

Defining Features of Nominal Clades of Diplopoda

Morphological descriptions of various millipede groupings are scattered in several works, span over 100 years and several languages. A critical compilation identifying putative apomorphies is needed since some of these morphological features are employed in various discussions on diplopod and myriapod phylogeny. For each nominal clade, we give putative morphological autapomorphies (PA), distinguished from other characters (OC), which may help to recognize the group. The morphological features that may represent putative apomorphies are often known from only a handful of species; a thorough taxon sampling with regards to these characters is required. The listing of the nominal clades follows the currently assumed phylogenetic hierarchy (see Figures 2 and 4 on the Milli-PEET web site, Page: Millipede Systematics). Abbreviations:

TO=Tömösvary organ, LP= leg pair; BR=Body ring(s); LTS=median longitudinal tergite suture; S-T= sperm transferring.

Pauropoda. – PA: branched antennae with segmented stalk and unique sense organ (Globulus). Putative synapomorphies with Diplopoda: collum segment (with leg rudiments in Pauropoda); dignath condition, Maxille1 forming a gnathochlarium-like plate; tracheal system (only in the Hexamerocerata). OC: TO present (called Pseudoculus in Pauropoda); ocelli absent; some tergites enlarged, covering two segments; 9-11 leg-bearing trunk segments; animals small.

Diplopoda. – PA: diplosegements of the trunk; legless collum segment; four antennal sense cones; aflagellate sperm.

Penicillata (Pselaphognatha, bristle millipedes). – PA: serrated setae arranged in tufts; head with transverse suture between antennae and ocellar clusters. OC: Cuticle soft, uncalcified; sternites, pleurites and tergites connected by membranes; head with trichobothria; BR2 and BR3 with spiracles; tracheae branched; mouth parts reduced, gnathochilarial palps large. TO small; most genera with ocelli. Animals small (a few millimeters); 11 -13 BR, 13-17 LP; neither gonopods nor telopods; no copulation, males with long penes at coxa of LP2, deposit a spermatophore.

Chilognatha. – comprises 15 millipede orders. PA: cuticle calcified; trichobothria absent; coxae of first leg pair fused to sternite in females.

Pentazonia (Opisthandria). – comprises orders Sphaerotheriida, Glomerida, Glomeridesmida. PA: sternites divided (see Regier, Wilson & Shultz, 2005, for alternative albeit unsubstantiated interpretation); labrum with single median tooth; lamellae linguales of gnathochilarium fused; mandible with molar plate process (Wesener & Sierwald, 2005); last tergite (Pygidium) enlarged covering anal segment. OC: head capsule lacks transverse median suture; TO present; tergites, pleurites and sternites free; spiracles present on BR2 and BR3, without closure mechanism; tracheae branched; LTS absent. At least last leg pair in males modified to telopods; the homology of these between Sphaerotheriida and Glomerida (=Oniscomorpha) on one hand and Glomeridesmida on the other hand is uncertain, even unlikely, since they are located on non-homologous segments. Regier et al. (2005) suggest that modified appendages at the body end of the fossil *Microdeceplex* may represent telopods (which would make this character symplesiomorphic for Pentazonia); however the very limited known

morphological details of these modified appendages do not substantiate such a homology assumption.

Glomeridesmida (superorder Limacomorpha). – PA: females with conspicuous, pleated ovipositor at coxa of LP2; last LP held straight out posteriorly. OC: 22BR; females 36 LP, males 35 LP and one pair of posterior telopods. TO large round pit; no ocelli. Order poorly known.

Oniscomorpha. – comprises orders Glomerida and Sphaerotheriida. PA: males with posterior telopods; Pygidium large. OC: up to 13BR; features adapted for volvation in both orders are unlikely to be homologous.

Glomerida. – PA: 2nd and 3rd tergites fused forming a large shield (=12 apparent BR); TO horseshoe-shaped; few ocelli in a row; dorsal repugnatory gland openings (unlikely to be homologous to lateral repugnatory glands of Helminthomorpha). OC: Gnathochilarium with cardines; antennae long and close to each other; small, 2.5-20mm, females 17 LP, males 19 LP; single pair of posterior telopods.

Sphaerotheriida. – PA: 2nd tergite enlarged forming a shield; 21 LP, males additionally with two pairs of telopods; gnathochilarium without cardines. OC: 13BR; TO small, round pit; many ocelli; antennae widely separated from each other, often with many apical sense cones. Males and females often with stridulatory organs at the posterior body end. Sphaerotheriida are among the heaviest millipedes known (*Zoosphaerium* sp. 49 grams, Wesener, pers. com.).

Helminthomorpha (Proterandria). – PA: lateral row of repugnatory gland openings starting at BR5; no spiracles on BR2 and BR3; tracheae not branched. OC: Lamellae linguales of gnathochilarium not fused; tergites consist of prozonum and metazonum;

undivided sterna; without posterior telopods and with gonopods in the anterior body region; gonopods in the supraordinal clades Colobognatha and Eugnatha most likely not homologous (different ontogeny, non-homologous appendages involved). The monophyly of most helminthomorph orders is undisputed, albeit not always supported by unambiguous apomorphies, characters of the male gonopod structure often serving as autapomorphies. However, primary homology hypotheses of gonopod elements are currently underdeveloped. Other character systems, such as the female gonopore opening and associated sclerites, are insufficiently known.

Colobognatha. – comprises orders Platydesmida, Siphonophorida, Polyzoniida and Siphonocryptida. PA: 2 pairs of leg-like gonopods with varying number of podomeres on BR7 (posterior pair, LP9 S-T) and BR8 (anterior pair, LP10); prospective gonopods modify step-wise over several molts (see Verhoeff, 1928. Klasse Diplopoda I. In *HG Bronn's Klassen und Ordnungen des Tierreichs* 5. 2. II. Leipzig, Ger.: Akademische Verlagsgesellschaft, pp 1071) (see Demange, 1967. Recherches sur la segmentation du tronc des chilopodes et des diplopodes chilognathes (Myriapodes). *Mèm. Mus. Nat. Hist. Nat. Ser. A* 44:188) from walking legs; gnathochilarial palps absent; lateral repugnatory glands tubular. OC: head distinctly narrower than body; at most one or two pairs of ocelli, labral teeth absent, TO absent; subanal scale absent (uncertain whether this is true for all species).

Typhlogena. – comprises orders Siphonophorida and Platydesmida; no PA defined (see Hoffman, 1982. Diplopoda. In *Synopsis and Classification of Living Organisms*).

Platydesmida. – PA uncertain: tergite-pleurites fused (state assumed non-homologous to Eugnatha); head triangular, with two less-pigmented lobes (not present in all species).

OC: gnathochilarium with basic set of sclerites, ocelli absent; long lateral tergite extensions (paranota), LTS present; 50 to 60 BR (up to 110); up to 60mm; animals rather flat.

Siphonophorida. – PA: head prolonged into a long ‘beak,’ mandibles strongly modified; body densely setose. OC: ocelli absent, gnathochilarium without basic set of sclerites; tergite-pleurites free; body narrow, no paranota, animals appear worm-shaped; LTS absent; up to 192BR; includes millipedes with the largest number of legs (Marek & Bond, 2006, *Nature*); up to 36mm in length.

Siphonocryptida. – PA: terga with transverse row of tubercles, tergite-pleurites fused (state assumed non-homologous to Eugnatha), lateral ozopores on the peritremata (see Enghoff & Golovatch, 1995. A revision of the Siphonocryptidae (Diplopoda, Polyzoniida). *Zoologica Scripta* **24(1)**, 29--41); telson completely covered by last tergite. OC: LTS present; body not setose; head cone-shaped, covered by large collum; gonopods with 6 (LP9) and 5 (LP10) podomeres; gnathochilarium not examined; up to 50BR; up to 10mm.

Polyzoniida. – PA: head cone-shaped, with one pair of macrosetae between antennal bases; with two large ocelli. OC: gnathochilarium without basic set of sclerites; tergite-pleurites free; LTS and paranota absent; body not setose but smooth and glabrous; head visible from above. Animals mostly small (less than 30mm long); more than 30 BR.

Eugnatha. – comprises all remaining millipede orders. PA: LP8 (anterior pair of BR7, Figure 1a) modified to gonopods, ontogenetic development via small bud-shaped primordial structures (see Verhoeff, 1928. Klasse Diplopoda I. In *HG Bronn's Klassen und Ordnungen des Tierreichs* 5. 2. II. Leipzig, Ger.: Akad. Verlag, pp 1071); tergite-

pleurites fused; globular defense glands. OC: gnathochilarium with palps and at least the sclerites stipities, lamellae linguales and mentum; stigmata often with closure mechanism.

Nematophora. – comprises orders Callipodida, Chordeumatida and Callipodida. PA: spinnerets at telson; tracheae leading to spinnerets branched, molar cusp at mandible (see Enghoff, 1984. Phylogeny of millipedes: a cladistic analysis. *Zoologische Zeitschrift für Systematik und Evolutionsforschung* **22(1)**, 8-26). OC: sternum free.

Coelocheta. – comprises orders Callipodida and Chordeumatida. PA uncertain: special structure of TO (Enghoff, Dohle & Blower, 1993. Anamorphosis in millipedes (Diplopoda): the present state of knowledge with some developmental and phylogenetic considerations. *Zoological Journal of the Linnean Society, London* **109**, 103-2340) (see Hennings C. 1906. Das Tömösvarische Organ der Myriopoden. II. *Zeitschrift für Wissenschaftliche Zoologie* **80**:576-641); mentum of gnathochilarium transversly divided (appears to be almost identical in both orders).

Callipodida. – PA: hypoproct divided into three sclerites; possibly the divided anal valves and characters in the female organs, i.e. the extrusable vulvae (Stoev and Enghoff pers. com.); characters of gonopod LP8, with large coxosternal elements, located deep inside body pouch. OC: TO small pit; ocelli grouped tightly, arranged in a triangle; LP9 unmodified; legs and antennae long and slender; LTS present; tergites in most species with longitudinal ridges and transverse row(s) of setae; 40-60 BR, 15-100 mm in length; tolerate drier habitats, are active foragers, some may be predatory.

Chordeumatida. – PA: 3+3 setal structure on tergites, coxal glands at least at LP11; ozopores absent; 26-32 BR. OC: TO small pit; body tapering towards end; LTS present;

LP8&LP9 gonopods, characteristic at suborder level (Chordeumatidea [*sensu* Shear, 2000. On the milliped family Heterochordeumatidae, with comments on the higher classification of the order Chordeumatida (Diplopoda). *Invertebrate Taxonomy* **14**, 363-376]); LP9 S-T, LP10 reduced, LP11 with coxal gland; Heterochordeumatidea LP9 S-T, LP10 reduced with coxal gland, LP11 with coxal gland; Craspedosomatidea and Striariidea LP8 S-T, LP9 modified, LP10 and LP11 with coxal glands); Chordeumatidea and (some?) Craspedosomatidea with complex spermatophores (see Verhoeff KW. 1910. Über Diplopoden. 19(39.) Aufsatz: Iuliden und Ascospemphora. *Jahreshefte des Vaterländischen Vereins für Naturkunde in Württemberg* **66**, 337-398) (see Shear WA. 1981. The milliped family Tingupidae (Diplopoda, Chordeumatida, Brannerioidea). *American Museum Novitates* **2715**, 1-20). Animals 3 to 35mm, paranota in some groups, many winter-active forms.

Stemmiulida. – PA: one or two large ocelli; LP2 in males strongly modified; characters of gonopod LP8, LP9 reduced; females with paired paramedian sperm receptacle separate from gonopores. OC: TO absent; gnathochilarium sexually dimorphic; animals very agile and can jump; more than 30 BR; up to 50 mm in length.

Polydesmida. – PA: 19-21 BR; finger-shaped organ at 7th antennomere; sternites fused without suture; ocelli absent; LP8 gonopod with cannula (absent in Rhachodesmidae and relatives); ozopores always absent on BR6; repugnatory glands with two compartments, production of cyanide. OC: TO pear-shaped; LP9 unmodified; number of ozopores reduced, in most members present at 5, 7, 9, 10, 12, 13, 15-18; often with paranota (lateral projections of the metazona); 3 to 130mm body length.

Juliformia. – comprises orders Julida, Spirobolida and Spirostreptida. PA: sternites fused to pleurotergites demarkated by suture; collum enlarged, covering posterior part of head capsule; spermatozoa with pseudoperforatorium; TO absent; produce benzoquinon containing defense secretions; OC: LP8&LP9 gonopods; LTS absent; animals mostly cylindrical, small to large.

Diplocheta. – comprises the orders Spirostreptida and Julida; no PA defined (see Hoffman, 1982. Diplopoda. In *Synopsis and Classification of Living Organisms*).

Julida. – PA: characters of gonopods LP8 and LP9, LP9 S-T; gnathochilarium structure unique, stipites of gnathochilarium adjacent; LP1 of males modified. OC: fresh specimens often with a fringe of setae around posterior end of each BR; median head suture line not extending to labrum; 30-90BR, animals small to moderate (10-120mm).

Spirostreptida. – PA: LP8 S-T. OC: gonopod structure characteristic for each suborder (Spirostreptidea and Epinannolenidea LP8 complex, withdrawn in pouch; LP9 reduced; Cambalidea LP8 not completely withdrawn, LP9 modified and not reduced); mentum of gnathochilarium large, located between stipites; median head suture line not extending to labrum; animals small (6mm) to very large (300mm), up to 90 BR. Note: The Cambalidea is most likely not a member of the Spirostreptida but may be closely related to the Julida (see Enghoff, 1979. Taxonomic significance of the mandibles in the millipede order Julida. In *Myriapod Biology*, ed. M Camatini, pp. 27--38. London: Academic Press).

Spirobolida. – PA: median head suture line extending to labrum; anterior legs moved orally, BR1 (=collum segment) to BR5 seemingly with a single leg pair each; characters of gonopods LP8 and LP9, LP9 S-T, OC: Spirobolidea gonopods in pouch, Trigoniulidea

gonopods extending outside the body; 35 to 60 BR; some Rhinocricidae up to 200mm in length.

Helminthomorpha incertae sedis

Siphoniulida. – PA: sternites fused (with suture); without ocelli or ozopores; characters of gonopod LP8 unique. OC: head drawn into a ‘beak;’ TO absent, LP9 unmodified; 30-40 BR; animals small (5–6 mm), resembling a large nematode.