

CHILOPODA – THE FOSSIL HISTORY

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The lightly sclerotised cuticle of chilopods, coupled with their predominantly litter and soil-dwelling habits, set constraints on their fossilisation potential. In spite of this, of the five extant chilopod orders, two (Scutigeromorpha and Scolopendromorpha) have a fossil record extending back to the Palaeozoic, and an extinct order in the Middle Devonian (Devonobiomorpha) dates the divergence of Lithobiomorpha and Phylactometria to at least that age, ca 385 million years ago. In addition to a few recent discoveries in Jurassic and Cretaceous rocks, chilopods are known from several species in Cretaceous and Cenozoic ambers.

Scutigeromorpha

The earliest known fossil centipedes, ca 418 million years old, can be confidently assigned to the Scutigeromorpha. The Silurian-Devonian genus *Crussolum* Shear et al., 1998 (Shear et al. 1998; Anderson and Trewin, 2003) has the polygonal cross section of the leg articles, with sawblade-like rows of spines along the ridges (carinae) at each angulation (Fig. 18.1D, E), that is retained by extant scutigeromorphs. Unlike extant scutigeromorphs the tarsus is not clearly differentiated into a tarsus 1 and tarsus 2, and several unique tarsal characters that are invariably observed in all extant scutigeromorphs (tarsal papillae, resilient sole-hairs) are lacking in the mid-Palaeozoic fossils. As such, *Crussolum* can be identified as a stem-group scutigeromorph.

The forcipules of *Crussolum* have a separation between the coxae that indicates flexibility, and has robust socketed setae along the margin of the coxae (Anderson and Trewin, 2003) (Fig. 18.1C). These latter setae differ from the invariable four spine-bristles on the coxal margin of crown-group Scutigeromorpha, an apomorphic character that reinforces the stem-group position of *Crussolum*. In the Windyfield Chert (Lower Devonian, Scotland), an antenna assigned to *Crussolum* sp. has at least 21 short articles, but its complete length is unknown, and Fayers and Trewin (2005) allowed that the material could be hexapod rather than chilopod. *Crussolum* is known from the Upper

Silurian (Přídolian) Ludford Lane deposits in England, the Lower Devonian (Pragian) Rhynie and Windyfield Cherts of Scotland, and the Middle Devonian (Givetian) of Gilboa, New York.

Stratigraphically later scutigeromorphs include the Upper Carboniferous *Latzelia* Scudder, 1890, and the Lower Cretaceous *Fulmenocursor* Wilson, 2001. *Latzelia* is known from a single species, *L. primordialis* Scudder, 1890, from the Mazon Creek deposits of Illinois, U.S.A. (Scudder, 1890; Mundel, 1979). It has been separated as a monotypic family, Latzeliidae, though diagnosed only as “a small-headed robust scutigeromorph” (Mundel, 1979). One feature that might place *Latzelia* outside the scutigeromorph crown group is its relatively short fourth tergite (plate covering leg-bearing segments 7–9), but in most respects it is decidedly similar to extant Scutigeromorpha. *Fulmenocursor* is likewise monotypic, based on *F. tenax* Wilson, 2001, from the Crato Formation (Aptian) in northeastern Brazil. The shape of the antennal articles (wider than long), presence of paired spine-bristles on the tibia of the second maxillae, and apparently styliform (male?) gonopods (Wilson, 2001) suggest that *Fulmenocursor* may be referable to the family Scutigeridae. Two scutigerid taxa, *Scutigera illigeri* and *S. leachi*, were named by Koch & Berendt (1854) from Eocene Baltic amber, though they have since been regarded as a single species (Keilbach, 1982).

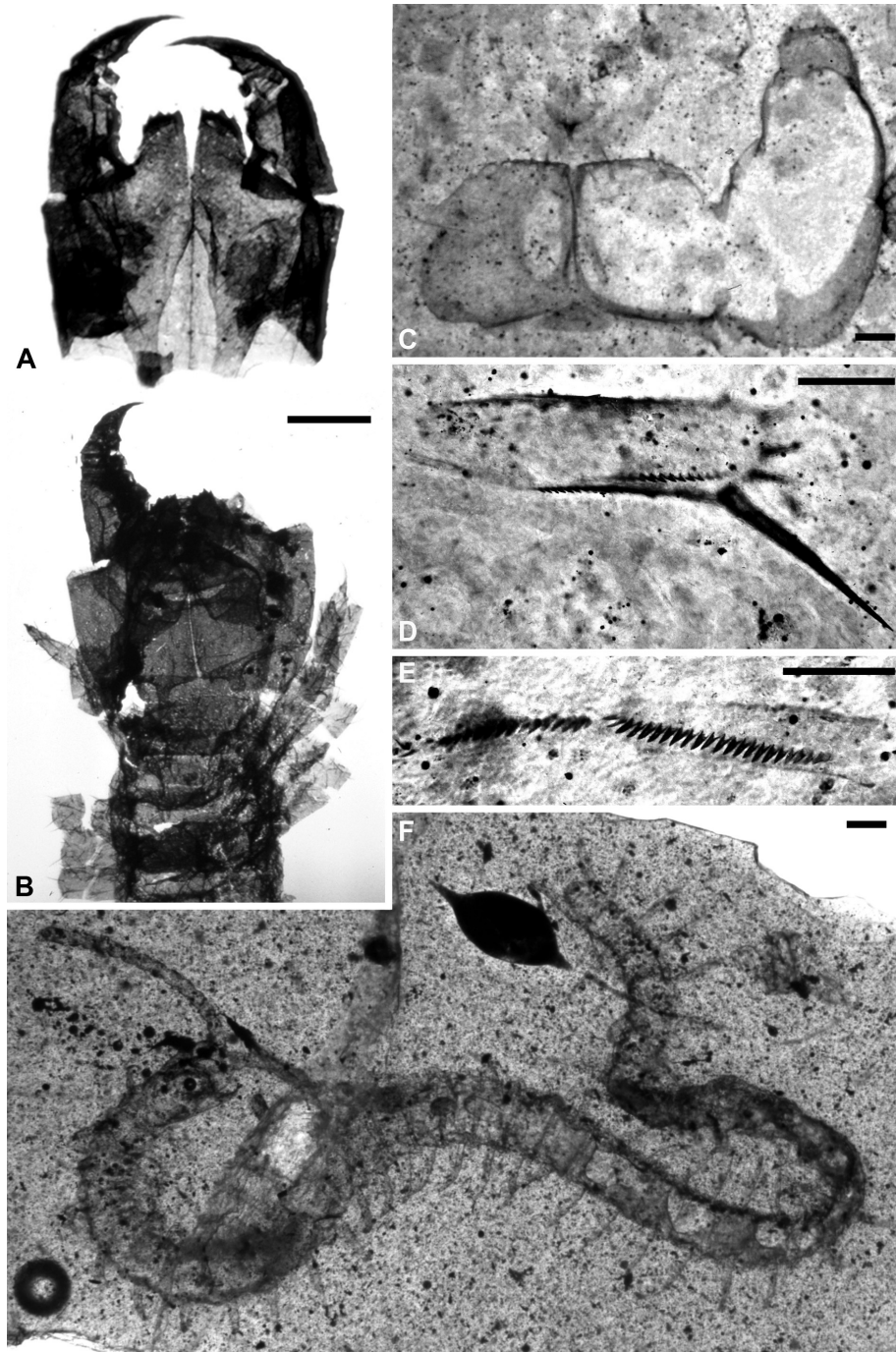
Lithobiomorpha

Although the widely endorsed cladogram for Chilopoda and available palaeontological data (occurrence of *Devonobius*; Shear and Bonamo, 1988) predict that stem-group lithobiomorphs should have evolved no later than the Middle Devonian, the record of fossil lithobiomorphs is confined to the Cenozoic. A specimen referred to *Lithobius* from the Rubielos de Mora site in Spain (Peñalver, 1998) is of Early Miocene age. The published drawing identifies it as a lithobiid rather than a henicopid based on the presence of spurs encircling the distal parts of leg articles, and the relative thickening of the ultimate legs is more typically lithobiid.

Additional fossil lithobiomorphs are represented in Cenozoic ambers. Baltic amber in-

Fig. 18.1 Fossil Chilopoda. Scale bars 0.2 mm. A–B *Devonobius delta*, Middle Devonian, Gilboa, New York, USA. A Forcipules. B. Head and anterior part of trunk. C–E Stem-group scutigeromorph *Crussolum* sp., Windyfield Chert (Lower Devonian), Scotland. C Forcipules. D Prefemur of a trunk leg. E Tibia of a trunk leg. F *Buziniphilus antiquus*, Upper Cretaceous amber, western France. A, B, W. A. Shear; C–E, L. I. Anderson; F, original G.D. Edgecombe

For a colour version of this figure, see Plate III.



cludes a few named lithobiid species (*Lithobius longicornis*, *L. maxillosus*, *L. planatus*; all by Koch & Berendt, 1854; plus several nomina nuda referred to *Lithobius* by Menge (1854)). None of this material has been examined in modern times and the detailed affinities of these species are unknown.

Fossils preserved in volcanic tephra in the Rhine floodplain, dated at ca 11,000 years, are identified as *Lithobius* cf. *forficatus* (Waldmann et al., 1996).

Devonobiomorpha

Devonobius delta Shear and Bonamo, 1988, from the Middle Devonian of Gilboa, New York, is known from magnificently preserved cuticular remains, with even fine details of setation known for parts of the exoskeleton. The head and anterior part of the trunk are preserved (Fig. 18.1A, B), including legs, but the complete number of segments is unknown, and the structure of the posterior segments is not well understood, being represented by a single telescoped exuvium.

Devonobius delta lacks ocelli. The antenna is composed of at least 13 articles but the most complete specimen (Shear and Bonamo 1988, their fig. 25) is fragmentary. The trunk has at least 16 segments with distinct alternation of long and short tergites (heterotergy). The most distinctive character is a pair of long ventral apodemes on the forcipular coxosternite, not known in other chilopods; like other pleurostigmophorans, *Devonobius* also has a pair of dorsal apodemes (Coxalplatten of Verhoeff). The coxosternite has “can opener” serrate endites as in *Craterostigmus* and many Scolopendromorpha (Fig. 18.1A).

Shear and Bonamo (1988) considered *Devonobius* to be sister group of Scolopendromorpha and Geophilomorpha based on the shared absence of a Tömösváry's organ. Borucki (1996) instead regarded *Devonobius* to be most closely related to *Craterostigmus*. The characters cited in support of this relationship, involving purported specializations of the forcipules, a sclerotized bridge between the antennal bases, and size and position of the mandible, were critiqued by Edgecombe and Giribet (2004), whose morphological analysis was unable to choose between the two alternatives (both were equally parsimonious).

Scolopendromorpha

Palaeozoic scolopendromorphs are known exclusively from the Upper Carboniferous of Mazon Creek, Illinois, USA. Two Mazon Creek species have been described,

Palenarthrus impressus Scudder, 1890, and *Mazoscolopendra richardsoni* Mundel, 1979. The better known *Mazoscolopendra* is a 21-segmented species that is currently unassignable to either of the main 21-segmented families (Cryptopidae and Scolopendridae). Taxonomically critical characters such as ocelli are inadequately preserved (pers. obs., Field Museum collections), and classification more detailed than Scolopendromorpha is not possible.

The Mesozoic record of scolopendromorphs is based on two species from the Lower Cretaceous Crato Formation in northeastern Brazil, *Velocipede betimar*, named and described by Martill and Barker (1998), and *Cratoraricrus oberlii* Wilson, 2003. The latter is the better understood of the two, though known from a single specimen. It possesses some characters typical of Scolopendridae, such as bipartite tarsi, and sternites having paired paramedian grooves (Wilson, 2003). More specifically, sternal paramedian grooves along the length of the trunk are apomorphic for Asanadini and Scolopendrini (Scolopendrinae). The presence of ocelli in *Cratoraricrus* can neither be confirmed nor discounted. An unassigned Crato Formation scolopendromorph with 21 pairs of trunk legs is distinct from *Cratoraricrus* but requires further comparison with *Velocipede* (Menon et al., 2003).

Baltic amber is the source of an unnamed cryptopid (*Cryptops* sp. of Bachofen-Echt, 1942) and *Scolopendra avita* Menge in Koch & Berendt, 1854. A scolopendromorph illustrated from Dominican amber (Poinar & Poinar, 1999, their fig. 87) is a member of Scolopocryptopinae, with a single large ventral spinous process on the ultimate leg prefemur that is consistent with a more precise identity as one of the two extant genera in the Neotropics, *Scolopocryptops* and *Dinocryptops*.

Geophilomorpha

Shear and Bonamo (1988) suggested that *Ilyodes attenuata* Matthew, 1894, from the Upper Carboniferous of New Brunswick, Canada, is a potential geophilomorph, but a subsequent examination of the material in the New Brunswick Museum by W. A. Shear (pers. comm.) leaves it doubtful that it is a chilopod.

The earliest well established geophilomorph is *Eogeophilus jurassicus* Schweigert and Dietl, 1997, from the Upper Jurassic Nusplingar Plattenkalk of southwestern Germany. Though the habitus of this species is unquestionably geophilomorph, based on the elongated body with a large number (50+) of trunk segments, its original description from a single specimen presents a puzzling incongruence with extant geophilomorphs in the form of the forcipules. Extant geophilomorphs share a joint between the first and

fourth articles of the telopodite, completely reducing the second and third articles (femur and tibia) on the outer side of the telopodite. This modification is shared with scolopendromorphs (observed in the Cretaceous *Cratoraricus*: Wilson, 2003, their fig. 4) and has classically been regarded as a synapomorphy for Scolopendromorpha and Geophilomorpha. *Eogeophilus* was depicted as having a complete femur and tibia on the forcipule (Schweigert and Dietl, 1997, their fig. 4) but this may be based on a mistaken anterior limit of the coxosternum (Edgecombe et al., 2009).

The only other Mesozoic geophilomorph is *Buziniphilus antiquus* Edgecombe, Minelli & Bonato, 2009, from La Buzinie amber (Late Cretaceous, early Cenomanian) in western France. This species is known from a single, evidently immature specimen (Fig. 18.1F) but it preserves sufficient morphological information to make membership in either of the families Geophilidae or Schendylidae probable.

Another geophilomorph, *Calciphilus abboti* Chamberlin, 1949, is known from a single incomplete specimen preserved in onyx of Late Cenozoic age from Arizona. It is apparently a member of the Geophilidae (Chamberlin, 1949).

Geophilomorphs from Baltic amber (e.g., Weitschat & Wichard 1998, their pl. 22, fig. d) have not received a recent taxonomic treatment, though a few species have been in the literature since the mid-19th century. A series of names proposed by Menge in Koch & Berendt (1854), including *Geophilus brevicaudatus*, *G. crassicornis* and *G. filiformis*, were regarded by Keilbach (1982) as nomina nuda.

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