MYRIAPODS

Myriapods are many-legged, terrestrial arthropods whose bodies are divided into two major parts, a head and a trunk. The head bears a single pair of antennae, highly differentiated mandibles (or jaws), and at least one pair of maxillary mouthparts; the trunk region consists of similar "metameres," each of which is a functional segment that bears one or two pairs of appendages. Gas exchange is accomplished by tracheae—a branching network of specialized tubules—although small forms respire through the body wall. Malpighian organs are used for excretion, and eyes consist of clusters of simple, unintegrated, light-sensitive elements that are termed ommatidia. These major features collectively characterize the five major myriapod clades: Diplopoda (millipeds), Chilopoda (centipeds), Pauropoda (pauropods), Symphyla (symphylans), and Arthropleurida (arthropleurids). Other features indicate differences among these clades. For example, chilopods are opisthogoneate in that the genital openings occur in the penultimate trunk segment, while all other myriapods are progoneate by having the second abdominal segment housing the genital openings. Chilopods and symphylans possess a second pair of maxillary (or labial) mouthparts similar to hexapods (insects and parainsects), but these structures are absent in pauropods and diplopods. These and other unevenly distributed characters have made it difficult to unravel the evolutionary relationships of the higher groups of myriapods.

Myriapod Relationships

More contentious than internal myriapodan relationships is the relationship of myriapods to the rest of the Arthropoda, particularly the issue of whether they are phylogenetically close to the Hexapoda. Current thought on the relationship of myriapods to other arthropods can be characterized by five major hypotheses (Figure 1). The oldest currently held proposal (Figure 1A) consists of a Schizoramia clade that unites the Trilobita and Chelicerata (horseshoe crabs, spiders, and relatives), and a Mandibulata clade that contains the Crustacea and a more derived Tracheata clade that consists of the Myriapoda + Hexapoda (Weygolt 1979). (The Tracheata also are known as the Atelocerata or Antennata.) A second hypothesis envisions a clade that combines the Myriapoda + Hexapoda and another that unites the Trilobita and the Chelicerata + Crustacea, or a "TCC" clade (Figure 1B). This scheme maintains that the Myriapoda is a monophyletic clade, that is one with a single common ancestor, whose sister group, or closest relative, is the Hexapoda. Accordingly, this clade has very distant links to the rest of the Arthropoda (Briggs et al. 1992; Wheeler et al. 1993).

A third proposal, the uniramian hypothesis, was advocated by S.M. Manton (1977) and is based on functional analyses of the structure of arthropods, including myriapods. According to this view, because of functionally disparate mechanisms in walking, feeding, and other activities, major arthropodan clades are polyphyletic, indicating scant evidence of a common ancestor (Figure 1C). At a much coarser level, this hypothesis does distinguish four arthropod groups, the Trilobita, Chelicerata, Crustacea, and the Uniramia, the last consisting of the Myriapoda, Hexapoda, and Onychophora (velvet worms). However, subsequent structural and molecular evidence indicates that there are several characters uniting major arthropod taxa. Moreover, paleobiologic, embryologic, and other evidence demonstrates that myriapods and hexapods are fundamentally polyramous, having two major articulating appendages per embryological body segment, like other arthropods.

A fourth proposal (Figure 1D) suggests that myriapods are an ancient, basal arthropod lineage, and that the Hexapoda emerged as an independent, relatively recent clade from a rather terminal crustacean lineage, perhaps the Malacostraca, which contains lobsters and crabs (Ballard et al. 1992). Because few crustacean taxa were examined in this analysis, and due to the Cambrian age of many major crustacean lineages, it is possible that myriapods and hexapods are distinct lineages embedded within the Crustacea. Recently, an analysis by Friedrich and Tautz (1995) arrived at an unconventional conclusion that the Myriapoda is related closely, perhaps as a sister group, to the Chelicerata (Figure 1E), although support for this relationship was weak. Notably, there was lack of support for a Myriapoda-Hexapoda connection in two of these schemes.

Several conclusions have resulted from these and other studies of internal and external myriapod relationships. First, when analyses are limited to myriapods and hexapods, perhaps including some crustacean taxa, the Myriapoda is not sustained as a group defined by distinctive structures. The Symphyla becomes the sister group to the Hexapoda (Figure 2A), or the Chilopoda often becomes a paraphyletic taxon whose sister group is the rest of the Myriapoda and the Hexapoda (Figure 2B). Second, in more global analyses that include representatives from the other major arthropod groups, the Myriapoda + Hexapoda becomes disassembled, frequently radically so, leading to a conclusion that the several features that unite the Tracheata may have originated independently from convergence. Characters such as a single pair of antennae, tracheae, uniramy, and Malpighian tubules probably originated independently in both clades as adaptations to a terrestrial existence.

Taxonomic Characterization and Fossil History

Six major clades, or classes, of myriapods have been recognized, including two that are extinct (Kampecarida and Arthropleuridea) and an extant class that lacks a fossil record (Pauropoda). Kampecarids are poorly understood Late Silurian to Late Devonian myriapods with weakly coalesced segments, a head as wide or wider than body segments, large eyes with numerous ommatidia, and a medially divided sternum. Nothing is known of their mouthparts. Kampecarids are presumed to have been amphibious or even aquatic (Almond 1985). They probably were related to diplopods, whose major Paleozoic representatives were the giant, spiny euphoberiids (Figure 3) that bore prominent, rigid, and laterally positioned spines that were often forked.
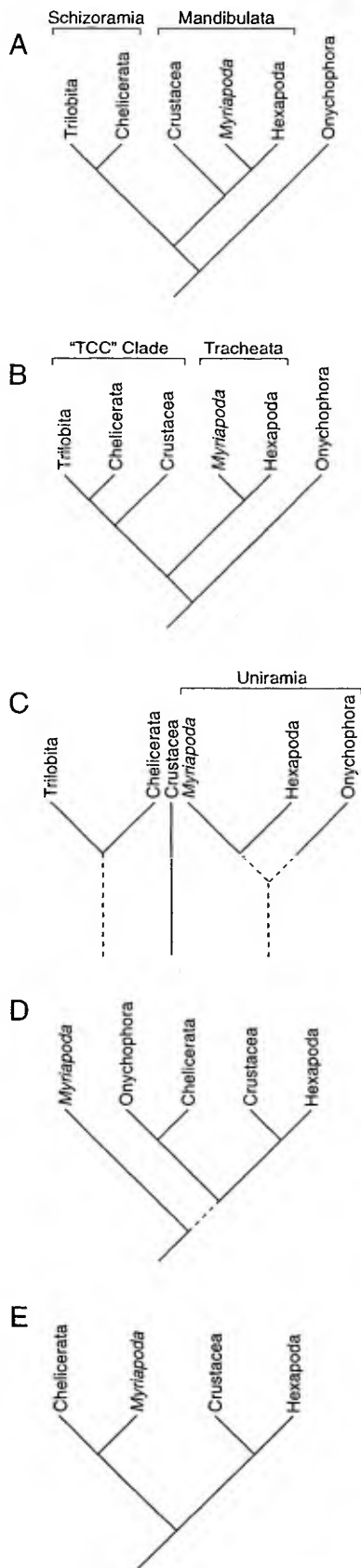
Figure 1. Summaries of five recent hypotheses indicating the relationship of myriapods to other major arthropod groups. All branch lengths are arbitrary; dotted lines indicate nodes that are theoretically inferred (c) or not statistically valid (others). This is not an exhaustive list. a, Schizoramia/Mandibulata Hypothesis; b, TCC/Tracheate Hypothesis, in which tracheates are recognized as a monophyletic clade but with the possibility of myriapods polyphyletic with respect to hexapods; some early Paleozoic subgroups, such as "trilobitoids," are not included; c, Uniramia Hypothesis, showing the polyphyletic origin of major arthropod clades from unspecified, lobopod ancestors; d, Basal Myriapod Hypothesis; e, Chelicerate/Myriapod Hypothesis. From: a, Weygolt (1979); b, Briggs et al. (1992), Wheeler et al. (1993); c, Manton (1977), see also Fryer (1996); d, Ballard et al. (1992); e, Turbeville et al. (1991).
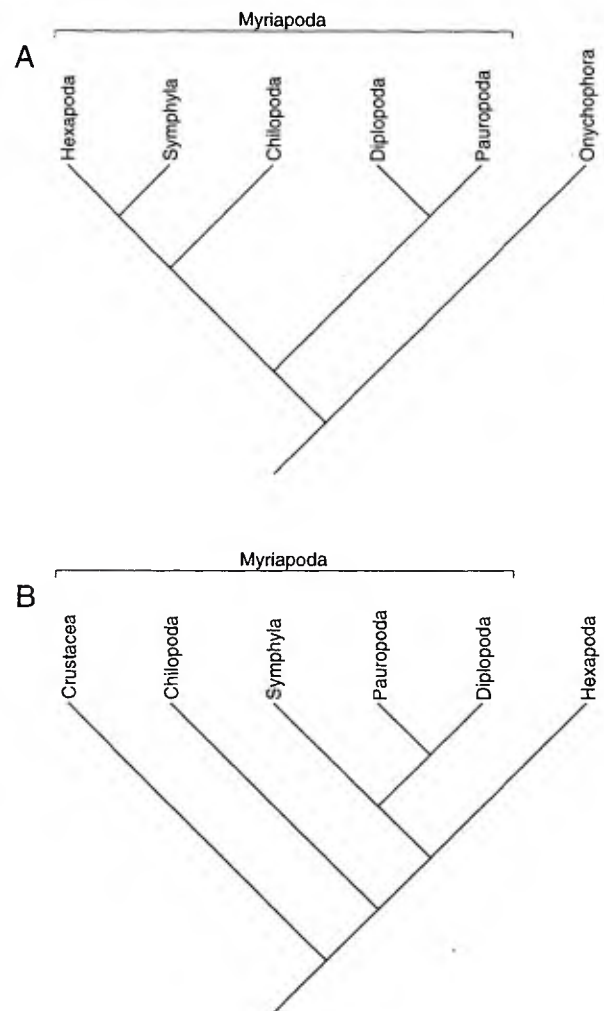

Figure 2. Two recent hypotheses for the phylogenetic relationships of myriapod classes and hexapods, based on morphological data. a, Briggs et al. (1992); b, Kraus and Kraus (1994).
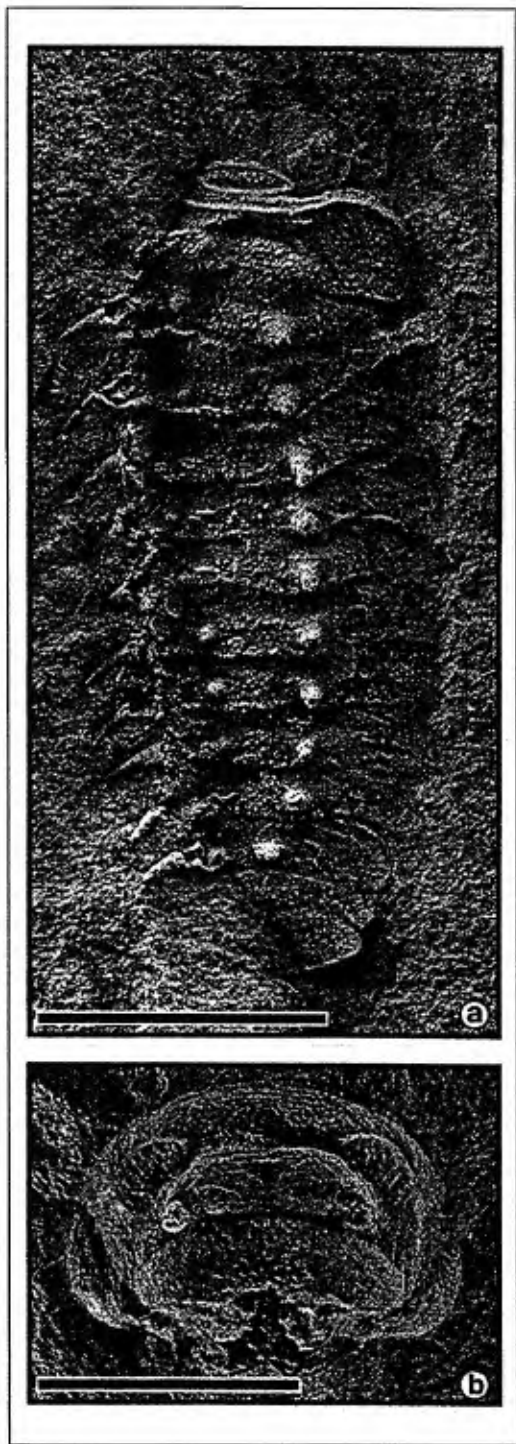

Diplopods have a head narrower than trunk segment width. On the head are lateral eyes, eight-segmented antennae above a labrum, and mouthparts that include robust, highly toothed mandibles and maxillae modified into a special, multielement structure, the gnathochilarium (Figure 4b, c). The gnathochilarium is attached by membranes to a sternum and consists of a basal mentum and a pair of distal stipes. Their trunk segments are diplosomites, each consisting of a coalesced anterior prozonite and posterior metazonite that are fused or connected by membranes into a single functional segment that bears two pairs of segmented appendages (Figure 4a). These diplosomites are telescoped under the margin of the segment immediately in front of it, allowing some forms to curl or enroll completely. Modern diplopods are sluggish and range in length from two millimeters in the Julida to 26 centimeters in the Spirostrepsida, although Late Carboniferous euphoberiids were longer. Diplopods have the best fossil record of all myriapods, predominantly because of a relatively durable exoskeleton impregnated with calcium carbonate. Diplopod fossils are overwhelmingly represented in Baltic amber, from which the earliest occurrences of six of the 12 fossil orders are known (Table 1).

Pauropods are progoneate myriapods possessing nine pairs of legs, 11 body segments, and a terminal pygidium that forms a distinctive end segment. Reaching a maximum length of only two millimeters, pauropods lack tracheae and a circulatory system. They bear distinctive, two-branched antennae and have reduced mouthparts that lack a labial region. Pauropods lack a fossil record.

Symphylans are small, colorless, progoneate myriapods that exhibit a stereotyped combination of 12 leg-bearing segments ventrally and 15 or 22 dorsal sclerotized plates, plus a terminal segment bearing cercilike appendages homologous to walking legs. The head juts forward, bearing two simple antennae with beadlike segments, and well developed mandibular, maxillary, and labial mouthparts, imparting a distinctive insectan appearance. Described fossil symphylans are very rare; two of the three extant families are represented by single occurrences—a scolopendrellid from Late Eocene Baltic amber and a scutigerellid from Late Oligocene Dominican amber.

Chilopods are actively moving, opisthogoneate, tracheate myriapods that bear a single pair of appendages per functional segment (Figure 5a). With the exception of the presence of a second maxilla with a conspicuous palp (Figure 5b), the gross head structures and mouthparts of chilopods are similar to those of diplopods. The head is dorsoventrally flattened and is forwardly directed. The pair of appendages on the first trunk segment are walking legs modified into a poison claw, which contains an internal poison gland that releases toxin from an orifice at the appendage tip for immobilizing prey (Figure 5b, c). The trunk is elongate, flattened, and flexible, and each segment consists of an unmineralized, dorsal tergite, a ventral exoskeletal sternite, and up to several, complexly arranged, small exoskeletal pleurites on the body sidewall. Chilopods may reach lengths approaching 30 centimeters and are exclusively carnivorous, feeding extensively on other terrestrial arthropods. The chilopod fossil record extends to the Late Silurian. This and the occurrence of relatively advanced Middle Devonian fossils containing original cuticle (Shear and Bonamo

Figure 3. Structure of Carboniferous euphoberiid diplopods. *a,* dorsal view of trunk of *Amynilyspes wortheni* Scudder, from Mazon Creek, Illinois (from Hannibal 1984); note dorsal and lateral spines. *b,* ventral view of head of *?Myriacantherpestes* (from Hannibal 1997); note two laterally placed manibles at bottom of photograph, broad arcuate region above, and two lateral knobs for insertion of antennae above the labrum. Scale bars represent one cm. Both photographs were taken by Bruce Frumker, Cleveland Museum of Natural History, and are reproduced with permission.
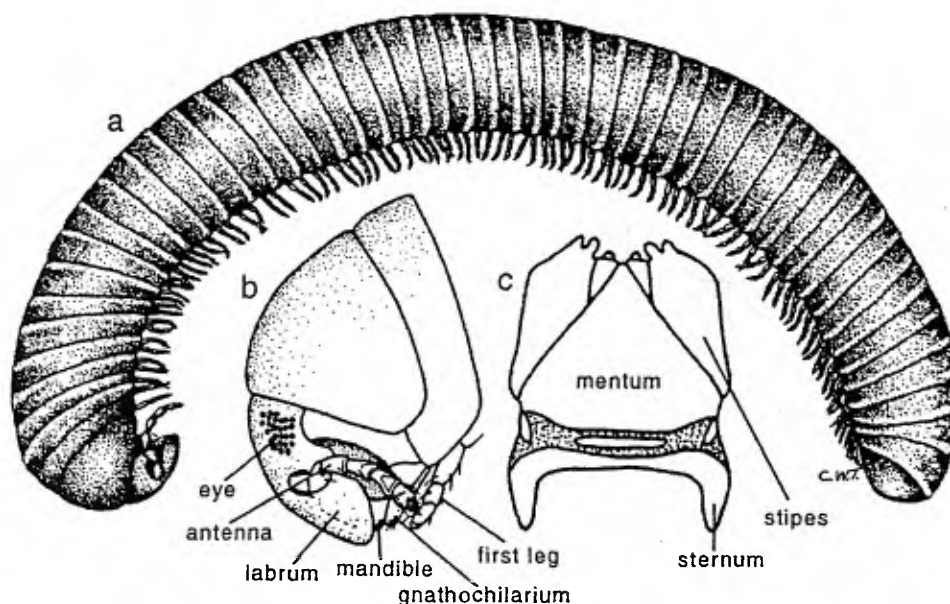
Figure 4. Major external features of the spirobolid milliped *Narceus*, representative of the myriapod class, Diplopoda. a, lateral view of the body; b, lateral view of head and first trunk segment; c, ventral view of the gnathochilarium. Figures from AN INTRODUCTION TO THE STUDY OF INSECTS, Sixth Edition by Donald J. Borror, Charles A. Triplehorn, and Norman F. Johnson, copyright © 1989 by Saunders College Publishing, reproduced by permission of the publisher.

1988) indicate that the initial radiation of chilopods probably was a Late Silurian event. Many chilopod fossils occur in Mid-Cenozoic Baltic amber, all assignable to modern families.

Arthropleurids are minute to gigantic myriapods up to two meters long, possibly slightly longer (Hahn et al. 1986), and are the largest terrestrial arthropods known (Figure 6). They are rare, occurring in two distinctive environments: Devonian *Eoarthropleura* is found in perimarine, early terrestrial deposits associated with diminutive and primitive vascular plants, whereas Late Carboniferous *Arthropleura* inhabited Late Carboniferous to Early Permian, equatorial, well-drained environments, especially seed-fern forests (Schneider and Barthel 1997). Segmentation consisted of two pairs of walking legs per functional segment (Briggs and Almond 1994), indicating that arthropleurids were anatomically close to diplopods. Arthropleurid cuticle was unmineralized and unusually thin, although it probably was sclerotized extensively (Rolfe 1969). The structure of the head is unknown, but it is inferred to have been significantly narrower than the total trunk width. The adult body consisted of at least 27 segments and probably a terminal telson; thoracic tergites were dorsolaterally expanded into anteriorly overlapping, trilobite-like structures. The tergites were ornamented by tubercles and blunt spines. Sternites were considerably complex, consisting of three major, characteristically shaped, ornamented plates. The limbs were comprised of eight to 10 tapering, imbricated segments, each bearing two spiny, ventral prongs. Arthropleurids probably were sluggish, yet capable of limited lateral and sinusoidal flexion. Late Carboniferous fossils of arthropleurids are associated with plants, and one specimen is known with club moss material filling its gut (Rolfe and Ingham

1967). These and other data indicate that arthropleurids lived on mineralic substrates and grazed on the forest floor.

Diversity

There are approximately 13,660 described species of extant myriapods (Borror et al. 1989). When compared to the extensive taxonomic diversity of other major terrestrial arthropod clades, namely the approximately 876,000 known hexapods and the 65,000 known arachnids (spiders, mites, and relatives) (Borror et al. 1989), myriapods are relatively undiverse. Of described extant species, 10,000, or 73 percent, are diplopods and 3,000, or 22 percent, are chilopods. Because myriapods are rarely of economic consequence, myriapodologists are significantly underrepresented when compared to the more economically applied fields of entomology and arachnology. This, in addition to major difficulties in recognizing genera and species of many myriapod groups, suggests that a significant hidden diversity probably exists for myriapods. As for past levels of diversity, the lack of a sufficiently diverse and abundant fossil record has prevented a robust evaluation. However, relative to insect diversity, documented myriapod diversity was greater during the Devonian and Early Carboniferous.

Biogeography

Myriapods have poor powers of dispersal, a reflection of several attributes, including an aversion to certain barriers such as deserts and the inability to fly. Consequently, myriapods, especially larger forms, have a high potential for delineating biogeographic pat-

Table 1.

Geochronologic Distribution of Myriapod Orders[1]

Order[2]	Common Name	First Occurrence[3]	Last Occurrence[3]
		Kampecarida	
Unnamed	kampecarids	Silurian (Pridoli)	Devonian (Lokhovian)
		Diplopoda	
Unnamed		Silurian (Pridoli)	Silurian (Pridoli)
Euphoberiida[4]	giant spined millipeds	Carboniferous (Moscovian)	Carboniferous (Kasimovian)
Polyxenida	bristly millipeds	Paleogene (Priabonian)	Recent
Glomerida	pill millipeds	Paleogene (Priabonian)	Recent
Amynilyspedida	pill millipeds	Carboniferous (Moscovian)	Carboniferous (Kasimovian)
Sphaerotheriida	sphaerotherids	Carboniferous (Moscovian)	Recent
Spirobolida	spirobolids	?Carboniferous (Moscovian)	Recent
Polyzoniida	polyzonids	Paleogene (Priabonian)	Recent
Julida	snake millipeds	Paleogene (Priabonian)	Recent
Spirostreptida	spirostreptids	?Carboniferous (Late)	Recent
Callipodida	callipodids	Paleogene (?Chattian)	Recent
Chordeumida	chordeumids	Paleogene (Priabonian)	Recent
Polydesmida	flatbacked millipeds	Paleogene (Priabonian)	Recent
[Uncertain]		Carboniferous (Moscovian)	
		Symphyla	
Scolopendrellida	scolopendrellids	Paleogene (Priabonian)	Recent
Scutigerellida	scutigerellids	Paleogene (Chattian)	Recent
		Chilopoda	
Devonobiomorpha	devonobiomorphs	Devonian (Givetian)	Devonian (Givetian)
Scutigeromorpha	scutigeromorphs	Silurian (Pridoli)	Recent
Lithobiomorpha	stone centipeds	Paleogene (Priabonian)	Recent
Geophilomorpha	soil centipeds	Paleogene (Priabonian)	Recent
Scolopendromorpha	scolopendromorphs	Carboniferous (Moscovian)	Recent
		Arthropleuridea	
Arthropleurida	arthropleurids	Devonian (Emsian)	Carboniferous (Kasimovian)

Notes

[1] This list is modified slightly from Ross and Briggs (1993). The Pauropoda lack a fossil record.

[2] The classification is from Hoffman (1969).

[3] Epoch and stage names are from Harland et al (1990).
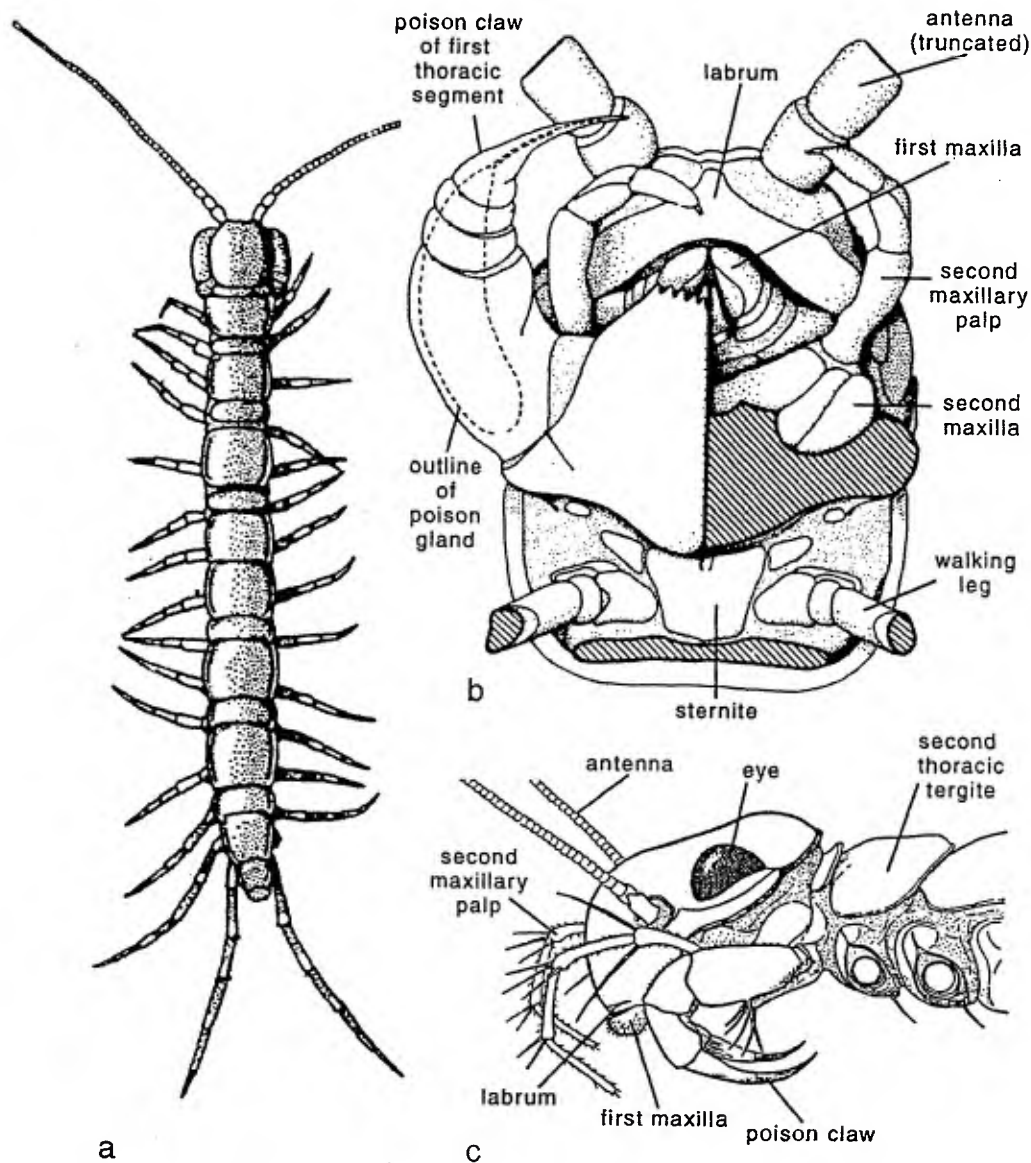
[4] This is the Archipolypoda of some authors.

Figure 5. Major external features of the myriapod class, Chilopoda. *a*, dorsal view of the body of the lithobiomorph centiped *Lithobius*; *b*, ventral view of head and mouthparts of *Lithobius*; *c*, left lateral view of head and anterior trunk region of the scutigeromorph centiped, *Scutigera*. From: *a*, *b*, Lewis (1981), reprinting granted by Cambridge University Press, from J.G.E. Lewis, *Biology of Centipedes* (1981), Figs. 3 and 4; *c*, reprinted from Snodgrass (1952), copyright © 1952 by Cornell University Press, used by permission of the publisher, Cornell University Press.

terns. Myriapod biogeography is in its infancy, and only a small fraction of this potential has been explored, principally in the context of Late Cenozoic environmental change. Nevertheless, tentative conclusions can be made from the fossil record. For example, Late Silurian and Devonian kampecarids and eoarthropleurids are found only in several localities adjacent to marine deposits in Europe and North America, called Laurussia to indicate the single continent once encompassing both of these areas. These animals occur amid other early terrestrialized arthropods such as springtails, bristletails, trigonotarbid spiders, and mites. Kampecarids were probably connected to aquatic habitats, whereas eoar-

thropleurids were more terrestrialized. During the Late Carboniferous the presumed eoarthropleuriid descendants, the arthropleurids, are also found in Laurussia but apparently were confined to interior equatorial basins, amid vegetation rooted in mineralic substrates. One report records arthropleurids from the smaller paleocontinent of Kazakhstania, northeast of Laurussia, and at a more temperate latitude.

Gondwanaland was the major continent occupying the Southern Hemisphere at this time; it has since split into Africa, Antarctica, Australia, India, and South America. The Gondwanan distributional patterns of some extant myriapods provide evidence

for Mesozoic taxa that still occur today. For example, the Spiros-treptidae occur in the tropics of Africa, Madagascar, and Central and South America, whereas the Harpagophoridae inhabit south-eastern Africa, Madagascar, Australia, New Zealand, and South-east Asia. These extant occurrences indicate broad Mesozoic distributions across Gondwanaland prior to its breakup during the Early Jurassic. One of the products of that breakup, India, formed the Himalaya Mountains as it became subducted under the south-ern margin of Eurasia. An analysis of the forest diplopod fauna of the Himalayas has revealed two fundamental biogeographic ele-ments that originated during the Early Cenozoic. One is a lowland diplopod fauna originating in the southeast, from western China and Indochina, and the other is a highland fauna emigrating from western Asia. Both immigrant faunal elements invaded the Hima-layas and subsequently diversified during the Pliocene and Pleis-tocene into the highly endemic fauna of today.

Functional Morphology

Myriapods derive their name from a multiplicity of trunk append-ages, and the role of these appendages in locomotion and copula-tion has inspired research in functional morphology—the analysis of form and its function. For example, biologists have speculated about the number of trunk walking legs in the ancestral myriapod. Suggestions have included a few pairs borne by short bodies to numerous pairs attached to long, winding bodies. An experimental solution to this question indicated that if the desirable trait was significant thrust involved in protracted burrowing, then numer-ous segments were necessary to gain purchase on the substrate for exertion of major physical forces. If rapid running is the optimized feature, then a small number of leg pairs is favored. However, it turns out that for a terrestrial running arthropod that has more than three pairs of walking legs, the answer is more complicated. Studies by Manton (1977) and others indicate that the distribu-tion of body weight across the pairs of legs is critical. Evidently, 13 pairs of legs is optimal, resulting in the fastest gaits.

Related to appendage number are the several gross specializa-tions of body form that characterize major myriapodan life habits. Combinations such as trunk segment number, a flattened or circular body cross section, and the length, articulation, segmentation, and musculation of the legs are important for determining how myria-pods feed, hunt prey, avoid prey, and seek shelter. In this context, the bulldozer life habit of julid diplopods is accomplished by a cylindri-cal body with numerous legs to provide forward thrust. In contrast, the geophilomorph centipede's burrowing life habit minimizes leg contact with the substrate but instead provides earthwormlike pro-pulsion by the interface of a flexible body surface with the soil sub-strate. The cursorial life habit of scolopendromorph and lithobiomorph centipedes, which rapidly run after and pursue other predators, is effected by numerous long legs and flattened bodies to penetrate narrow crevices. Scutigeromorph centipedes are active pursuit predators that modified this morphology by reducing leg pair number to an optimum for achieving high speed. The symphy-lan life habit of living among soil particles is conditioned by extreme trunk flexibility to achieve forward movement by twisting and turn-ing rather than by leg-directed thrust.
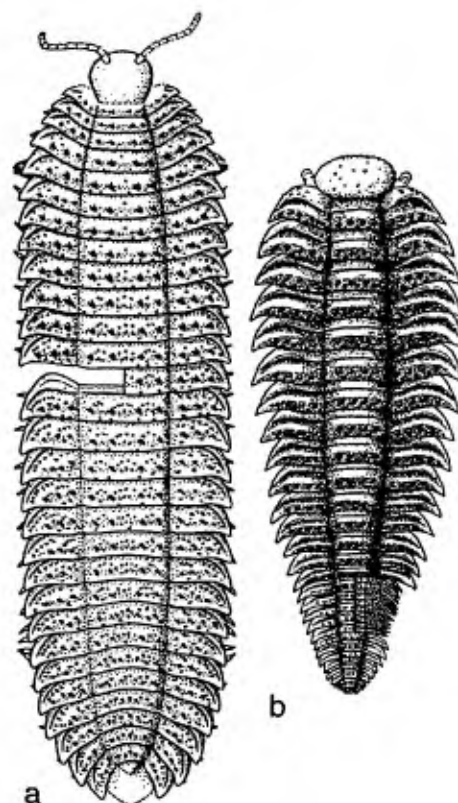

Figure 6. Dorsal views of adult and juvenile arthropleurids. a, dorsal view of adult *Arthropleura armata;* total body length approximately 1.8 meters; b, dorsal view of juvenile instar of *Arthropleura;* total body length approximately four centimeters. The reconstruction of the adult is shown with one pair of walking legs per functional segment, whereas recent data indicates that two walking legs occurred per functional segment, as illustrated in the juvenile. From: a, Rolfe and Ingham (1967), reprinted with permission from the *Scottish Journal* of *Geology,* volume 3, page 121; b, Briggs and Almond (1994).

Certain trunk appendages are modified for copulation, such as claspers, which males use for grasping the female during sperm transfer. Carboniferous euphoberiids have extensive spines along the sides and back of the trunk, rendering impossible the typical diplo-pod behavior of copulation through intertwining. However, it was found recently that a modified midtrunk segment with elongate legs was present in several Late Carboniferous euphoberiid taxa (Hanni-bal 1995). This structure was most likely a pair of clasping append-ages used by males to grasp females without becoming impaled.

Interactions with Other Organisms

Virtually all interactions of myriapods with other organisms involve feeding or the avoidance of being eaten. The dietary reper-toire of myriapods is broad, but unlike insects and mites, they

rarely consume live plants and are largely confined to detritivory, a diet based upon the dead remains of other organisms, and to a lesser extent carnivory or the more eclectic spectrum of omnivory. Thus, myriapods are basically creatures of soil and litter. A few inhabit special habitats such as bark or fungi. Herbivory, the consumption of live plant tissue, has been documented only in a few diplopod species that consume roots or foliage, but such associations are either among rare detritivores or are confined to a handful of species. Most likely, myriapods never have had intimate or even diffuse associations with live plants during their evolutionary history. Myriapods typically are the prey of small vertebrates and large predatory arthropods.

Although we know the dietary spectra in detail for only a limited number of myriapod species, we can make broad characterizations. Diplopods are overwhelmingly detritivorous (Hopkin and Read 1992), although one family is insectivorous, and limited herbivory is known for a few pest species. Chilopods are almost exclusively carnivorous on other terrestrial arthropods and occasionally small vertebrates (Lewis 1981), indicated by the ubiquitous presence of poison glands on the first trunk segment (Figure 5). Depending on the higher-level taxon, chilopods are pursuit predators on the ground or will ambush prey in the soil or other cryptic habitats. Soil-inhabiting symphylans and pauropods are detritivorous on dead plants, but some will consume live rootlets (Snodgrass 1952; Eisenbeis and Wichard 1985). Arthropleurids were likely detritivores, as evidenced by the occurrence of macerated club-moss tissue in the gut of one specimen (Rolfe and Ingham 1967). It is highly likely that arthropleurids possessed symbiotic gut microbes to digest cellulose and perhaps lignin, similar to those documented in extant diplopods.

Fossil Record and History of Discovery

Five types of deposits account for virtually all myriapod fossils. In order of decreasing age, they are terrestrial deposits that border marine settings, ironstone nodules, bituminous coal and organic rich shales, amber, and mineral deposits associated with hot springs. These deposits represent relatively narrow windows of geologic time that preserve unique environments. No single deposit occurs throughout the 410-million-year-old myriapod fossil record, or even an appreciably long interval within it. Thus, what is presented are rare snapshots in time and space.

The earliest known deposits containing myriapods are Late Silurian and Devonian in age and are confined to the Old Red Sandstone continent of Laurussia, in water-lain deposits adjacent to major ocean basins. These clastic deposits have yielded kampecarids, eoarthropleurids, diplopods, and chilopods. During the Late Carboniferous to Early Permian, two fossilization modes are overwhelmingly responsible for preservation of myriapods. The first is ironstone nodules from better-drained clastic environments such as Mazon Creek (Illinois) and Montceau-les-Mines (France), which represent lowland deltaic and associated environments in the humid equatorial tropics. The second is coals and organic-rich shales such as those, respectively, from the bituminous Gaskohle Formation of the Czech Republic and the Anthracite Basin of Pennsylvania. These environments contain euphoberiid diplopods

and were associated with swamp forests. After a prolonged hiatus during the Late Permian to Eocene, in which myriapod fossils are very rare, the next most notable occurrence is that of Mid-Cenozoic Baltic amber, which has yielded the most diverse assemblage of fossil myriapods, including the earliest occurrences of many modern lineages (Table 1). Rivaling this diversity is somewhat younger Dominican amber, which recently has yielded a diverse assemblage of myriapods. During the Late Cenozoic several hot spring deposits, most in the southwestern United States and central Europe, have preserved myriapods in mineral deposits, presumably by rapid entombment of individuals by mineral-laden waters.

The two most important students of fossil myriapods were Samuel Scudder and Anton Fritsch. Scudder, who described and interpreted the life habits of many Late Carboniferous myriapods from Mazon Creek, was the first to reveal the taxonomic and structural diversity of Late Paleozoic myriapods. Fritsch complemented Scudder's work on Late Paleozoic myriapods, focusing on the exceptional deposits at Nyrany, in the Czech Republic, documenting similar Laurussian myriapods from another equatorial environment. Several, mostly German, researchers during the early and mid–twentieth century described myriapods from Baltic amber, although this work has been extensively supplemented by recently documented amber from the Dominican Republic (e.g., Santiago-Blay and Poinar 1992). By the late 1960s there was a sufficient myriapod fossil record that a major summary was provided by R.L. Hoffman (1969). Recently, new and exquisitely preserved chilopods from the Middle Devonian Gilboa site of New York state have been documented by W.A. Shear and P.A. Bonamo (1988).

CONRAD C. LABANDEIRA

See also Terrestrialization of Animals

Works Cited

Almond, J.E. 1985. The Silurian-Devonian fossil record of the Myriapoda. *Philosophical Transactions of the Royal Society of London*, ser. B, 309:227–37.

Ballard, J.W.O., G.J. Olsen, D.P. Faith, W.A. Odgers, D.M. Rowell, and P.W. Atkinson. 1992. Evidence from 12S ribosomal RNA sequences that onychophorans are modified arthropods. *Science* 258:1345–48.

Borror, D.J., C.A. Triplehorn, and N.F. Johnson. 1989. *An Introduction to the Study of Insects*. Philadelphia: Saunders College.

Briggs, D.E.G., and J.E. Almond. 1994. The arthropleurids from the Stephanian (Late Carboniferous) of Montceau-les-Mines (Massif Central-France). *Mémoires de la Section des Sciences* 12:127–35.

Briggs, D.E.G., R.A. Fortey, and M.A. Wills. 1992. Morphological disparity in the Cambrian. *Science* 256:1670–73.

Eisenbeis, G., and W. Wichard. 1985. *Atlas on the Biology of Soil Arthropods.* New York and Berlin: Springer; as *Atlas zur Biologie der Bodenarthropoden,* Stuttgart: Fischer Verlag, 1985.

Friedrich, M., and D. Tautz. 1995. Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature* 376:165–67.

Fryer, G. 1996. Reflections on arthropod evolution. *Biological Journal of the Linnean Society* 58:1–55.

Hahn, G., R. Hahn, and C. Brauckmann. 1986. Zur Kenntnis von Arthropleura (Myriapoda; Ober-Karbon). *Geologica et Palaeontologica* 20:125–37.

Hannibal, J.T. 1984. Pill millipedes from the Coal Age. *Field Museum of Natural History Bulletin* 55:12–16.

———. 1995. Modified legs (clasping appendages?) of Carboniferous euphoberiid millipeds (Diplopoda: Euphoberiida). *Journal of Paleontology* 69:932–38.

———. 1997. Myriapods and arthropleurids. *In* C.W. Shabica and A.A. Hay (eds.), *Richardson's Guide to the Fossil Fauna of Mazon Creek.* Chicago: Northeastern Illinois University Press.

Harland, W.B., R.L. Armstrong, A.V. Cox, L.E. Craig, A.G. Smith, and D.G. Smith. 1990. *A Geologic Time Scale: 1989.* Cambridge and New York: Cambridge University Press.

Hoffman, R.L. 1969. Myriapoda, exclusive of Insecta. *In* R.C. Moore (ed.), *Treatise of Invertebrate Paleontology.* Part R, *Arthropoda 4, 2.* Boulder, Colorado: Geological Society of America; Lawrence: University of Kansas.

Hopkin, S.P., and H.J. Read. 1992. *The Biology of Millipedes.* Oxford: Clarendon; New York: Oxford University Press.

Kraus, O., and M. Kraus. 1994. Phylogenetic system of the Tracheata (Mandibulata): On "Myriapoda"-Insecta interrelationships, phylogenetic age and primary ecological niches. *Verhandlungen des Naturwissenschaftenlichen Vereins in Hamburg (N.F.)* 34:5–31.

Lewis, J.G.E. 1981. *The Biology of Centipedes.* Cambridge and New York: Cambridge University Press.

Manton, S.M. 1977. *The Arthropoda: Habits, Functional Morphology, and Evolution.* Oxford: Clarendon Press.

Rolfe, W.D.I. 1969. Arthropleurida. *In* R.C. Moore (ed.), *Treatise of Invertebrate Paleontology.* Part R, *Arthropoda 4, 2.* Boulder, Colorado: Geological Society of America; Lawrence: University of Kansas Press.

Rolfe, W.D.I., and J.K. Ingham. 1967. Limb structure, affinity, and diet of the Carboniferous "centipede" Arthropleura. *Scottish Journal of Geology* 3:118–24.

Ross, A.J., and D.E.G. Briggs. 1993. Arthropoda (Euthycarcinoidea and Myriapoda). *In* M.J. Benton (ed.), *The Fossil Record 2.* London and New York: Chapman and Hall.

Santiago-Blay, J.A., and G.O. Poinar Jr. 1992. Millipeds from Dominican amber, with the description of two new species (Diplopoda: Siphonophoridae) of Siphonophora. *Annals of the Entomological Society of America* 85:363–69.

Schneider, J., and M. Barthel. 1997. Eine Taphocoenose mit Arthropleura aus dem Rotliegend (?Unterperm) des Döhlen-Becken (Elbe-Zone, Sachsen). *Freiberger Forschungsheft,* ser. C, 466:193–223.

Shear, W.A., and P.A. Bonamo. 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. *American Museum Novitates* 2927:1–30.

Snodgrass, R.E. 1952. *A Textbook of Arthropod Anatomy.* Ithaca, New York: Cornell University Press.

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. *Molecular Biology and Evolution* 8:669–86.

Weygolt, P. 1979. Significance of later embryonic stages and head development in arthropod phylogeny. *In* A.P. Gupta (ed.), *Arthropod Phylogeny.* New York: Van Nostrand Reinhold.

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

Further Reading

Borror, D.J., C.A. Triplehorn, and N.F. Johnson. 1954. *An Introduction to the Study of Insects.* New York: Rinehart; 6th ed., Philadelphia: Saunders College.

Gupta, A.P. (ed.). 1979. *Arthropod Phylogeny.* New York: Van Nostrand Reinhold.

Hopkin, S.P., and H.J. Read. 1992. *The Biology of Millipedes.* Oxford: Clarendon; New York: Oxford University Press.

Lewis, J.G.E. 1981. *The Biology of Centipedes.* Cambridge and New York: Cambridge University Press.

Manton, S.M. 1977. *The Arthropoda: Habits, Functional Morphology, and Evolution.* Oxford: Clarendon.

Moore, R.C. (ed.). 1969. *Treatise of Invertebrate Paleontology.* Boulder, Colorado: Geological Society of America; Lawrence: University of Kansas Press.

Snodgrass, R.E. 1952. *A Textbook of Arthropod Anatomy.* Ithaca, New York: Cornell University Press.