DIPLOPODA — GENERAL MORPHOLOGY

BY

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THE MILLIPEDE BODY — SHAPE AND STRUCTURE

The body of millipedes consists of a head and a largely homonomous trunk composed of units generally called diplosegments or rings. Most trunk rings are typically equipped with two pairs of segmented legs each (diplopodous). The legs are articulated to the trunk paramedially on its ventral side. The total number of leg pairs in adults ranges from 11 up to 375. Body size of adults varies conspicuously; extant species include dwarves with a body length of only 1.4 millimeter as well as giants reaching body lengths of more than 30 cm (Hoffman et al., 2002).

The body is usually elongate. Most common forms are (sub-) cylindrical and worm-like, short-legged and capable of enrolling into a tight spiral when disturbed; or are broadly flattened (flat-backed) and equipped with lateral wing- or keel-like cuticular extensions of the body wall called paranota that may cover the legs. Anterior and/or posterior ends of the body taper in some species. The head may be partially or entirely hidden by the anteriormost body ring(s). The most posterior unit of the body (telson) bears the anal opening and lacks legs but may be equipped with filamentous outgrowths (‘spinnerets’) onto which fibre-producing glands open. The telson usually forms the rear of the body; in some species it is hidden by the posteriormost body ring(s). Paired genital openings (gonopores) lie medioventrally in the anterior part of the trunk (progoneate condition). In females the gonopores open on eversible devices called vulvae, which are sometimes transformed into elongate ovipositors or into sclerotized, leg-like appendages called cyphopods. In males the gonopores lie directly on leg bases or on paired, rarely unpaired penes. Males that transfer sperm directly onto females show specialized legs for copulation: gonopods closely behind the body ring bearing the gonopores/penes (Helminthomorpha), or modified ultimate legs called telopods (Pentazonia). Spiracles (tracheal openings, also called stigmata) occur close to the leg bases on stigmatic plates. Openings of repugnatorial glands (ozopores) may be present as an unpaired, inconspicuous row along the dorsal midline (Pentazonia: Glomerida), or as paired rows in the lateral...
body wall (Helminthomorpha); in juliformian millipedes they often form a conspicuous longitudinal line of dots on each side of the trunk.

The exoskeleton is soft in penicillate millipedes only; in all other millipedes (Chilognatha), as far as known (reviewed by Enghoff, 1990), the cuticle becomes calcified and therefore hard and rigid in the course of their postembryonic development. The body surface may either be largely smooth, variably microsculptured (e.g., Akkari & Enghoff, 2011), or ornamented with prominent cuticular tubercles, ridges, or spines as in the “dragon millipedes” (e.g., Likhitrakarn et al., 2015). Rarely is the body surface densely covered by setae, as in the thread-like *Mitocybe* species (Platydesmida) (Shelley, 2010). Distinct, often aposematic colouration or colour patterns (longitudinal bands, transverse stripes, or spots) are widespread in millipedes (reviewed by Enghoff, 2011), especially in polydesmidans (e.g., Marek & Bond, 2009) and generally in tropical species. Millipedes of temperate zones are more uniformly brown, gray or black. Some lack pigmentation entirely such as species inhabiting caves.

**FUNCTIONAL TYPES**

Since Manton’s studies on the functional morphology of millipedes (summarized in 1977) five main types of body shapes are related to particular life habits and distinguished as *Lebensformtypen* (e.g., Dunger, 1993), *ecomorphological types* (Hopkin & Read, 1992), or *morphotypes* (Kime & Golovatch, 2000; Golovatch & Kime, 2009). Three of them concern different specializations to burrowing life habits: *Bulldozers or rammers* are represented by cylindrical forms with numerous short walking legs and a broad front end, as exemplified by the Juliformia. The front end of the trunk forms a rigid cap used as a ram with the head bent underneath, followed by a stiff, largely inflexible trunk with an even width made of round, relatively short, telescopically invaginated and incompressible body rings. The power needed by the walking legs to push the body through substrate is optimized by the relatively broad size of the path determined by the front end, and by the minimal resistance of the body rings and legs against the penetration of the substrate. In millipedes of the *wedge type*, as represented by the Polydesmida, a tapering front end facilitates entering crevices. The stiff, incompressible body rings are equipped with paranota that broaden the rigid, flat backs and provide a thrust to widen the penetrated crevice laterally in one plane, thus allowing for relatively longer and stronger legs; their power for pulling the body forward is two to five times greater than in juliformian millipedes (Manton, 1977). Another type of wedge-burrowing characterizes the *borers* among the Colobognatha and Nematophora. Borers have strongly tapering front ends, some also possessing keel-like paranota. They basically differ from the ‘flat-backed’ millipedes of the wedge type in the greater flexibility of their body rings that allows movements in an earthworm-like manner. The three main types of burrowers among millipedes show considerable variation and include transitional forms, such as juliformian species with tapered front ends (Manton, 1977) as well as ‘habit reversals’ like fast-running species among the Callipodida (Dunger, 1993) and other species that apparently abandoned burrowing in favour of a surface active lifestyle (Shelley, 1999).