd-A* expression in the thorax and *abd-B* in the genital segment (Averof and Patel 1997).

Copepoda (Fig. 1.9G) most clearly present the pattern of 5-7-4. The gonopores of both sexes occur on the seventh thoracomere. Thecostraca conform to the basic maxillopodan pattern with some variations. *Ascothoracica* exhibit 5-7-4. *Facetotecta* appear to manifest 5-7-3, based on the anatomy of the Y-cypris. *Cirripedia* exhibit 5-7-0, considering the cypris larva as a stand-in model for the highly derived adults. While male gonopores in the cirripedes appear on the seventh thoracic segment, the female pore has shifted forward onto the first thoracic segment. Furthermore, the cirripedes lack an abdomen and coincidentally also lack any expression of *Abd-A* (Mouchel-Vielh et al. 1998).

The parasitic *Tantulocarida* present problems since these microscopic forms have an extremely aberrant life cycle. However, recent advances in elucidating that life cycle (Huys et al. 1993) allow us to conclude that the tantulocarids express a 5-7-2 pattern, with the male gonopore appearing on the seventh thoracic somite and the single median female pore occurring on the first. This latter feature clearly unites tantulocarids and thecostracans as sister groups.

The constraints exerted by a limbless abdomen on lifestyle may explain much of what we see in maxillopodan evolution. The maxillopodans certainly thrive under unusual conditions. Parasitism is widespread in the group, especially among thecostracans, and those thecostracans that are not parasites have lost the abdomen altogether and settled (literally) into the completely sedentary, highly aberrant body plan seen in the barnacles. Only the copepods possess the kind of biodiversity and habitat variability we associate with "successful" groups. Even so, the small sizes of copepods could be related to the limits engendered by an abdomen lacking limbs.

Ostracoda

These animals remain the most vexing of arthropods to place phylogenetically and, if molecular sequences are to be believed, may not be a monophyletic group. Their extreme reduction of body plan (oligomery), complete enclosure within a calcareous shell, and specializations directed at life carried on at a microscale have hindered attempts to link them to other crustaceomorphs. There are contentious debates about homologies within Ostracoda (Horne et al. 2005), and ostracodes do not appear to share obvious apomorphies with other crustaceomorphs. Most textbooks and reference books consign ostracodes to the maxillopodans (see Schram 1986), but that is more of a default placement.

K. Martens (personal communication, 2004) and R.A. Jenner (personal communication, 2009) expressed an informal view of at least some researchers that Ostracoda might not be a monophyletic group. This possibility obtains some support from molecular data that sometimes finds Podocopa and Mydocopa in different parts of cladograms (see Spears and Abele 1997, Regier et al. 2008, 2010, Koenemann et al. 2010). However, most of these analyses have a very limited taxon sample with sequences from only a handful of ostracode species.

There is much variation in form in ostracode limbs, but there is a consensus at least that both the mydocopes and the podocopes are themselves monophyletic (Horne et al. 2005). However, debates about the number of somites in each group are not settled. At first glance, one perceives that only very few thoracic segments bear limbs, but Schulz (1976) presented some evidence that indicates *Cytherella pori*, a podocopan, might have 11 trunk somites (a 5-7-4 pattern) and that the penis appears to be associated with the sixth or seventh of these segments (see Schram 1986, their fig. 33-1C). Tsukagoshi and Parker (2000) confirmed this in other species of podocopans. No similar information is available yet for Mydocopa.

From this, it might appear that podocopan ostracodes are possibly maxillopodans. Some authorities classified Ostracoda as a subclass of Maxillopoda (Schram 1986), but others maintain them as an independent class (Martin and Davis 2001). Most recently, Koenemann et al. (2010) and Regier et al. (2010), on the basis of molecular sequences, obtained both podocopan and mydocopan ostracodes as a sister group to a clade of mystacocarids, branchiurans, and pentastomids. This arrangement would then unite all the short-bodied "oligostracans" into a single clade near the base of the crustaceomorph tree (Fig. 1.6).

However, there existed Paleozoic, especially Cambrian, taxa that may have some bearing on eventually determining ostracode affinities. Several such groups are under active study, such as the bradoriids, Phosphatocopida (Maas et al. 2003), and perhaps even the thylacocephalans. These groups will eventually have to be integrated into any classification of the crustaceomorphs, and undoubtedly they will prove very interesting in this regard.

Remipedia

This most recently discovered group of crustaceomorphs is noteworthy for several reasons. The trunk is not differentiated into a thorax and abdomen/pleon. If we consider the

maxilliped-bearing segment as a modified trunk somite (even though it is completely merged into the cephalon), then the female gonopore occurs on the eighth postmaxillary segment, and the male gonopore, on the fifteenth. However, as noted above (Koenemann et al. 2007, 2009), the distinctive maxillipeds, virtually identical in general form to the maxillae, display no developmental evidence that this limb is modified from a thoracopod format. In addition, the number of trunk segments is not fixed, either within or between species (Koenemann et al. 2006), with many long-bodied forms recognized (Fig. 1.9E)—although there appears to be at least a lower limit of 16 trunk segments in the adults (Fig. 1.9F). The significance of all this variability remains to be explored.

The remipede body plan ensured that these animals are excellent swimmers, on a par with anything seen among the malacostracans. Even so, their habitat restrictions are quite profound; they prefer anchialine cave habitats in low-oxygen conditions.

CLASSIFICATION

The above review indicates there have to be changes in our concepts of crustaceomorph classification, but this is not the place to present any new or radical higher taxonomy. In principle, we want our taxonomies to reflect phylogeny, but that is not always possible. There is much conflicting evidence from molecular analyses, which along with morphological data often suffers from limited taxon sampling, and the latter often ignores or minimizes input from fossils. We still need to more effectively integrate data from gross morphology, molecular sequencing, and paleontology into a coherent whole. Nevertheless, we should extend some effort to recognize the monophyletic groups about which we are certain (Fig. 1.10); there are patterns that should be acknowledged.

To these ends, we can make good use of the concept of the *plesion*, a particular taxon that does not fit well into another category and that eventually might be assigned to its own higher category. I believe that, in this instance, we should begin to think of the infraphyla below as monophyletic groups on a par with other well-established arthropod monophyla such as Hexapoda, Chelicerata, Trilobita, and Pycnogonida. What fossils and where they will fall within or between these monophyletic groups will be explored elsewhere. The scheme is not complete in terms of all possible fossil plesions but does include most of those mentioned in the text above (Table 1.4).

WHAT MIGHT THE CRUSTACEOMORPH ANCESTOR HAVE LOOKED LIKE?

At one time, there was a fair consensus as to what the ancestor of Crustacea might have looked like. Hessler and Newman (1975) devised an ancestor with a long, homonomously segmented body, each segment bearing a set of limbs not unlike a cephalocarid, for which Newman preferred a form with a carapace, and Hessler one without (Fig. 1.11A). Cisne (1982) believed that crustaceans arose from a trilobite-like ancestor. Schram (1982) concurred with Hessler and Newman (1975), although he would have preferred a somewhat more foliaceous limb, intermediate between cephalocarids and branchiopods (Fig. 1.11B). However, Schram's 1982 paper had been written in 1978 (delayed due to a delay in the publication of the book in which it appeared), and in the intervening years the remipedes had come to light. By 1983, Schram had altered his views as to the form of an ancestor, which, while still in possession of a long homonomous body, was viewed as equipped with biramous, paddlelike limbs (Schram 1983). Schram positioned this biramous theory as an alternative hypothesis to the mixopodial theory of Hessler and Newman, and this then postulated a remipede-like alternative ancestor as opposed to a cephalocarid-like forebear.

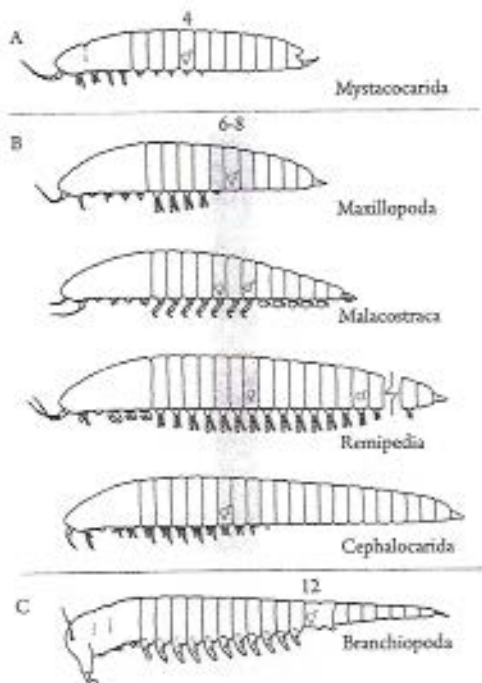


Fig. 1.10.

Major crustaceomorph body plans based on gonopore position. (A) *Mystacocarida*, an "oligostracan." (B) "Eucrustaceans." (C) *Branchiopoda*. From Schram and Koenemann (2004a).

The debate outlined above was based on morphology. Some information derived from molecular sequences now suggests that hexapods could factor into this mix. One fossil that might have facilitated a visual understanding of how this transition might have occurred is *Wingertschellia backesi* Briggs and Bartels, 2001 (= *Devonohexapodus bocksbergensis* Haas et al., 2003). A recent reexamination of all available fossils of this species from the famous Devonian Hunsrück Shale (Kühl and Rust 2009) synonymized the two names, but the original reconstruction of Haas et al. (2003) presented a strange chimera—it appears to have a dragonfly anterior end and a very long myriapodous posterior end (Fig. 1.11C). Although the interpretation of Haas et al. (2003) of *D. bocksbergensis* offered a head (of possibly four segments) and a short three-segment thorax followed by a long abdomen, the new interpretation presents a six- or seven-segment head, with the posteriormost three pairs of cephalic limbs as long, possibly prehensile appendages and followed by a long trunk with biramous limbs. Neither Briggs and Bartels (2001) nor Kühl and Rust (2009) offer a reconstruction of *W. backesi*, but the latter believe that this species is neither a stem hexapod nor within crown group Malacostraca. Of these I am not so sure, having once had the opportunity to examine *D. bocksbergensis* courtesy of Dieter Walossek. Even though what this Devonian species might represent remains uncertain, nevertheless, it does demonstrate that there is an abundance of long-bodied forms in the Paleozoic that may have significance for understanding the early evolution and possible origins of surviving groups of arthropods.

Another source of information that is relevant for understanding crustacean ancestry is derived from the study of the Cambrian Orsten microfossils (a few of which were mentioned

Table 1.4. A classification of tetraconate arthropods with inclusion of fossil plesions.

| |
|--|
| Subphylum: Tetraconata (= Crustaceomorpha = Pancrustacea) |
| Infraphylum: Hexapoda |
| Infraphylum: unnamed (short-bodied crustaceomorphs—"Oligostraca") |
| Class Branchiura |
| Order: Arguloidea |
| Order: Pentastomida |
| Class: Mystacocarida |
| Plesion: Skaracarida |
| Plesion: Ostracoda (one possible position; includes <i>Myodocopa</i> and <i>Podocopa</i>) |
| Infraphylum: Branchiopoda |
| Class: Phyllopoda (= Calmanostraca) |
| Order: Laevicaudata |
| Order: Notostraca |
| Order: Spinicaudata |
| Order: Cyclestherida |
| Order: Cladocera |
| Class: Sarsostraca |
| Order: Anostraca |
| Plesion: Lipostraca (= <i>Lepidocaris</i>) |
| Plesion: Rebbachiellida (= <i>Rebbachiella</i>) |
| Plesion: Waptiidae |
| Infraphylum: Crustacea |
| Class: Cephalocarida |
| Class: Maxillopoda |
| Subclass: Copepoda |
| Subclass: Thecostraca |
| Infraclass: Ascothoracica |
| Infraclass: Cirripedia |
| Infraclass: Facetotecta |
| Infraclass: Tantulocarida |
| Plesion: Ostracoda (one possible position; includes <i>Myodocopa</i> and <i>Podocopa</i>) |
| Class: Malacostraca |
| Subclass: Eumalacostraca |
| Subclass: Hoplocarida |
| Subclass: Phyllocarida |
| Class: Remipedia |

Cephalocarida and Remipedia might constitute a single class, Xeoocarida, based on molecular evidence. Ostracoda could occupy two possible positions: among oligostracans, based on molecular data, or within maxillopodans, based on some morphological data. Hoplocarida and Eumalacostraca (*sensu stricto*) could be arranged as a single subclass Eumalacostraca (*sensu lato*) with infraclasses Caridoidea and Hoplocarida.

above), and these have raised the possibility of alternative hypotheses. Incompletely understood in the 1980s, the depth of knowledge about these animals is now astounding, extending as it does to even developmental stages for many of these species (see chapter 2). The full impact of these studies remains to be assessed within the larger framework of the anatomy of modern forms, molecular sequences, and gene expressions, but much of this work suggests a

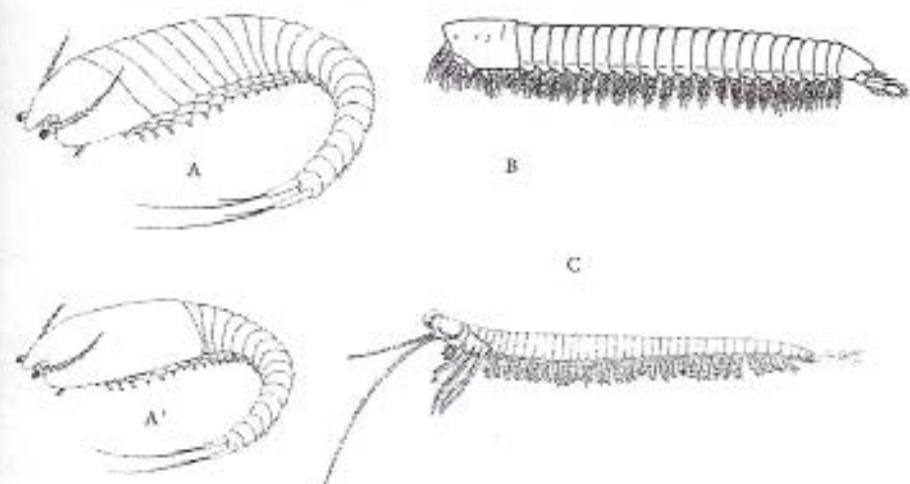


Fig. 1.11.

Crustaceomorph ancestors (see text for details). (A and A') Without and with a carapace, according to Hessler and Newman (1975). (B) According to Schram (1981). (C) *Devonoheteropodus bocksbergensis* (from Haas et al. 2003).

possible alternative hypothesis: a short-bodied ancestor rather than a long-bodied one. This merits consideration (Schram and Koenemann 2004a), but it is not possible or appropriate to examine here.

CONCLUSIONS

It would appear that we are little closer to understanding the origin of crustaceomorphs than we were 30 years ago. While the larger assemblage of the crustaceomorphs (or pancrustaceans, or tetraconatans, if you prefer) might be in some way monophyletic, just how it can (or even if it can) be diagnosed with a single set of apomorphies is not clear at this point. There are, however, good monophyletic groups within this vast array that can be clearly defined. Furthermore, these body plans appear to be constrained regarding biodiversity, functional morphology, and habitats they can occupy. In addition, we have a growing array of fascinating fossil taxa scattered within and between these monophyla, but how these are related to the monophyletic groups for which they may serve as stem forms remains to be determined.

But take heart! It is a time not to mourn the demise of the monophylum Crustacea but to embrace what will be a new world order and a better understanding of this whole branch of the crustaceomorph arthropods.

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