UNRAVELING THE HISTORY OF ARTHROPOD BIODIVERSIFICATION[1]

Richard C. Brusca[2]

ABSTRACT

Current views of arthropod phylogeny are assessed in light of recent research in morphological and molecular phylogenetics, developmental biology, neurobiology, and paleontology. Recent fossil discoveries and molecular clock data inform us that arthropod diversification began in the Precambrian, and suggest that by the Cambrian the arthropods were already the most speciose metazoan phylum on earth. The combination of metamerism and jointed appendages (with intrinsic musculature), and the evolutionary potential of homeotic genes, has profoundly affected arthropod evolution and created many morphological homoplasies. Evidence strongly favors a monophyletic Arthropoda. Accumulating evidence supports a hypothesis that insects and modern crustaceans comprise a phylogenetic sister group, and that they, and perhaps also trilobites, chelicerates, and myriapods, all could have evolved out of an ancient crustacean stem line. Two implications of this hypothesis are that Crustacea comprise a paraphyletic taxon and insects may be viewed as "flying crustaceans."

Key words: Arthropoda, arthropod evolution, Crustacea, insects, Metazoa.

PREFACE. THE CHALLENGE OF UNRAVELING METAZOAN PHYLOGENY

Despite great progress made in zoology during the 20th century, there remain many fundamental, unanswered questions concerning metazoan evolutionary history. The origins and relationships of many animal phyla remain unclear or in dispute. In large part, this stems from the challenge of recovering unambiguous phylogenetic signals from ancient lineages. Recent molecular and paleontological studies suggest that major splits among the Metazoa occurred in the Precambrian, some perhaps nearly a billion years ago (Wray et al., 1996; Ayala et al., 1998; Seilacher et al., 1998; Li et al., 1998). In part, it may also be because the field of comparative morphology has lost popularity (and employment opportunities). And finally, the emerging field of molecular phylogenetics is still so new that every year sees improvements in the data analyzed and the phylogenetic inference methods used. For example, prior to 1997 most molecular analyses were based on small numbers of taxa and short sequences of a single gene, usually the inherently problematic 18S rDNA gene. Recently, however, new (and larger) molecular data sets have been developed based on other conserved nuclear genes, mitochondrial gene order, and gene duplication data. Because it is unlikely that a single gene will recover the full phylogeny of Metazoa, the future will no doubt see analyses of multiple gene sets.

Emerging molecular studies have corroborated many, and challenged some, paradigms of metazoan phylogeny. For example, whereas some molecular studies have supported the long-held close relationship between annelids and arthropods (Wheeler et al., 1993), recent studies have not done so (Lake, 1990; Halanych et al., 1995; Eernisse, 1997; Aguinaldo et al., 1997). Furthermore, the discovery of new animal phyla, and thus new fundamental body plans, continues to occur. The first edition of Linnaeus's (1735) *Systema Naturae* listed 14 groups that we now recognize as distinct animal phyla. Today, we recognize 34 animal phyla. Three former phyla have recently been sunk: Pentastomids are now placed within the Arthropoda (allied with the Maxillopoda), and vestimentiferans and pogonophorans are now regarded as annelids (probably highly modified polychaetes) (McHugh, 1997; Brusca & Brusca, in press).

Most of the large-bodied animal groups were discovered by the end of the 19th century. We are now on a track of discovery of microscopic metazoa, and three new animal phyla have been discovered just since 1956: Gnathostomulida (1956), Loricifera (1983), and Cycliophora (1995). There is a correlation between the discovery of new animal phyla and their body sizes: phyla described in the period of 1901–1920 have maximum body lengths of 3–10 mm; phyla described in the period of 1941–1960 have maximum body lengths of just 1 mm;

[1] This paper benefited from reviews by Wendy Moore, Lisa Nagy, and an anonymous reviewer. This work was supported in part by an NSF-PEET grant (DEB-9521649) to the author. Special thanks go to the indefatigable Peter Raven for encouraging the writing of this paper.

[2] Columbia University, Biosphere 2 Center, P.O. Box 689, Oracle, Arizona 85623, U.S.A.

phyla described in the 1980s and 1990s have maximum body lengths of less than 0.5 mm. Most of the small-bodied phyla are meiofaunal, although cycliophorans live as commensals on the mouth appendages of various marine crustaceans (Funch & Kristensen, 1997). The discovery of these minute animals presents challenges to those of us interested in animal phylogeny. They are so small that a great deal of their anatomy is reduced or otherwise altered. We know almost nothing about their developmental biology, and they are so rare that molecular biologists have not yet extracted gene sequences from them. I predict that the discovery of new microscopic phyla will continue for another half-century.

The challenges of unraveling animal phylogeny are not unique to molecular biology, small animals, or new phyla. Biology has a long history of skirmishing over phylogenetic issues at all levels. The evolutionary history of the Arthropoda has been one of the most challenging issues biologists struggled with throughout the 20th century. What follows is an update (as of mid 1998) on what we know about arthropod evolutionary history.

Arthropod Evolution: Background

There are five clearly distinguished groups of arthropods: trilobites (extinct since the end of the Paleozoic; ~ 4000 described species); Cheliceriformes (horseshoe crabs, eurypterids, arachnids, pycnogonids; ~ 75,000 described living species); crustaceans (crabs, shrimp, isopods, and their kin; ~ 50,000 described living species); hexapods (insects and their kin; 878,000 to 1.5 million described living species); and myriapods (centipedes, millipedes, and their kin; ~ 14,000 described living species). And, there are two close allies of the arthropods, tardigrades (water bears) and onychophorans (*Peripatus* and their kin). The close relationship between the Tardigrada and the Arthropoda has never been seriously questioned (Brusca & Brusca, 1990), and recent molecular work continues to support a sister-group relationship between these two phyla (Garey et al., 1996). There are now 1.02 to 1.64 million described arthropods, known from virtually all environments on earth. Estimates of undescribed arthropod species range from 3 to 100 million. The arthropods (Table 1) comprise about 85% of all described metazoan species.

The arthropods also encompass an unparalleled range of structural and taxonomic diversity, have a rich fossil record, and have become favored animals of evolutionary developmental biology. Arthropods were among the earliest animals to evolve.

Table 1. Fossil record of major arthropod groups.

Tardigrades: Middle Cambrian to present
Onychophora: Middle Cambrian to present
Trilobita: Early Cambrian to Permian
Xiphosura: Early Ordovician/Silurian to present
Eurypterida: Early Ordovician through mid-Permian
Arachnida: Upper Silurian to present
Pycnogonida: Devonian to present
Crustacea: Early Cambrian (or Vendian) to present
Hexapoda: Lower Devonian to present
Myriapoda: Upper Silurian to present

Recent work (Waggoner, 1996) suggests that even the Ediacaran (Vendian) fauna, of the latest Precambrian, included early arthropod taxa, perhaps true Crustacea.

Ever since Darwin, biologists have asked the question, "How has the incredibly successful diversification of arthropods come about?" Why are there so many arthropods? Is there something "special" about these animals? What is the phylogenetic history of the Arthropoda? Specifically, are the arthropods monophyletic and what are the relationships of the major arthropod groups to one another? There have been four great challenges to biologists in answering these questions. (1) Until the last decade of the 20th century, there had been a lack of hypotheses on arthropod evolution based on principles of explicit phylogenetic inference. (2) We have a very incomplete understanding of arthropod development, though this is improving quickly with the advent of molecular developmental biology. (3) There has been a paucity of comprehensive studies based on fossils from the earliest ages of arthropod evolution (late Precambrian and early Paleozoic). (4) It is apparent that high levels of homoplasy exist among the arthropods. In just the past 10 years, major discoveries have begun to address each of these challenges, as discussed below.

Work by the great comparative biologist Robert Snodgrass in the 1930s established a benchmark in arthropod biodiversity research. Table 2 shows a classification of the arthropods at that time, and it is this classification that one still finds in most modern biology textbooks. The Snodgrass classification embraces three important hypotheses:

(1) Arthropods comprise a monophyletic taxon.
(2) Myriapods and hexapods form a sister group, a taxon called Atelocerata (= Tracheata, or Uniramia of some authors). The Atelocerata have been united by several seemingly powerful attributes:

Table 2. Classification of the arthropods and their allies sensu Snodgrass (1938).

Phylum Arthropoda
Subphylum Trilobita
Subphylum Chelicerata
Class Merostomata
Subclass Xiphosura. Horseshoe crabs
Subclass Eurypterida. Eurypterids; extinct Paleozoic arthropods
Class Arachnida. Land spiders, mites, etc.
Class Pycnogonida. Sea spiders
Subphylum Mandibulata
Class Crustacea. Crabs, shrimps, isopods, etc.
Class Tracheata (= Atelocerata)
Subclass Hexapoda
Superorder Protura. Proturans
Superorder Insecta. Insects
Subclass Myriapoda
Superorder Chilopoda. Centipedes
Superorder Diplopoda. Millipedes
Superorder Symphyla. Symphylans
Superorder Pauropoda. Pauropodans

(a) A tracheal respiratory system.
(b) Uniramous legs.
(c) Use of Malpighian tubules for excretion.
(d) Loss of the second head appendages—the second antennae (as the name Atelocerata implies). Vestiges of the anlagen of this appendage can be seen during the embryogeny of some insects (e.g., Sharov, 1953; Brukmoser, 1965).

(3) The Crustacea and the Tracheata form a sister group, the Mandibulata—a name that Snodgrass himself coined.

For a brief period of time in the mid-century the concept of a polyphyletic Arthropoda, championed mainly by S. Manton and D. Anderson, enjoyed some popularity (Manton, 1973, 1977; Manton & Anderson, 1979; Anderson, 1979), and Anderson (1996) still maintains this view. The Mantonian view of arthropods placed the myriapods, hexapods, and onychophorans in a separate lineage (Manton's phylum "Uniramia") with an origin apart from the rest of the arthropods. However, this idea, based on flawed phylogenetic argumentation and an inadequate embryological foundation, did not long survive the rigors of scientific testing and modern methods of phylogenetic inference (see below). In addition to phylogenetic analyses, studies of Permian diaphanopteroid insects (Kukalová-Peck, 1991a, b, 1992; Kukalová-Peck & Brauckmann, 1990) have shown that early pterygotes probably possessed polyramous appendages, further undermining the Manton-Anderson Uniramia hypothesis. Additional support for arthropod monophyly has come from studies of compound eyes using a monoclonal antibody raised against a specific glycoprotein (3G6), to crystalline cones, cucones, and other elements in a variety of insect and crustacean retinas (Edwards & Meyer, 1990).

It was not until the late 1980s that Snodgrass's long-standing view of arthropod relationships began to be seriously questioned with: (1) the appearance of explicit morphological and molecular phylogenetic analyses, (2) the discovery of the amazing potential of homeobox genes in arthropod development and evolution, (3) the emergence of molecular-based evolutionary developmental biology, and (4) the discovery of exquisite new Cambrian preservations from Sweden, China, and elsewhere.

Morphological Phylogenetic Studies of Arthropods

Morphological phylogenetic studies of the arthropods are summarized in Table 3. Overall, these analyses suggest three important conclusions:

(1) The arthropods are a monophyletic taxon.
(2) The relationship of the Crustacea to the insects and myriapods is ambiguous; that is, Snodgrass's Mandibulata is a taxon of questionable validity.
(3) The monophyly of the Atelocerata (insects + myriapods) is also questionable.

Waggoner (1996) included in his analysis a number of arthropod-like fossils belonging to the "Vendian fauna," from the latest Precambrian (= Ediacara Period) that had generally been regarded as

Table 3. Morphological views of monophyly within the arthropods.

Year	Author(s)	Arthropods monophyletic	Mandibulates monophyletic	Tracheata monophyletic
1990	Brusca & Brusca	Yes	Yes	n.a.
1991	Schram	Yes	No	n.a.
1992	Eernisse et al.	Yes	n.a.	n.a.
1993	Backeljau et al.	Yes	n.a.	n.a.
1993	Wheeler et al.	Yes	Yes	Yes
1994	Wills et al.	Yes	Yes	Yes
1995	Wills et al.	Yes	No	No
1996	Nielsen et al.	Yes	Yes	Yes
1996	Waggoner	Yes	No	No
1997	Emerson & Schram	Yes	No	No
1998	Strausfeld	Yes	No	No

"problematica." He also included 21 Cambrian arthropods, and various modern taxa. He concluded that: (a) the Arthropoda are monophyletic, (b) the Ediacaran arthropod-like fossils are, in fact, true arthropods, and (c) the anomalocarids (and their kin) fall out very close to the base, and are probably the most primitive known arthropods. Anomalocarids were giant predatory arthropods (arguably, true Crustacea) that reached a meter in length. They are known from both the Precambrian and the Cambrian, and they were probably the largest predators of that time (Briggs, 1994; Chen et al., 1994).

The most recent phylogenetic analysis of arthropods was based on anatomical features of the central nervous system (Strausfeld, 1998). Strausfeld used 100 conserved neural characters in the brains of a variety of segmented invertebrates to reconstruct phylogenetic relationships among the arthropods. His analysis suggested that insects and crustaceans comprise a sister group, that the myriapods are a polyphyletic group (i.e., chilopods and diplopods are not sister taxa), and that pycnogonids are true chelicerates. The most important neuronal synapomorphies of Crustacea–Insecta are elements of the optic lobes and mid-brain, particularly features of the midline neuropils and neuropils associated with the compound eyes. This analysis corroborated earlier neurological descriptive work by Strausfeld et al. (1995), which also concluded that insects are closer to crustaceans than to any other arthropod group.

All arthropod central nervous systems use the same fundamental embryonic plan of construction (Whitington et al., 1993; Thomas et al., 1984; Strausfeld, 1998). However, a fundamental distinction between the early embryonic development of the myriapod nervous system and that of insects + crustaceans was recognized some time ago. Whitington et al. (1991) found that in insects and crustaceans longitudinal connectives are pioneered by segmental neurons, whereas in the centipede *Ethmostigmus rubipres* longitudinal connectives are pioneered from neurons in the brain that send their axons posteriorly to set up the parallel connectives. This difference between centipede and insect-crustacean ventral nervous systems is compounded by the fact that the pattern of segmental neurons in centipedes is quite different from that found in insects and crustaceans; centipede ganglia receive contributions from more widely distributed neurons, and there are more neurons in the centipede ventral cord when segmental axons are laid down. Comparisons of early neuronal outgrowth during embryonic development of the brain and thoracic ganglia also suggest a close affinity between crustaceans and insects (Harzsch et al., 1997; Therianos et al., 1995; Whitington et al., 1991). Paulus (1979) argued for arthropod monophyly on the basis of shared characters in the organization of photoreceptors and their satellite cells in compound and single-lens eyes. He further noted that insect and crustacean ommatidia, with their developmentally fixed numbers of cells, share more fine structural characters than either do with the chilopod ommatidia (which comprise an indeterminate number of elements).

Molecular Phylogenetic Studies of Arthropods

Molecular phylogenetic studies of the Arthropoda are summarized in Table 4. Field et al. (1988) sequenced a short segment of 18S rRNA but used representatives of just 10 phyla (only 4 of which were arthropods). Despite its limitations, the Field et al. work was pioneering. It was the first molecular phylogenetic study to test the monophyly of the arthropods, which it supported, and the work ini-

Table 4. Molecular views of monophyly within the arthropods.

Year	Author(s)	Arthropods monophyletic	Crustacea + Hexapoda	Myriapoda + Hexapoda (Tracheata)	Data
1988	Field et al.	Yes	Yes	No	18S rRNA
1989	Patterson	Yes	Yes	No	18S rRNA
1990	Lake	No	No	Yes	18S rRNA
1990	Field et al.	Yes	Yes	No	18S rRNA
1991	Turbeville et al.	Yes	Yes	No	18S rRNA
1992	Ballard et al.	Yes	Yes	No	12S rRNA (mitochondrial)
1992	Winnepenninckx et al.	Yes	Yes	n.a.	18S rDNA
1993	Van de Peer et al.	Yes	Yes	?	18S rDNA
1993	Wheeler et al.	Yes	Yes	No	18S rDNA + ubiquitin
1995	Winnepenninckx et al.	Yes	Yes	n.a.	18S rDNA
1995	Friedrich & Tautz	Yes	Yes	No	18S + 28S rDNA
1996	Garey et al.	Yes	Yes	n.a.	18S rDNA
1997	Regier & Shultz	Yes	Yes	No	EF-1a + POLII
1997	Eernisse	Yes	Yes	No	18S rDNA
1997	Spears & Abele	Yes	Yes	No	18S rDNA

tiated a stream of follow-up studies, continuing to use 18S rRNA sequences, and later the 18S rDNA gene itself. Each subsequent study has tended to use more taxa and longer nucleotide sequences for its data base, but until very recently most also continued to rely on the 18S gene. Problems associated with the 18S gene, use of short gene sequences, and single-gene phylogenetic inferences are well known and need not be repeated here. Furthermore, although there are now over 300 metazoan 18S sequences available, most published phylogenies have been based on fewer than 20 sequences (Eernisse, 1997). This is despite studies that suggest a minimum of 30–40 taxa are needed to accurately identify the root node of a large clade (Lecointre et al., 1993a, b; Sanderson, 1996; Hillis, 1996). In spite of methodological and sampling problems, recent molecular studies are beginning to converge on some similar conclusions. However, as Spears and Abele (1997) pointed out, "... in the crusade for understanding relationships among crustacean and other arthropod lineages, the rDNA data represent but a relic, and not the Holy Grail itself."

The most recent 18S sequence data suggest that insects share fewer similarities with the myriapods than they do with the Crustacea. Spears and Abele (1997) analyzed 31 18S sequences, and their results suggested that neither crustaceans nor insects were monophyletic. When they removed the "problematic" long-branched crustacean taxa (Remipedia, Cephalocarida, Mystacocarida), a myriapod + chelicerate clade emerged first, with insects as the sister group to a paraphyletic Crustacea. The Spears and Abele analysis also strongly supported malacostracan monophyly. Eernisse (1997) analyzed 103 sequences and concluded that (1) the Arthropoda are monophyletic, but only if the tardigrades are included [probably another 18S artifact], and (2) hexapods are more closely related to crustaceans than they are to myriapods. Regier and Shultz (1997) made a complete and welcome break with the 18S gene, using sequences from two other nuclear genes, the elongation factor (EF-1α) gene and the RNA polymerase II (POLII) gene. These trees were robust and mostly in agreement with the 18S work, concluding that: (1) Arthropods are monophyletic, (2) Crustacea are paraphyletic, and (3) insects are not the sister group of the myriapods, but arose from within the Crustacea.

Recent work by Boore et al. (1995) examined not gene sequences, but the linear arrangement of mitochondrial genes. This new type of data corroborates the gene sequence work and recognizes a mitochondrial gene arrangement that is unique to the crustaceans and insects alone.

In summary, the majority opinion from the molecular research, and the most recent opinions from both the morphological and molecular work, recognize four key features in arthropod phylogeny:

(1) Arthropods are monophyletic.
(2) Neither the Mandibulata nor the Atelocerata are natural groups.
(3) Crustaceans and insects constitute a sister group, exclusive of the myriapods.

(4) Crustacea are likely to constitute a paraphyletic taxon.

These last three conclusions are in conflict with 150 years of morphology-based thinking. Thus, two profound implications of these new studies are that the morphological attributes linking insects to myriapods might all be convergences (e.g., uniramous legs, tracheal system, Malpighian tubules), and that insects are actually "flying crustaceans" (in the same sense that birds are flying reptiles).

Emerging Views from Developmental Studies

The unique combination of segmentation and jointed appendages has allowed arthropods to develop modes of locomotion and feeding, and body region specialization, unavailable to other metazoan phyla. We now know that the fates of these segmental units and their appendages are under the ultimate orchestration of homeotic genes. These genes select the critical developmental pathways to be followed by cells during morphogenesis. Homeobox genes determine such basic body architecture as the dorso-ventral and the anterior-posterior body axes, where body appendages form, and the general types of appendages that form (Averof & Patel, 1997; Panganiban et al., 1997; Shubin et al., 1997). Homeobox genes can either suppress limb development, or modify it to create alternative appendage morphologies. A growing body of evidence suggests that these unique genes have probably played major roles in the evolution of new body plans among arthropods and the Metazoa in general (Davidson et al., 1995; Williams & Nagy, 1995; Panganiban et al., 1995).

The degree to which homeobox genes have been conserved is remarkable, and most of them probably date back at least to the Cambrian. For example, homologues of the *Pax-6* gene seem to dictate where eyes will develop in all animal phyla. *Pax-6* is so similar in protostomes (insects) and deuterostomes (mammals) that the genes can be experimentally interchanged and still function correctly. Homeobox genes modulate the expression of dozens of interacting, downstream, developmental genes whose products drive morphogenesis. The profound evolutionary potential of homeobox genes lies in this hierarchical nature. Variation in the output of these multigene networks can arise at many levels, simply by tinkering with the relative timing of gene expression—an evolutionary process we know as heterochrony. To understand the profound potential of homeobox genes to drive evolutionary change, consider that within the *Drosophila* genome 85–170 different genes might be regulated by the product of a single homeobox gene, the Ultrabithorax (*Ubx*) gene (Carroll, 1995).

A good example of the evolutionary potential of homeobox genes is seen in the abdominal limbs of insects. Abdominal limbs ("prolegs") occur on larvae of various insects in several orders, and they are ubiquitous in the order Lepidoptera, i.e., caterpillars. Abdominal limbs were almost certainly present in adult insect ancestors. Hence prolegs may have reappeared in such groups as the Lepidoptera through something as simple as the de-repression of an ancestral limb development program (i.e., they represent an atavism). We now know that proleg formation is initiated by a change in the regulation and expression of the *BX-C* gene complex (i.e., the Bithorax complex, which includes the *Hox* genes *Ubx*, *abdA*, and *abdB*) during embryogenesis (Carroll, 1995).

Molecular and developmental biology also seem to have broken the deadlock on the arguments over origins of uniramous and biramous limbs (e.g., Popadic et al., 1996; Panganiban et al., 1995, 1997; Shubin et al., 1997; Emerson & Schram, 1997). We now know that limb branching is a second-order phenomenon, probably orchestrated largely by the homeobox gene *Distal-less* (*Dll*). This single gene initiates development of unbranched limbs in insects and branched limbs in crustaceans. Antibodies that recognize *Dll* proteins show expression at the tips of insect limbs and also in biramous crustacean limbs (Panganiban et al., 1995). Branched limbs are formed when the gene is expressed ectopically in *Drosophila* (Diaz-Benjumea et al., 1994). In fact, *Dll* occurs in many animal phyla, where it is expressed at the tips of ectodermal body outgrowths in such different structures as the limbs of vertebrates, parapodia and antennae of polychaete worms, tube feet of echinoderms, siphons of tunicates, and appendages of arthropods. Furthermore, recent work suggests that whether an arthropod mandible is "whole-limb" (i.e., built of many segments) or "gnathobasic" (i.e., built of only the basalmost segments) also depends on the expression of the gene Distal-less. Thus, *Dll* is expressed in the whole limb (or multisegmented) jaws of myriapods, but not in the gnathobasic jaws of crustaceans and insects—still further testimony to the probable sister-group relationship of insects and Crustacea.

The Paleontological Data

Recent work has shown the fossil record of arthropods dates back to the early Cambrian, or perhaps the late Precambrian. And, by the mid-Paleo-

Table 5. Some important Precambrian and Cambrian arthropod *Lagerstätten* faunas.

Name	Age	Principal location
Orsten fauna	Upper Cambrian (~510 MYA)	Southern Sweden
Burgess Shale fauna	Middle Cambrian (~520 MYA)	British Columbia
Chengjiang fauna	Lower Cambrian (~530 MYA)	Southern China
Ediacaran fauna	Latest Precambrian (~560–600 MYA)	Ediacara Hills, Aust.

zoic, all five arthropod lineages were in existence and had already undergone substantial radiation. Arthropods are also the first land animals for which we have a geological record (Labandeira et al., 1988; Kukalová-Peck, 1990), and by the Late Silurian the first terrestrial scorpions and myriapods were already present. In fact, both terrestrial and marine myriapods have been reported from this period (Almond, 1985; Hahn et al., 1986; Labandeira et al., 1988), although molecular data suggest that myriapods might have arisen as early as the Cambrian (Friedrich & Tautz, 1995). The first centipede fossils occur in the Upper Silurian (~ 414 MYA) and, along with trigonotarbid arachnids, constitute the earliest known land animals (Jeram et al., 1990). The first millipede fossils occur in Devonian deposits (Almond, 1985; Robison, 1990); they are similar to the extant genus *Craterstigmus* (Shear et al., 1984) and are contemporaneous with the first terrestrial mites, pseudoscorpions, and scorpions (Størmer, 1969, 1977; Shear et al., 1987), as well as the first hexapods (Greenslade, 1988). The earliest known fossil hexapods are bristletails and collembolans from 390-million-year-old Gaspé mudstone (Labandeira et al., 1988). Some good records of these early creatures now exist, and the presence of these predatory arthropods suggests that complex terrestrial ecosystems were in place at least as early as the late Silurian. Perhaps the most important ancient arthropod fossils are those in which even the soft parts of the animal were preserved—the so-called ancient *Lagerstätten* (Table 5).

These ancient fossils have pushed the age of origin for the arthropods back to at least 600 MYA, and they provide us with critically important data on early arthropod anatomy and evolution. These extraordinary faunas are now telling us that Crustacea probably predate the appearance of trilobites in the fossil record, running counter to a long-held belief that trilobites were the most ancient arthropods. The recently exploited Chengjiang fauna of south China is Lower Cambrian, about 10 million years older than the Middle Cambrian Burgess Shale fauna (Chen et al., 1994). The Chengjiang fauna is very well preserved and includes at least 100 species of animals, many without hard skeletons, including the first known members of many modern groups. However, it is the arthropods that dominate this fauna, including trilobites and bradoriid "crustaceans" (and also tardigrades and onychophorans). The largest of the Chengjiang animals is *Anomalocaris*, also known from Ediacaran and Middle Cambrian deposits (Briggs, 1994). The Chengjiang fauna is very similar to that of the Burgess Shale, and it demonstrates that the arthropods were already far advanced by this early date.

The spectacular recent discovery by Klaus Müller and Dieter Walossek (Müller, 1983, 1992; Müller & Walossek, 1985; Müller et al., 1995; Walossek & Müller, 1992, 1997) of microscopic arthropods from the Upper Cambrian *Orsten* deposits of Sweden, has brought to light a rich fauna of minute crustaceans, crustacean larvae, and various crustacean-like arthropods. Among them, for example, is *Skara*, a cephalocarid-, or mystacocarid-like crustacean for which both naupliar larvae and adults have been recovered (the nauplius larvae are only a couple hundred microns long; adults are about 1 mm in length) (Müller & Walossek, 1986). *Skara*, and many other *Orsten* Crustacea, were surely meiofaunal animals not unlike modern marine meiofaunal crustaceans.

Fossils from this Cambrian site in Sweden have been collected since the days of Linnaeus, who actually described the first fossils from this area in 1757 (trilobites and conodonts). However, a brand-new kind of collecting began with Müller and Walossek's work in the 1980s. This new *Orsten* material is all microscopic, three-dimensional fossils. The *Orsten* arthropods show little or no signs of decomposition. They preserve details less than 1 micrometer in size (e.g., cuticular pores, the bristles on setae). Dozens of *Orsten* microcrustacea have so far been described. The recovery of these three-dimensionally preserved animals and the developmental series that have been found (with successive larval, juvenile, and adult instars—in animals less than 1 mm in length) have provided us with information on the detailed anatomy of body segments and appendages of many ancient stem-arthropods. The *Orsten* fauna shows that Cambrian Crustacea had all the attributes of modern crustaceans, such as com-

pound eyes, a head shield, naupliar larvae (with locomotory first antennae), and biramous appendages on the second and third head somites (the second antennae and mandibles).

Taken together, this recent paleontological work corroborates Whitington's observations long ago about the Burgess Shale fauna, that during Cambrian times the non-trilobite arthropods were both morphologically more varied and more numerous than were the trilobites (despite popular belief). We also now know that arthropods have probably been the dominant animals in terms of species diversity since the Cambrian. Arthropods comprise over one-third of all species described from Lower Cambrian strata.

Briggs and Fortey (1989) cladistically analyzed 23 of the Cambrian arthropod taxa, plus 5 extant groups. Their tree placed the Crustacea at the very base, as a paraphyletic sequence of taxa, and placed the trilobites and chelicerates near the top of the tree. The most recent molecular work does not conflict with this tree, in viewing the Crustacea as a paraphyletic group from which the other major arthropod clades emerged.

The Pentastomida

Pentastomids are obligatory parasites of vertebrate respiratory systems. There are about 100 described species, all of which infest various tetrapods, including two cosmopolitan species that infest humans. The blood-sucking adults inhabit respiratory tracts of their hosts, where they anchor themselves by means of their hooklike head appendages. For years it was believed that pentastomids were allied with the onychophorans as vermiform, pre-arthropod creatures. However, several recent molecular studies (using 18S gene sequences) have revealed the pentastomids to be highly modified crustaceans (Abele et al., 1989, 1992; Garey et al., 1996). Corroborative independent work over the past few years has come from cladistic analyses of sperm and larval morphology, nervous system anatomy, and cuticular fine structure (Wingstrand, 1972, 1978; Storch, 1984; Storch & Jamieson, 1992). Furthermore, Müller and Walossek's work on the Swedish *Orsten* fauna proves that the pentastomids (and also the tardigrades) had appeared at least by the Upper Cambrian, long before the land vertebrates had even evolved (Müller & Walossek, 1988; Walossek & Müller, 1994). So, we must ask what the original hosts of these parasitic crustaceans might have been. Walossek, Müller, and even Stephen Jay Gould have noted that Conodont fossils are common in all the Cambrian localities that have yielded pentastomids, and thus the conodonts (also long a mystery, but now widely regarded as parts of early fish-like vertebrates) might have been the original hosts of the pentastomids.

The Onychophora

As with pentastomids, onychophorans, too, were part of the amazing, early-Cambrian, explosive marine diversification. They have been found in Burgess Shale-type faunas at several localities, in Cambrian deposits from China and Siberia, and in the Swedish *Orsten* fauna (Xianguang & Weiguo, 1988; Xianguang & Junyuan, 1989; Ramsköld & Hou, 1991). And, we now know that Conway Morris's original reconstruction of *Hallucigenia* (from the Burgess Shale) had the animal turned upside-down. Ramsköld and Hou (1991) recently turned *Hallucigenia* over and found a second pair of legs, concluding it was an onychophoran with long dorsal spines. And there is now an onychophoran known from the Chengjiang deposits of China with side plates and spines (Ramsköld & Hou, 1991). *Aysheaia* (also from the Burgess Shale) was originally described by Walcott as an annelid, but it, too, is now regarded as an early marine onychophoran.

Conclusions

Let us now return to our two fundamental questions regarding arthropod evolution: Why are there so many arthropods, and what is the phylogenetic history of the arthropods? As to the first question, I propose six over-arching scenarios, each complex in its own right.

(1) The numerical superiority of arthropods is not a recent event. Recent fossil discoveries, and molecular clock data, inform us that arthropod diversification began very early in the history of the Metazoa, in the Precambrian, and by the Cambrian the arthropods were probably already the most speciose metazoan phylum on earth. Arthropods have been on a powerful phylogenetic trajectory for well over 600 MY. They have had a great deal of time to radiate, and with the exception of the trilobites and the eurypterids, all the major lineages have survived and continue to radiate.

(2) Their great size range, especially on the smaller end of the scale, adapts arthropods for a great variety of ecological niches. The Cambrian *Orsten* deposits tell us that a whole fauna of interstitial/meiofaunal arthropods already existed as early as the mid-Cambrian, and this habitat

has continued to be rich in adaptive radiation and specialized species ever since. Similar small-body-size niches are filled in a great many specialized environments today. We find high diversities of minute arthropods in habitats such as marine sediments, coral reefs, among the fronds of algae, on mosses and other primitive plants, and on the bodies of every kind of animal imaginable. There are even arthropod faunas that live strictly on the gills of other crustaceans (mites and small crustaceans). Small insects and mites have exploited virtually every terrestrial microhabitat available.

(3) The close relationship and coevolution with flowering plants (on land) and algae (in aquatic environments) have been a powerful force in the radiation of the arthropods. It is not just the insects that have been on a coevolutionary trajectory with plants—many crustaceans utilize algae as both a living substrate and a food source and show strong evidence of coevolution.

(4) The arthropods (insects) were the first flying animals, and the ability to fly led them into niches other invertebrates simply could not penetrate.

(5) Metamerism (the serially repeated body segments and appendages of arthropods) provides an enormous amount of easily manipulated body plan material upon which evolutionary processes can act. Given the great age, sheer diversity, and our emerging knowledge of regulatory genes in these animals, a high level of homoplasy is no longer surprising.

(6) The potential for major changes in body plans due to variations in homeobox genes, and the downstream genes they regulate, is just beginning to be realized, but this potential is clearly enormous. There seems little doubt that changes in homeotic genes over time have profoundly affected arthropod evolution. Considering the number and position of limbs in arthropods, and the flexibility of homeobox and regulatory switches, it is little wonder that arthropod anatomical diversity seems so endless.

As to the second question—what is the phylogenetic history of the Arthropods—it seems the plasticity of the arthropod body and homeobox gene expression may have produced an even higher level of homoplasy than once thought. As a result, some traditional morphological classifications are in conflict with molecular classifications. All the evidence suggests that the arthropods are monophyletic. However, fossil data, recent comparative neuroanatomical research, and molecular data all suggest that Crustacea are a paraphyletic group, and that the Crustacea and Insecta are very closely related to one another, but not to the Myriapoda. In fact, the insects appear to have arisen from within a crustacean stem line. Further, recent molecular and fossil data are beginning to suggest that the trilobites, chelicerates, insects, myriapods, and recent crustaceans *all* might have emerged from crustacean stem-line ancestors. This view of a paraphyletic Crustacea spinning off a series of other major arthropod lineages might explain why morphologists have been unable to come to agreement on the sister-group relationships of the major arthropod lineages. Resolution of this conflict will come, I predict, within the next two decades, with further understanding of the genetic regulation of developmental processes, examination of new nuclear and mitochondrial genes (and use of multiple gene data sets in phylogenetic analyses), and as more cladistic analyses include fossil species, particularly the growing series of Chengjiang, *Orsten*, and related arthropods.

A Speculation

The realization that insects might have arisen out of an ancestral crustacean stem line leads to many new implications concerning arthropod evolution. For example, given this scenario, one could search about among the Crustacea for a likely ancestor to the insects and in doing so recognize the presence of a "fixed" 19-segmented body plan in insects and certain crustaceans (or more likely a 20-segmented plan in each, Kukalová-Peck, 1991a, b; Scholtz et al., 1994; Scholtz, 1995). All insects are fixed on this body plan. Of all the crustacean higher taxa, this body plan consistently occurs only in the subclass Eumalacostraca—the crabs, shrimps, isopods, and their kin. Thus, if the insects did evolve from a crustacean ancestor, one might speculate that they could have evolved from a eumalacostracan. Examining the Eumalacostraca for a possible insect ancestry, there is only one group that is truly terrestrial, has evolved gas-exchange tracheae (granted, probably convergently to those of insects), has reduced/lost one pair of antennae (antennae one reduced in oniscideans, antennae two reduced in hexapods), and has strictly uniramous walking legs (as do the insects)—the terresttial isopods (Isopoda: Oniscidea). Could it be that insects are not only flying crustaceans, but flying isopods?

The concept of a Eumalacostraca–Insecta sister-group relationship finds strong support in the comparative anatomy of arthropod central nervous systems. Development of the compound eye follows

similar morphogenetic events in insects and eumalacostracans (Hafner & Tokarski, in press). In addition, the optic lobes of pterygote insects and eumalacostracans are distinguished by nested retinotopic neuropils, each of which represents the whole eye. In these two taxa, these neuropils comprise an anatomically distinct lamina, medulla, and lobula complex (Strausfeld, 1996). The presence of these structures in pterygote insects and eumalacostracans was viewed as a homology indicating a sister-group relationship between these taxa by Osorio and Bacon (1994) and Nilsson and Osorio (1997). Further, eumalacostracans that have so far been examined also possess a distinctive form of neuron, called a bushy T-cell, which was first recognized in insects on the basis of its characteristic dendritic "tree" situated near the inner face of the medulla (Strausfeld, 1976). Bushy T-cells in insects and eumalacostracan crustaceans send their axons to large tangential dendrites that extend across substantial areas of the retinotopic mosaic. In those pterygote orders investigated, bushy T-cells comprise part of an evolutionarily conserved subset of retinotopic elements that contribute to elementary motion detector circuits (Strausfeld & Lee, 1991; Douglass & Strausfeld, 1995, 1996). The presence of these cell types in eumalacostracan crustaceans and pterygote insects implies that either identical circuits have arisen independently in the two groups, or the circuit for motion detection evolved in a common ancestor to insects and crustaceans has been maintained basically unchanged throughout the history of both groups. That the latter is more likely is suggested by the presence of small field retinotopic neurons that arise from the inner layer of the medulla of the apterygote *Thermobia* and extend into the lateral lobe of the protocerebrum (Strausfeld, 1998).

All crustacean nervous systems so far examined possess the architectonic and positional equivalent of a fan-shaped body, the neurons of which extend laterally into the protocerebral lobes, as they do in insects (Strausfeld, 1998). However, except in isopods there is no evidence in Crustacea of other components of the central body complex seen in insects. Further, in pterygote insects and isopods (but not in decapods or apterygotes) the fan-shaped body is supplied by a bridge of neuropil that lies posteriorly in the brain and connects the left and right protocerebral hemispheres. Strausfeld (1998) concluded that, while fan-shaped bodies are synapomorphic to insects and crustaceans, the protocerebral bridge may have evolved independently in insects and isopods.

Many morphological features are in conflict with a close malacostracan-insect relationship, including differences in tagmata arrangement and locations of the gonopores. The fossil record also does not support an isopod + insect sister-group relationship. The oldest known isopod fossils are only 300 million years in age (Phreatoicidea: *Hesslerella*, Carboniferous) (Brusca & Wilson, 1991). However, a recent analysis of phreatoicidean phylogeny suggests the isopods might have had their origin considerably earlier than this (Wilson & Keable, in press), and further examination of this unconventional idea may be warranted.

Literature Cited

Abele, L., W. Kim & B. E. Felgenhauer. 1989. Molecular evidence for inclusion of the phylum Pentastomida in the Crustacea. Molec. Biol. Evol. 6: 685–691.

———, T. Spears, W. Kim & M. Applegate. 1992. Phylogeny of selected maxillopodan and other crustacean taxa based on 18S ribosomal nucleotide sequences: A preliminary analysis. Acta Zool. 73: 373–382.

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff & J. A. Lake. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. Nature 387: 489–493.

Almond, J. E. 1985. The Silurian–Devonian fossil record of the Myriapoda. Philos. Trans., Ser. B 309: 227–237.

Anderson, D. T. 1979. Embryos, fate maps, and the phylogeny of arthropods. Pp. 59–106 *in* A. P. Gupta (editor), Arthropod Phylogeny. Van Nostrand, New York.

———. 1996. Atlas of Invertebrate Anatomy. Univ. New South Wales Press, NSW, Australia.

Averof, M. & N. H. Patel. 1997. Crustacean appendage evolution associated with changes in Hox gene expression. Nature 388: 682–686.

Ayala, F. J., A. Rzhetsky & F. J. Ayala. 1998. Origin of the metazoan phyla: Molecular clocks confirm paleontological estimates. Proc. Natl. Acad. Sci. 95: 606–611.

Backeljau, T., B. Winnepenninckx & L. de Bruyn. 1993. Cladistic analysis of metazoan relationships: A reappraisal. Cladistics 9: 167–181.

Ballard, J. W. O., G. J. Olsen, D. P. Faith, W. A. Odgers, D. M. Rowell & P. W. Atkinson. 1992. Evidence from 12S ribosomal RNA sequences that onychophorans are modified arthropods. Science 258: 1345–1348.

Boore, J. L., T. M. Collins, D. Stanton, L. L. Daehler & W. M. Brown. 1995. Deducing the pattern of arthropod phylogeny from mitochondrial DNA rearrangements. Nature 376: 163–165.

Briggs, D. E. G. 1994. Giant predators from the Cambrian of China. Science 264: 1283–1284.

——— & R. A. Fortey. 1989. The early radiation and relationships of the major arthropod groups. Science 246: 241–243.

Brukmoser, P. 1965. Untersuchungen über den Kopfbau der Collembole *Orchesella villosa*. L. Zool. Jahrb. Anat. Ontog. 82: 299–364.

Brusca, R. C. & G. J. Brusca. 1990. Invertebrates. Sinauer Associates, Sunderland, Massachusetts.

——— & ———. Invertebrates, 2nd ed. Sinauer Associates, Sunderland, Massachusetts (in press).

——— & G. D. F. Wilson. 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations. Mem. Queensland Mus. 31: 143–204.

Carroll, S. B. 1995. Homeotic genes and the evolution of arthropods and chordates. Nature 376: 479–485.

Chen, J.-Y., L. Ramsköld & G.-Q. Zhou. 1994. Evidence for monophyly and arthropod affinity of Cambrian giant predators. Science 264: 1304–1308.

Davidson, E. H., K. J. Peterson & R. A. Cameron. 1995. Origin of bilaterian body plans: Evolution of developmental regulatory mechanisms. Science 270: 1319–1325.

Diaz-Benjumea, F. J., B. Cohen & S. M. Cohen. 1994. Cell interaction between compartments established the proximal-distal axis of *Drosophila* legs. Nature 372: 175–179.

Douglass, J. K. & N. J. Strausfeld. 1995. Visual motion detection circuits in flies: Peripheral motion computation by identified small field retinotopic neurons. J. Neurosci. 15: 5596–5611.

——— & N. J. Strausfeld. 1996. Visual motion detection circuits in flies: Parallel direction- and non-direction-sensitive pathways between the medulla and lobula plate. J. Neurosci. 16: 4551–4562.

Edwards, J. S. & M. R. Meyer. 1990. Conservation of antigen 3G6: a crystalline cone constituent in the compound eye of arthropods. J. Neurobiol. 21: 441–452.

Eernisse, D. S. 1997. Arthropod and annelid relationships re-examined. Pp. 43–56 *in* R. A. Fortey & R. H. Thomas (editors), Arthropod Relationships. Chapman & Hall, London.

———, J. S. Albert & F. E. Anderson. 1992. Annelida and Arthropoda are not sister taxa: A phylogenetic analysis of spiralian metazoan morphology. Syst. Biol. 41: 305–330.

Emerson, M. J. & F. R. Schram. 1997. Theories, patterns and reality: Game plan for arthropod phylogeny. Pp. 67–86 *in* R. A. Fortey & R. H. Thomas (editors), Arthropod Relationships. Chapman & Hall, London.

Field, K. G., A. J. Olsen, D. J. Lane, S. J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace & R. A. Raff. 1988. Molecular phylogeny of the animal kingdom. Science 239: 748–753.

———, J. M. Turbeville, R. A. Raff & B. A. Best. 1990. Evolutionary relationships of phylum Cnidaria inferred from 18S rRNA sequence data. Fourth Int. Congr. Syst. Evol. Biol. [Abstract].

Friedrich, M. & D. Tautz. 1995. Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. Nature 376: 165–166.

Funch, P. & R. M. Kristensen. 1997. Cycliophora. Pp. 409–474 *in* F. W. Harrison & E. E. Ruppert (editors), Microscopic Anatomy of Invertebrates. Vol. 13, Lophophorates, Entoprocta, and Cycliophora. Wiley-Liss, New York.

Garey, J. R., M. Krotec, D. R. Nelson & J. Brooks. 1996. Molecular analysis supports a tardigrade-arthropod association. Invertebrate Biol. 115(1): 79–88.

Greenslade, P. J. M. 1988. Reply to R. A. Crowson's 'Comments on Insecta of the Rhynie Chert' [1985 Entomol. Gener. 11: 097–098]. Entomol. Gener. 13: 115–117.

Hafner, G. S. & T. R. Tokarski. Morphogenesis and pattern formation in the retina of the crayfish *Procambarus clarkii*. Cell Tissue Res. (in press).

Hahn, G., R. Hahn & C. Brauckmann. 1986. Zur Kenntnis von *Arthropleura* (Myriapoda; Ober-Karbon). Geol. Palaeontol. 20: 125–137.

Halanych, K. M., J. D. Bacheller, A. M. A. Aguinaldo, S. M. Liva, D. M. Hillis & J. A. Lake. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. Science 267: 1641–1643.

Harzsch, S., K. Anger & R. R. Dewers. 1997. Immunocytochemcal detection of acetylated alpha-tubulin and *Drosophila* synapsis in the embryonic crustacean nervous system. Int. J. Developm. Biol. 41: 411–494.

Hillis, D. M. 1996. Inferring complex phylogenies. Nature 383: 130–131.

Jeram, A. J., P. A. Selden & D. Edwards. 1990. Land animals in the Silurian: Arachnids and myriapods from Shropshire, England. Science 250: 658–661.

Kukalová-Peck, J. 1990. Fossil history and the evolution of hexapod structures. *In* T. D. Naumann (editor), The Insects of Australia, 2nd ed. CSIRO and Melbourne Univ. Press, Melbourne.

———. 1991a. The "Uniramia" do not exist: The ground plan of the Pterygota as revealed by Permian Diaphanopteroidea from Russia (Insecta: Paleodictyopteroidea). Canad. J. Zool. 70: 236–255.

———. 1991b. Fossil history and the evolution of hexapod structures. Pp. 141–179 *in* I. D. Naumann (editor), The Insects of Australia, Vol. 1. Cornell Univ. Press, Ithaca, New York.

———. 1992. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). Canad. J. Zool. 65: 2327–2345.

——— & C. Brauckmann. 1990. Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany. Canad. J. Zool. 68: 1104–1111.

Labandeira, C., B. Beall & F. Hueber. 1988. Early insect diversification: Evidence from a lower Devonian bristletail from Quebec. Science 242: 913–916.

Lake, J. A. 1990. Origin of the Metazoa. Proc. Natl. Acad. Sci. U.S.A. 87: 763–766.

Lecointre, G., H. Philippe, H. L. Van Le & H. Le Guyader. 1993a. Species sampling has a major impact on phylogenetic inference. Molec. Phylogenetics & Evol. 2: 205–224.

———, ———, ——— & ———. 1993b. How many nucleotides are required to resolve a phylogenetic problem? The use of a new statistical method applicable to available sequences. Molec. Phylogenetics & Evol. 3: 292–309.

Li, C.-W., J.-Y. Chen & T.-E. Hua. 1998. Precambrian sponges with cellular structures. Science 279: 879–882.

Linnaeus, C. 1758. Systema Naturae. Regnum Animale, 10th ed., tomus I; Salvii, Hominae.

Manton, S. M. 1973. Arthropod phylogeny—A modern synthesis. J. Zool. 171: 111–130.

———. 1977. The Arthropoda. Oxford Univ. Press, Oxford.

——— & D. T. Anderson. 1979. Polyphyly and the evolution of arthropods. Pp. 269–321 *in* M. R. House (editor), The Origin of Major Invertebrate Groups. Systematics Assoc. Special Vol. No. 12. Academic Press, London.

McHugh, D. 1997. Molecular evidence that echiurans and pogonophorans are derived annelids. Proc. Natl. Acad. Sci. U.S.A. 94: 8006–8009.

Müller, K. J. 1983. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. Lethaia 16: 93–109.

———. 1992. Upper Cambrian "Orsten." Pp. 274–277 *in* D. E. G. Briggs & P. R. Crowther (editors), Palaeobiology. A Synthesis. Blackwell Sci. Publ., London.

——— & D. Walossek. 1985. A remarkable arthropod fauna from the Upper Cambrian "Orsten" of Sweden. Trans. Roy. Soc. Edinburgh, Earth Sci. 76: 161–172.
——— & ———. 1986. *Martinssonia elongata* gen. et sp. n., a crustacean-like euarthropod from Upper Cambrian "Orsten" of Sweden. Zool. Scripta 15: 73–92.
——— & ———. 1988. Arthropod larvae from the Upper Cambrian of Sweden. Trans. Roy. Soc. Edinburgh, Earth Sci. 77: 157–179.
———, ——— & A. Zakharov. 1995. "Orsten" type phosphatized soft-integument preservation and a new record from the Middle Cambrian Kuonamka Formation in Siberia. Neues Jahrb. Geol. Paläontol., Abh. 197: 101–118.
Nielsen, C., N. Scharff & D. Eibye-Jacobsen. 1996. Cladistic analyses of the animal kingdom. Biol. J. Linn. Soc. 57: 385–410.
Nilsson, D.-E. & D. Osorio. 1997. Homology and parallelism in arthropod sensory processing. Pp. 333–347 *in* R. A. Fortey & R. H. Thomas (editors), Arthropod Relationships. Chapman & Hall, London.
Osorio, D. & J. P. Bacon. 1994. A good eye for arthropod evolution. BioEssays 16: 419–424.
Panganiban, G., A. Sebring, L. Nagy & S. Carroll. 1995. The development of crustacean limbs and the evolution of arthropods. Science 270: 1363–1366.
———, S. M. Irvine, C. Lowe, H. Roehl, L. S. Corley, B. Sherbon, J. K. Grenier, J. F. Fallon, J. Kimble, M. Walker, G. A. Wray, B. J. Swalla, M. Q. Martindale & S. B. Carroll. 1997. The origin and evolution of animal appendages. Proc. Natl. Acad. Sci. U.S.A. 94: 5162–5166.
Patterson, C. 1989. Phylogenetic relationships of major groups: Conclusions and prospects. Pp. 471–488 *in* B. Fernholm, K. Bremer, & H. J. Jörnvall (editors), The Hierarchy of Life. Elsevier, Amsterdam.
Paulus, H. F. 1979. Eye structure and the monophyly of the Arthropoda. Pp. 299–383 *in* A. P. Gupta (editor), Comparative Insect Morphology and Arthropod Phylogeny. Van Nostrand Reinhold, New York.
Peer, Y. J. van der, M. Neefs, P. De Rijk & R. De Wachter. 1993. Reconstructing evolution from eukaryotic small-ribosomal-subunit RNA sequences: Calibration of the molecular clock. J. Molec. Evol. 37: 221–232.
Popadic, A., D. Rusch, M. Peterson, B. T. Rogers & T. C. Kaufman. 1996. Origin of the arthropod mandible. Nature 380: 395.
Ramsköld, L. & X. Hou. 1991. New early Cambrian animal and onychophoran affinities for enigmatic metazoa. Nature 351: 225–228.
Regier, J. C. & J. W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis of the origin of hexapods. Molec. Biol. Evol. 14: 902–913.
Robison, R. A. 1990. Earliest known uniramous arthropod. Nature 343: 163.
Sanderson, M. J. 1996. How many taxa must be sampled to identify the root node of a large clade? Syst. Biol. 45: 168–173.
Scholtz, G., N. H. Patel & W. Dohle. 1994. Serially homologous engrailed stripes are generated via different cell lineages in the germ band of amphipod crustaceans. Int. J. Dev. Biol. 38: 471–478.
———. 1995. Head segmentation in Crustacea—an immuno cytochemical study. Zoology 98: 104–114.
Schram, F. R. 1991. Cladistic analysis of metazoan phyla and the placement of fossil problematica. Pp. 35–46 *in* A. M. Simonetta & S. Conway Morris (editors), The Early Evolution of the Metazoa and the Significance of Problematic Taxa. Cambridge Univ. Press, Cambridge.
Seilacher, A., P. K. Bose & F. Pflüger. 1998. Triploblastic animals more than 1 billion years ago: Trace fossil evidence from India. Science 282: 80–83.
Sharov, A. G. 1953. Razvitiye shchetinokhvostok (Thysanura, Apterygota) v svyzi s problemoi filogenii nasekomykh [Development of bristletails in connection with the problem of insect phylogeny]. Trudy Inst. Morf. Zhizot. 8: 63–127.
Shear, W. A., P. M. Bonamo, J. D. Grierson, W. D. I. Rolfe, E. L. Smith & R. A. Norton. 1984. Early land animals in North America. Evidence from Devonian age arthropods from Gilboa, New York. Science 224: 492–494.
———, P. A. Selden, W. D. I. Rolfe, P. M. Bonamo & J. D. Grierson. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). Amer. Mus. Novit. 2901: 1–74.
Shubin, N., C. Tabin & S. Carroll. 1997. Fossils, genes and the evolution of animal limbs. Nature 388: 639–648.
Snodgrass, R. E. 1938. Evolution of the Annelida, Onychophora and Arthropoda. Smithsonian Misc. Collect. 97: 1–159.
Spears, T. & L. G. Abele. 1997. Crustacean phylogeny inferred from 18S rDNA. Pp. 169–187 *in* R. A. Fortey & R. H. Thomas (editors), Arthropod Relationships. Chapman & Hall, London.
Storch, V. 1984. 37. Pentastomida. Pp. 709–713 *in* J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards (editors), Biology of the Integument. 1, Invertebrates. Springer, Berlin.
——— & B. G. M. Jamieson. 1992. Further spermatological evidence for including the Pentastomida (tongue worms) in the Crustacea. Int. J. Parasitology 22: 95–103.
Størmer, L. 1969. Oldest known terrestrial arachnids. Science 164: 1276–1277.
———. 1977. Arthropod invasion during late Silurian and Devonian times. Science 197: 1362–1364.
Strausfeld, N. J. 1976. Atlas of an Insect Brain. Springer, Heidelberg.
———. 1996. Oculomotor control in flies: From muscles to elementary motion detectors. Pp. 277–284 *in* P. S. G. Stein & D. Stuart (editors), Neurons, Networks, and Motor Behavior. Oxford Univ. Press, Oxford.
———. 1998. Crustacean-insect relationships: The use of brain characters to derive phylogeny amongst segmented invertebrates. Brain, Behavior, Evol. 52: 186–206.
———, E. K. Bushbeck & R. S. Gomez. 1995. The arthropod mushroom body: Its roles, evolutionary enigmas and mistaken identities. Pp. 349–381 *in* O. Breidbach & W. Kutsch (editors), The Nervous Systems of Invertebrates: An Evolutionary and Comparative Approach. Birkhäuser Verlag, Basel.
——— & J.-K. Lee. 1991. Neuronal basis for parallel visual processing in the fly. Visual Neurosci. 7: 13–33.
Therianos, S., S. Leuzinger, F. Hirth, C. S. Goodman & H. Reichert. 1995. Embryonic development of the *Drosophila* brain: Formation of commissural and descending pathways. Development 121: 3849–3860.
Thomas, J. B., M. J. Bastiani & C. S. Goodman. 1984. From grasshopper to *Drosophila*: A common plan for neuronal development. Nature 310: 203–207.
Turbeville, J. M., D. M. Pfeifer, K. G. Field & R. A. Raff.

1991. The phylogenetic status of arthropods, as inferred from 18S rRNA sequences. Molec. Biol. Evol. 8: 669–686.

Waggoner, B. M. 1996. Phylogenetic hypotheses of the relationships of arthropods to Precambrian and Cambrian problematic fossil taxa. Syst. Biol. 45: 190–222.

Walossek, D. & K. J. Müller. 1992. The "Alum Shale Window"—Contribution of "Orsten" arthropods to the phylogeny of Crustacea. Acta Zool. 73: 305–312.

——— & ———. 1994. Pentastomid parasites from the Lower Palaeozoic of Sweden. Trans. Roy. Soc. Edinburgh, Earth Sci. 85: 1–37.

——— & ———. 1997. Cambrian "Orsten"-type arthropods and the phylogeny of Crustacea. Pp. 139–153 *in* R. A. Fortey & R. H. Thomas (editors), Arthropod Relationships. Systematics Assoc. Special Vol. 55. Chapman & Hall, London.

Wheeler, W. C., P. Cartwright & C. Y. Hayashi. 1993. Arthropod phylogeny: A combined approach. Cladistics 9: 1–39.

Whitington, P. M., T. Meier & P. King. 1991. Segmentation, neurogenesis and formation of early axonal pathways in the centipede *Ethmostigmus rubripes* (Brandt). Roux's Arch. Developmental Biol. 199: 349–363.

———, D. Leach & R. Sandeman. 1993. Evolutionary change in neural development within the arthropods: Axonogensis in the embryos of two crustaceans. Development 118: 449–461.

Williams, T. A. & L. M. Nagy. 1995. Brine shrimp add salt to the stew. Curr. Biol. 5: 1330–1333.

Wills, M. A., D. E. Briggs & R. A. Fortey. 1994. Disparity as an evolutionary index: A comparison of Cambrian and Recent arthropods. Paleobiology 20: 93–130.

———, ———, ——— & M. Wilkinson. 1995. The significance of fossils in understanding arthropod evolution. Verh. Deutsch. Zool. Ges. 88: 203–215.

Wilson, G. D. F. & S. Keable. A phylogenetic analysis of the isopod suborder Phreatoicidea. *In:* R. C. Brusca & B. Kensley, Proceedings of the Second Int. Isopod Conference, Amsterdam, 1998. Crustacean Issues, Balkema, Rotterdam (in press).

Wingstrand, K. G. 1972. Comparative spermatology of a pentastomid, *Raillietiella hemidactyli*, and a branchiuran crustacean, *Argulus foliaceus*, with a discussion of pentastomid relationships. Kongel. Danske Vidensk. Selsk. Biol.-Skr. 19: 1–72.

———. 1978. Comparative spermatology of the Crustacea Entomostraca. I. Subclass Branchiopoda. Kongel. Danske Vidensk. Selsk. Biol.-Skr. 22: 1–66.

Winnepenninckx, B., T. Backeljau, L. Y. Mackey, J. M. Brooks, R. de Wachter, S. Kumar & J. R. Garey. 1995. 18s rRNA data indicate that Aschelminthes are polyphyletic in origin and consist of at least three distinct clades. Molec. Biol. & Evol. 12: 1132–1137.

———, ———, Y. Van de Peer & R. De Wachter. 1992. Structure of the small ribosomal subunit RNA of the pulmonate snail *Lunicolaria kambeul*, and phylogenetic analysis of the Metazoa. Federation of European Biochemical Societies 309: 123–126.

Wray, G. A., J. S. Levinton & L. H. Shapiro. 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. Science 274: 568–573.

Xianguang, H. & S. Weiguo. 1988. Discovery of Chengjiang fauna at Meichucun, Jinning, Yunnan. Acta Palaeontol. Sin. 27: 1–12.

——— & C. Junyuan. 1989. Early Cambrian arthropod-annelid intermediate sea animal, gen. nov. from Chengjiang, Yunnan. Acta Palaeontol. Sin. 28: 207–213.