Evolutionary Biology of Centipedes (Myriapoda: Chilopoda)

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Key Words
arthropod phylogeny, biogeography, evodevo

Abstract
New insights into the anatomy, systematics, and biogeography of centipedes have put these predatory terrestrial arthropods at the forefront of evolutionary studies. Centipedes have also played a pivotal role in understanding high-level arthropod relationships. Their deep evolutionary history, with a fossil record spanning 420 million years, explains their current worldwide distribution. Recent analyses of combined morphological and molecular data provide a stable phylogeny that underpins evolutionary interpretations of their biology. The centipede trunk, with its first pair of legs modified into a venom-delivering organ followed by 15 to 191 leg pairs, is a focus of arthropod segmentation studies. Gene expression studies and phylogenetics shed light on key questions in evolutionary developmental biology concerning the often group-specific fixed number of trunk segments, how some centipedes add segments after hatching whereas others hatch with the complete segment count, the addition of segments through evolution, and the invariably odd number of leg-bearing trunk segments.
INTRODUCTION

Centipedes (Chilopoda)—one of the four major lineages of myriapods—are an important group of predatory arthropods in many terrestrial habitats. They comprise approximately 3300 species belonging to the five extant orders illustrated in Figure 1, and one extinct order represented by a single species (84).

Centipedes are known from all continents except Antarctica, with the greatest diversity occurring in the tropics and warm temperate regions, and have a fossil record spanning 420 million years. Most species inhabit leaf litter and soil or are found under stones, bark, or wood in forests, although grassland, desert, caves, and the littoral zone are occupied by some species.

Centipedes are typically solitary except when brooding their eggs or hatchlings. Adult body length ranges from 4 to 300 mm, with most species measuring 10 to 100 mm long. They are almost exclusively predatory and, commensurate with their size range, in most cases feed on small live arthropods and other invertebrates, although large scolopendrids can take vertebrate prey (67). The prey is immobilized by venom injected from the poison glands, which are housed in a modified first pair of trunk legs (63). In all centipedes these legs are functionally incorporated into the head as a pair of maxillipeds (also called forcipulae), this modified pair of appendages being the most conspicuous shared derived character of Chilopoda. The majority of species are nocturnal, and they live most of their lives cryptically.

Centipedes have fascinated all kinds of biologists, including ecologists interested in their modes of life and biodiversity, biogeographers interested in understanding their current and past distributions, and systematists interested in the pivotal role of centipedes in understanding arthropod phylogeny. Evolutionary developmental biologists use centipedes as models to understand segmentation because of the uniqueness of the myriapod body plan based on its serial repetition of segments. In addition, centipedes are of medical importance owing to the presence of powerful neurotoxic venoms (11).

Aside from taxonomy and systematics, some of the most interesting topics in centipede evolution are the modes of development and the number of trunk segments, as well as the different modes of maternal care displayed by some centipede groups. The study of these characters and trends requires a sound understanding of centipede relationships. The typical centipede body plan includes six head segments followed by the pair of maxillipeds, a series of trunk leg-bearing segments with one pair of legs per segment, and two genital segments. The number of leg-bearing trunk segments (pairs of walking legs) varies between groups (Table 1). Several groups have 15 leg-bearing trunk segments, while some have up to 191 pairs of legs. Intermediate states with 21 and 23 pairs of legs occur in the scolopendromorphs, and in geophilomorphs the number of leg-bearing segments ranges from 27 to the aforementioned 191. Interestingly, this is always an odd number, so the number of trunk segments (including the maxillipede segment) is always even. The raw number of segments in each species can be fixed or it can vary within the different orders (Table 1). The number of leg pairs is conserved in the members of the orders Scutigeromorpha, Lithobiomorpha, and Craterostigmomorpha, whereas it varies slightly in Scolopendromorpha and enormously in Geophilomorpha. The number of segments has relevance to the development of models for segmentation, both within centipedes and in arthropods, questions that have recently received attention from the perspective of gene expression data in embryos (13, 45).

The addition of segments through development is another key question in centipede evolution, because some groups hatch with the complete adult number of segments (epimorphosis), whereas others add segments after hatching (anamorphosis) (see Sidebar). Whether epimorphosis or anamorphosis is
Figure 1

Life images of the five extant centipede orders. (a) Scutigeromorpha: Parascutigera sp., a scutigerid from Lane Poole Reserve (Western Australia). (b) Lithobiomorpha: Ceratobius japonicus, a henicopid from Mount Takao (Japan). (c) Craterostigmomorpha: Craterostigmus cf. tasmanianus from Mount Cook/Aoraki National Park (New Zealand). (d) Scolopendromorpha: Cormocephalus aurantiipes, a scolopendrid from Lane Poole Reserve (Western Australia). (e) Scolopendromorpha: Cormocephalus hartmeyeri from Porongurup National Park (Western Australia) brooding peripatoid stage hatchlings. (f) Geophilomorpha: Zelanophilus provocator, a geophilid from Hinewai Scenic Reserve (New Zealand). Photographs by the authors.
Table 1  Number of adult and hatchling leg-bearing trunk segments and mode of development

<table>
<thead>
<tr>
<th>Order</th>
<th>Adult</th>
<th>Hatchling</th>
<th>Development</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scutigeromorpha</td>
<td>15</td>
<td>4</td>
<td>Anamorphic</td>
</tr>
<tr>
<td>Lithobiomorpha</td>
<td>15</td>
<td>6–8 (7)*</td>
<td>Anamorphic</td>
</tr>
<tr>
<td>Craterostigmomorpha</td>
<td>15</td>
<td>12</td>
<td>Anamorphic</td>
</tr>
<tr>
<td>Scolopendromorpha</td>
<td>21–23</td>
<td>21–23</td>
<td>Epimorphic</td>
</tr>
<tr>
<td>Scolopocryptopidae</td>
<td>23</td>
<td>23</td>
<td>Epimorphic</td>
</tr>
<tr>
<td>Geophilomorpha</td>
<td>27–191</td>
<td>27–191</td>
<td>Epimorphic</td>
</tr>
<tr>
<td>Mecistocephalidae</td>
<td>47–101</td>
<td>47–101</td>
<td>Epimorphic</td>
</tr>
<tr>
<td>Adesmata</td>
<td>27–191</td>
<td>27–191</td>
<td>Epimorphic</td>
</tr>
</tbody>
</table>

*Value in parenthesis indicates most common number of hatchling leg-bearing trunk segments.

the primitive condition in centipedes has been extensively debated in the literature, but only through a rigorous phylogenetic framework can we understand this important evolutionary trend. Finally, some centipedes display maternal brood care, although whether the mother guards the brood with her sternal (ventral) or tergal (dorsal) regions is also of evolutionary significance.

In this article we review these important aspects of centipede evolutionary biology and place them in a phylogenetic context. We also revise the most current interpretations of the position of centipedes within the arthropod tree of life and focus on relationships between centipede orders, a topic that has received enormous attention from detailed morphoanatomical studies and their combination with multiple sources of molecular data. The intention of this review is to further the current understanding of this fascinating and ancient group of terrestrial arthropods, which plays a major role as predators in most terrestrial ecosystems.

CENTIPEDES AND ARTHROPOD PHYLOGENY

Myriapod Monophyly?

The position of centipedes in the arthropod tree of life is tied to a question concerning the monophyly of Myriapoda. In addition to Chilopoda, Myriapoda includes three other groups: Symphyla, Pauropoda, and Diplopoda. Symphylans and pauropods are relatively minor groups, known from only 200 and 700 species (1), respectively, whereas Diplopoda (millipedes) includes 11,000 described species (1). Pauropods and diplopods are nearly universally recognized as each others’ closest relatives, together forming the clade Dignatha, and most morphologists identify Symphyla as their sister group (16, 23, 54). Collectively these three myriapod classes comprise the clade Progoneata, named for the positioning of the genital opening anteriorly on the trunk, behind the second pair of legs—in contrast, Chilopoda are opisthogoneate, with the genital opening located terminally on the body, as in insects. The fundamental question over Myriapoda is then whether centipedes are part of a natural group with the progoneate myriapods (16). Recent studies using either morphology or molecular data have variably resolved myriapods as monophyletic (23, 36, 37, 79, 80), paraphyletic (53, 55, 71), or polyphyletic (57), although the case for monophyly is sustained by the largest amount of evidence.
Morphological arguments in favor of the monophyly of Myriapoda are principally derived from the structure and movements of the cephalic tentorial endoskeleton and the structure of the mandibles (23). The classic argument for myriapod monophyly is the abduction of the mandibles by the movements of the anterior tentorial arms, the so-called swinging tentorium (60). The tentorium of Chilopoda and Progoneata shares a common pattern of fusion of its posterior process to a transverse bar that extends to the lateral cranial wall (7, 52). Myriapod mandibles are structurally unique in that they are divided into a movable, independently musculated gnathal lobe and a base plate. The separation of the gnathal lobe is marked by a large flexor muscle with a common point of origin on the cranial roof.

**Mandibulata**

For most of the past century, most morphologists have united myriapods with hexapods and crustaceans on the basis of the shared presence of mandibles as the anterior-most adult mouthpart, formed from the appendages of the post-tritocerebral segment. This clade has been named Mandibulata. Mandibles are embedded in a chewing chamber in the head capsule; their musculature indicates a common identity as a coxal gnathobase, and they share similar substructures on their biting edge (30). Classical morphological arguments for the homology of mandibles have been strengthened by gene expression data. For example, mandibles are differentiated from other appendages in their gradient of decreasing expression of the homeobox-containing gene _distal-less_ through ontogeny (74, 82); the expression pattern of this gene as well as _dachsbrund_ (75) reinforces the uniformly gnathobasic identity of mandibles. In addition to the mandible itself, monophyly of Mandibulata finds support from the ultrastructure of the compound eyes, notably the presence of a crystalline cone composed of four cone cells, primary pigment cells, and interommatidial pigment cells that are found in scutigeromorph centipedes as well as in crustaceans and hexapods (69). Other evidence for a natural grouping of Mandibulata includes the expression patterns of Hox genes in the head [(45, 46); data for Chilopoda based on _Lithobius atkinsoni_), specific serotonin-immunoreactive neurons [(39); data for Chilopoda based on _L. forficatus_ and _Scolopendra_ sp.], the organization of the brain neuropils (40), and hemocyanin sequence data (56).

In the context of the Mandibulata hypothesis, myriapods have traditionally been united with hexapods to form a group named Atelocerata or Tracheata (54). The Atelocerata hypothesis has been seriously challenged by the analysis of molecular data, many kinds of which instead suggest a crustacean-hexapod grouping. These include sequence data for nuclear ribosomal genes (58), nuclear coding genes (79), mitochondrial genes (48), Hox genes (15), hemocyanin (56), or the combination of multiple loci and morphology (36, 37). Morphological support for a crustacean-hexapod clade includes several neurological characters, including brain structure (87), generation of ganglion mother cells by the mitotic division of neuroblasts (40), and specific early-differentiating neurons (20) and pairs of serotonergic neurons (39).

If hexapods are most closely related to—or derived from—crustaceans, as favored by virtually all kinds of molecular data and a suite of neurological characters, then there is little question that myriapods are monophyletic because the atelocerate characters [such as a limbless intercalary (tritocerebral) segment in the head, the ectodermally derived Malpighian tubules, and a cuticular cephalic tentorial endoskeleton] would serve as additional myriapod characters.

**Paradoxopoda**

A closer relationship between myriapods and chelicerates than either shares with hexapods...
or crustaceans has been found in some molecular studies, including analyses of nuclear ribosomal genes (58) as well as mitochondrial genes (48, 71, 73) and Hox genes (15). The myriapod-chelicerate group has been named Paradoxopoda (58) or Myriochelata (73) and has never been previously proposed on the basis of anatomical data.

The Paradoxopoda hypothesis conflicts with the substantial body of morphological support for Mandibulata and is itself without compelling morphological support. To date, the only suggestion for a myriapod-chelicerate group from the perspective of morphology is derived from a shared pattern of neurogenesis in a spider, a millipede, and a lithobiomorph centipede (19, 49). In each of these arthropods, the neural precursors form similar groups of cells that invaginate from the neuroectoderm. It cannot be ruled out that the myriapod-chelicerate pattern of neurogenesis is simply plesiomorphic for arthropods, in contrast to the shared role of neuroblasts in generating the neuronal precursor cells in crustaceans and hexapods (40).

The most comprehensively sampled analysis of combined morphological and molecular sequence data (37) support the monophyly of Mandibulata over more analytical conditions that support the Paradoxopoda hypothesis (14 versus 2), including the conditions that maximize overall congruence among all data. A crustacean-hexapod clade, Tetraconata, is also stable to analytical variation, and Myriapoda is monophyletic under most analytical regimes (Figure 2).

**MORPHOLOGY, MOLECULES, AND SYSTEMATICS OF THE FIVE EXTANT CENTIPEDE ORDERS**

Extant centipedes are grouped in five orders, all of which are currently recognized as monophyletic entities. In this section we discuss each of these orders and provide the evidence that has been used to support their monophyly.

**Scutigeromorpha**

Scutigeromorpha (Figure 1a) consists of 100 valid species (~200 named species) assigned to three families: Psellidiidae, Scutigeridae, and Scutigerinidae. The most familiar and best-studied species is *Scutigera*...
**Figure 3**

External morphological characters distinguishing Notostigmophora (*a, e, Scutigera coleoptrata; c, Theranoema tuberculata*) and Pleurostigmophora (*b, d, f, Lithobius obscurus*). (*a*) Domed head capsule, showing antennae (ant), compound eye (c.e), maxillipede (mxpd), and second maxillae (mx2). (*b*) Flattened head capsule, with cluster of ocelli (oc); other abbreviations as in *a*. (*c*) Maxillipeds, with flexible hinge between coxae indicated by arrow. (*d*) Maxillipeds, with coxae joined (arrow). (*e*) Head (at right) and first two tergal plates, showing spiracles (sp) opening dorsally. (*f*) Tergal plates 3–5, showing spiracles (sp) opening above leg bases. Scanning electron micrographs by Sue Lindsay (Australian Museum). Scale: 0.25 mm.

*coleoptrata*, a circum-Mediterranean native that is the synanthropic house centipede in many other parts of the world. The monophyly of Scutigeromorpha is amply supported by numerous unique characters (27). The antennae are multiannulated flagella usually composed of a few hundred ring-like articles (*Figure 3a*). The respiratory system features tracheal lungs opening to a spiracle on the posterior part of the tergites (*Figure 3e*)—in all other chilopods the spiracles open above the leg bases, at the sides of the body.
Scutigeromorphs are the only centipedes that use hemocyanin as the oxygen transport molecule (59). Eight elongate tergal plates cover the 15 pairs of trunk legs. Scutigeromorphs have faceted eyes (Figure 3a), the ultrastructure of which corresponds to ommatidia of the compound eyes of crustaceans and hexapods (69). The head contains several distinctive organs and glands (44).

Scutigeromorphs are remarkably fleet-footed, running at speeds of up to 40 cm s$^{-1}$ (61). Mothers lay single eggs, which are abandoned in the soil. Hatchlings have four pairs of legs and are active; the remaining segments are added through a series of molts.

### Lithobiomorpha

The order Lithobiomorpha (Figure 1b) includes 1100 valid species among more than 1800 named species. Its most familiar species is the common European and North American Lithobius forficatus. Two families are recognized, one principally Laurasian (Lithobiidae) and the other principally Gondwanan (Henicopidae). Lithobiomorpha is the only centipede order whose monophyly has been questioned, but ample evidence from morphology and molecular sequence data has accumulated in recent studies to defend the group’s monophyly (22, 25).

Lithobiomorphs are rarely more than 30 mm long and have 15 pairs of trunk legs. The head shield is flattened, with either a cluster of ocelli on each side of the head (in Lithobiidae) (Figure 3b) or a single ocellus on each side of the head (in Henicopidae). The antenna consists of 15 to more than 100 articles. The trunk has long tergites on leg-bearing segments 1, 3, 5, 7, 8, 10, 12, and 14 and short tergites on the alternating segments. Postembryonic development is anamorphic, as in scutigeromorphs, and eggs are likewise laid singly without maternal care. Hatchlings usually have seven (although in some species six or eight) leg pairs. Characters that unite Lithobiomorpha as a monophyletic group include plumose setae on the second maxillary tarsus, a transverse seta that projects medially from the labral sidepiece, and a female gonopod with its basal article bearing macrosetae (spurs) and having a broad claw.

### Craterostigmomorpha

Craterostigmus tasmanianus is the sole described species of the order Craterostigmomorpha. Originally known from and widespread throughout the Australian state of Tasmania, Craterostigmus also occurs throughout New Zealand (Figure 1c). The New Zealand collections are morphologically indistinct from C. tasmanianus. Unique characters of Craterostigmus include subdivision of the long tergites so that the trunk appears to have 21 tergites covering the 15 pairs of trunk legs; long maxillipedes, projecting in front of the head plate; sclerites of the fifteenth leg-bearing segment fused as a complete cylindrical ring; and the anogenital region enclosed in a bivalved capsule that opens ventrally to expose a meshwork of openings for the coxal organs.

Because of its isolated systematic position, the morphology, ultrastructure, and genetics of C. tasmanianus have been investigated in detail. Important contributions have been made on external morphology and internal anatomy (10, 18, 61), together with detailed studies of the genital systems (78), spermatophore and sperm ultrastructure (12), anal organs (81), tracheae (42), eyes (68a), and the circulatory system (91).

### Scolopendromorpha

The order Scolopendromorpha (Figure 1d,e) is the most aggressive and most voracious predators among the centipedes, with body length reaching up to 30 cm in the Neotropical Scolopendra gigantea. More than 800 valid species (from nearly 1300 named species) are known, generally classified into three families: Latreilleidae, Bifididae, and Scolopendridae, on the basis of body length.
Scolopendrids and cryptopids have 21 pairs of trunk legs, whereas scolopocryptopids have 23 pairs.

Unique characters that define Scolopendromorpha include a single tergite covering both the maxillipede segment and the first leg-bearing trunk segment; the spiracles served by muscles that have an apodemal function (42); a bean-shaped spermatophore with a tough, multilayered wall; and a rudimentary left oviduct and ejaculatory duct (77).

Scolopendromorphs share important aspects of their embryology and early postembryonic development with Geophilomorpha. Both have epimorphic development and the mother broods the eggs and two nonfeeding posthatching stages.

**Geophilomorpha**

Geophilomorpha (Figure 1f) is by far the most diverse centipede order at the familial level, with 14 families currently recognized to accommodate approximately 1300 valid species among more than 1700 named species. Derived characters shared by all geophilomorphs include the nearly homonomous trunk segments with a spiracle on all leg-bearing trunk segments except the last, and a greater number of segments than in other centipedes. Geophilomorphs differ from other chilopods in that the number of trunk segments is usually variable within a species [sometimes greatly so, e.g., 87 to 177 segments in *Himantarium gabrielis* (2)], despite the fact that no segments are added after hatching, with females usually having more segments than males. All species are blind, and the brain has a less clear differentiation of its three lobes compared with the other centipedes. The antennal segment number is precisely fixed at 14 segments. The antennal segment number is precisely fixed at 14 segments. The trunk tergites are divided into prominent pretergites and metatergites, each independently muscled, a feature that has been linked to the burrowing habits of these centipedes (61).

A compelling suite of morphological, behavioral, and molecular characters divides Geophilomorpha into the clades Placodesmata (composed of a single family, Mecistocephalidae) and Adesmata (all other families). Mecistocephalids are the only geophilomorphs in which mothers brood with the sternum against the eggs or hatchlings, as is also the case in scolopendromorphs (9). All other geophilomorphs brood with the sternum upward. This behavioral shift is associated with a significant morphological innovation; in Adesmata, defensive glands are developed along the trunk, and the brooding ritual has evidently been modified to keep the noxious defensive secretions out of contact from the brood (9). An additional argument for a basal position of mecistocephalids within Geophilomorpha is the fixed numbers of segments within species (without sexual dimorphism), as in all other centipede orders.
Figure 4
Summary tree of the relationships among centipede families. This tree is based mostly on data provided in Reference 25; geophilomorph relationships are based on data provided in Reference 32.

Notostigmophora-Pleurostigmophora split that has also been recognized by studies based on either non-numerical cladistic analysis (84, 86) or studies of particular character systems (81, 91). Pleurostigmophora is supported by such apomorphic characters as the flattening of the head plate (Figure 3b), medial coalescence of the maxillipede coxae (Figure 3d), a maxillipede tarsungulum (fused tarsus and pretarsus), pleural spiracles (Figure 3f), coxal organs, spermatophore deposition on a web, and ultrastructure of the lateral ocelli (68, 68a).

Acceptance of the Pleurostigmophora concept means that the division of Chilopoda into Anamorpha and Epimorpha (4) on the basis of anamorphic versus epimorphic development is unwarranted. Anamorphosis is instead resolved as a plesiomorphic character shared between Scutigeromorpha, Lithobiomorpha, and Craterostigmomorpha, the last reducing the anamorphic phase to a single instar with 12 leg pairs. Epimorphosis maps onto the cladogram as a synapomorphy for Scolopendromorpha + Geophilomorpha, a clade named Epimorpha (Figure 4).

Other morphogenetic characters are correlated with the difference between anamorphic and epimorphic development. The two orders with prolonged anamorphic phases...
regenerate legs after loss, whereas in the epi-
morphic orders regeneration happens for the 
last legs only or not at all (66). Geophilom-
orphs, which have the lowest number of an-
tennal segments, are unique in not adding an-
tennal segments after hatching and in lacking 
the capacity to regenerate antennae (66).

Most morphological and combined mor-
phological and molecular analyses unite 
Craterostigmomorpha with Epimorpha. This 
group shares maternal care of the eggs and 
hatchlings and has been named Phylactome-
tria for this behavior (25). Other diagnostic 
characters include a strengthening of the max-
ilipeds, with the hinge between the coxos-
ternites fused, and the testes having lateral 
vesicles (76).

A topology conflicting with the morpho-
logical cladogram is produced by analyses 
of three nuclear coding genes (80). These 
data resolve *Craterostigmus* as sister to all 
other chilopods and support a sister group 
relationship between Scutigeromorpha and 
Scolopendromorpha. When these data are 
combined with four other genes and morphol-
ogy, two basic tree topologies are obtained 
(34). The classical topology emerges under 
certain parameter sets in which the riboso-
mal genes represent a larger portion of the 
total cladogram length, while under the com-
plementary parameter sets the topology ob-
tained from the nuclear protein-coding genes 
dominates.

**BIOGEOGRAPHY AND 
CENTIPEDES**

Many groups of centipedes have relatively 
narrow geographic distributions. Low in-
dividual vagility and restricted geographic 
distributions of species render these taxa 
useful subjects for historical biogeographic 
udies. Exceptions to narrow-range en-
demism are known within each of the major 
groups. Among the most widespread dis-
tributions, each known from several contin-
ents across a range of climatic zones, are 
*Pachymerium ferrugineum* (Geophilomorpha), 
*Lamyces emarginatus* (Lithobiomorpha), and 
*Scutigera coleoptrata* (Scutigeromorpha). *P. fer-
rugineum* is highly resistant to immersion in 
water, which may account for its occurrence 
on far-flung islands. *L. emarginatus* repro-
duces by parthenogenesis throughout most 
of its range, a strategy that has facilitated 
its nearly cosmopolitan distribution. *S. coleop-
trata* is synanthropic through much of its ange, as described above, and although it is 
identified as a single morphospecies, it ex-
hibits substantial genetic variation (27).

The three families of Scutigeromorpha 
have largely disjunct distributions, and two 
of them are restricted to only two continen-
tal fragments (Figure 5). Scutigerinidae is 
edemic to southern Africa and Madagascar 
and Pselliidiidae is restricted to the Neotrop-
ics and tropical Africa. Scutigeridae is the 
most widespread family, including all of the 
scutigeromorphs in Europe, North Africa, 
Asia, Australia, and the Pacific Islands.

In Lithobiomorpha, the mostly Southern 
Hemisphere family Henicopidae has been 
subjected to cladistic analyses that pro-
vide a framework for biogeographic analy-
ses (24, 29). The most persistent problems in 
the higher-level systematics of Henicopidae 
involves groups with disjunct biogeographic 
distributions (24). The small, blind Anop-
sobiinae are resolved as sister to all other 
Henicopidae in most analyses. Within this 
group, most species diversity belongs to a 
well-defined Gondwanan clade, with mem-
bers in Australia, New Zealand, New Cale-
donia, southern South America, and southern 
Africa (26). Five monotypic genera of Anop-
sobiinae have widely separated occurrences in 
the Northern Hemisphere, including Japan, 
 Tajikistan, the island of Rhodes (likely a 
synanthropic introduction), and Kazakhstan.

The henicopine tribe *Zygethobiini* has 
likewise proved to be of uncertain monophyly 
(24) and involves a disjunct trans-Pacific dis-
tribution. Its members include two or three 
Nearctic genera and two Oriental genera. The 
trans-Pacific distribution of *Zygethobiini* is 
largely congruent with that of the lithobiid
Figure 5
Exemplar taxon distributions for Scutigerinidae, Pselliodidae, and Bothropolys.

Gondwana: southern supercontinent including the present Africa, Antarctica, Australia, India, Madagascar, and South America that began rifting apart in the Jurassic period

genus Bothropolys (21), which is found in East and Southeast Asia and in North America (Figure 5).

The most comprehensive phylogenetic and biogeographic data are available for the predominantly southern temperate Henicopini. The genus Paralatomyctes has been used for biogeographic analyses because of its endemicity to most major fragments of Gondwana, including southern Africa, Madagascar, India, Patagonia, eastern Australia, and New Zealand. A cladogram for Paralatomyctes has been constructed using 20 of the 26 known species of the genus (35). The phylogenetic analysis identified two main clades: One unites species from southern Africa, Madagascar, tropical to subtropical Australia, and New Zealand, and the other includes species found in temperate Australia, New Zealand, and Chile. The biogeographic analysis concluded that Australian clades have closest affinities to other Gondwanan fragments.

The disjunct populations of Craterostigmas in Tasmania and in New Zealand pose a biogeographic enigma because no morphological differentiation has been found between them. However, genetic differentiation in mitochondrial genes is substantial (25). Analysis of 16S rRNA shows levels of divergence similar to those among different species of lithobiomorphs and scolopendromorphs.

A detailed morphological cladistic analysis of the geophilomorph family Mecistocephalidae suggests an evolutionary trend toward an increase in segment number (8). Certain groups have highly disjunct biogeographic distributions (e.g., Dicellophilus in central Europe, Japan, and California) that may suggest that the current distribution is a relict of a formerly more widespread condition. Similarly, a revision of the Neotropical geophilomorph taxa suggests that certain clades preserve relictual Gondwanan distributions, although the majority of the biota has a cosmopolitan distribution that originated through more recent dispersal (72).

Because of their typical variation in segment numbers within a species, adesmatan geophilomorphs can be examined from the perspective of geographic variation in segmentation. Latitudinal clines in segment numbers have been documented in several species in Britain (3, 50), indicating an increase in the number of segments in more
southerly populations compared with their more northerly conspecifics.

CENTIPEDES AND THE FOSSIL RECORD

Because centipedes have an unmineralized exoskeleton and generally inhabit nonaquatic sites with low fossilization potential, their fossil record is patchy. Even so, their history extends back to the latest Silurian, approximately 418 Mya. Each of the four diverse centipede orders is known from amber fossils, and of these only Lithobiomorpha lacks a pre-Cenozoic fossil record. As is the case for myriapods in general, geologically early centipede fossils are surprisingly modern and can be identified as members of the crown-group of Chilopoda (84, 85).

The earliest known fossil centipedes can be confidently assigned to Scutigeromorpha. The Silurian-Devonian genus *Crussolum* (1a, 85) has the pentagonal cross-section of the leg podomeres with rows of sawblade-like spines that are retained in extant scutigeromorphs. The maxillipede has a separation between the coxosternites and robust spine bristles along the margin of the coxosternum, as in extant Scutigeromorpha (1a). *Crussolum* is known from the latest Silurian in England, the Lower Devonian of Scotland, and the Middle Devonian of Gilboa, New York. Other fossil scutigeromorphs include the Upper Carboniferous *Latzelia*, from the Mazon Creek deposits of Illinois (70), and the Lower Cretaceous *Fulmenocursor*, from the Crato Formation in northeastern Brazil (89). *Fulmenocursor* has short antennal articles and style-like male gonopods that suggest membership in the extant family Scutigeridae.

*Devonobius delta*, from the Middle Devonian of Gilboa, New York, is a representative of the monotypic order Devono- bionomorpha and is known from magnificently preserved cuticular remains (84). The head and anterior part of the trunk are preserved, but the complete number of segments (at least 16) is unknown. Its most distinctive character is the presence of long ventral apodemes on the maxillipede that are unknown in extant chilopods. *Devonobius* was initially interpreted as the sister group of Epimorpha (84) but was subsequently regarded as most closely related to *Craterostigmus* (10). The characters cited in support of this latter relationship do not withstand scrutiny (25), and parsimony analysis of morphology leaves the position of *Devonobius* unresolved with respect to *Craterostigmus* and Epimorpha.

Paleozoic scolopendromorphs are known exclusively from two species in the Upper Carboniferous deposits of Mazon Creek, Illinois. The better known, *Mazoscolopendra richardsoni* (70), has 21 leg-bearing trunk segments as in Scolopendridae and Cryptopidae. The Mesozoic record of scolopendromorphs is based on two species from the Lower Cretaceous of northeastern Brazil, *Velocipede betimari* and *Cratoraricrus oberlii* (62, 90). The latter is the better understood of the two, possessing some characters typical of Scolopendridae (90).

The earliest reasonably established geophilomorph is *Eogeophilus jurassicus*, from the Upper Jurassic Solnhofen limestones of Germany (83). Although the habitus of this species is unquestionably geophilomorph, it presents a puzzling incongruence in the form of the maxillipede. Extant geophilomorphs share a joint between the first and fourth articles of the telopodite. This modification is shared with scolopendromorphs and has been regarded as a synapomorphy for Scolopendromorpha and Geophilomorpha. *Eogeophilus* has complete (unreduced) second and third articles. Interpreting the form of *Eogeophilus* to be plesiomorphic forces a convergence between extant geophilomorphs and scolopendromorphs.

CENTIPEDES AND EVOLUTIONARY DEVELOPMENTAL BIOLOGY

Two important aspects of centipedes are currently at the forefront of evolutionary and developmental biology studies—the patterns
Tagmosis: type of segmentation in which groups of segments acquire a specific function and delimit different body regions.

and modes of segmentation. The addition of segments through evolution is an important theme in the group. The fixed number of trunk segments in most centipede species and the switch from an anamorphic developmental mode to an epimorphic one in the course of centipede phylogeny—including an intermediate stage in Craterostigmus—have captivated evolutionary developmental biologists interested in the evolution of segmentation in arthropods in general and in myriapods in particular.

One of the peculiarities of centipede segmentation is the invariant odd number of leg-bearing trunk segments. The basis of this developmental constraint on pairing of segments that leads to an odd segment number has been elucidated in Strigamia maritima, which is also the only exception to the rule, with a mutant having 48 pairs of legs (produced by a duplication of the ultimate leg-bearing segment) (51). Recent embryological studies of this species, including expression data for segmentation genes (14), have corrected a fundamental error in the description of the anterior-posterior body axis in centipede embryos introduced by Heymons (41) and widely perpetuated in subsequent literature. The corrected description recognizes segmentation originating in a terminal growth zone, with rings of expression of segmentation genes around the proctodeum that fade anteriorly. Expression bands for odd-skipped and caudal show that the odd trunk segment number arises via a double-segmental pair-rule patterning involving two phases of segmentation (13). Intriguingly, the double phase of segmentation described for S. maritima was not detected in Lithobius atkinsoni for which segmentation genes indicate a strictly one-by-one formation of segments (45).

Variation in numbers of trunk segments in centipedes has been explored using a merомерic model of segmentation (64). The model implies a trunk originally consisting of eight primary units called eosegments, each of which subsequently divided into secondary units known as merosegments. The 16-segment trunk—maxillipede plus the 15 leg-bearing segments—would thus be generated by a single phase of meromeric duplication of the original eight eosegments. Additional phases of meromeric duplication would yield 24 segments (as in Scolopocryptopidae in Scolopendromorpha) and the modal numbers of trunk segments observed in different groups of Geophilomorpha. In geophilomorphs as a whole, numbers of segments are separated into regular intervals of 2, 4, 8, or 16 segments (65). The model is largely consistent with observed variation in trunk segment numbers across centipedes, although it requires modifications to explain the common pattern of 22 trunk segments found in most scolopendromorphs.

Data on the identity of the Hox gene cluster and Hox sequences in centipedes were first generated for a scolopendromorph (38), a lithobiomorph (15), and a geophilomorph (6). Patterns of Hox gene expression are best documented in L. atkinsoni (46, 47). These studies show that centipedes have the complete arthropod cluster of 10 Hox genes (47). Expression domains of myriapods are in some respects intermediate between the broadly overlapping domains of chelicerates and the generally more restricted domains of insects and crustaceans. The head-trunk tagmosis of centipedes is marked by relatively restricted expression domains in the head and maxillipede and broad overlap of Ubx, Abd-A, and Abd-B in the rest of the trunk, which corresponds to its structural homonymy.

Expression patterns for other segmentation genes in L. atkinsoni generally show that their roles are conserved across arthropods. For example, even-skipped expression is similar to that in other arthropods with short germ-band embryos, showing strong posterior expression stripes that fade anteriorly. The initial study on expression of the segment polarity gene engrailed in a scolopendromorpha suggested that centipedes have unique patterns compared with other arthropods (88). Subsequent work on a lithobiomorph (45)
and a geophilomorph (14, 51a) instead shows the typical arthropod expression of *engrailed* stripes at the posterior end of segments. Expression of *engrailed* and other segmentation genes show that the centipede head is composed of six segments (45), as is generally accepted for other mandibulate arthropods. Sequence data derived from *engrailed* are highly conserved between centipede orders, although some instances of gene duplication can be posited (5).

**Conclusion**

The segmentation process in centipedes has mostly been studied to the stage when segment polarity genes are expressed (14, 51a). Data are emerging on more upstream segmentation genes, including homologs of the *Drosophila* pair-rule genes (13, 45). Additional work on these as well as other important pattern-formation genes would help to clarify the evolution of centipede segmentation.

**SUMMARY POINTS**

1. Morphology, molecular sequences, and combined analyses of both sources of data generally unite centipedes and other myriapods as a monophyletic group. In such schemes, myriapods are sister to an insect-crustacean assemblage within the Mandibulata clade (jawed arthropods).

2. Phylogeny based on morphology and sequence data from multiple molecular markers shows that the addition of segments in postembryonic life history is a primitive trait for centipedes. Similarly, the number of trunk segments in centipedes increased through evolutionary time.

3. Fossil centipedes from the Paleozoic Era can be accommodated within living clades. Along with their geological antiquity, certain centipede clades have ancient (e.g., Gondwanan) biogeographic distributions.

4. Recent studies of expression patterns of Hox and other genes show that centipedes generally conform to segmentation mechanisms in other arthropods with short germ-band embryos.

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**LITERATURE CITED**


43. Deleted in proof.

47. Key report reviewing gene expression data and segmentation across arthropods, including original data on Lithobius.
of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan hemocoel. *J. Linn. Soc.* 45:251–484


**RELATED RESOURCES**

Centre International de Myriapodologie: [http://www.mnhn.fr/assoc/myriapoda/INDEX.HTM](http://www.mnhn.fr/assoc/myriapoda/INDEX.HTM)
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