Out on a Limb: Arthropod Origins

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WITHOUT PRECEDENT, AND IN STUNNING DIVERSITY, A group of metameric animals with hardened cuticles and tubular articulated appendages—the arthropods—made their debut throughout the Paleozoic (*1*). The survivors of the early arthropods fall into four groups separated primarily along lines of limb structure and position, as well as patterns of segmental regionalization (that is, tagmatization). The crustaceans (shrimp, copepods, barnacles, crabs), like the trilobites and many other extinct Cambrian arthropods, have fundamentally branched, or biramous, appendages. The other three surviving groups—the chelicerates (spiders, scorpions, horseshoe crabs), the myriapods (centipedes, millipedes, and the like), and the insects—characteristically bear uniramous appendages. Insects and myriapods are undeniably more closely related to each other than either is to the crustaceans and chelicerates; most systematists combine them into the taxon Uniramia. In turn, the chelicerates and crustaceans are so distinct from each other, and from the Uniramia, that they each are placed into separate taxa of equal rank to the Uniramia.

Beyond this gross taxonomy, there is little agreement on how the arthropods, extant and extinct, are related. One view of the genealogy of the arthropods traces a monophyletic history, with the Uniramia, Crustacea, and Cheliceriformes each descending from a single ancestral taxon that was itself an arthropod, and with all arthropods being more closely related to each other than any other organisms (*2–4*). Nevertheless, the profound morphological gaps among the major groups, set against the background of sudden appearances in the fossil record of many novel taxa and the absence of easily recognizable transitional forms, bear witness to another possibility: the different groups of arthropods represent a grade of organization that arose independently from several metameric, nonarthropod, ancestors whose cuticles hardened (*1, 5*). From this polyphyletic perspective, the morphological features shared by the arthropods primarily reflect constraints imposed by sclerotization of the cuticle.

The often acrimonious debate over monophyly versus polyphyly now centers partly on differences in approach to phylogenetic reconstruction. Polyphyleticists stress the diversity of arthropod morphologies and embryologies (*1, 5, 6*); most advocates of monophyly take a cladistic perspective (*3, 4, 7*), seeking classes of shared, derived characters to build phylogenies. But the central evolutionary question remains: How, in terms of both pattern and process, did the unparalleled diversity and persistence of the arthropods come about? To answer such questions requires the identification of traits that distinguish major groups but also have an evolutionary history amenable to phylogenetic reconstruction. Paleontology, functional morphology, comparative embryology, and molecular biology each offer different sorts of potentially useful traits.

Among metazoans, the arthropods have an ancient and relatively complete fossil record. To advocates of polyphyly, studies of taxa once relegated to the Trilobitomorpha reveal far more independent lines of arthropod evolution than previously imagined (*1, 5*). However, a cladistic phylogeny that incorporates these "problematic" taxa portrays a monophyletic topology and places many of the problematic fossil arthropods as conceivable transitional taxa (*7*).

Some discrepancies of paleontological and phylogenetic interpretation arise from the paucity of fossils prior to the sudden appearance of the mid-Cambrian arthropod faunas. For example, the uniramous, onychophoran-like *Aysheaia*, and the biramous phyllocarid-like crustaceans appear nearly synchronously during the Cambrian (*8*), leaving open the pivotal mysteries of whether uniramous or biramous appendages evolved first, and what the polarity and nature of the transformations might have been. More importantly, do morphological gaps between taxa represent breaks in the record, plausible phenotypic transformations, or genealogical independence?

Studies of comparative morphology and embryology have only further polarized the debate over monophyly versus polyphyly. In fact, it was comparative morphologists who first seriously questioned the monophyletic tradition. They concluded, along with some embryologists, that many attributes once assumed to be homologous among the major taxa were not, and that gradual transitions from one appendage type to another would not have been biomechanically efficient, hence selectively advantageous (*5*).

This led them to depict the course of arthropod evolution as an unrooted bush, with four major branches. Molecular evolutionary studies promise to untangle some of this confusion. But for now, the molecular data are too sparse, and the diversification too rapid and ancient, to permit the reconstruction of unambiguous phylogenies (*9*).

That each approach comes up short of a definitive phylogeny is not surprising, in part simply because it is difficult to find enough characters of the right sort to generate a statistically reliable tree. But even if the historically correct phylogeny could be deciphered from distributions of character states, we would still only have half an answer to the central evolutionary question. The challenge would remain to reconcile phylogenetic pattern with evolutionary process.

Emerson and Schram (*10*) have taken on part of this challenge. They propose a novel hypothesis for how the uniramous appendages of insects and myriapods might be related morphologically, developmentally, and historically to the biramous appendages of crustaceans. The crux of their argument requires some basic understanding of the form of arthropod appendages and their relation to the segments that bear them.

Crustaceans possess limbs with a proximal section (the coxa), upon which rests the basis. From the basis arise two segmented branches: the exopod, directed laterally, and the midventrally directed endopod. The Uniramia, in contrast, lack any such branches.

In principle, uniramous limbs could be transformed by the gradual elaboration of a basal projection into a biramous appendage. If, however, the polarity of the transformation were from biramous to uniramous appendage, the exopod (and its accessory branches) may simply have been reduced leading to the uniramous conformation. Emerson and Schram argue that both of these scenarios are potentially flawed. For example, the gradual transformation from uniramous to biramous appendage should have left at least some fossils with transitional morphologies, yet there appear to be none. If the polarity were in the opposite direction, then the problem remains of how biramous appendages originated in the first place.

By abandoning the usual comparisons of the limbs themselves, and shifting the level of comparative analysis to the body segments from which the limbs developmentally and morphologically arise, the authors reach the simple and original conclusion that biramous appendages evolved by the consolidation of pairs of appendages originally on adjacent body segments.

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To trace the history of segment-appendage relationships, they first identify three types of segment-appendage conformation. The trunk of an adult insect is constructed of serially repeated single units, or monosegments. Because each trunk segment bears a single pair of uniramous limbs, insects monosegments are also monopodous. In modern myriapods such as millipedes and pauropods, as well as the long extinct euthycarcinoideans, the relation between segment and appendage is somewhat more complex, because some pairs of segments have dorsally fused. When two adjacent monosegments become dorsally, but not ventrally, fused, they form a diplosegment. Thus, from a dorsal perspective, each segment appears diplopodous, carrying two pairs of appendages, whereas from a ventral perspective, each segment bears a single pair of appendages. The third arrangement, termed duplosegmentation, is seen most clearly in one of the problematic arthropods of the Mississippian *Tesnusocaris goldichi* (*11*). *Tesnusocaris* now seems to be most closely related to the Remipedia, a recently discovered class of crustacean that most carcinologists agree retains numerous primitive crustacean traits (*12*); but, unlike all modern crustaceans, including extant remipedians, *Tesnusocaris* bore two pairs of uniramous appendages per segment.

In developmental terms, Emerson and Schram view duplomery to be the result of dorsal fusion of the tergites of adjacent segments, with incomplete fusion of ventral sclerites, internal parts, and appendages. Duplomery, as manifested in *Tesnusocaris*, is a developmentally and evolutionarily more derived state, involving complete fusion of adjacent segments, but incomplete fusion of appendage anlagen. This still incomplete consolidation leaves two separate pairs of appendages per adult duplosegment. They consider the most derived state of duplomery to involve the basal fusion of the pairs of appendages borne on duplosegments, producing a single pair of biramous appendages per somite. This is the segment-appendage conformation seen in most extant crustaceans, and many extinct arthropods. If this developmental and evolutionary scenario is correct, then a single crustacean duplosegment would be homologous to two uniramian monosegments (or a diplosegment of a millipede). Two predictions follow: first, the ontogeny and morphology of crustacean segments should reflect, to some extent, their duplicitous ancestry; second, monosegmental uniramians should have a duplicitous developmental basis.

The double sets of segmental commissures, ganglia, and ganglionic anlagen (*13*) may be telling remnants of the diplosegmental ancestry of the Crustacea. Even more intriguing evidence comes from comparisons of the ontogeny of segmentally repeated structures in Uniramia and Crustacea. In general, uniramian segmental growth appears to be underlain by an ontogenetic program of pairing (*14*). The pair-rule genes of *Drosophila*, which act in concert to regulate segment number, may also belie an underlying pairwise organization of monosegments in other Uniramia (*15*).

In contrast, it appears that crustacean segments and appendages are always produced singly during ontogeny (*13, 16*). This contrast between paired segmental expression in uniramians and the lack of pairing in crustaceans is exactly what would be expected if a single crustacean duplosegment were homologous to two uniramian monosegments (*10*). Based primarily on these patterns of growth and segment-appendage relationships, Emerson and Schram propose that the uniramous, monosegmental condition of insects and geophilomorph centipedes and the biramous, duplosegmental arrangement of crustaceans were both derived from a uniramous, diplosegmental ancestor. They speculate that this diplosegmental ancestor, which was akin to *Tesnusocaris*, but certainly much older and less derived in details of appendage and cephalic characters, arose from some onychophoran-like form.

Far from closing the debate on monophyly versus polyphyly, these speculations raise entirely new lines of argument, and potentially set the controversy in a new mechanistic framework. Emerson and Schram's study implies that changes in limb morphology are not the most dependable character states for reconstructing arthropod limb phylogeny. Instead, alterations in the limb-segment complex, because it appears to evolve as a developmental unit linked with other such units, may be more informative. To the extent this is true, the evolution of the three major types of limb-segment relationship may be proximally controlled by shifts in the relative timing of expression of genes that mediate intersegmental and segment-appendage relationships.

Not surprisingly, phylogenetic analyses based on limb-segment conformation yield a different set of transitional character states between uniramous and biramous appendages than analyses based on the appendages alone. Schram and Emerson (*13*) cast this novel transformational series as a monophyletic arthropod tree, but with a diplosegmental uniramous ancestral rooting, rather than a monosegmental biramous or uniramous ancestral one.

Emerson and Schram's analysis yields a monophyletic genealogy of the arthropods that is remarkably consistent with recent phylogenies based on molecular, paleontological, and developmental characters. All these approaches show that the foundations upon which arthropod phylogenies have been built will need more than just reshoring. For instance, until recently, few disputed that the ancestors of the arthropods were metameric, annelid-like creatures. Molecular phylogenies, however, now depict annelids arising after arthropods. This not only casts into doubt the traditional view of the nature of the ancestral taxon to the metameric protostomes, but raises anew the old question of wheter metamerism itself evolved independently in annelids and arthropods. The answer to this question is not yet clear, but immunohistochemical studies show that the highly conserved regulatory gene, *engrailed*, is expressed segmentally in crustaceans and insects, but not in annelids. In concert with the phylogenies based on 18*S* ribosomal RNA sequences (*9*) and limb-segment relationships, these data imply that metamerism evolved once in arthropod lineage, but independently in annelids (*17*).

The most demanding challenge for all concerned will be to assemble enough independent characters—be they molecular, morphological, physiological, or developmental—so that unambiguous and statistically robust phylogenies can be built. Whether further molecular and developmental studies of other arthropods narrow or broaden the bounds on these phylogenies remains to be seen.

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