Ward C. Wheeler

Gonzalo Giribet

Gregory D. Edgecombe

Arthropod Systematics

The Comparative Study of Genomic, Anatomical, and Paleontological Information

Arthropods are perhaps the most diverse creatures on Earth, with the number of known species approaching one million, and perhaps 10 times as many left to discover. Comprised today of Hexapoda (insects and relatives), Myriapoda (centipedes, millipedes, and allies), Crustacea (shrimps, crabs, lobsters, crayfish, barnacles, etc.), and Chelicerata (arachnids, horseshoe crabs, and sea spiders), the arthropods vary over four orders of magnitude in size (from <1 mm mites and parasitic wasps to >4 m spider crabs), are herbivores and carnivores, free-living and parasitic (endo and ecto), and solitary and social, and constitute the great majority of animal biomass. Arthropods are ubiquitous. They are found on all continents, the deepest oceans, and highest mountains. Extinct groups include trilobites, marrellomorphs, anomalocaridids, and euthycarcinoids, some of which may well be equal in taxonomic status to those we know today.

As members of the triploblastic Metazoa, arthropods are characterized by a segmented, hardened, chitinous cuticular exoskeleton and paired, jointed appendages. This exoskeleton is composed of a series of dorsal, ventral, and lateral plates that undergoes molting (ecdysis), sometimes periodically. Primitively, arthropods share a compound eye with a subunit structure that is unique within the animal kingdom.

The geological history of arthropods extends back over 520 million years (to the Lower Cambrian) with extinct lineages of great diversity (e.g., trilobites). This history has undergone several dramatic rounds of extinction and diversification, most prominently in the Paleozoic Era near the end of the Ordovician Period and at the Permian-Triassic boundary. The Cambrian and Ordovician body fossil record of arthropods is exclusively marine, but terrestrial forms (including arachnids, millipedes, and centipedes) appear from the Upper Silurian, more than 400 million years ago.

Relatives

The closest relatives of the arthropods are the enigmatic water bears (Tardigrada) and velvet worms (Onychophora). All of these animals share paired appendages and a chitinous cuticle. There are approximately 800 species of tardigrades that live in marine, freshwater, and terrestrial habitats. Marine tardigrades are an important component of the meiofauna, crawling between sand grains. Terrestrial tardigrades are mostly found on mosses and bryophytes and may occur in huge densities (hundreds of thousands to millions per square meter). Tardigrades are small (between 150 and 1000 μm); have a round mouth and four pairs of legs, the last one being terminal; and, like arthropods and a few other phyla, grow by molting. Terrestrial tardigrades can live in extreme environments, surviving desiccation or freezing by entering into cryptobiosis. The cryptobiotic stage has been recorded to last more than 100 years, and in this stage they can be dispersed by wind. The Onychophora are a group of exclusively terrestrial, predatory creatures that live in humid temperate (mostly southern hemisphere) and tropical forests of

America, Southern Africa, Australia, and New Zealand. The velvet worms are characterized by a soft body with pairs of "lobopod" walking limbs, a pair of annulated antennae, jaws, and oral ("slime") papillae. About 150 extant species have been named, but there were many more types including marine "armored" or plated lobopods in the Early Paleozoic. Onychophorans and arthropods share a dorsal heart with segmental openings (ostia) and a unique structure of the nephridia, the excretory organs. Lack of these organs in tardigrades may be due to miniaturization. It is thought that Tardigrada is the sister taxon of Arthropoda and Onychophora, the next closest relative (Giribet et al. 1996, 2001).

It has been long thought that there was an evolutionary progression from wormlike creatures, to lobopodous forms like Onychophora, to modern arthropods. This was expressed in the "Articulata" hypothesis that linked annelid worms (polychaetes and oligochaetes, including leeches) to Onychophora and Arthropoda. Recent work, especially from DNA sequences, has largely replaced this view, instead allying arthropods, tardigrades, and onychophorans with other molting creatures such as the nematodes, kinorhynchs, and priapulids in Ecdysozoa (after ecdysis or molting; Aguinaldo et al. 1997, Giribet and Ribera 1998, Schmidt-Rhaesa et al. 1998), and uniting the annelids with mollusks, nemerteans, sipunculans, and entoprocts in Trochozoa (Eernisse et al. 1992, Halanych et al. 1995, Giribet et al. 2000).

Extant Groups

The major extant arthropod groups are discussed in separate chapters and so are only briefly discussed here.

Hexapoda

The insects are by far the most diverse known arthropod group (but mites might come close), with hundreds of thousands of species known to science. Hexapods are characterized by possession of three body tagma (head, thorax, abdomen), the second of which possesses three limb-bearing segments. Insecta comprise most of the diversity within Hexapoda, insects being those hexapods with an antenna developed as a flagellum without muscles between segments. The hexapod head (like that of crustaceans and myriapods) has a large, generally robust mandible used for food maceration, a single pair of sensory antennae, and both compound and simple eyes. There are 30 commonly recognized hexapod "orders" further organized into several higher groups: Entognatha (those with internal mouthparts)—Protura, Diplura, and Collembola (springtails); Archaeognatha (bristletails); Zygentoma (silverfish); Ephemerida (mayflies), Odonata (damselflies and dragonflies); orthopteroids—Plecoptera (stoneflies), Embiidina (web spinners), Dermaptera (earwigs), Grylloblattaria (ice insects), Phasmida (walking sticks), Orthoptera (crickets, grasshoppers), Zoraptera, Isoptera (termites), Man-todea (praying mantises), Blattaria (roaches), Mantophasmatodea; hemipteroids—Hemiptera (true bugs and hoppers), Thysanoptera (thrips), Psocoptera, Pthiraptera (lice); and the Holometabola—Coleoptera (beetles), Neuroptera (lacewings, dobsonflies, snakeflies), Hymenoptera (bees, ants, wasps), Trichoptera, Lepidoptera (moths and butterflies), Siphonaptera (fleas), Mecoptera (snow fleas), Strepsiptera, and Diptera (flies). Basal hexapods (Protura, Collembola, Diplura, Archaeognatha, and Zygentoma) are wingless, whereas the more derived insect orders generally possess two pairs of wings. Members of Neoptera (Pterygota—winged insects except for the "paleopteran" ephemerids and odonates) possess wing hinge structures that allow folding their wings back over their abdomen. Those insects with complex development, Holometabola, are the most diverse, with beetles leading the way with more than 300,000 recognized species. Insects are found over the world in terrestrial and freshwater habitats, and many have economic importance as pests or medical interest for causing or carrying disease. An extensive fossil record of hexapods commences with the Devonian collembolan *Rhyniella* (Whalley and Jarzembowski 1981), through other Paleozoic and Mesozoic deposits, to the dramatic and beautiful amber-preserved insects from Lebanon, the Baltic, and the Dominican Republic (Carpenter 1992, Grimaldi 2001).

Myriapoda

The centipedes, millipedes, symphylans, and pauropods are multilegged, mostly soil-adapted creatures. Generally without compound eyes (except for scutigeromorph centipedes) but possessing a single pair of sensory antennae, the myriapods are most easily recognized by their large numbers of legs and the trunk not being differentiated into distinct tagmata. Almost all postcephalic segments bear a single (centipedes, pauropods, symphylans) or double (millipedes) pair of legs, numbering into the hundreds in some taxa. These arthropods are generally small (<5–10 cm), but there are several dramatically larger examples (*Scolopendra gigantea* at 30 cm). There are four main lineages of myriapods: Diplopoda (millipedes), Chilopoda (centipedes), Pauropoda, and Symphyla. The basic division among myriapods lies between Chilopoda, whose members have the genital opening at the posterior end of the body, and the other three lineages, grouped as Progoneata on the basis of the genital opening being located anteriorly on the trunk, behind the second pair of legs (Dohle 1998). The millipedes are by far the most diverse group, with approximately 11,000 described species. The chilopods are the other diverse group (~2,800 known species). Pauropods and symphylans are less speciose, with a few hundred described taxa. In general, myriapods are soil creatures feeding on detritus, with the centipedes exclusively predatory and possessing a modified fang and the ability to deliver toxins to their prey. It is probable, but far from universally agreed, that the myriapods share a single common

ancestor (Edgecombe and Giribet 2002). The movement and connections of the head endoskeleton (the tentorium), structure and musculature of the mandible, and most DNA sequence evidence support the single origin of Myriapoda, but several hypotheses place myriapod lineages with hexapods (Kraus 1998). There are few well preserved myriapod fossils, but the extant chilopod order Scutigeromorpha and the diplopod group Chilognatha both have fossil representatives from the Late Silurian (Almond 1985, Shear et al. 1998). The extinct group Arthropleurida, thought to be members of Diplopoda (Wilson and Shear 2000), may have reached 2 m in length.

Crustacea

Crustaceans are perhaps the most morphologically diverse group of arthropods (>30,000 species known), with huge variation in numbers and morphology of appendages, body organization (tagmosis), mode of development, and size (<1 mm to >4 m). These creatures are generally characterized by having two pairs of antennae (first and second), biramous (branched) appendages, and a specialized swimming larval stage (nauplius). They usually possess both simple ("naupliar") and compound eyes (the latter frequently stalked). Like myriapods and hexapods, crustaceans possess strongly sclerotized mandibles that are distinguished by frequently having a segmented palp. The Crustacea are generally marine, with several freshwater and terrestrial groups (e.g., some isopods, the woodlice). Crustacean phylogeny is an area of active debate with the status of some long-recognized groups under discussion (see Schram and Koenemann, ch. 19 in this vol.). Currently, several higher groups are recognized (Martin and Davis 2001) with their interrelationships (and even interdigitiation) unclear: Remipedia (12 species; *Speleonectes*, *Lasionectes*, and three other genera), Cephalocarida (few species; *Hutchinsoniella* and three other genera), Branchiopoda (1000 species; fairy shrimp, water fleas, tadpole shrimp, clam shrimp), Maxillopoda (10,000 species; copepods, barnacles, ostracods, fish lice), and Malacostraca (20,000 species; mantis shrimp, crayfish, lobsters, crabs, isopods, amphipods). Many of the debates on crustacean relationships center on the position of the recently discovered remipedes as either the most basal lineage resembling, in some respects, the first Crustacea, or a more derived position having little to do with crustacean origins. The fossil group Phosphatocopina is probably the earliest Crustacea or the closest relative of the extant Crustacea (Walossek 1999), first occurring in the Lower Cambrian in England and being known from fine preservational quality, notably in the three-dimensional Orsten Cambrian fauna (Müller 1979).

Chelicerata

The sea spiders, horseshoe crabs, and arachnids are characterized by division of body segments into two tagmata: pro-soma and opisthosoma (generally), and the first leg-bearing head segment being modified into chelifores or chelicerae. With the exception of horseshoe crabs (the American *Limulus* and the Asian *Carcinoscorpius* and *Tachypleus*), extant chelicerates do not possess compound eyes, and none have antennae. Horseshoe crabs and arachnids have one pair of median eyes, whereas sea spiders have a second pair. Of the three main divisions of chelicerates [Pycnogonida—sea spiders (1000 species), Xiphosura—horseshoe crabs (four species), and Arachnida—spiders, scorpions, etc. (92,000 species)], the sea spiders and horseshoe crabs are marine and arachnids are terrestrial, with the exception of some groups of mites. Many groups of Acari (mites and ticks) are parasites of plants and animals, both vertebrates and invertebrates, and being ecto- and endoparasitic, mostly of respiratory organs. The arachnids are the most diverse component of the Chelicerata, with the Acari and Araneae (spiders) constituting the vast majority of taxa. Other arachnid groups include Opiliones (harvestmen, daddy longlegs), Scorpiones (scorpions), Solifugae (sun, camel, or wind spiders), Pseudoscorpiones ("false" scorpions), Ricinulei, Palpigradi (micro-whip scorpions), Amblypygi (tailless whip scorpions or whip spiders), Uropygi (vinegaroons), and Schizomida. The Paleozoic eurypterids are an aquatic (mostly brackish water) group, generally considered to be the closest relatives of Arachnida, although some workers consider them especially related to scorpions (see Dunlop and Braddy 2001 for a discussion of the evidence). The largest eurypterids are 1.8 m long, among the largest arthropods ever. The sea spiders graze on corals, anemones, or seaweeds and vary in size from quite small (<1 cm) to almost a meter in leg span. Horseshoe crabs and arachnids are almost entirely predatory, with spiders the dominant arthropod predators in many environments. Horseshoe crabs scavenge and prey on small animals in seaweeds, and like the Opiliones, they digest their food internally. Most arachnids, however, digest food extraorally, ingesting their prey in the form of digested fluids.

Fossil History and Extinct Lineages

No doubt there are more extinct lineages of arthropods than extant. More likely than not, most will remain unknown to science, but several major groups we do know about have a great effect on our notions of higher level relationships among the arthropods (living and extinct). Trilobites are among the best-known group of extinct arthropods. First known from the Lower Cambrian, trilobites had huge radiations in the Paleozoic. Trilobites were an exclusively marine group (10,000 species described) characterized by two longitudinal furrows dividing the body into three lobes (hence the name). The body segments are organized into three tagmata (cephalon, thorax, pygidium). Trilobites possessed compound eyes and a single pair of antennae and had biramous appendages. All post-antennal appendages in trilobites are

basically similar in structure (Whittington 1975). The imbricated lamellar setae in the exopods suggest that trilobites are closely related to the Chelicerata (being similar to the book gills of Xiphosura and Eurypterida), together with numerous other extinct lineages constituting the group Arachnata. Anomalocaridids or Dinocarida: Radiodonta are a group of large (up to 2 m), predatory Cambrian arthropod relatives. With unmineralized but sclerotized cuticle, they were known initially only by their raptorial feeding/grasping appendages that were anterior to a circular mouth that was surrounded by a ring of plates (Collins 1996). Their phylogenetic affinities are uncertain, but most recent work places them in the stem group of Arthropoda (Budd 2002), probably more closely related to extant arthropods than are tardigrades (Dewel et al. 1999). Marrellomorphs comprise a clade known from the Burgess Shale (Middle Cambrian, Canada) and Hunsrück Slate (Lower Devonian, Germany) that possess two pairs of antenniform limbs and two pairs of long spines that curve back over the body. Marrella is the most abundant arthropod in the Burgess Shale fauna (Whittington 1971). Euthycarcinoids are an enigmatic group that ranges from the Ordovician or Lower Silurian to the Middle Triassic, having potential affinities with myriapods or crustaceans (Edgecombe and Morgan 1999). They possessed a single pair of antennae and numerous pairs of uniramous legs. A diversity of lobopodian taxa has recently come to light via soft-part-preserved specimens, mainly from the Lower Cambrian of China. The marine lobopodians are thought to be related to living terrestrial Onychophora or Tardigrada, or some may be positioned higher on the arthropod stem group. Several of the Cambrian lobopodians possessed elaborate spines and armored plates (Ramsköld and Chen 1998). The "Orsten" fauna of Sweden contains amazingly well-preserved, three-dimensional Upper Cambrian fossils, most importantly of basal crustacean-like taxa (Walossek and Müller 1998). Several of these forms (e.g., Martinssonia) are important to understanding the origins and relationships of Crustacea. Among the most productive Paleozoic fossil deposits are the Burgess Shale, Chengjiang and Orsten (Cambrian), Rhynie Chert and Gilboa (Devonian), and Mazon Creek (Carboniferous) deposits.

The Relationships of the Arthropod "Classes"

The question of arthropod relationships has been and is still unsettled, despite the large effort invested by researchers. Excellent literature sources and reviews on many issues about arthropod relationships can be found in the recent volumes edited by Edgecombe (1998), Fortey and Thomas (1998), and Melic et al. (1999). These volumes complement the classical treatises by Snodgrass (1938), Boudreaux (1979), and Gupta (1979).

Of the living taxa (Chelicerata, Crustacea, Myriapoda, Hexapoda), it seems clear that those groups that possess mandibles (robust, sclerotized, chewing mouthparts), the clade Mandibulata: Crustacea, Myriapoda, and Hexapoda, share a unique common ancestor (fig. 17.1). The biting edge of mandibles is formed by the same segment, the coxa, of the same limb (third limb-bearing segment in Crustacea), with a distinctive expression pattern of the Distal-less gene (Popadić et al. 1998, Scholtz et al. 1998). Within this group, things become less clear. There are two main competing hypotheses: Tracheata or Atelocerata (myriapods and insects) versus Tetraconata or Pancrustacea (crustaceans and insects). The Tracheata hypothesis is supported by some anatomical evidence, notably the similar tentorial head endoskeleton, an absence of limbs on the head segment (intercalary segment) innervated by the third brain ganglia, and similar respiratory and excretory organs (Klass and Kristensen 2001). Molecular sequence data and an alternative set of anatomical features, notably ommatidium structure, the optic neuropils, and neurogenesis, support the Tetraconata hypothesis (Dohle 2001).

This is a somewhat simplistic view of arthropod relationships that assumes that the four main classes are each monophyletic. However, pycnogonids may challenge this premise, and recent studies have shown them as the putative sister group to all remaining arthropods (Zrzavý et al. 1998, Giribet et al. 2001), in part supported by the presence of a terminal mouth as in many other non-arthropod ecdysozoans (Schmidt-Rhaesa et al. 1998) and absence of arthropod-type nephridia and intersegmental tendons. Fossil pycnogonids demonstrate their presence as far back as the Cambrian (Waloszek and Dunlop 2002). Also, many proponents of the Tracheata hypothesis supported myriapod paraphyly (Snodgrass 1938, Tiegs 1947, Dohle 1965). Paraphyly or polyphyly of crustaceans has also been proposed (Moura and Christoffersen 1996).

Mandibulata is supported by most molecular and total evidence analyses (Wheeler et al. 1993, Giribet and Ribera 1998, Wheeler 1998a, 1998b, Zrzavý et al. 1998, Edgecombe et al. 2000, Giribet et al. 2001). Alternatives to the clade Mandibulata have also appeared based on molecular sequence data analyses (Turbeville et al. 1991, Friedrich and Tautz 1995, Giribet et al. 1996, Hwang et al. 2001), although this seems to be an artifact of deficient taxonomic sampling because most other molecular analyses support Mandibulata (Regier and Shultz 1997, 1998). A second molecular alternative places Chelicerata as sister to Tetraconata (Regier and Shultz 2001, Shultz and Regier 1999), but again this result seems to be a bias toward particular genes.

Although relationships within Mandibulata are debated, molecular data from all sources tend to agree that crustaceans and insects form a monophyletic group, with the exception of some total evidence analyses (Wheeler et al. 1993, Wheeler 1998b, Edgecombe et al. 2000), but not from the most recent one including eight genes and morphology (Giribet et al. 2001).

The addition of fossil arthropods to the phylogenetic mix has rendered a strikingly different view from that of mor-
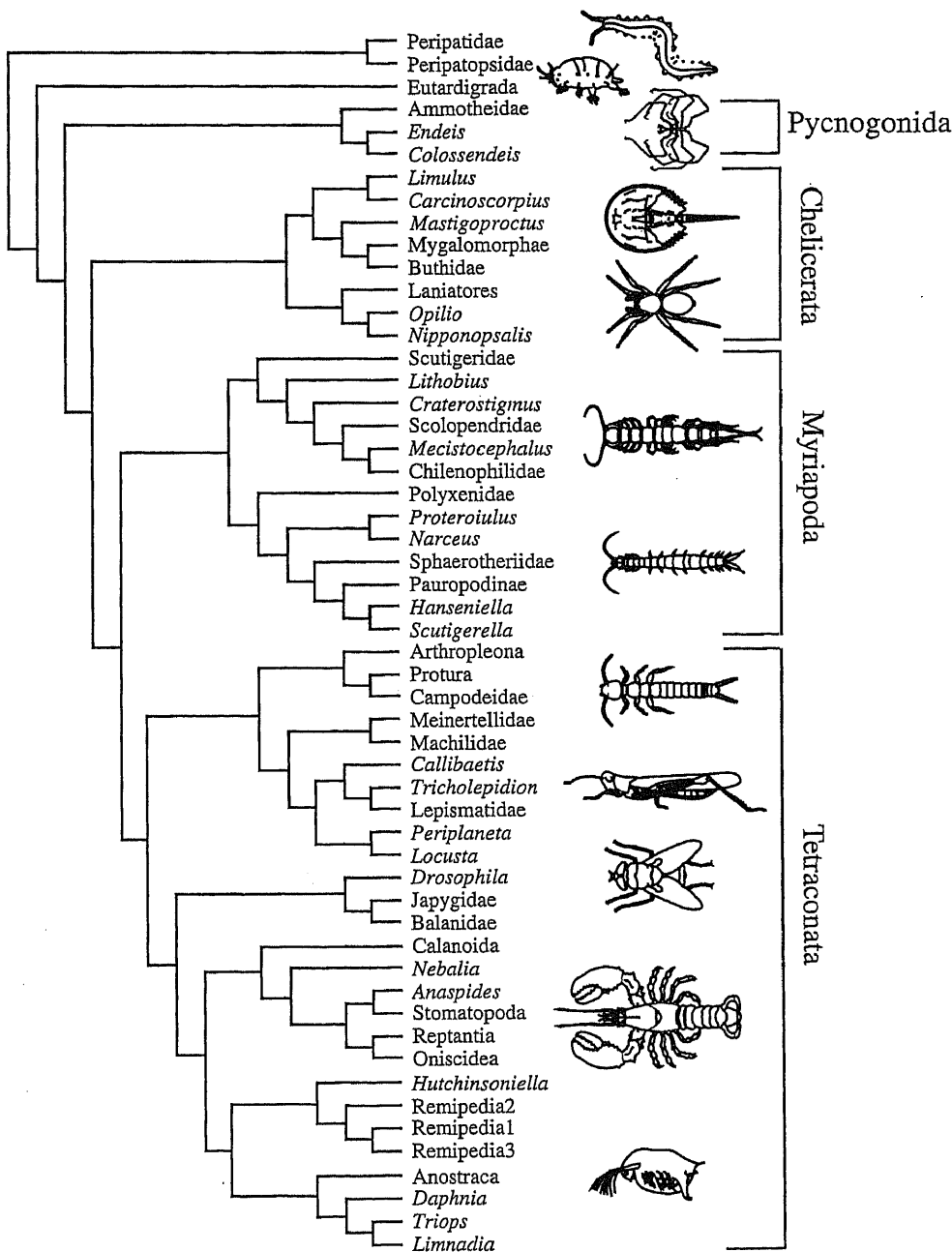
Figure 17.1. Cladogram of extant arthropod relationships, after Giribet et al. (2001).

phologists and molecular biologists, notably a hypothesis uniting all arthropods with biramous appendages in a clade named Schizoramia (Cisne 1974, Briggs et al. 1992, Budd 1996, Wills et al. 1998). Schizoramia contains the extant crustaceans and chelicerates, as well as many extinct lineages, including trilobites.

Monophyly versus Polyphyly

Arthropods were considered to be monophyletic since the 19th century (Siebold and Stannius 1848, Haeckel 1866) and were treated as such by most zoologists until the mid 20th century (Snodgrass 1938). A diphyletic current then ap-

peared, grouping the myriapods and hexapods together with the velvet worms to form Uniramia, versus Trilobita, Crustacea, and Chelicerata (Tiegs 1947, Tiegs and Manton 1958; named TCC by Cisne 1974). The diphyletic theory relied upon functional morphology arguments, based on the idea that the synapomorphies defining arthropods, such as the presence of a chitinous exoskeleton with jointed appendages and the presence of compound eyes, were convergences due to a similar mode of life.

The diphyletic theory further evolved into a polyphyletic theory in which the only previous taxon to be maintained was Uniramia. This was proposed by Manton (1964, 1973, 1977, 1979) and Anderson (1973, 1979). Manton proposed

that the mandibles of crustaceans were not homologous to those of insects and myriapods, although she did not indicate an explicit relationship for the crustaceans or chelicerates. Anderson (1979) used embryonic fate maps to suggest a close relationship among annelids, onychophorans, and atelocerates (insects and myriapods). Subsequently, Schram (1978) joined the polyphyletists and used fate maps to endorse a relationship between pycnogonids and chelicerates.

The arguments in defense of arthropod polyphyly were not based on phylogenetic thinking or identifying alternative sister groups to different arthropod clades and were refuted by morphological (e.g., Weygoldt 1986, Kukalová-Peck 1992, 1998, Shear 1992, Wägele 1993), developmental (e.g., Weygoldt 1979, Panganiban et al. 1995, Popadić et al. 1996, 1998, Scholtz et al. 1998, Abzhanov and Kaufman 1999), and molecular (e.g., Wheeler et al. 1993, Edgecombe et al. 2000, Giribet et al. 2001) evidence. Also recently, homeobox genes have suggested homology between the chelicerae and the antennae of myriapods and insects and the first antennae of crustaceans (Damen et al. 1998, Telford and Thomas 1998, Abzhanov et al. 1999, Mittmann and Scholtz 2001). The only recent defenses of arthropod polyphyly (Fryer 1996, 1998) have resorted to imaginary worms rather than real taxa to force arthropod non-monophyly.

Schizoramia versus Mandibulata

With the issue of arthropod monophyly settled, arguments about the relationships among the main arthropod lineages grew, especially in relation to Schizoramia versus Mandi-

bulata. The TCC (Tiegs 1947, Cisne 1974) concept groups extinct trilobites and allied "trilobitomorophs" with extant chelicerates and crustaceans based on the primitive biramous nature of their appendages (Hessler and Newman 1975, Briggs and Fortey 1989, Bergström 1992, Briggs et al. 1992, Wills et al. 1995, 1998). This hypothesis, however, does not find support in molecular analyses, but this is not unexpected because TCC is based on the combinations of character states found in the extinct fauna. The Schizoramia concept obviously conflicts with Mandibulata (fig. 17.2), which finds support in morphological and molecular analyses (see discussion above).

Tracheata versus Tetraconata

Another major issue in arthropod systematics is the relative position of the mandibulate taxa. Classically, myriapods and insects were grouped together in Tracheata (or Atelocerata; Snodgrass 1938, 1950, 1951, Wägele 1993, Kraus and Kraus 1994, 1996, Kraus 1998, 2001, Wheeler 1998a, 1998b) based on morphological evidence (see discussion above). The addition of molecular data to study arthropod relationships, however, suggested an alternate relationship of crustaceans and hexapods (Boore et al. 1995, 1998, Friedrich and Tautz 1995, Giribet et al. 1996, 2001, Regier and Shultz 1997, 1998, Giribet and Ribera 1998), originally named Pancrustacea (Zrzavý et al. 1998) and later on formalized as Tetraconata (Dohle 2001) in reference to the ommatidium structure (four-part crystalline cone) shared by crustaceans and insects.

Figure 17.2. Signal synapomorphies for Mandibulata (mandible, shown for the chilopod *Ethmostigmus*) versus Schizoramia (biramous appendages, shown for the cephalocarid *Hutchinsoniella*).
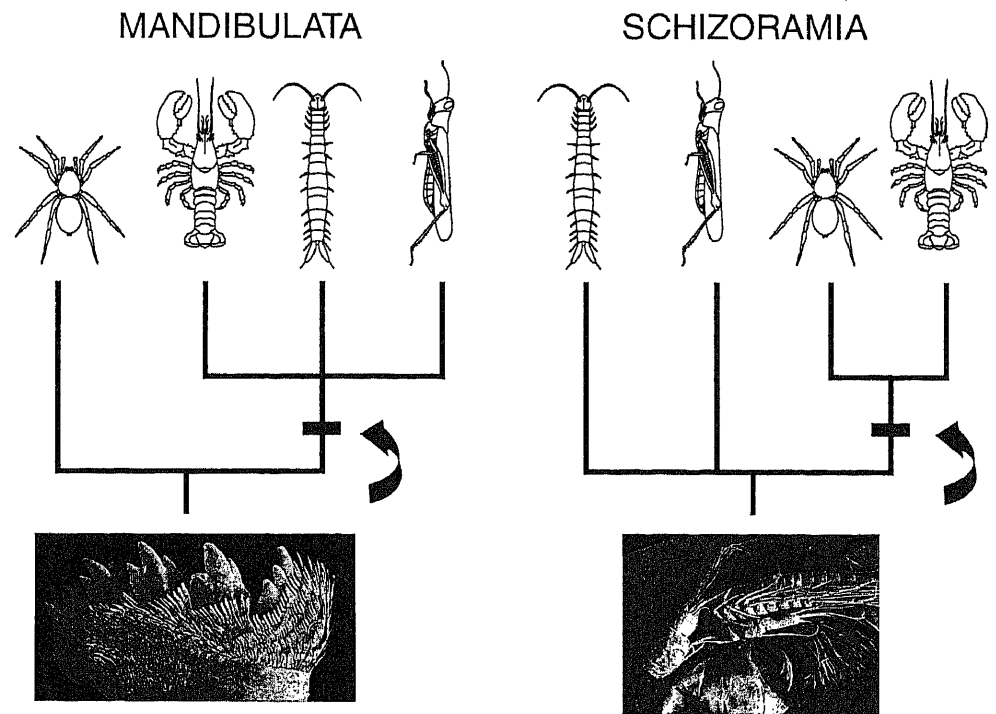
Other aspects of heated argumentation about arthropod evolution are the monophyly of Crustacea (see Schram and Koenemann, ch. 19 in this vol.) and the monophyly of Myriapoda (see Edgecombe and Giribet 2002).

Current Status and the Role of Fossils

In summary, arthropod systematists recognize the monophyly of the group, with Euarthropoda closely related to velvet worms (Onychophora) and water bears (Tardigrada). The arthropods can be divided into four main lineages, Chelicerata, Myriapoda, Crustacea, and Hexapoda, and a minor lineage of more uncertain affinities, Pycnogonida. Agreement about the monophyly of Mandibulata and Tetraconata seems to emerge from combined analyses of morphology and molecules (e.g., Giribet et al. 2001; fig. 17.1), but these groupings are not recognized universally, especially not so when the extinct diversity is brought into the picture. With regard to the sea spiders, emerging evidence suggests that they could be the sister group to the remaining arthropods, although a relationship to chelicerates cannot be rejected.

To evaluate these and other hypotheses, we attempted an analysis including almost 250 arthropods, living and extinct, and other related animals, together with information on more than 800 morphological characters and more than 2 kb (kilobases) of molecular sequence data. The aim of this study was to bring together the vast array of information known for extant arthropods and begin the integration of extinct taxa.

New Analysis

Taxa

The analysis of Giribet et al. (2001) contained 54 well-sampled, extant taxa but did not attempt any examination of extinct lineages. Here we have enlarged the sample of living taxa from 54 to 247, including seven Paleozoic taxa. These extinct lineages were Trilobita, coded largely from Whittington (1975: *Olenoides*); *Emeraldella* (from Bruton and Whittington 1983); *Sidneyia* (from Bruton 1981); Eurypterida, coded largely from Selden (1981); the Devonian pycnogonid *Palaeoisopus* (from Bergström et al. 1980); and the putative stem group crustacean *Martinssonia* (from Müller and Walossek 1986). Anomalocaridids are coded from *Parapeytoia* (Hou et al. 1995), but the coding precedes the reinterpretation (Budd 2002) of the grasping appendage as pre-antennal (with respect to crown group euarthropods). These morphological data were coded for 128 lineages, and the specific molecular taxa were treated as exemplars, with each member of the morphologically defined lineage (if there are several) receiving the same character coding (see supporting materials, see Wheeler 2003).

Of the 247 total taxa, 227 were sampled for molecular data [227 taxa for 18S ribosomal DNA (rDNA) and 135 taxa for 28S rDNA]. The remaining 20 taxa were sampled only for morphological data, seven because they are extinct, and the remainder due to the unavailability of sequence data.

Characters

Three sources of data were used in this study: morphological, small subunit rDNA (18S), and large subunit (28S) rDNA. The morphological characters include information from external and internal anatomy, behavior, ultrastructure, gene order, and development (see Wheeler 2003 for data). Overall, the morphological data had 13 additive multistate and 795 non-additive characters. The small- and large-subunit sequence data are the same fragments used·in Giribet et al. (2001). There were 10.7% missing and 14.5% inapplicable anatomical cells, 8.10% missing 18S rDNA sequences, and 45.3% missing 28S rDNA sequences (including extinct lineages).

Analysis

Morphological and molecular data were analyzed under parsimony using the program POY (vers. 2.7; Gladstein and Wheeler 1997–2002) on a 560 CPU PIII Linux cluster at the American Museum of Natural History and morphological analyses verified with NONA (vers. 2.0; Goloboff 1998). Cladogram costs were calculated for unequal length sequences using direct optimization (Wheeler 1996). A sensitivity analysis (Wheeler 1995) was performed using a variety of indel:transversion cost ratios (1:1, 2:1, 4:1, 8:1, and 16:1) and transversion:transition costs (1:1, 2:1, 4:1, and 8:1). This diversity of analyses was performed to assess the effects of analytical assumptions on phylogenetic conclusions.

Results

Analysis of the living taxa data set via NONA produced 100 equally parsimonious cladograms of length 1669, consistency index (CI) 0.60, and retention index (RI) 0.87, the strict consensus of which is shown in figure 17.3A. The inclusion of the seven extinct lineages resulted in 110 equally parsimonious cladograms of length 1720 (CI, 0.58; RI, 0.87), the strict consensus of which is shown in figure 17.3B. The two analyses jibe nearly completely with each other except for three areas: pycnogonids, remipedes/cephalocarids, and tracheates.

The living-taxa-only analysis shows a rather standard extant taxon hierarchy with the sea spiders as sister group to a clade of Xiphosura (horseshoe crabs) + arachnids. This is consistent with Snodgrass (1938), Wheeler et al. (1993), and the basal placement of pycnogonids by Giribet et al. (2001). The total taxon analysis (extinct + extant), however, inverts this relationship, placing Pycnogonida as sister to

Figure 17.3. Phylogenetic analysis of morphological data for major groups of arthropods. (A) Extant taxa data set, and (B) extant + extinct data sets. Cladogram realized using WINCLADA (ver. 1.0; Nixon 2002).

Figure 17.4. Phylogenetic analysis of molecular data for arthropods. (A) 18S, (B) 28S, and (C) combined molecular data with indels costing 8; transversions, 1; and transitions, 1; and morphological transformations costing 8. Cladogram realized using WINCLADA (ver. 1.0; Nixon 2002).

Arachnida, with the eurypterids, Xiphosura, trilobites, and *Emeraldella* + *Sidneyia* as successive sister groups. The inclusion of extinct lineages inverts the pattern based on living taxa. This is in part because of the additional scorable states in the pycnogonid opisthosoma due to *Palaeoisopus*, and the biramous limbs of the trilobites and other basal arachnates.

A second difference comes in the basal lineages of Crustacea. Both analyses support a major division between the malacostracan and maxillopodan + branchiopodan lineages. The placement of the remipedes and cephalocarids differs. In the more restrictive analysis (extant taxa only), these two putatively basal taxa group with Malacostraca, whereas in the complete taxon analysis the remipedes are the sister group to the remaining crustaceans, with *Hutchinsoniella* grouping with the non-malacostracan lineages.

The highest-level disagreement between these analyses is in the relative placement of Crustacea, Myriapoda, and Hexapoda. The extant taxa analysis supports Crustacea + Hexapoda (= Tetraconata), whereas the total-taxon analysis supports Hexapoda + Myriapoda (= Tracheata). The interactions here are complex. Certainly the role of the crustacean-like *Martinssonia* as a basal mandibulate (Wägele 1993, Moura and Christoffersen 1996) is central. The extinct lineages have altered the basal relationships of both the crustaceans and the chelicerates, and therefore their basalmost character states. Uniramy, as an example, has gone from the primitive condition in arthropods to a derived condition uniting tracheates on one side and arachnids + pycnogonids on the other. This is reinforced by both *Martinssonia* and the status of the anomalocarids (i.e., *Parapeytoia*) as sister group to crown group Euarthropoda (Dewel et al. 1999).

Molecular analyses show a diversity of patterns depending on the analytical parameters used to derive cladograms. There is a general pattern, however, of linking and even intermixing the crustacean and hexapod taxa (fig. 17.4). This pattern has been seen in molecular analyses of arthropod data for some time (e.g., Wheeler et al. 1993, Regier and Shultz 1997, Zrzavý et al. 1998, Giribet et al. 2001). The four pycnogonid representatives group together and separate from the arachnid lineages.

Combined analyses show an interesting distinction between extant and total-taxon analysis. As far as the relationships among the "classes," the extant taxa analyses are completely robust (fig. 17.5, left panel). In each of the 20 cases examined (e.g., fig. 17.6A), the crustaceans and hexapods form a clade. This is not terribly surprising in that both the morphological analysis of living taxa and the molecular data show this pattern. The Tetraconata (Dohle 2001) ["Pancrustacea" of Zrzavý et al. (1998) is based on crustacean paraphyly] is ubiquitous. When the extinct taxa are included, however, the pattern becomes less clear. At lower indel costs, Tetraconata is favored, whereas at higher indel costs (>2:1 over base substitutions), Tracheata is most parsimonious (figs. 17.5, right panel, and 17.6B). The "TCC" grouping was never found. Several patterns are common to the analyses. In both cases, the major groups (Crustacea, Chelicerata, Myriapoda, and Hexapoda) are monophyletic. Furthermore, the pycnogonids are brought to the base of chelicerates (sister group to Xiphosura + Arachnida), with *Emeraldella* + *Sidneyia* as stem-group chelicerates in the total-taxa analysis. Both analyses also support Remipedia + Cephalocarida (found in Giribet et al. 2001), which is not supported by either morphological taxon set. However, this clade is sister to the remaining crustaceans when the extinct lineages are included. Another noteworthy difference concerns the status of the entomostracan crustaceans, monophyletic based on the extant taxa (see Walossek and Müller 1998) but paraphyletic with respect to Malacostraca when fossils are included.

Inclusion of the molecular data affects the position of some of the extinct groups. Morphology alone resolves Trilobita in a frequently endorsed position in an arachnate clade (fig. 17.3B), in the chelicerate stem group (Wills et al. 1995, 1998, among many others). Analysis with the molecular data, however, shifts the trilobites outside Arachnata (fig. 17.6B), perhaps in part caused by character conflict when pycnogonids are placed as sister group of euchelicerates. This latter resolution, with trilobites as sister group to other euarthropods, allows that the lack of differentiation of post-antennal appendages in trilobites could be a primitive condition, rather than the reversal forced by their deep nesting in Arachnata.
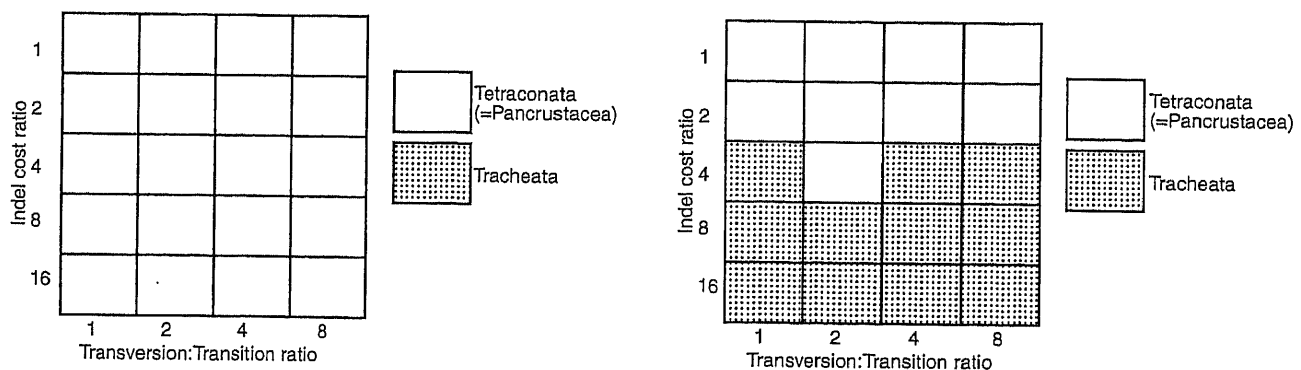

Figure 17.5. Sensitivity plots for (left panel) extant and (right panel) extant + extinct taxa showing the support for Tetraconata and Tracheata over varied analytical parameter assumptions.
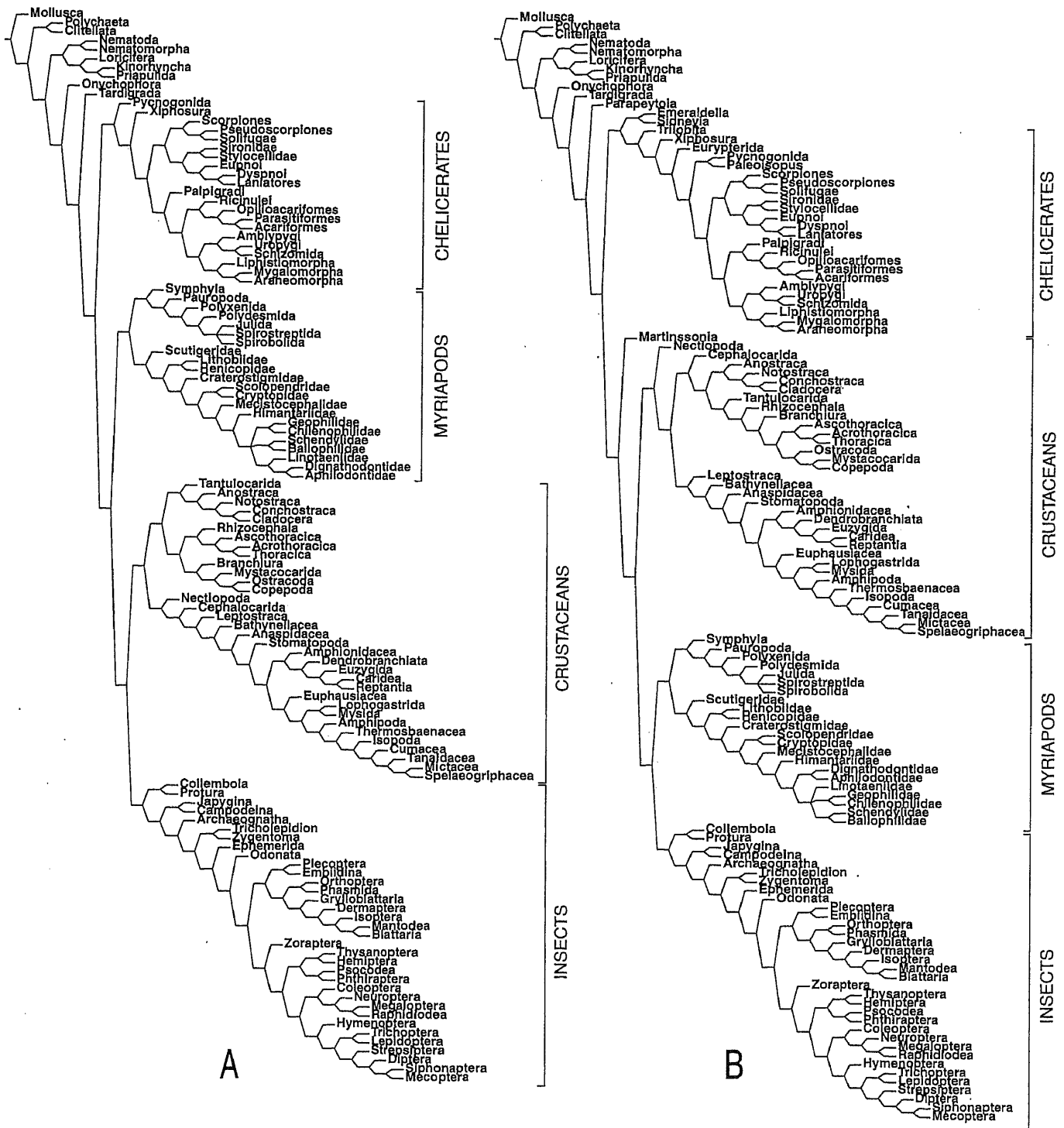
Figure 17.6. Combined (all data) analysis for (A) extant and (B) extant + extinct taxa with indels costing 8 transversions 1 and transitions 1 and morphological transformations 8. Cladogram realized using WINCLADA (ver. 1.0; Nixon 2002).

Discussion

The most striking result of this analysis and summary of current data on arthropod relationships is the importance of extinct lineages. Although we are able to examine a great deal of extant arthropod anatomy and molecular biology, the patterns of diversification and extinction in these groups make sampling limited to living taxa insufficient. Furthermore, even though this initial attempt at uniting these lineages resulted in unavoidably large levels of missing data in

both molecular and morphological analysis, the effects of including even a few extinct taxa were profound.

At this point, several overall patterns in arthropod relationships can be identified as having support: monophyly of each of the major groups, Crustacea, Myriapoda, Hexapoda, and Chelicerata (with the possible exception of the Pycnogonida); monophyly of Mandibulata (crustaceans, hexapods, and myriapods); and outgroup status of Tardigrada and Onychophora. Several other important questions remain, including the position of the pycnogonids, the basalmost lineages of Crustacea and the sister group to Hexapoda. As we have shown here, these problems are sensitive to the inclusion of extinct lineages and are unlikely to be resolved with any great confidence until a broader sample of extinct diversity is incorporated into this analysis. Our results changed radically when we had 3% extinct lineages; what will happen when we have 99%?

Literature Cited

Abzhanov, A., and T. C. Kaufman. 1999. Homeotic genes and the arthropod head: expression patterns of the *labial*, *proboscipedia*, and *deformed* genes in crustaceans and insects. Proc. Natl. Acad. Sci. USA 96:10224–10229.

Abzhanov, A., A. Popadić, and T. C. Kaufman. 1999. Chelicerate Hox genes and the homology of arthropod segments. Evol. Dev. 1:77–89.

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Lindford, M. C. Rivera, J. R. Garey, R. A. Raff, and 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 and Devonian fossil record of the Myriapoda. Philos. Trans. R. Soc. Lond. B. 309:227–237.

Anderson, D. T. 1973. Embryology and phylogeny in annelids and arthropods. Pergamon, Oxford.

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

Bergström, J. 1992. The oldest Arthropoda and the origin of the Crustacea. Acta Zool. 73:287–291.

Bergström, J., W. Sturmer, and G. Winter. 1980. *Palaeoisopus*, *Palaeopantopus* and *Palaeothea*, pycnogonid arthropods from the Lower Devonian Hunsrück Slate, West Germany. Paläont. Z. 54:7–54.

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

Boore, J. L., D. V. Lavrow, and W. M. Brown. 1998. Gene translocation links insects and crustaceans. Nature 392:667–668.

Boudreaux, H. B. 1979. Arthropod phylogeny with special reference to insects. John Wiley and Sons, New York.

Briggs, D. E. G., and R. A. Fortey. 1989. The early radiation and relationships of the major Arthropod groups. Science 246:241–243.

Briggs, D. E. G., R. A. Fortey, and M. A. Wills. 1992. Morphological disparity in the Cambrian. Science 256:1670–1673.

Bruton, D. L. 1981. The arthropod *Sidneyia inexpectans*, Middle Cambrian, Burgess Shale, British Columbia. Philos. Trans. R. Soc. Lond. B. 295:619–656.

Bruton, D. L., and H. B. Whittington. 1983. *Emeraldella* and *Leanchoilia*, two arthropods from the Burgess Shale, Middle Cambrian, British Columbia. Philos. Trans. R. Soc. Lond. B. 300:553–585.

Budd, G. E. 1996. The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. Lethaia 29:1–14.

Budd, G. E. 2002. A palaeontological solution to the arthropod head problem. Nature 417:271–275.

Carpenter, F. M. 1992. Hexapoda. Treatise on invertebrate paleontology: Pt. R, Arthropoda 4. Geological Society of America, University of Kansas Press, Lawrence.

Cisne, J. L. 1974. Trilobites and the origin of arthropods. Science 186:13–18.

Collins, D. 1996. The "evolution" of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.). J. Paleontol. 70:280–293.

Damen, W. G. M., M. Hausdorf, E. A. Seyfarth, and D. Tautz. 1998. A conserved mode of head segmentation in arthropods revealed by the expression pattern of hox genes in a spider. Proc. Natl. Acad. Sci. USA 95:10665–10670.

Dewel, R. A., G. E. Budd, D. F. Castano, and W. C. Dewel. 1999. The organization of the subesophageal nervous system in tardigrades: insights into the evolution of the arthropod hypostome and tritocerebrum. Zool. Anz. 238:191–203.

Dohle, W. 1965. Über die Stellung der Diplopoden im System. Zool. Anz. 28(suppl.):597–606.

Dohle, W. 1998. Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship. Pp. 305–315 *in* Arthropod relationships (R. A. Fortey and R. H. Thomas, eds.). Systematics Association spec. ser. vol. 55. Chapman and Hall, London.

Dohle, W. 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name Tetraconata for the monophyletic unit Crustacea + Hexapoda. Ann. Soc. Entomol. Fr. (n.s.) 37:85–103.

Dunlop, J. A., and Braddy, S. J. 2001. Scorpions and their sister-group relationships. Pp. 1–24 *in* Scorpions 2001. In Memoriam Gary A. Polis (V. Fet and P. A. Selden, eds.). British Arachnological Society, Burham Beeches, Buckinghamshire, UK.

Edgecombe, G. D. 1998. Arthropod fossils and phylogeny. Columbia University Press, New York.

Edgecombe, G. D., and G. Giribet. 2002. Myriapod phylogeny and the relationships of Chilopoda. Pp. 143–168 *in* Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento (J. E. Llorente Bousquets and J. J. Morrone, eds.). Prensas de Ciencias, Universidad Nacional Autónoma de México, Mexico DF.

Edgecombe, G. D., and H. Morgan. 1999. *Synaustrus* and the euthycarcinoid puzzle. Alcheringa 23:193–213.

Edgecombe, G. D., G. D. F. Wilson, D. J. Colgan, M. R. Gray, and G. Cassis. 2000. Arthropod cladistics: combined analysis of Histone H3 and U2 snRNA sequences and morphology. Cladistics 16:155–203.

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

Fortey, R. A., and R. H. Thomas. 1998. Arthropod relationships. Chapman and Hall, London.

Friedrich, M., and D. Tautz. 1995. Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. Nature 376:165–167.

Fryer, G. 1996. Reflections on arthropod evolution. Biol. J. Linn. Soc. 58:1–55.

Fryer, G. 1998. A defence of arthropod polyphyly. Pp. 23–33 *in* Arthropod relationships (R. A. Fortey and R. H. Thomas, eds.). Chapman and Hall, London.

Giribet, G., S. Carranza, J. Baguñà, M. Riutort, and C. Ribera. 1996. First molecular evidence for the existence of a Tardigrada + Arthropoda clade. Mol. Biol. Evol. 13:76–84.

Giribet, G., D. L. Distel, M. Polz, W. Sterrer, and W. C. Wheeler. 2000. Triploblastic relationships with emphasis on the acoelomates and the position of Gnathostomulida, Cycliophora, Plathelminthes, and Chaetognatha: a combined approach of 18S rDNA sequences and morphology. Syst. Biol. 49:539–562.

Giribet, G., G. D. Edgecombe, and W. C. Wheeler. 2001. Arthropod phylogeny based on eight molecular loci and morphology. Nature 413:157–161.

Giribet, G., and C. Ribera. 1998. The position of arthropods in the animal kingdom: a search for a reliable outgroup for internal arthropod phylogeny. Mol. Phylogenet. Evol. 9:481–488.

Gladstein, D. S., and W. C. Wheeler. 1997–2002. POY: the optimization of alignment characters, ver. 2.7 [program and documentation]. New York. Available: ftp.amnh.org/pub/molecular. Last accessed 15 December 2003.

Goloboff, P. A. 1998. NONA, ver. 2.0 [program and documentation]. Available: www.cladistics.com. Last accessed 15 December 2003.

Grimaldi, D. 2001. Insect evolutionary history from Handlirsch to Hennig, and beyond. J. Paleontol. 75:1152–1160.

Gupta, A. P. 1979. Arthropod phylogeny. Van Nostrand Reinhold, New York.

Haeckel, E. 1866. Generelle Morphologie der Organismen. Georg Reimer, Berlin.

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

Hessler, R. R., and W. A. Newman. 1975. A trilobitomorph origin for the Crustacea. Fossils and Strata 4:437–459.

Hou, X.-G., J. Bergström, and P. Ahlberg. 1995. *Anomalocaris* and other large animals in the Lower cambrian Chengjiang fauna of southwest China. Geologisk. Föreningens Förhandl. 117:163–183.

Hwang, U. W., M. Friedrich, D. Tautz, C. J. Park, and W. Kim.

2001. Mitochondrial protein phylogeny joins myriapods with chelicerates. Nature 413:154–157.

Klass, K.-D., and N. P. Kristensen. 2001. The ground plan and affinities of hexapods: recent progress and open problems. Ann. Soc. Entomol. Fr. (n.s.) 37:265–298.

Kraus, O. 1998. Phylogenetic relationships between higher taxa of tracheate arthropods. Pp. 295–303 *in* Arthropod relationships (R. A. Fortey and R. H. Thomas, eds.). Systematics Association spec. ser. vol. 55. Chapman and Hall, London.

Kraus, O. 2001. "Myriapoda" and the ancestry of the Hexapoda. Ann. Soc. Entomol. Fr. (n.s.) 37:105–127.

Kraus, O., and M. Kraus. 1994. Phylogenetic system of the Tracheata (Mandibulata): on "Myriapoda": Insecta interrelationships, phylogenetic age and primary ecological niches. Verh. Naturwiss. Ver. Hamburg 34:5–31.

Kraus, O., and M. Kraus. 1996. On myriapod/insect interrelationships. Mem. Mus. Natl. Hist. Nat. 169:283–290.

Kukalová-Peck, J. 1992. The "Uniramia" do not exist: the ground plan of the Pterygota as revealed by Permian Diaphanopterodea from Russia (Insecta: Paleodictyopteroidea). Can. J. Zool. 70:236–255.

Kukalová-Peck, J. 1998. Arthropod phylogeny and 'basal' morphological structures. Pp. 249–268 *in* Arthropod relationships (R. A. Fortey and R. H. Thomas, eds.). Chapman and Hall, London.

Manton, S. M. 1964. Mandibular mechanisms and the evolution of Arthropods. Philos. Trans. R. Soc. Lond. B 247:1–183.

Manton, S. M. 1973. Arthropod phylogeny—a modern synthesis. J. Zool. Lond. 171:11–130.

Manton, S. M. 1977. The Arthropoda: habits, functional morphology, and evolution. Clarendon Press, Oxford.

Manton, S. M. 1979. Functional morphology and the evolution of the hexapod classes. Pp. 387–466 *in* Arthropod phylogeny (A. P. Gupta, ed.). Van Nostrand Reinhold, New York.

Martin, J. W., and G. E. Davis. 2001. An updated classification of the Recent Crustacea. Nat. Hist. Mus. LA County Contrib. Sci. 39:1–124.

Melic, A., J. J. de Haro M. Méndez, and I. Ribera (eds.). 1999. Evolución y filogenia de Arthropoda [monograph]. Bol. Soc. Entomol. Aragonesa no. 26.

Mittmann, B., and G. Scholtz. 2001. Distal-less expression in embryos of *Limulus polyphemus* (Chelicerata, Xiphosura) and *Lepisma saccharina* (Insecta, Zygentoma) suggests a role in the development of mechanoreceptors, chemoreceptors, and the CNS. Dev. Gen. Evol. 211:232–243.

Moura, G., and M. Christoffersen. 1996. The system of the mandibulate arthropods; Tracheata and Remipedia as sister groups, "Crustacea" non-monophyletic. J. Comp. Biol. 1:95–113.

Müller, K. J. 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. Lethaia 12:1–27.

Müller, K. J., and D. Walossek. 1986. *Martinssonia elongata* gen. et sp. n.: a crustacean-like euarthropod from the Upper Cambrian of Sweden. Zool. Scr. 15:73–92.

Nixon, K. G. 2002. WINCLADA ver. 1.0. Available: http://cladistics.com. Last accessed 15 December 2003.

Panganiban, G., A. Sebring, L. Nagy, and S. Carroll. 1995. The

development of crustacean limbs and the evolution of arthropods. Science 270:1363–1366.

Popadić, A., G. Panganiban, D. Rusch, W. A. Shear, and T. C. Kaufman. 1998. Molecular evidence for the gnathobasic derivation of arthropod mandibles and for the appendicular origin of the labrum and other structures. Dev. Gen. Evol. 208:142–150.

Popadić, A., D. Rusch, M. Peterson, B. T. Rogers, and T. C. Kaufman. 1996. Origin of the arthropod mandible. Nature 380: 395.

Ramsköld, L., and J.-Y. Chen. 1998. Cambrian lobopodians: morphology and phylogeny. Pp. 107–150 in Arthropod fossils and phylogeny (G. D. Edgecombe, ed.). Columbia University Press, New York.

Regier, J. C., and J. W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. Mol. Biol. Evol. 14:902–913.

Regier, J. C., and J. W. Shultz. 1998. Molecular phylogeny of arthropods and the significance of the Cambrian "explosion" for molecular systematics. Am. Zool. 38:918–928.

Regier, J. C., and J. W. Shultz. 2001. Elongation factor-2: a useful gene for arthropod phylogenetics. Mol. Phylogenet. Evol. 20:136–148.

Schmidt-Rhaesa, A., T. Bartolomaeus, C. Lemburg, U. Ehlers, and J. R. Garey. 1998. The position of the Arthropoda in the phylogenetic system. J. Morphol. 238:263–285.

Scholtz, G., B. Mittmann, and M. Gerberding. 1998. The pattern of Distal-less expression in the mouthparts of crustaceans, myriapods and insects: new evidence for a gnathobasic mandible and the common origin of Mandibulata. Int. J. Dev. Biol. 42:801–810.

Schram, F. R. 1978. Arthropods: a convergent phenomenon. Fieldiana Geol. 39:61–108.

Selden, P. A. 1981. Functional morphology of the prosoma of Baltoeurypterus tetragnophthalmus (Fischer) (Chelicerata: Eurypterida). Trans. R. Soc. Edinb. Earth Sci. 72:9–48.

Shear, W. A. 1992. End of the "Uniramia" taxon. Nature 359:477–478.

Shear, W. A., A. J. Jeram, and P. A. Selden. 1998. Centipede legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America. Am. Mus. Nov. 3231:1–16.

Shultz, J. W., and J. C. Regier. 2000. Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean + hexapod clade. Proc. R. Soc. Lond. B 267:1011–1019.

Siebold, C. T. W. V., and H. Stannius. 1848. Lehrbuch der vergliechenden Anatomie der Wirbellosen Tiere. Veit, Berlin.

Snodgrass, R. E. 1938. Evolution of the Annelida, Onychophora and Arthropoda. Smithson. Misc. Coll. 97:1–159.

Snodgrass, R. E. 1950. Comparative studies on the jaws of mandibulate arthropods. Smithson. Misc. Coll. 116:1–85.

Snodgrass, R. E. 1951. Comparative studies on the head of mandibulate arthropods. Comstock Publishing, Ithaca, NY.

Telford, M. J., and R. H. Thomas. 1998. Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proc. Natl. Acad. Sci. USA 95:10671–10675.

Tiegs, O. W. 1947. The development and affinities of the Pauropoda, based on a study of Pauropus silvaticus. Q. J. Microsc. Sci. 88:275–336.

Tiegs, O. W., and S. M. Manton. 1958. The evolution of the Arthropoda. Biol. Rev. 33:255–337.

Turbeville, J. M., D. M. Pfeifer, K. G. Field, and R. A. Raff. 1991. The phylogenetic status of arthropods, as inferred from 18S rRNA sequences. Mol. Biol. Evol. 8:669–686.

Wägele, J. W. 1993. Rejection of the "Uniramia" hypothesis and implications of the Mandibulata concept. Zool. Jb. Syst. 120:253–288.

Walossek, D. 1999. On the Cambrian diversity of Crustacea. Pp. 3–27 in Crustaceans and the biodiversity crisis (F. R. Schram and J. C. von Vaupel Klein, eds.). Brill, Leiden.

Walossek, D., and K. J. Muller. 1998. Early arthropod phylogeny in light of the Cambrian "Orsten" fossils. Pp. 107–150 in Arthropod fossils and phylogeny (G. D. Edgecombe, ed.). Columbia University Press, New York.

Waloszek, D., and J. A. Dunlop. 2002. A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian "Orsten" of Sweden, and the phylogenetic position of pycnogonids. Palaeontology 45:421–446.

Weygoldt, P. 1979. Significance of later embryonic stages and head development in arthropod phylogeny. Pp. 107–136 in Arthropod phylogeny (A. P. Gupta, ed.). Van Nostrand, New York.

Weygoldt, P. 1986. Arthropod interrelationships—the phylogenetic–systematic approach. Z. Zool. Syst. Evol. 24:19–35.

Whalley, P. E. S., and E. A. Jarzembowski. 1981. A new assessment of Rhyniella, the earliest known insect, from the Devonian of Rhynie, Scotland. Nature 291:317.

Wheeler, W. C. 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. Syst. Biol. 44:321–331.

Wheeler, W. C. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics 12:1–9.

Wheeler, W. C. 1998a. Molecular systematics and arthropods. Pp. 9–32 in Arthropod fossils and phylogeny (G. D. Edgecombe, ed.). Columbia University Press, New York.

Wheeler, W. C. 1998b. Sampling, groundplans, total evidence and the systematics of arthropods. Pp. 87–96 in Arthropod relationships (R. A. Fortey and R. H. Thomas, eds.). Chapman and Hall, London.

Wheeler, W. C. 2003. Supporting data. Available: ftp.amnh.org/pub/molecular/data/tol-appendices.doc.

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

Whittington, H. B. 1971. Redescription of Marrella splendens (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia. Bull. Geol. Soc. Can. 209:1–24.

Whittington, H. B. 1975. Trilobites with appendages from the Middle Cambrian Burgess Shale, British Columbia. Fossils Strata 4:97–136.

Wills, M. A., D. E. G. Briggs, R. A. Fortey, and M. Wilkinson. 1995. The significance of fossils in understanding arthropod evolution. Verh. Deutsch. Zool. Ges. 88:203–215.

Wills, M. A., D. E. G. Briggs, R. A. Fortey, M. Wilkinson, and P. H. A. Sneath. 1998. An arthropod phylogeny based on fossil and recent taxa. Pp. 33–105 *in* Arthropod fossils and phylogeny (G. D. Edgecombe, ed.). Columbia University Press, New York.

Wilson, H. M., and W. A. Shear. 2000. Microdecemplicida, a new order of minute arthropleurideans (Arthropoda;

Myriapoda) from the Devonian of New York State, U.S.A. Trans. R. Soc. Edinburgh Earth Sci. 90:351–375.

Zrzavý, J., V. Hypsa, and M. Vlaskova. 1998. Arthropod phylogeny: taxonomic congruence, total evidence and conditional combination approaches to morphological and molecular data sets. Pp. 97–107 *in* Arthropod relationships (R. A. Fortey and R. H. Thomas, eds.). Chapman and Hall, London.