Quick Guide
Myriapoda

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IN BRIEF: Paul Marek and William Shear introduce the arthropod sub-phylum Myriapoda, which includes centipedes, millipedes and other multi-legged animals.

What is a myriapod? A myriapod is a many-legged terrestrial arthropod in the subphylum Myriapoda. Myriapods include centipedes, millipedes, and the poorly known symphylans and pauropods. Among the most spectacular myriapods are species that glow in the dark, dangle from the ceiling of caves and seize bats from the air, or roll up into a baseball-sized sphere for defense against predators. The name Myriapoda means 'countless feet'. All species have over eight pairs of legs as adults; millipedes have 34 – 1306 individual legs, centipedes: 30 – 382, pauropods: 16 – 22, and symphylans: 12. *Eumillipes persephone*, a millipede discovered 60 meters below ground in Australia, has the most legs of any animal with 1306.

When did myriapods originate?
The first evidence of land animals are late Silurian fossil millipedes from 425 million years ago. Molecular clock analyses date the origin of myriapods to the Cambrian. This earlier date coincides with probable marine myriapod taxa from that time, and millipede burrows first appear in late Ordovician sediments. Myriapods were nearly fully adapted to life on land over 45 million years earlier than vertebrates such as *Tiktaalik*. Fossil myriapods represent the first case of an animal breathing atmospheric oxygen and the earliest instances of an intromittent organ and chemical defenses on land. Some fossilized myriapods were among the largest arthropods ever to exist, reaching up to 2.63 meters in length and weighing an estimated 50 kg. Myriapods and their close relatives, hexapods and crustaceans, make up the Mandibulata (mandible-bearing arthropods), the most species diverse group of animals on the planet with over one million species.

Why so many legs?
Myriapods, like their mandibulate relatives, originated from many-legged ancestral marine species. During the earliest diversification of arthropods, most lineages bore numerous legs ($\geq$10) for metachronal swimming. The metachronal wave gait of millipedes, a primitive style of locomotion, is likely to be a vestige of this metachronal swimming using the paddle-like legs of their marine ancestors. In a metachronal wave gait, each leg pair steps with a slight phase difference between the adjacent pairs, imparting a traveling wave phenomenon that propagates from the hind to the front legs and propels the animal's body forward. In millipedes, legs are in bilateral phase symmetry, an adaptation for burrowing, but in centipedes the legs have a 180° phase asymmetry for running. Subsequently, and from their many-legged ancestors with fairly uniform limbs, specialized limbs originated in myriapod groups such as centipedes, with

their first walking legs modified into venom jaws (forcipules), and helminthomorph millipedes, with their eighth leg pair modified into gonopods, intromittent organs for transferring sperm; a 414 million-year-old fossil, exhibits the first occurrence of an intromittent organ on land. Centipedes, symphylans, and pauropods primarily use their multiple legs for locomotion. These classes have one pair of legs per segment, although dorsal plates may cover more than one pair of legs to confer rigidity to the body while running. In the case of millipedes, a unique feature is the fusion of the ancestral single leg-bearing segments into segments with two pairs of legs termed ‘diplosegments’. Diplosegmentation is implicated in the origin of burrowing; further fusion of the plates that comprise the diplosegment (tergites, pleurites and sternites) into a fully coalesced ring in the millipede group Juliformia makes burrowing efficiency even greater. Called “bulldozer ecomorphs,” juliformian millipedes are the strongest burrowers, using their power to push through the soil with brute force. Other ecomorphs include wedgers and bark dwellers. For burrowing deeper underground, the squeezer or borer ecomorph is exhibited by super-elongated millipedes such as *E. persephone*. These 700+ legged millipedes have primitively unfused rings that are compressible, an extensible trunk, and flexible body, allowing them to squeeze through narrow underground crevices. The continuous metachronal wave gait and biomechanical action of concentric tubular diplosegments sliding within one another provide continuous pushing force. In combination with the many legs, longitudinal and oblique muscles pull the rings together, facilitating forward locomotion. This accordion-like fashion of burrowing resembles that used by earthworms and centipedes of the order Geophilomorpha, another group of greatly elongated myriapods that includes the leggiest centipede, *Gonibregmatus plurimipes* from Fiji with 191 segments and 382 legs. Pauropods are tiny (ca. 2 mm long), pale, blind litter-dwelling myriapods. Evolutionary sister to millipedes, they share features, such as a limbless collum immediately behind the head, hatchlings with 6 or 12 legs and a gnathochilarium—a bottom lip-like mouthpart. Symphylans, which share the same microhabitat with pauropods are small (ca. 6 mm long), pale, blind myriapods with spinnerets and an unusual mating behavior, in which the male leaves stalked spermatophores for the female to find and store in her head.

How do myriapods avoid predators?

Fossil myriapods show the first evidence of chemical defenses on land. In a 385 million-year-old fossil millipede, ozopores, openings of chemical defense glands, are present on rings along the length of the body. Symphylans and pauropods, which lack chemical defenses, likely run and hide from predators, and centipedes are defended with hypodermic, needle-like venom jaws. (Some centipede venom has experimentally been shown to be a more effective pain reliever than morphine.) Other centipedes are capable of producing a bioluminescent mucus from their undersides, probably to misdirect or entangle their predators. Millipedes are chemically defended with toxins such as hydrogen cyanide, alkaloids, phenols, cresols, quinazolinones, and benzoquinones. Some cyanogenic millipedes are capable of producing 600 μg of hydrogen cyanide, 18X the amount lethal to a pigeon-sized bird. With the phylogeny of millipedes and identification of their chemical defenses, researchers have traced the evolution of chemicals from an ancestral phenol-like precursor to complex and higher molecular weight molecules such as (1),7-(4-methylpent-3-en-1-yl)-1,2,3,5,8,8a-hexahydroindolizine. Some millipede chemical defenses have a mode of action similar to methaqualone muscle relaxants, and some members of the millipede order Platydesmida produce some of the most structurally diverse and bioreactive chemicals of the subphylum. Capuchins and lemurs learned of the toxicity and insect repellency of millipedes defended with benzoquinone and anoint their own fur with recently disturbed millipedes for protection against biting insects. Other millipedes use mechanical means of defense; for example, using hooked bristles that ensnare ants and the ability to roll into a defensive ball like an armadillo. Upon the backs of some millipedes in Colombia, grow lichens, bryophytes, and liverworts, perhaps as a form of adaptive camouflage.

Why study myriapods?

Myriapods play an especially important function in ecosystems. Centipedes are carnivorous predators that are natural enemies of pest species, thus maintaining community composition. Millipedes are important detritivores; by feeding on decaying leaves, wood and other detritus, they break up organic material, freeing up nutrients for biogeochemical cycling. Based on natural history observations, scientists described the astounding composting abilities of *Narceus americanus*, the ironworm millipede. They estimated that this species annually produces over two tons of compost per acre of forest. From a soil conservation perspective, maintaining the detritivore community (millipedes, fungi, earthworms, *etc.*) is critical for ecosystem health. Myriapods have roamed Earth for more than 500 million years, but we know little about them. There are about 13,000 described millipede species; researchers estimate that as many 65,000 species may exist. Some myriapods are extremely small (1 – 2 mm long), and there are few experts to study them, so even discoveries in familiar places are probable. Backyard discoveries of larger millipedes are also common; for example, a new species, a rather large 20 mm-long millipede, was discovered on the campus of Virginia Tech in 2021 and named *Nannaria hokie*. Some species are restricted to tiny geographical areas, occurring nowhere else on Earth. Micro-range endemic species are limited to ≤1000 km^2 and can occur in regional mosaics. Overly prone to extinction, even small disturbances can cause significant losses of species diversity. Loss of an ecologically significant detritivore, or a millipede with a new bioreactive chemical that might inspire a new medication is devastating enough; larger scale extinction seriously threatens nature's resilience and biodiversity that has persisted for over 500 million years. *Eumillipes persephone* was discovered last year under 60 meters of semiarid desert soil in a resource-rich region of Australia and is imminently threatened by surface mining. Interesting and new myriapod discoveries await discovery by taxonomists, and their conservation is critically important. Without robust conservation, documentation, and taxonomic description, many species of millipedes will continue undergoing anonymous extinction.

Figure 1. Representatives of the four classes of the subphylum Myriapoda. Diplopoda, millipedes (top); mimic species *Brachoria gracilipes* and *Apheloria virginiensis corrugata*. Symphyla, symphylans or garden centipedes (middle left); *Hanseniella caldaria*. Pauropoda, pauropods (middle right); *Donzelotauropus* sp. Chilopoda, centipedes (bottom); *Strigamia branneri*. [*H. caldaria* photo by S. Chiyoda.]

Where can I find out more?

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