

Review Article

The geological record and phylogeny of the Myriapoda

William A. Shear^{a,*}, Gregory D. Edgecombe^b^a Department of Biology, Hampden-Sydney College, 200 Via Sacra, Hampden-Sydney, VA 23943, USA^b Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

ARTICLE INFO

Article history:

Received 17 November 2009

Accepted 18 November 2009

Keywords:

Chilopoda
Diplopoda
Symphyla
Pauropoda
Arthropleurida

ABSTRACT

We review issues of myriapod phylogeny, from the position of the Myriapoda amongst arthropods to the relationships of the orders of the classes Chilopoda and Diplopoda. The fossil record of each myriapod class is reviewed, with an emphasis on developments since 1997. We accept as working hypotheses that Myriapoda is monophyletic and belongs in Mandibulata, that the classes of Myriapoda are monophyletic, and that they are related as (Chilopoda (Symphyla (Diplopoda + Pauropoda))). The most pressing challenges to these hypotheses are some molecular and developmental evidence for an alliance between myriapods and chelicerates, and the attraction of symphylans to pauropods in some molecular analyses. While the phylogeny of the orders of Chilopoda appears settled, the relationships within Diplopoda remain unclear at several levels. Chilopoda and Diplopoda have a relatively sparse representation as fossils, and Symphyla and Pauropoda fossils are known only from Tertiary ambers. Fossils are difficult to place in trees based on living forms because many morphological characters are not very likely to be preserved in the fossils; as a consequence, most diplopod fossils have been placed in extinct higher taxa. Nevertheless, important information from diplopod fossils includes the first documented occurrence of air-breathing, and the first evidence for the use of a chemical defense. Stem-group myriapods are unknown, but evidence suggests the group must have arisen in the Early Cambrian, with a major period of cladogenesis in the Late Ordovician and early Silurian. Large terrestrial myriapods were on land at least by mid-Silurian.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The fossil record and evolution of the Myriapoda were last reviewed in depth by Shear, in 1997. Since that time, new discoveries and new descriptions of important fossils, as well as recent broad-scale analyses of arthropod phylogeny and ingroup relationships of the extant myriapod taxa, have made desirable an updated overview of the field. In this article we first assess developments in our understanding of myriapod phylogeny, as a framework for a discussion of the fossils. We discuss fossil chilopods in a taxonomic framework, since there are only 5 extant orders and all known fossils except for the Devonian *Devonobius* can be confidently included in extant orders. Diplopod fossils are taken up chronologically, since no Palaeozoic representatives can be assigned with confidence to any of the 16 extant orders.

In the larger context of the Euarthropoda, myriapods have been difficult to place. Traditionally they have been regarded as closely allied to the Hexapoda, either as the hexapod sister group

(i.e., Bäcker et al., 2008; Bitsch and Bitsch, 2004), or with the hexapods nested within a paraphyletic Myriapoda (i.e., Kraus, 2001; Willmann, 2003). But recent work utilizing both morphological and molecular characters (see Edgecombe and Giribet, 2002) has presented strong evidence that Myriapoda is not to be included in a clade with Hexapoda, now regarded as more closely related to Crustacea (Dohle, 2001). So do some myriapods belong near the base of the arthropod tree (Strausfeld et al., 2006), are they a part of the Mandibulata along with Tetraconata or Pancrustacea (Crustacea + Hexapoda; Harzsch et al., 2005), or do they form a taxon Paradoxopoda/Myriochelata with the Chelicerata (Negrisolo et al., 2004; Mayer and Whittington, 2009)? Is Myriapoda monophyletic, paraphyletic, or polyphyletic? Are the myriapod classes themselves monophyletic? And within those classes, how are the included orders related? The evidence available to be brought to bear on these questions is variable. Much morphological and diverse molecular data have been gathered for the Chilopoda (Edgecombe and Giribet 2004; Giribet and Edgecombe, 2006), for example, and the internal phylogeny of the class now seems stable, while in the case of the Diplopoda, morphological analyses rely on relatively few characters, and only one kind of molecular marker (three nuclear coding genes) has been surveyed for a fairly

* Corresponding author.

E-mail addresses: w.shear@hsc.edu (W.A. Shear), g.edgecombe@nhm.ac.uk (G.D. Edgecombe).

restricted number of species, such that the analyses are sensitive to sampling breadth (Sierwald et al., 2001) as well as to parameters of analysis (Regier and Shultz, 2001; Regier et al., 2005; Sierwald and Bond, 2007). Exemplars of the Pauropoda and Symphyla have been included in few analyses, but in general data for these two classes are sparse, and nothing has been done regarding their internal phylogenies.

The myriapod fossil record is uneven both in a chronological and taxonomic sense. A small number of Silurian and Devonian fossils are available and their mode of preservation, as impressions in fine-grained sediments, as organically preserved cuticle, or embedded in translucent chert often allows for detailed morphological observations (Almond, 1985; Shear and Bonamo, 1988; Shear et al., 1998; Anderson and Trewin, 2003; Wilson, 2005a; Wilson and Anderson, 2004; Wilson et al., 2005). The Carboniferous holds perhaps the richest trove of myriapod fossils, albeit taxonomically biased toward the Diplopoda, and sampled from only limited habitats (Hoffman, 1969; Hannibal, 1987; Shear, 1997). In contrast, only a few myriapod fossils are known from the Permian, and none of them have been described in detail (Hannibal, 2006; Wilson, 2006a). The entire Mesozoic is similarly bereft, with but a handful of fossil myriapods (Edgecombe et al., 2009; Shear et al., 2009; Wilson, 2001, 2003). Cenozoic myriapod fossils are almost entirely limited to a few amber *Lagerstätten* and are assignable to extant taxa (i.e., Santiago-Blay and Poinar, 1992).

The taxonomic distribution of myriapod fossils is strongly biased toward the Diplopoda, likely due to their greater fossilization potential; except for one small group, their cuticle is reinforced with calcium carbonate and is quite robust. However, since the cuticle is almost always consumed by the animal after moulting (to recycle the calcium), cast cuticles, which potentially enable one animal to leave behind more than a single fossil remnant, are unlikely to be available for fossilization. Further, diplopods are ecologically bound to an environment where rapid decay of organic matter, including arthropod cuticles, is facilitated by abundant bacteria and fungi. So despite their strong, mineralized cuticles, millipedes are likely to become fossils only when carcasses are quickly washed into a basin of deposition. The preservation potential of chilopods is even less. Their cuticles are relatively thin and unmineralized and their habitats similarly inimical to the survival of undecayed bodies. Fossils of symphylans and pauropods, with cuticle like that of centipedes, a soil and litter habitat, and mostly minute size, are unknown except for a few examples from Tertiary ambers (Scheller and Wunderlich, 2001, 2004).

The usefulness of the fossil record in myriapod phylogenetics is further complicated by the fact that the characters used to construct trees of living myriapods are rarely available in the fossils, with the result that a number of extinct taxa simply cannot be placed, either systematically or phylogenetically. Nevertheless, we believe that significant information can be derived from them, especially as regards the timing of cladogenesis, and in some cases studies of fossils can provide additional evidence in support of phylogenetic trees. Study of fossil myriapods is also essential to our understanding of the process of terrestrialization in arthropods, since the earliest trace fossils as well as the earliest body fossils of such creatures are of myriapods. Fossil millipedes also provide the earliest evidence of air-breathing (the Silurian *Pneumodesmus newmani* Wilson and Anderson has spiracles; Wilson and Anderson, 2004) and of chemical defense against predators (Devonian xyloidiulideans have ozopores; Wilson, 2006a).

2. Myriapod phylogeny

Here we briefly review a variety of competing hypotheses regarding myriapod phylogeny, as set out above. Our conclusions

are that the data favour a position for Myriapoda within the more inclusive Mandibulata, myriapod monophyly, and monophyly of each of the myriapod classes. Although the traditional systematic arrangement with Chilopoda sister to Progoneata, and the division of Progoneata into Dignatha (Diplopoda + Pauropoda) and Symphyla has been challenged, we find no strong basis for rejecting it.

2.1. Mandibulata or Paradoxopoda?

The Mandibulata and Paradoxopoda hypotheses differ in their placement of a monophyletic or paraphyletic Myriapoda. Mandibulata unites all arthropods with mandibles (morphological evidence reviewed by Harzsch et al., 2005; Scholtz and Edgecombe, 2006), while Paradoxopoda places myriapods closer to, or paraphyletic with respect to, chelicerates.

Until recently, Paradoxopoda has not been well supported by morphological characters. Only one plausible character—a similar mode of neurogenesis involving post-mitotic cells immigrating as clusters found in diplopods, chilopods and chelicerates—had been proposed as a potential autapomorphy (Dove and Stollewerk, 2004; Kadner and Stollewerk, 2004; Stollewerk and Chipman, 2006). However, the polarity of this character could only be resolved when similar data for onychophorans were obtained. Study of nervous system development in peripatid and peripatopsid onychophorans by Mayer and Whittington (2009) led them to propose that three characters of neurogenesis and one of the split in the embryonic germ disc shared by myriapods and chelicerates are apomorphic for Paradoxopoda because crustaceans and hexapods share states with onychophorans. Several kinds of molecular data have likewise recovered Paradoxopoda, including Hox gene sequences, some analyses of hemocyanin sequences, mitochondrial genomics, and nuclear ribosomal genes (see Edgecombe, 2010, for citations). Limited taxon sampling is problematical for some of these studies; for example, with some samples, ribosomal 18S and 28S rRNA have provided support for Paradoxopoda (Mallatt et al., 2004), but a larger sample tested under parametric bootstrapping showed that the monophyly of Mandibulata could not be rejected (Mallatt and Giribet, 2006). Rota-Stabelli and Telford (2008) explored the mitochondrial genomic data and showed them to be sensitive to the choice of outgroups; Mandibulata is retrieved in certain cases. The very large nuclear protein-coding gene data set analyzed by Regier et al. (2008) showed stronger support for Mandibulata than for Paradoxopoda, and additional sequences reversed the conclusions of the hemocyanin sequence analysis (Kusche et al., 2003).

Thus while the presently available data show Mandibulata to be supported by more morphological characters, Paradoxopoda does have some support as well. The molecular data remain sensitive to analytical methods and the choice between Mandibulata and Paradoxopoda is equivocal.

2.2. Myriapod monophyly

The question of myriapod monophyly is inextricably intertwined with debates about the position of the Myriapoda in the arthropod tree as a whole, since the two strongest competing hypotheses postulate either myriapod monophyly or paraphyly in connection with the relationship of Myriapoda and Hexapoda. The Atelocerata hypothesis (Bitsch and Bitsch, 2004; Bäcker et al., 2008) maintains that Hexapoda is nested within a paraphyletic Myriapoda, Chilopoda being the sister group to a taxon that includes Hexapoda and Progoneata. The Tetraconata hypothesis (Dohle, 2001; Strausfeld et al., 2006; Ungerer and Scholtz, 2008) calls for a close relationship between Crustacea and Hexapoda, to the exclusion of Myriapoda, which may be monophyletic or not, but is generally taken as part of the Mandibulata, which also includes Tetraconata. However, some

Tetraconata proponents have suggested paraphyly of Myriapoda with Chelicerata (Negrisolo et al., 2004) or a basal position in the Euarthropoda for Diplopoda, with chilopods close to the other mandibulate arthropods (Strausfeld, 1998; Strausfeld et al., 2006; Loesel et al., 2002).

Support for the Tetraconata hypothesis is now very strong in terms of both morphological and molecular evidence (in fact, all molecular evidence available supports it). Morphological support is concentrated in detailed similarities between Crustacea and Hexapoda in the structure and development of the nervous system (see Edgecombe, 2010, for characters and citations). Coding these apomorphies in cladistic analyses with other morphological characters recovers Tetraconata as a clade and Myriapoda as its sister group (Giribet et al., 2005). Molecular support for Atelocerata is lacking, while evidence for Tetraconata comes from analyses of nuclear ribosomal genes, nuclear protein-coding genes, mitochondrial genomics, *Hox* gene sequences, hemocyanin sequences, mitochondrial gene order, and expressed sequence tags (citations listed by Edgecombe, 2010). Thus we adopt Tetraconata as a working hypothesis for considering myriapod relationships in this article.

Data from brain anatomy (Loesel et al., 2002; Strausfeld et al., 2006), analyzed in isolation, have been used to argue for myriapod polyphyly in a Tetraconata context. A single midline neuropil in diplopods and the presence of a second one in Chilopoda and Tetraconata seems to resolve Diplopoda at the base of the Euarthropoda, while chilopods group closer to pancrustaceans. Pauropoda and Symphyla were not included in the analyses. However, the analysis of many of these brain characters together with other morphological character systems yields a monophyletic Myriapoda (Giribet et al., 2005); it has been suggested that diplopod brains show some reverses or losses, rather than their being the most basal lineage in the arthropod crown group.

Myriapod paraphyly with respect to Hexapoda has been rendered unparsimonious by strong support for Tetraconata. Paraphyly with Chelicerata (Paradoxopoda/Myriochelata hypothesis), has been suggested based on one analysis of mitochondrial protein-coding genes (Negrisolo et al., 2004) but support was weak, and when the data were reanalyzed with alternative methods, myriapod monophyly was retrieved. The former molecular results are highly contradicted by morphology; we know of no apomorphies that any myriapod class share with chelicerates as a whole and not with other myriapods.

Recent reviews (Bitsch and Bitsch, 2002, 2004; Koch, 2003; Edgecombe, 2004) have set forth morphological characters that serve as putative autapomorphies of Myriapoda. The most important of these deal with the structure of the tentorium and its functional relationship to the mandible. In particular, a transverse bar, supporting the apodemes that give rise to the mandibular adductor muscles, is found in all myriapod classes, and is absent from any hexapods or crustaceans (Bitsch and Bitsch, 2002; Koch, 2003). The tentorial apodemes serve to adduct the mandibles, with their separate, movable gnathal lobes, as a result of the shift of the dorsoventral mandibular muscles to the tentorial apodemes. This creates the “swinging tentorium” seen by Manton (1964) and Kluge (1999) as strongly supporting myriapod monophyly. Klass and Kristensen (2001) argued that the tentorial movement in myriapods could be the plesiomorphic precursor of a fixed tentorium in insects, but the argument makes sense only if Atelocerata is monophyletic. Additional characters reinforcing myriapod monophyly include details of the nervous system and eyes. Harzsch (2004) found two groups of serotonin-reactive neurons in both chilopods and diplopods that are not found in Chelicerata or Tetraconata. Müller et al. (2007) found that the eucone cells of the ommatidia of Scutigera and Penicillata have their nuclei

displaced outside and proximal to the cone compartments. Analysis of morphological data sets for arthropods in general most frequently recovers myriapod monophyly, though sometimes with low support (Edgecombe, 2004; Giribet et al., 2005; Bitsch and Bitsch, 2004).

Myriapod monophyly is supported by many molecular analyses, but some of these are weakened by the failure to include Symphyla and/or Pauropoda. Diplopoda, Symphyla and Chilopoda were retrieved as a monophylum when the 28S and 18S loci were analyzed by Mallatt et al. (2004), and myriapod monophyly held up when a pauropod was added for these same nuclear ribosomal genes (Gai et al., 2006). Alternatively, however, other taxonomic samples for the same genes find that symphylans and pauropods do not unite with a well-supported clade of chilopods and diplopods (von Reumont et al., 2009). Analyses of first three nuclear protein-coding genes (Regier et al., 2005) and later 62 such genes for a subset of the taxa (totalling 41 kb of sequence data; Regier et al., 2008) returned myriapod monophyly. When Giribet et al. (2005) studied 9 molecular loci and morphology, Myriapoda was monophyletic under 13 of 20 explored analytical conditions. Thus it is reasonable to adopt myriapod monophyly as the best-supported hypothesis at present.

2.3. Monophyly of the myriapod classes and their relationships

The monophyly of Chilopoda, Diplopoda, Symphyla and Pauropoda as taxa is not controversial and is strongly supported by morphological, developmental and molecular characters (see reviews in Dohle, 1980, 1997; Kraus, 1997; Edgecombe and Giribet, 2002). We list some of these below.

Chilopoda: Appendage of first trunk segment a maxilliped with an internal poison gland; eggtooth on second maxilla of embryo; trochanters of trunk legs immobile at prefemoral joint; 15 pairs of trunk legs (secondarily increased in scolopendromorphs and geophilomorphs); trunk heterotery; anisostigmophory.

Symphyla: One pair of tracheal stigmata on head; eyes absent; 12 pairs of trunk legs; paired terminal spinnerets derived from appendages; labium with distal sensory cones; genital opening unpaired; anal segment with a pair of long trichobothria.

Pauropoda: Antennae three-branched, one branch a unique sensory organ (globulus); paired pseudoculi (perhaps homologous to Tömösváry organs); exsertile vesicles ventral on the collum; paired trichobothria at tergal margins.

Diplopoda: Trunk segments posterior to the fourth fused as diplosegments; antennae with 8 articles, the last with unique sensory cones (usually 4 in number); aflagellate spermatozoa.

Almost all conceivable relationships of the 4 classes have found support in at least one study, but we will discuss only those groupings that have obvious and compelling support, as opposed to those found in only single molecular analyses and even then, weakly supported, or groupings based on few morphological characters that have been rejected in later investigations. Morphological analyses tend to strongly support (Chilopoda ((Symphyla (Diplopoda + Pauropoda))), but molecular data have resulted in some surprising and discordant arrangements. The fact that these latter trees generally have feeble support (but see discussion of a symphylan-pauropod grouping below) leaves them as only weak arguments against the tree strongly favoured by morphology.

Morphological characters strongly support a sister group relationship between Chilopoda and Progoneata (Symphyla + Diplopoda + Pauropoda); the monophyly of the latter was

defended in detail by Dohle (1980), and even earlier by Anderson (1973) based on a suite of embryological characters. Apomorphies include the anterior gonopore (situated between or just behind the second legpair), development of the midgut within the yolk and of the fat body from yolk vitellophages, the gonoduct being a secondary ectodermal invagination, sternal apodemes (only in Hexamerocera in Pauropoda), and trichobothria with a basal bulb (only in Pselaphognatha in Diplopoda). Progoneata was monophyletic in morphological analyses by Edgecombe (2004) and Giribet et al. (2005). Bitsch and Bitsch (2004) rejected Progoneata, but did not include the developmental characters. Some molecular analyses have indicated support for Progoneata as well. Analyses of mitochondrial genomes by Gai et al. (2008) united Symphyla and Diplopoda to the exclusion of Chilopoda (Gai et al., 2008; also analyses of amino acids by Podsiadlowski et al., 2007), though mitogenomic studies to date have not included Pauropoda.

Within the Progoneata, Dignatha (Diplopoda + Pauropoda) is likewise favoured by morphological analysis. Apomorphies include a limbless postmaxillary (collum) segment, vas deferens opening at the tip of a conical penis, sternal spiracles opening into a tracheal pouch that also functions as an apodeme, a motionless pupoid stage after hatching, and the first free-living juvenile with three pairs of legs (Dohle, 1980; Enghoff et al., 1993). Differing views exist as to the composition of the gnathochilarium: first maxilla alone (Dohle, 1980, 1997) or both pairs of maxillae (Hilken and Kraus, 1994; Kraus and Kraus, 1994). Embryology, gene expression and anatomy favour the former view. In any case, as Ax (1999) pointed out, regardless of which opinion prevails, the structural and functional union of the maxillae is an apomorphy of Dignatha.

Despite the comparatively strong body of anatomical evidence that supports Dignatha, a recurring theme of molecular analyses has been a grouping of Symphyla and Pauropoda to the exclusion of other myriapods. Symphylans and pauropods unite under varied analytical conditions in analyses of combined small and large nuclear ribosomal RNA by Gai et al. (2006), and were also found (though with weak support) in the shortest cladogram based on combined morphological and multi-locus sequence data by Giribet et al. (2005), as well as in some analyses of nucleotide data for three nuclear protein-coding genes by Regier et al. (2005), but likewise with weak support. The lack of obvious morphological synapomorphies for Symphyla + Pauropoda (to the exclusion of Diplopoda) opens the question whether their grouping in several molecular analyses could derive from the difficulties that sequence length heterogeneity in symphylans and pauropods may pose for tree reconstruction methods. This is especially obvious for the widely used nuclear ribosomal genes, for which some well sampled analyses fail to resolve symphylans and pauropods as euarthropods, instead being attracted to the onychophoran and tardigrade outgroups (von Reumont et al., 2009).

3. Chilopoda

3.1. Interrelationships of Chilopoda

From the perspective of morphology, the relationships between the 5 extant orders of Chilopoda have widespread consensus. The relationships depicted in Fig. 1 conform to groupings recognized in early classifications (Pocock, 1902; Verhoeff, 1902–1925), were depicted in pre-Hennigian phylogenetic diagrams (Prunescu, 1965; Shinohara, 1970), were likewise retrieved when cladistic argumentation was applied to the problem (Dohle, 1985, 1990; Shear and Bonamo, 1988; Borucki, 1996), and are supported by parsimony analyses of morphological datasets (Edgecombe et al., 1999; Edgecombe and Giribet, 2004). Other studies that were principally focused on the phylogenetic significance of particular character

systems have found that the relationships in Fig. 1 parsimoniously accommodate new character evidence, and have added further support for these groupings (Hilken, 1997; Wirkner and Pass, 2002; Müller and Meyer-Rochow, 2006a,b; Müller and Rosenberg, 2006). Among contemporary studies, the only discord with the scheme favoured here was in an idiosyncratic reclassification by Ax (1999), wherein the cladogram was rerooted between Geophilomorpha and all other chilopods, as in the “contraction theory” endorsed by Brölemann (1930) and other pre-cladistic workers. Ax’s rerooted cladogram led him to establish new names for groupings that are instead resolved as grades in Fig. 1. The Ax cladogram was based on a depauperate subset of relevant character evidence and his classification has never been used.

The morphology-based relationships in Fig. 1 are highly congruent with cladograms retrieved using the best sampled molecular markers, small (18S) and large (28S) nuclear ribosomal RNA (Giribet et al., 1999; Edgecombe et al., 1999; Edgecombe and Giribet, 2002, 2004). Addition of mitochondrial sequence data to the character sample contributed to some groupings that conflict with morphology, such as Craterostigmomorpha + Geophilomorpha (Giribet and Edgecombe, 2006). Analyses based on three nuclear protein-encoding genes have found support for the monophyly of the large chilopod orders, but interordinal relationships from these markers are grossly incongruent with morphology (Regier and Shultz, 2001; Regier et al., 2005), e.g., resolving *Craterostigma* basally and allying scolopendromorphs and scutigermorphs. When the nuclear coding genes are added to nuclear ribosomal, mitochondrial and morphological data, two topologies are found under different analytical conditions: (1) the cladogram based on the nuclear coding genes alone; (2) the cladogram shown in Fig. 1 (Giribet and Edgecombe, 2006). Because the latter cladogram is emphatically supported by morphology and is congruent with the best sampled subset of the molecular data, chilopod phylogeny cannot be described as showing conflict between molecules and morphology, but rather conflict between different kinds of molecular data.

Monophyletic supraordinal groups in Chilopoda shown as clades in Fig. 1 (but not named in the figure) include Pleurostigmophora (clade composed of all non-scutigeromorph chilopods), Phylactometria (a clade named for maternal brood care, a behavioural synapomorphy that groups *Craterostigma* and Epimorpha), and a clade united by strictly epimorphic post-embryonic development, Epimorpha (Scolopendromorpha + Geophilomorpha). The apomorphic characters of these groups have been listed and discussed numerous times in recent studies, and are not repeated here (see Borucki, 1996; Edgecombe and Giribet, 2004, for analyses based on Hennigian argumentation/groundpatterns and numerical cladistic analysis, respectively). Each of these three groups is supported by at least 5 unambiguous apomorphic characters (Giribet and Edgecombe, 2006, Fig. 1).

3.2. The fossil record and timing of chilopod diversification

Two of the 5 extant chilopod orders (Scutigermorpha and Scolopendromorpha) are known from Palaeozoic fossils (Fig. 1). The scutigermorph fossils are especially informative for dating the crown group of Chilopoda to at least the Late Silurian (418 m.y.a.), and an extinct order in the Middle Devonian (Devonobiomorpha) dates the divergence of Lithobiomorpha and Phylactometria in Fig. 1 to at least 385 m.y.a.

The earliest known fossil chilopods are confidently assigned to Scutigermorpha based on leg morphology and the structure of the maxillipedes. Silurian and Devonian occurrences have been grouped in the genus *Crussolum* (Shear et al., 1998; Anderson and Trewin, 2003), known from the Late Silurian (Pridolian) Ludford Lane

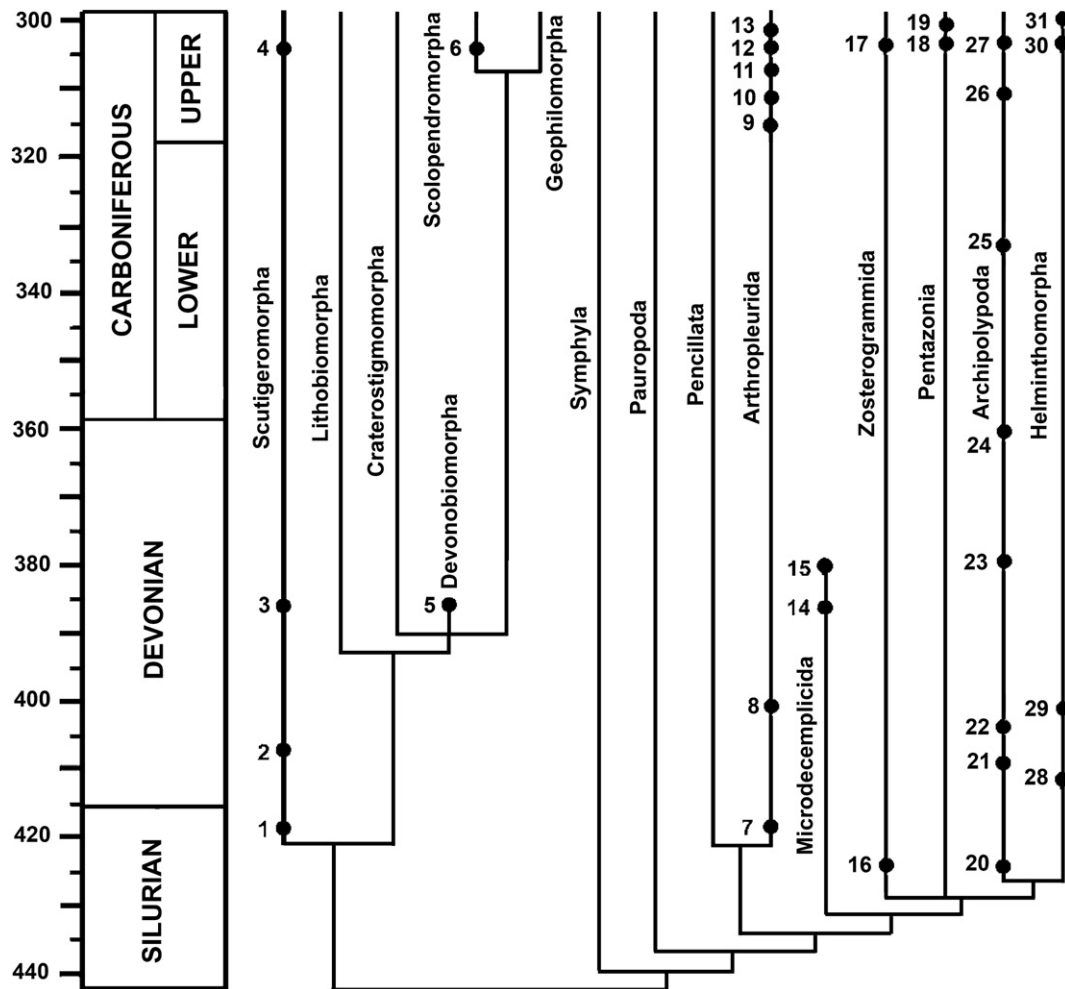


Fig. 1. Phylogeny of Myriapoda with minimal divergence dates calibrated by Silurian-Carboniferous fossil occurrences. Phylogenetic position of Arthropleurida and Microdeceplpicida follows Kraus and Brauckman (2003) but see Fig. 7 for an alternative resolution. Numbers refer to records as follows: 1–3. *Crussolum* spp. (Shear et al., 1998; Anderson and Trewin, 2003); 4. *Latzelia* (Mundel, 1979); 5. *Devonobius* (Shear and Bonamo, 1988); 6. *Mazoscolopendra* (Mundel, 1979); 7,8. *Eoarthropleura* spp. (Shear and Selden, 1995); 9–13. *Arthropleura* spp. (Hahn et al., 1986; Hannibal, 1987, and references therein); 14,15. *Microdeceplplex* (Wilson and Shear, 2000); 16. *Casiogrammus* (Wilson, 2005b); 17. *Purkynia*, *Zosterogrammus* (Wilson, 2005b); 18. *Amynilyspes*, *Archiscudderia*, *Glomerospis* (Hannibal and Feldmann, 1981); 19. *Amynilyspes* (Racheboeuf et al., 2004); 20. *Albadesmus*, *Cowiedesmus*, *Pneumodesmus* (Wilson and Anderson, 2004); 21. *Archidesmus* (Wilson and Anderson, 2004); 22. *Palaeodesmus* (Wilson and Anderson, 2004); 23. *Zanclodesmus* (Wilson et al., 2005); 24. *Orsadesmus* (Wilson et al., 2005); 25. *Anthracodesmus* (Wilson and Anderson, 2004), unnamed species (Shear, 1994); 26. *Myriacanthepestes* (Burke, 1979), *Anaxedesmus* (Wilson, 2005a); 27. *Acantherpestes*, *Euphoberia*, *Myriacanthepestes* (Burke, 1979); 28. *Sigmastria* (Wilson, 2006a); 29. *Gaspestria* (Wilson, 2006a); 30. *Xyloiulus*, *Nyranius*, *Plagiascetus* (Hoffman, 1963), *Isojulus*, *Pleurojulus* (Wilson and Hannibal, 2005), *Hexecontasoma* (Hannibal, 2000); 31, unnamed species (Hannibal et al., 2004).

deposits in England, the Lower Devonian (Pragian) Rhynie and Windyfield Cherts of Scotland, and the Middle Devonian (Givetian) of Gilboa, New York. Unlike extant scutigermorphs the tarsus is not clearly differentiated into a basitarsus and distitarsus, and tarsal substructures that are invariably present in extant scutigermorphs (tarsal papillae, resilient sole hairs) are lacking in *Crussolum*. As such, *Crussolum* is assigned to the scutigermorph stem-group. A second scutigermorph in the Windyfield Chert has been identified as taxonomically distinct from *Crussolum* (Fayers and Trewin, 2003, 2005, Fig. 7c).

Younger fossil scutigermorphs are the Upper Carboniferous *Latzelia* Scudder, 1890, and the Lower Cretaceous *Fulmenocursor* Wilson, 2001, known from single species in the Mazon Creek deposits of Illinois and the Crato Formation of Brazil, respectively. Both are similar to extant scutigermorphs in as much as their preserved details reveal, and *Fulmenocursor* (Fig. 3B) can possibly be assigned to an extant family, Scutigeridae (Edgecombe et al., 2009). This assignment would date the crown group of Scutigermorpha to at least the Early Cretaceous (Aptian).

The lithobiomorph fossil record is confined to the Cenozoic, with several taxa having been named from Baltic amber, though none has received modern study. A specimen referred to *Lithobius* from the Early Miocene of Spain (Peñalver, 1998) conforms to Lithobiidae in the presence of spurs encircling the distal parts of podomeres and the relative thickening of the ultimate legs.

Devonobius delta (Shear and Bonamo, 1988), known from cuticular material from the Middle Devonian of Gilboa, New York (Fig. 2A,B), is the basis for the extinct order Devonobiomorpha. The head and anterior part of the trunk, including legs, are the best understood parts of *Devonobius*. Its ordinal status can be defended based on its isolated phylogenetic position, being sister group to Epimorpha fide (Shear and Bonamo, 1988), and a peculiar autapomorphic character, a pair of long ventral apodemes on the maxillipede coxosternum that are not seen in other chilopods (Fig. 2B, cf. Fig. 2C). Affinities to Epimorpha were based on the shared absence of a Tömösváry organ (whereas Craterostigmorpha retain this organ; Edgecombe et al., 2002, Fig. 1H). Borucki (1996) instead regarded *Devonobius* to be most closely related to *Craterostigmus*,

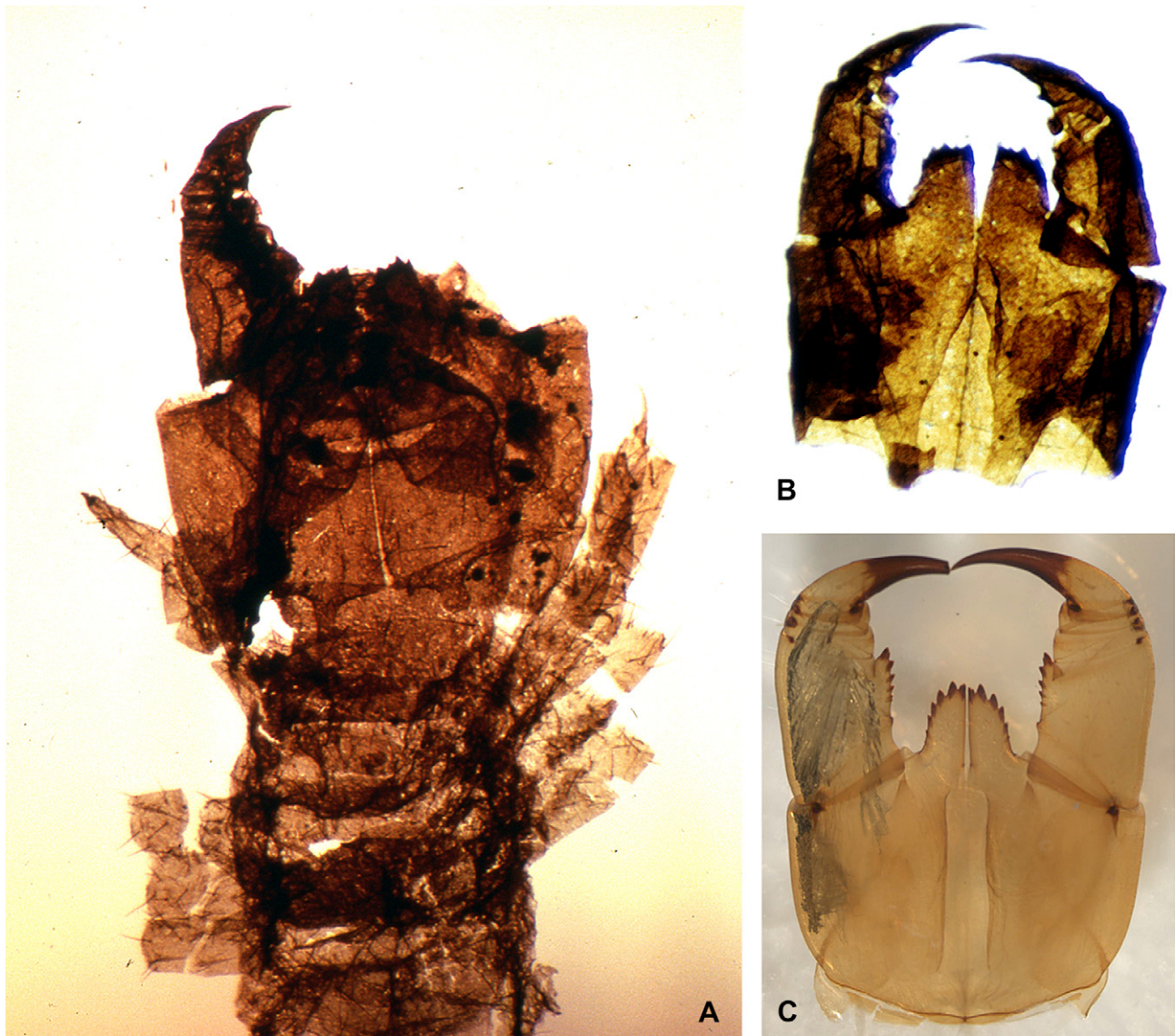


Fig. 2. (A,B) *Devonobius delta* Shear & Bonamo, 1988, a pleurostigmophoran chilopod from the Middle Devonian of New York. (A) Dorsal view of head and anterior part of trunk; (B) maxillipedes. (C) *Craterostigma tasmanianus* maxillipedes (cleared in Hoyer's) for comparison with those of *Devonobius delta*; note absence in *C. tasmanianus* of ventral apodemes.

but the characters cited in support of this relationship are either misinterpreted or are shared with other orders as well (Edgecombe and Giribet, 2004). From the perspective of morphology, all three possible resolutions for *Devonobius*, *Craterostigma* and *Epimorpha* are equally costly in the dataset of Edgecombe and Giribet (2004), but combination with sequence data favours a sister group relationship between *Devonobius* and crown group Phylactometria.

The oldest fossil *Epimorpha* are scolopendromorphs. The Upper Carboniferous of Mazon Creek, Illinois, is the source of both known Palaeozoic scolopendromorphs, of which *Mazoscolopendra richardsoni* (Mundel, 1979) is the better known. Even so, too few taxonomically informative details are preserved to permit an assignment to one of the extant families that likewise has 21 pedigerous trunk segments, and its status as a crown-grown scolopendromorph has not been established. In the Mesozoic, Scolopendromorpha are sampled from two monotypic genera from the Lower Cretaceous Crato Formation in northeastern Brazil (Martill and Barker 1998; Wilson, 2003). The better known *Cratoracricrus oberlii* (Fig. 3A) has tarsal articulations and paired paramedian trunk sutures as in Scolopendridae (Wilson 2003) and

a minimum dating for crown group Scolopendromorpha can be based upon it.

The divergence of Geophilomorpha is minimally dated by *Eogeophilus jurassicus* (Schweigert and Dietl, 1997) from the Upper Jurassic of southwestern Germany. This species is known from a single specimen, and its relationship to extant geophilomorphs has not been assessed in any detail. The crown group of Geophilomorpha and some of its subgroups (such as *Adesmata*) can be dated to at least the Late Cretaceous (early Cenomanian) based on *Buziniphilus antiquus* Edgecombe (Bonato and Minelli, 2002) from French amber. Although known from a single, apparently immature specimen, its preserved characters support membership in one of the extant families Geophilidae or Schendylidae.

4. Diplopoda

4.1. Interrelationships of Diplopoda

As indicated in Section 1, the phylogeny of millipedes is unsettled when compared to that of centipedes. Phylogenetic

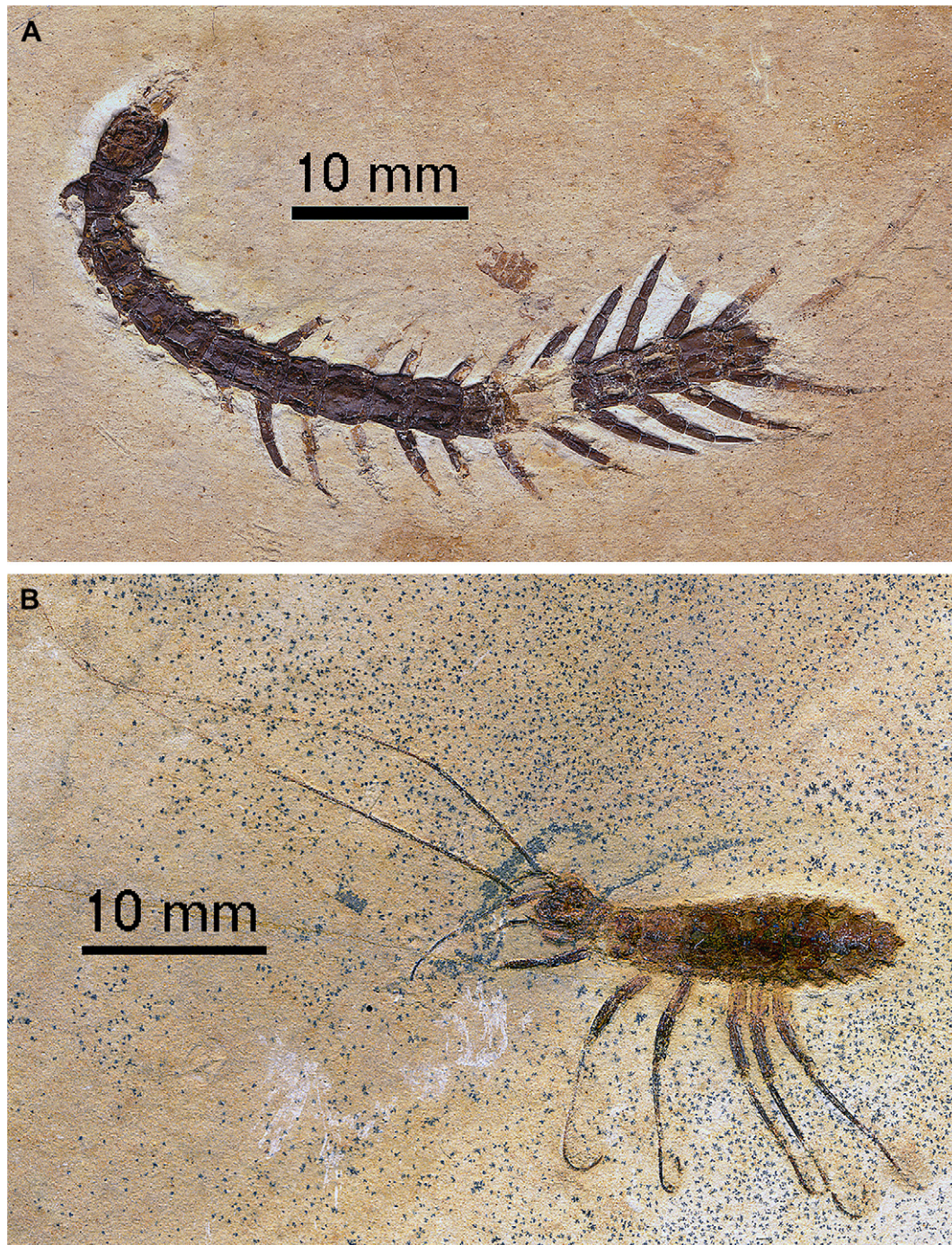


Fig. 3. Fossil Chilopoda from the Crato Formation (Early Cretaceous), Brazil. (A) *Cratoraricrus oberlii* (Scolopendromorpha). (B) *Fulmenocursor tevox* (Scutigleromorpha). Photos by G. Bechley (SMN Stuttgart).

problems in the Diplopoda are inherently more complex, since 16 extant orders of millipedes (including 144 families; [Shelley, 2003](#)) are currently recognized, as opposed to only 5 orders in centipedes. Fewer morphological characters have been studied, and entire potentially valuable character systems, such as the mouthparts, female external genitalia, and legs have either not been studied or have been underutilized. Only recently, [Shear \(2008\)](#) preliminarily explored the morphology of epiproctal spinnerets in the orders Polydesmida, Chordeumatida, Callipodida, Stemmiulida and Siphoniulida. Similar work may be expected to reveal additional characters of phylogenetic value. Within the

Helminthomorpha, the gonopods of the males have been a rich source of characters, but few of these have been subjected to strict tests of homology. As is the case with centipedes, few of these useful characters can be expected to be visible on fossils. Molecular analyses have also lagged behind. The most recent work ([Regier et al., 2005](#)) used sequences from three nuclear coding genes, *EF-1-alpha*, *EF-2* and *RNA Polymerase II*, from 28 millipede species distributed through 14 of the 16 orders, but data complete enough to be informative from such standard genes as 18S and 28S nuclear ribosomal RNA, or from any mitochondrial or *Hox* genes, are absent.

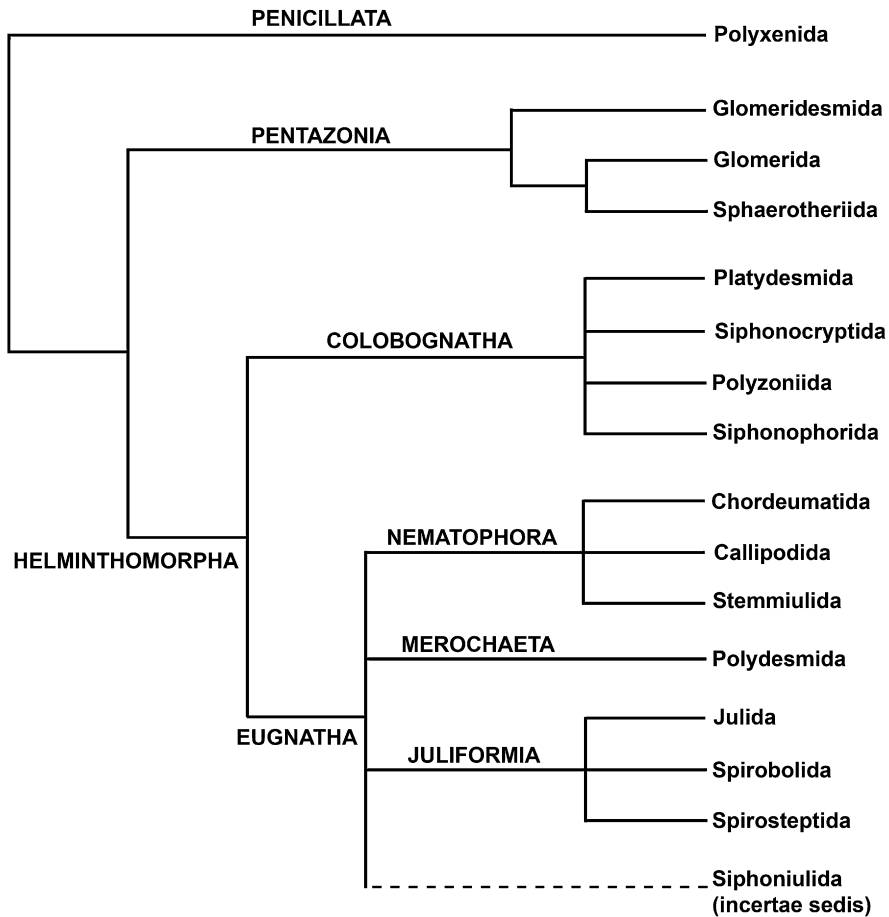


Fig. 4. Relationships among orders of Diplopoda based on the classification of Shelley (2003).

Each of the diplopod orders is regarded as monophyletic, and there has been little argument (see characters in Sierwald et al., 2003; supplement to Sierwald and Bond, 2007) except in the case of the suborder Cambalidea, which has variably been regarded as an independent order, a suborder of Julida, or a suborder of Spirostreptida (Shelley, 2003). Regier et al. (2005) sampled more than one species from the orders Julida (5 species), Chordeumatida (2), Spirostreptida (2), Polyzoniida (2), Polydesmida (3), Spirobolida (3), Sphaerotheriida (2) and Polyxenida (3) and found strong molecular support for the monophyly of those orders. The single cambalidean they studied grouped with a spirostreptidan (Regier et al., 2005).

Verhoeff (1928) presented an early hypothesis of millipede phylogeny which Sierwald and Bond (2007) updated with current clade names. The orders Siphonocryptida and Siphoniulida were not included because siphonocryptids were considered polyzoniids at that time, and Verhoeff was evidently unaware of siphoniulids.

The presently accepted classification (Shelley, 2003) contains phylogenetic hypotheses in its grouping of the orders (Fig. 4). The subclass Penicillata (Pselaphognatha) contains only the order Polyxenida, and is generally opposed to a subclass Chilognatha, comprised of the remaining 15 orders. The three orders Glomeridesmida, Glomerida, and Sphaerotheriida make up the infraclass Pentazonia, distinguished by an absence of gonopods (modified legs on segment 7 or segments 7 and 8 of the males, used to transfer sperm) and the presence of terminal telopods which clasp females during mating. Glomeridesmida are in their own superorder, Limacomorpha, while the remaining two pentazonian orders are in superorder Onsicomorpha (reduced number of segments, ability to

completely enroll). The remaining 12 orders make up the infraclass Helminthomorpha. This taxon comprises two superclasses, Colobognatha and Eugnatha. The colobognath orders (reduced or partially fused mouthparts, gonopods from legpairs 9 and 10) are Platydesmida, Polyzoniida, Siphonocryptida and Siphonophorida; no grouping of them within Colobognatha is currently in the classification (Shelley, 2003). Seven of the 8 orders in Eugnatha (unreduced mouthparts, gonopods from legpair 8 or legpairs 8 and 9) are grouped as follows: Superorder Juliformia (orders Julida, Spirostreptida and Spirobolida), Superorder Nematophora (orders Chordeumatida, Callipodida and Stemmiulida) and Superorder Merochaeta (order Polydesmida). The order Siphoniulida is not placed in the classification, but since it has both spinnerets and gonopods developed only from legpair 8, it could be either in Nematophora or Merochaeta. Converting this classification to a phylogenetic tree produces Fig. 4.

Sierwald et al. (2001) adapted and augmented the morphological character matrix originated by Enghoff (1984), who had earlier produced the first cladistic hypothesis of superordinal relationships in diplopods. Their cladogram is shown in Fig. 5. The order Siphonocryptida had not been recognized at the time; siphonocryptids were considered a suborder under Polyzoniida. When the order Siphoniulida, whose characters had just been observed from newly collected material, was added, considerable resolution was lost in a consensus tree.

Regier et al. (2005) presented two trees (both were for myriapods in general), one based on a Bayesian analysis of nucleotides with third codon positions excluded, the second a strict consensus

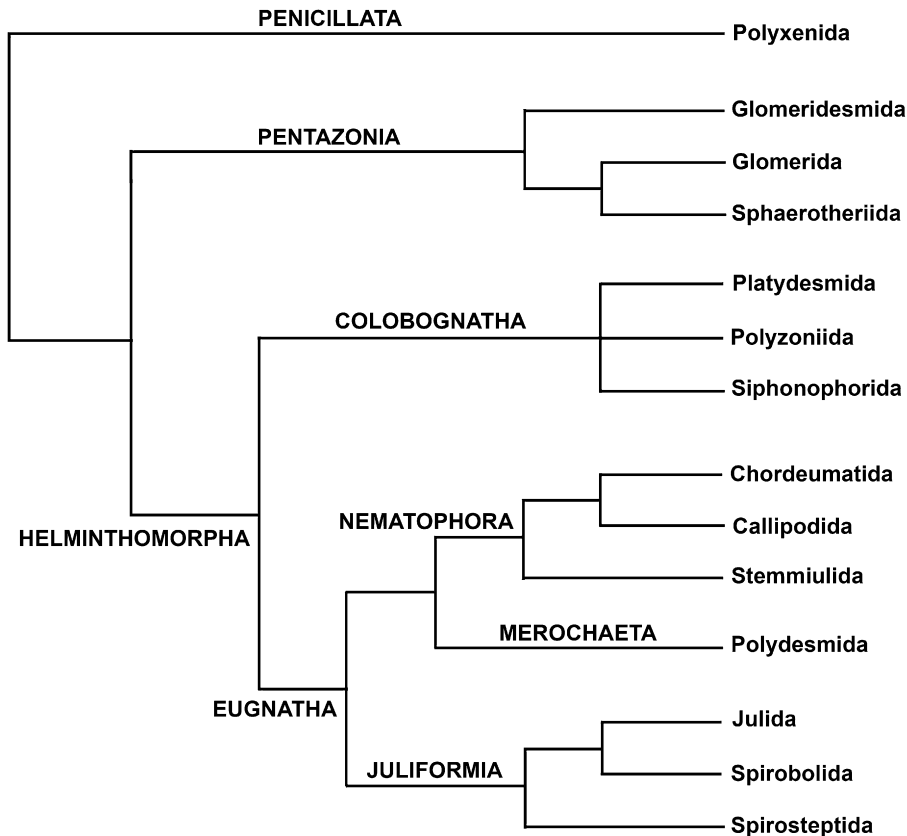


Fig. 5. Relationships among diplopod orders shown as strict consensus from cladistic analysis of morphological characters by Sierwald et al. (2001).

tree based on a parsimony analysis of amino acids. As indicated above, millipede orders in which more than a single species was sampled were strongly supported as monophyletic. However, support for only a few superordinal relationships was strong enough to be taken seriously, as follows (non-parametric bootstrap percentages from amino acid tree in parentheses): Helminthomorpha (up to 90%), Colobognatha (up to 84%), and Glomerida + Glomeridesmida (up to 97%). All other interordinal relationships were inconsistently recovered and had low bootstrap percentages. The grouping Glomerida + Glomeridesmida contradicts the morphological evidence.

Sierwald and Bond (2007) combined the morphological matrix of Sierwald et al. (2001) with the amino acid residue data of Regier et al. (2005); their tree (Fig. 6) differed from both the earlier morphological tree and the amino acid tree. In a Bayesian analysis, nearly all nodes showed high posterior probabilities, with lower probabilities (for example, 0.71 for a clade Platydesmida + Siphonocryptida) for those branches involving a clade for which there were no molecular data. This most recent tree, the only one based on total evidence, must be taken as a working hypothesis for the present, though it shows several traditionally accepted supraordinal groupings as polyphyletic (for example, Eugnatha and Nematophora). We concur with the recommendations of Sierwald and Bond (2007) and Shear (2008) that more complete taxon sampling, more morphological characters, and data from additional genes are urgently required.

The placement of any fossil millipede in this tree is speculative, as no fossils have been included in any analysis to this point, though Sierwald and Bond (2007) presented a hypothetical tree in which they attempted to show the relationships of extinct orders to extant ones; we present a slightly modified version in Fig. 7. Their presentation was based mostly on the conclusions of Wilson and

Anderson (2004). The extinct (Late Carboniferous) order Amynilypedida is undoubtedly a member of the Pentazonia (Hannibal and Feldmann, 1981). The majority of Palaeozoic fossil diplopods is placed in a superorder Archipolyпода under Helminthomorpha; archipolyпода differ from other helminthomorphs in having paired pores on the sternites, often with complex valve-like closures, that probably contained eversible sacs (Shear, 1997; Wilson and Anderson, 2004; Wilson, 2006a). Four orders, Cowiedesmida, Archidesmida, Palaeosomatida (not shown in Fig. 7) and Euphoberiida, are included. Wilson (2005b) described the order Zosterogrammida from Silurian and Carboniferous specimens, but it remains *Chilognatha incertae sedis*. The order Pleurojulida was considered by Wilson and Hannibal (2005) as sister taxon to the Colobognatha, but was placed by Sierwald and Bond (2007) in a trichotomy Pleurojulida-Colobognatha-Eugnatha. Wilson (2006a) included a Superfamily Xyloiuloidea (Lower Devonian–Upper Carboniferous) in the Julimorpha; Hoffman (1969) considered xyloiulids as spirobolidan. A few Mesozoic fossils strongly resemble spirobolids and have been placed there (Dzik, 1975), while others may be nematophorans (Shear and Selden, 2009) as might also be the Carboniferous *Hexecontasoma* Hannibal (Hannibal, 2000). Considerable controversy surrounds the systematic and phylogenetic position of three orders (Arthropleurida [Carboniferous], Microdecemplicida [Devonian] and Eoarthropleurida [Silurian–Devonian]) informally grouped as “arthropleurideans.” The arthropleurids and eoarthropleurids were originally thought to represent a separate, extinct class of myriapods (Shear, 1997) until Wilson and Shear (2000) presented evidence that they shared at least some of the diagnostic features of millipedes, and the consensus has now shifted to viewing them as belonging to Diplopoda. Wilson and Shear

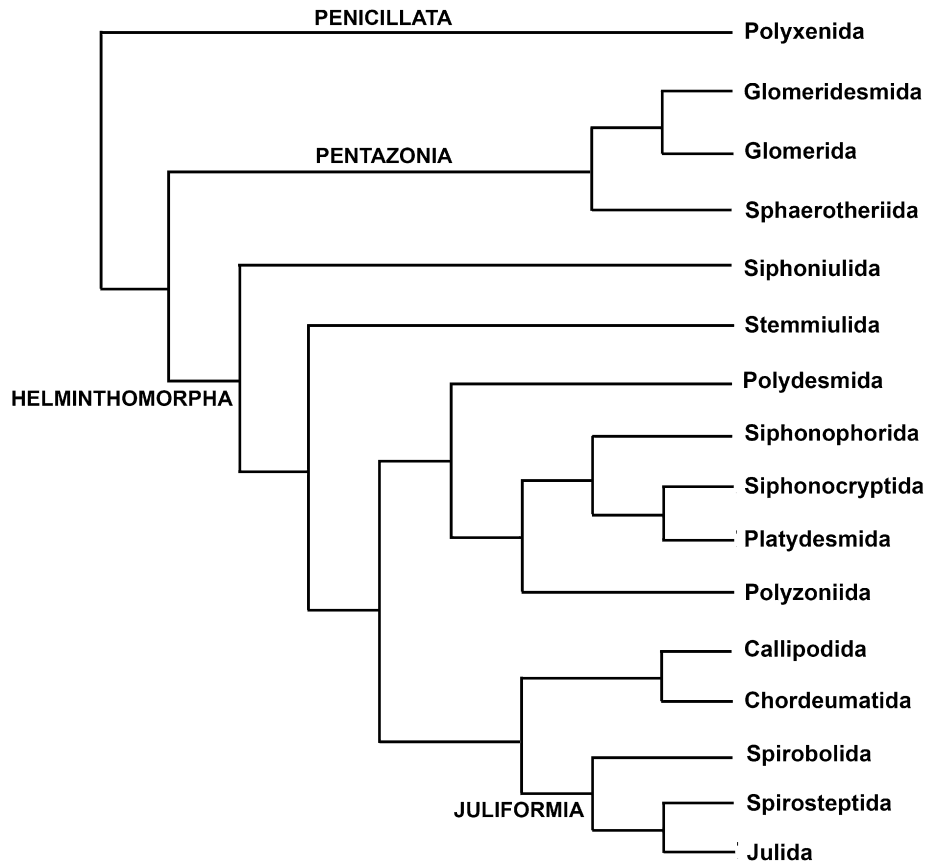


Fig. 6. Relationships among orders of Diplopoda (from Sierwald and Bond, 2007) based on Bayesian analysis of combined morphological data (Sierwald et al., 2001) and amino acid data of Regier et al. (2005).

(2000) considered all three orders to form a sister taxon to the Chilognatha, but Kraus and Brauckman (2003) placed Arthropleurida and Eoarthropleurida in the Penicillata, leaving only Microdeceplidica as sister to the Chilognatha. Wilson and Anderson (2004) showed microdeceplidids sister to chilognaths, but the other two arthropleurid orders as sister to Penicillata, rather than included therein. The question remains unresolved; we show the Kraus and Brauckmann view in Fig. 1 and the Wilson alternative in Fig. 7.

4.2. The fossil record of the Diplopoda

Because millipede fossils have been comprehensively reviewed recently (Shear, 1997; Almond 1985), the following focuses on post-1996 developments. We recognize in particular the significant contributions of Heather M. Wilson and Joseph T. Hannibal. Despite the work of a half-dozen specialists in myriapod fossils, many specimens remain unstudied and much of the material collected and described in the nineteenth century is in urgent need of re-examination.

4.2.1. Silurian

The fossil record of the Diplopoda begins in the Middle Silurian of Scotland with three archipolypod species (Wilson and Anderson, 2004). *Cowiedesmus eroticopodus* Wilson and Anderson is the only species in its order (Cowiedesmida) and is clearly an archipolypod helminthomorph. *Albadesmus almondi* Wilson and Anderson, and *Pneumodesmus newmani* Wilson and Anderson are also archipolypodans but are not assigned to orders. The major significance of these species is that the helminthomorph body plan had already

been established by the Middle Silurian, and that the “litter-splitting” ecotype, marked by well-developed paranota in all three, was also present. Further, gonopod-like modified legs are seen in the vicinity of segment 8 of *C. eroticopodus*, suggesting that some form of indirect sperm transfer was already taking place. The exact segmental placement of these possible gonopods is difficult to establish because counts of legs anterior to the modified ones may be disputed (are legs from one or both sides of the body preserved in the specimen, or a mixture of both?), but Wilson and Anderson (2004) favoured the modification of the posterior pair of legs of segment 8 (legpair 11), a condition not seen in any extant millipede order. *Pneumodesmus newmani* provides not only the earliest preserved air-breathing spiracles in millipedes, but the earliest direct evidence of air-breathing in any animal.

Casiogrammus ichthyeros (Wilson 2005) from the Wenlock of Scotland, was included by Wilson (2005b) in an order Zosterogrammida, which also included two Upper Carboniferous genera. Zosterogrammida cannot be placed with any more precision other than to say that it appears to be a chilognath, but the breadth of the tergites and possibly divided sternites suggest a similarity to pentazonians (Wilson, 2005b).

Eoarthropleura ludfordensis Shear and Selden (Eoarthropleurida) is a part of the earliest terrestrial fauna, cuticular remains macerated from Upper Silurian shales of Ludford Lane, Wales (Shear and Selden, 1995). Two additional species of this genus are known from the Devonian of New York and Germany (Shear, 1997).

4.2.2. Devonian

The Lower Devonian marks the first appearance of julimorph millipedes, a significant fact due to the consideration by most

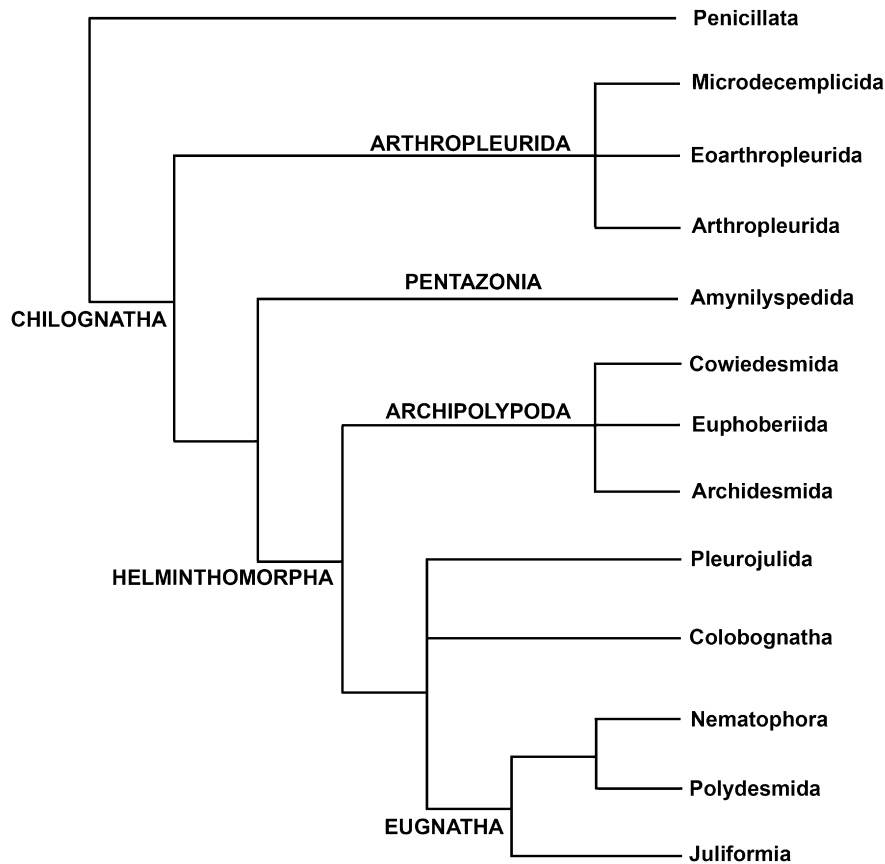


Fig. 7. Placement of fossil diplopod orders, as suggested by Sierwald and Bond (2007). The order Zosterogrammida, not shown, is *Chilognatha incertae sedis*.

myriapodologists that the julimorphs are the most highly evolved taxon in Diplopoda. *Gaspestria genselorum* Wilson is from the Late Emsian of Québec, and *Sigmastria dilata* Wilson was found in the Lochkovian of Scotland. Neither includes much more evidence for systematic placement than a julimorph body plan and diplopleurotergal striations thought to be diagnostic for xyloiuulideans. Of some significance is the presence in these specimens of the first known ozopores, thus the earliest evidence in millipedes and in all animals of a chemical defense (Wilson, 2006a).

Archidesmus macnicoli Peach was redescribed by Wilson and Anderson (2004) and typifies the order Archidesmida of the superorder Archipolypoda. As with the cowiedesmidan *Cowiedesmus eroticopodus*, *A. macnicoli* has a modified legpair (gonopods?) which Wilson and Anderson (2004) considered to be legpair 10, the anterior pair of segment 8. Again, the leg counts can be disputed, but legpair 10 is modified for sperm transfer in the extant colobognaths. This legpair is evidently the effective one in sperm transfer, while the legs of pair 9 are also modified as sheaths for the gonopods. It does not appear that legpair 9 is modified in *Archidesmus*. The nature of the modification—a swollen, clavate, multi-segmented structure with some small details visible at the tip—is similar in both archidesmidans and cowiedesmidans. Additional archidesmidans of a new family Zanclodesmidae, from the Upper Devonian, were described by Wilson et al. (2005) from Pennsylvania (late Famennian; *Orsadesmus rubecollis* Wilson, Daeschler and Desbiens) and Québec (Frasnian; *Zanclodesmus willetti* Wilson, Daeschler and Desbiens). Placement in Archidesmida is based on the general similarity of the dorsum in these genera to *Archidesmus*, since ventral features cannot be seen in the fossils, including any modified anterior legs that may be present. *Palaeodesmus*

tuberculata (Brade-Birks), from the Siegenian of Scotland (Fig. 8A) is *Archipolypoda incertae sedis*.

Devonian arthropleurids were represented by two distinct orders, Eoarthropleurida and Microdecemplicida. The eoarthropleuridans are known from disarticulated parts found in New York, Canada, Britain and Germany (Shear and Selden, 1995). Knowledge of the exact details of their structure awaits the discovery of more complete specimens. *Microdecemplex rolfei* Wilson and Shear, on the other hand, is known from fairly complete material macerated from rocks in New York. The animals were minute, less than 10 mm long, with bizarre heads evidently lacking antennae, and sexually dimorphic posterior limbs (Shear, 1997; Wilson and Shear, 2000). Somewhat different interpretations of these animals were given by Kraus and Brauckman (2003).

4.2.3. Carboniferous

Millipede fossils from the Lower Carboniferous require restudy. *Anthracodesmus macconochiei* Peach (Viséan of Scotland) was examined by Wilson and Anderson (2004) but they were only able to conclude that it was probably an archipolypod. Shear (1994) illustrated, but did not name, a cylindrical-bodied millipede with free sternites, also from the Viséan of Scotland (Fig. 8E). The specimen displayed ozopores, a well-preserved head and sternal spiracles, but no sternal pores with eversible sacs. This specimen also had small lateral spines on the metazonites; it probably represents an undiagnosed order.

The great majority of millipede fossils come from the Upper Carboniferous, and most of those from deposits associated with coal swamps. This association with wet habitats led some workers to hypothesize that many Upper Carboniferous diplopods were

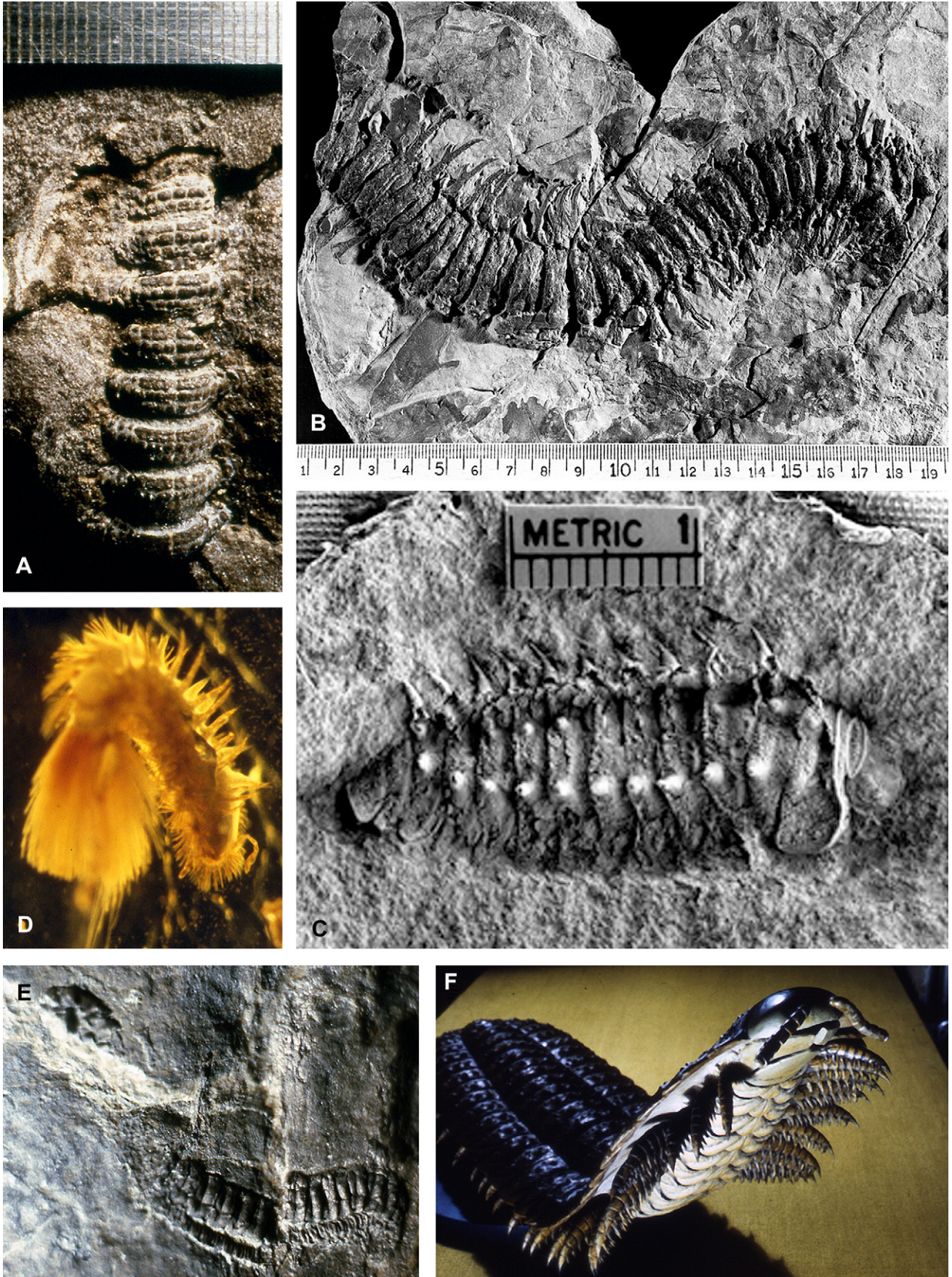


Fig. 8. Fossil diplopods. (A) *Paleodesmus tuberculatus* (Brade-Birks), Lower Devonian of Scotland. (B) *Myriacanthepestes clarkorum* (Burke), Upper Carboniferous of West Virginia. (C) *Amynilyspes wortheni* Scudder, Upper Carboniferous of Illinois. (D) Unidentified polyxenid from Baltic Amber. (E) unnamed helminthomorph, Lower Carboniferous of Scotland. (F) Reconstruction of *Arthropleura* sp. (B) and (C) courtesy of Cleveland Museum of Natural History, (A) and (F) courtesy of Hunterian Museum, Glasgow.

semiaquatic, an idea mostly rejected today (Hannibal, 1981). An aquatic or semiaquatic habit was also postulated by Kraus and Brauckman (2003) for the gigantic *Arthropleura*, on the basis of a supposed “paper-thin” cuticle. However, Kraus (2005) later suggested that all known *Arthropleura* fossils were of exuvia, which could explain the apparent thin cuticle. Many ichnofossils attributed to *Arthropleura* are known from Europe and North America (i.e. Briggs et al., 1979, 1984; Martino and Greb, 2009) in which the animal was clearly locomoting for some distance subaerially over wet sediment, leaving marks only of its leg tips; it is hard to imagine this stance in an animal as large as *Arthropleura*, if, as Kraus and Brauckman (2003) postulated, the only skeletal support for it was hemolymph pressure. Further, Lucas et al. (2005) comment that the deep impressions of *Arthropleura* trackways studied by them indicate strong sclerotization of the cuticle. According to Kraus and Brauckman (2003) and Kraus (2005), *Arthropleura* was a gigantic representative of the Penicillata, a group represented today by animals generally less than 3 mm long. Wilson and Shear (2000) on the other hand, placed Arthropleuridea (including the orders Arthropleurida, Eoarthropleurida and Microdecemplicida) as a sister taxon to all chilognaths. Whatever their taxonomic or phylogenetic position, the largest *Arthropleura* were estimated to be 2 m or more in length (Fig. 8F) and were very likely the most massive arthropods that ever existed (Hahn et al., 1986).

Pentazonia were represented in the Upper Carboniferous by members of the order Amynilyspedida. Species of *Amynilyspes* (Fig. 8C) occurred in North America, Britain and continental Europe. They were characterized by long, paired spines on the metatergites, which, in enrolled animals, would have been a potent defense (Hannibal and Feldmann, 1981; Hannibal, 1984; Racheboeuf et al., 2004). *Archiscudderia* and *Glomeropsis*, on the other hand, lacked spines but were otherwise similar to *Amynilyspes* (Hannibal, 1984). Hannibal and Feldmann (1981) also postulated that the extant order Sphaerotheriida was present in the Upper Carboniferous, based on a specimen with 13 tergites, as opposed to 14 in the amynilyspedidans. Zosterogrammidans, which Wilson (2005b) thought may be allied to pentazonians, were represented by *Zosterogrammus stichostethus* Wilson, from Mazon Creek.

The coal swamps were also home to at least three evolutionary lines of archipolypods, represented by three genera in the order Euphoberiida, *Euphoberia*, *Acantherpestes* and *Myriacanthepestes*. Known examples were all rather large millipedes, up to 30 cm long (Hannibal, 1981), and fitted out on each metatergite with long, branched spines that were presumably defensive in nature, speaking to a possible “arms race” with large predatory tetrapods. Nevertheless, Hannibal and Feldmann (1988) found euphoberiid remains in coprolites in limestones from Hamilton, Kansas. While most of the known examples were first described by Scudder and by Fritsch in the nineteenth century, the best studies of euphoberiids (*Myriacanthepestes*) were those by Burke (1973, 1979). *Myriacanthepestes* (Fig. 8B) was a rather flattened animal, but both *Acantherpestes* and *Euphoberia* have been reconstructed with cylindrical segments and erect spines (Hannibal, 1981). The heads of euphoberiids were very different from those of extant millipedes, with large, possibly compound eyes, small antennae that arose from bulging sockets, and a labrum without teeth (Burke, 1973). Kraus (1974) suggested that the euphoberiids were only lightly sclerotized and had thin cuticle, but this was refuted by Shear (1997); Kraus (1974) also placed the tracheal stigmata in “pleurites” but these are clearly lateral to the legs, in the sternites. Euphoberiids do not have free pleurites. At least some euphoberiids had modified legs about midlength in the body (around the 20th to 25th segment), but these were probably not gonopods; instead it seems likely they may have been used to clasp the opposite sex while mating (Hannibal, 1995). In two ironstone nodules from Mazon Creek, Wilson (2006b) found

aggregations of 10–19 juvenile *Euphoberia*, and suggested that the aggregation/migration behaviour seen in some extant diplopods was present even in the Carboniferous, and may have been associated with increasing the efficiency of individual chemical defenses (euphoberiids have ozopores). Additional archipolypods lacking spines were also present, including *Anaxodesmus diambonotusi* Wilson, from Coseley, England. It may have been an archidesmid (Wilson, 2005b). The order Palaeosomatida is known from species of *Paleosoma* found in England and Poland; these were large millipedes lacking tergal spines, but with distinct ozopores located on dorsal bosses (Hannibal and Krzemiński, 2005). A comprehensive restudy of all available Carboniferous archipolypod material would be very valuable.

Pleuroiulidans, possibly related to modern colobognaths, were moderately large millipedes (up to 10 cm long), round in cross-section, but with free diplopleurites (Wilson and Hannibal, 2005). *Pleurojulus* and *Isojulus* were found in the Czech Republic and North America. The evidence is ambiguous, but either legpair 10 alone, or legpairs 9 and 10 (as in living colobognaths) may have been modified as gonopods in males (Wilson and Hannibal, 2005). However, the discussions of gonopods by Wilson and Hannibal (2005) and Wilson and Anderson (2004) are marred by some misconceptions regarding these appendages in living forms. For example, Wilson and Hannibal (2005) stated that “All extant helminthomorph millipedes, with only a few notable exceptions ... have at least legpair 9 modified, either as intromittant organs or accessory gonopods (p. 1117)”. However, in the orders Chordeumatida, Polydesmida, Siphoniulida, Stemmilulida, Callipodida and Spirostreptida, together accounting for more than 70% of known millipede species, it is the eighth legpair that is invariably modified, the ninth being modified only in apomorphic taxa of Chordeumatida (the ninth pair also may be completely reduced, for example in Spirostreptida). In julimorphs such as spirobolids and julids, the eighth pair is also invariably modified, but as an accessory. Thus the significance of possible male gonopods in Palaeozoic millipedes needs restudy.

Hoffman (1963) re-examined specimens of *Xyloilulus*, *Nyranius* and *Plagiascetus*, and considered all three (united by him in a suborder Xyloilulidea) to be possible spirobolidans, which would make the Spirobolida the oldest known order of millipedes still in existence. Despite his suggestion that the xyloilulideans were spirobolids, Hoffman (1963) characterized a possible gonopod on *Plagiascetus lateralis* Hoffman as spirostreptid-like. Another possible spirobolid from the Late Carboniferous is represented by an unnamed species reported by Hannibal et al. (2004) from the Virgilian of New Mexico. *Hexecontasoma* was described by Hannibal (2000) as a possible callipodidan from Mazon Creek, but despite a general resemblance to the living genus *Abacion*, does not show any of the autapomorphies of the order Callipodida.

There still remains, in collections in North America and Europe, much unstudied material of Carboniferous millipedes, and as mentioned above, many of the taxa described in the nineteenth century desperately need restudy, especially in view of the recent reinterpretation of some of these fossils by Wilson, Hannibal, and others.

4.2.4. Permian

The Permian Period is virtually a blank as far as millipede fossils are concerned. Hannibal (2006) noted, but did not describe, Permian millipede fossils from fissure fills in Oklahoma. *Arthropleura* evidently survived at least into the Lower Permian (Kraus, 2005).

4.2.5. Mesozoic

Like the Permian Period, the entire Mesozoic Era is remarkably depauperate in millipede fossils. Shear et al. (2009) recently reviewed what is known, but missed the paper of Nguyen Duy-

Jacquemin and Azar (2004), which described two new genera and species of penicillate millipedes from the Cretaceous amber of Lebanon, and noted the occurrence of the established genus *Phryssonotus* in Cretaceous amber from France. Earlier, Cockerell (1917) had mentioned a penicillate from Burmese amber, now dated as Albian (Nguyen Duy-Jacquemin and Azar, 2004). Shear et al. (2009) also described a new species, *Hannibaliulus wilsonae* Shear, Selden and Gall, from the Triassic Lagerstätte of Grès à Voltzia, France. This species has cylindrical segments composed of diplopleurotergites with a midline suture, and free sternites; it may be an early nematophoran. *Tomius angulatus* Dzik is from the Triassic of Siberia and was said by Dzik (1981) to be a xyloiuclidean, which would indicate the survival by this clade of the Permian–Triassic Crisis, but the taxonomic placement is based only on the striate ornament of the segments and is open to dispute. Jell (1983) described *Decorotergum warrenae* Jell from the early Jurassic of Australia, but the specimen is very poorly preserved, and neither of Jell's taxonomic suggestions—Aminylispedida or Polydesmida—is at all convincing. Dzik (1975) maintained that *Gobiulus sabulosus* Dzik, from the middle Campanian (Cretaceous) of Mongolia was actually a member of the extant spirobolid family Atopetholidae, but he evidently completely misunderstood the morphology and geographic distribution of this family (Shear et al., 2009). Nevertheless, it seems quite likely that *Gobiulus* is at least a julimorph, and possibly in the order Spirobolida. If this is so, and the xyloiuclidean are also spirobolids, they too survived the mass extinction at the end of the Permian.

4.2.6. Cenozoic

Numerous millipede fossils (Fig. 8D) have been described from Cenozoic ambers (i.e. Bachofen von Echt, 1942; Hoffman, 1969; Shear, 1981; Santiago-Blay and Poinar, 1992), from limestone caves in Jamaica (Donovan and Velkamp, 1994), from mineral deposits in Australia (Duncan et al, 1998), and North American asphalt (Pierce, 1946), and onyx-marble (Pierce, 1951, 1957). Especially the material from the Baltic amber requires restudy, but there is no reason not to believe that all Cenozoic millipede fossils can be placed in extant orders, and perhaps even families and genera (i.e. Santiago-Blay and Poinar, 1992).

4.3. Cladogenesis in Diplopoda

Wilson (2006a) constructed a stratocladogram for the Myriapoda, and we adopt her conclusions here (Fig. 1). As far as the Diplopoda are concerned, the key piece of evidence is the presence in the Early Devonian of what are very probably juliforms. Since these diplopods are generally accepted as being the most apomorphic extant clade, Wilson argued for a sustained burst of rapid cladogenesis during the Early and mid-Silurian, producing almost all of the superordinal taxa by the beginning of the Devonian. Only the Nematophora and Merochaeta (Polydesmida) may have originated late in the Carboniferous, but this is based on considering *Hexecontasoma* a nematophoran, which is by no means certain. Millipedes are thought by Wilson (2006a) to have originated at some time in the Late Ordovician, a date set by the trackways in the Llanvirn-Caradoc of Britain discovered by Johnson et al. (1994) and attributed to millipedes with a penicillate/arthropleuridean body plan based on studies of modern tracks of *Polyxenus* (Wilson, 2003). Wilson (2006a) rejected the Cambrian–Ordovician trackways found in Canada by MacNaughton et al. (2002) as diplopod traces. Burrows described from the Late Ordovician of Pennsylvania by Retallack (2001) as the ichnogenus *Scoyenia* were interpreted by him as made by diplopods, but a recent study of burrowing by living juliforms (Hembree 2009) demonstrated that such burrows have nothing in common with *Scoyenia*; Wilson (2006a) also

disputed Retallack's interpretation. Indeed, an implication of Wilson's analysis is a single terrestrialization event for an ancestral myriapod sometime prior to the Middle Ordovician.

5. Pauropoda and Symphyla

No reliable internal phylogenies for these orders have been proposed, and they are taxonomically understudied, despite the herculean efforts of Ulf Scheller, virtually the only active specialist apart from pauropod taxonomist Yasunori Hagino. Although symphylans and pauropods are known as fossils only from the Baltic (Scheller and Wunderlich 2001, 2004) and Dominican ambers (Poinar and Edwards 1995), specimens which can be placed in extant families and genera, the presence of both these orders at least by the mid-Silurian is predicted by the occurrence of diplopod fossils from that time.

6. Kampecarida

Kampecarids are enigmatic but relatively common myriapod-like fossils from Late Silurian and Early Devonian deposits in Britain. They were examined in an unpublished thesis by J.E. Almond (with an overview in Almond, 1985), upon which Shear (1997) based some tentative conclusions and a reconstruction. The kampecarid head may have been diplopod-like, with antennae and mandibles, and may either have been covered by two separate plates or followed by a legless collum. At least some of the trunk segments were diplosegments, and a few legless segments are found at the posterior end of the body. The legs articulated with the sternum, as in millipedes. It is likely they represent an extinct high-level taxon within Diplopoda; they have never been included in any phylogenetic analysis and are not mentioned by Wilson (2006a) in her discussion of myriapod cladogenesis.

7. Fossil stem-group myriapods?

The problem of identifying a fossil stem-group myriapod was addressed by Edgecombe (2004). While conceding that the presence of stem-group myriapods in the Cambrian is phylogenetically sound, and is indeed strengthened by the discovery of apparent crown group representatives of its sister group, Tetraconata, in the early Cambrian (Harvey and Butterfield, 2008), Edgecombe (2004) found that a variety of candidate fossils from the Lower and Upper Cambrian had in common with Myriapoda only a series of homonomous trunk segments. None preserve heads with detail enough to allow the detection of myriapod synapomorphies (e.g., the transverse bar of the tentorium or a mobile mandibular gnathal lobe) found there. Edgecombe (2004) suggested that an as yet undescribed and unnamed myriapod-like animal from the Lower Silurian of Waukesha, Wisconsin (Mikulic et al, 1985) or the enigmatic *Leverhulmia* from the Lower Devonian Rhynie Chert (Anderson et al, 2003) might represent late-surviving relicts of a myriapod stem-group. However, Wilson et al. (2004) examined the Waukesha animal, represented by 30 or more specimens, and found no evidence of myriapod affinities, suggesting instead that it was closer to lobopodians. Fayers and Trewin (2005) reinterpreted *Leverhulmia* as a hexapod, delineating characters of the limbs that would exclude it from Myriapoda. Identifying early Palaeozoic stem-group myriapods remains one of the challenges of the arthropod fossil record.

Acknowledgements

Günther Bechly kindly provided the photographs of chilopods from the Cretaceous of Brazil. Markus Koch prepared and

photographed the *Craterostigma* maxillipedes in Fig. 2C. Joe Hannibal provided photographs of Paleozoic diplopods. Work on this article by WAS was supported by a grant from the National Science Foundation of the United States (DEB05-29715) to WAS, Petra Sierwald and Jason Bond, and by the Faculty Professional Development Committee of Hampden-Sydney College.

References

- Almond, J.E., 1985. The Silurian-Devonian fossil record of the Myriapoda. *Philosophical Transactions of the Royal Society of London B* 309, 227–237.
- Anderson, D.T., 1973. *Embryology and Phylogeny in Annelids and Arthropods*. Pergamon Press, Oxford.
- Anderson, L.L., Trewin, N.H., 2003. An Early Devonian arthropod fauna from the Windyfield Cherts, Aberdeenshire, Scotland. *Palaeontology* 46, 457–509.
- Ax, P., 1999. *Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik*. Gustav Fischer Verlag, Stuttgart.
- Bachofen von Echt, A.F., 1942. Über die Myriapoden des Bernsteins. *Palaeobiologica* 7, 394–403.
- Bäcker, H., Fanenbruck, M., Wägele, J.-W., 2008. A forgotten homology supporting the monophyly of Tracheata: the subcoxa of insects and myriapods re-visited. *Zoologischer Anzeiger* 247, 185–207.
- Bitsch, C., Bitsch, J., 2002. The endoskeletal structures in arthropods: cytology, morphology and evolution. *Arthropod Structure & Development* 30, 159–177.
- Bitsch, C., Bitsch, J., 2004. Phylogenetic relationships of basal hexapods among the mandibulate arthropods: a cladistic analysis based on comparative morphological characters. *Zoologica Scripta* 33, 511–550.
- Bonato, L., Minelli, A., 2002. Parental care in *Dicelloglyphus carniolensis* (C.L. Koch, 1847): new behavioural evidence with implications for the higher phylogeny of centipedes (Chilopoda). *Zoologischer Anzeiger* 241, 193–198.
- Borucki, H., 1996. Evolution und Phylogenetisches System der Chilopoda (Mandibulata, Tracheata). *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg* 35, 95–226.
- Brölemann, H.-W., 1930. *Myriapodes Chilopodes*. Faune de France 25. Imprimerie Toulousaine, Paris, 405 pp.
- Briggs, D.E.G., Rolfe, W.D.I., Brannan, J., 1979. A giant myriapod trail from the Namurian of Arran, Scotland. *Palaeontology* 22, 273–291.
- Briggs, D.E.G., Plint, A.G., Pickerill, R.K., 1984. *Arthropleura* trails from the Westphalian of eastern Canada. *Palaeontology* 27, 843–855.
- Burke, J.J., 1973. Notes on the morphology of *Acantherpestes* (Myriapoda, Archipolypoda) with the description of a new species from the Pennsylvania of West Virginia. *Kirtlandia* 17, 1–24.
- Burke, J.J., 1979. A new millipede genus, *Myriacanthepestes*, (Diplopoda, Archipolypoda) and a new species, *Myriacanthepestes bradebirksi*, from the English coal measures. *Kirtlandia* 30, 1–23.
- Cockerell, T.D.A., 1917. Arthropods in Burmese amber. *Psyche* 24, 40–45.
- Dohle, W., 1980. Sind die Myriapoden eine monophyletische Gruppe? Eine Diskussion der Verwandtschaftsbeziehungen der Antennaten. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 23, 45–104.
- Dohle, W., 1985. Phylogenetic pathways in the Chilopoda. *Bijdragen tot de Dierkunde* 55, 55–66.
- Dohle, W., 1990. Some observations on morphology and affinities of *Craterostigma tasmanianus* (Chilopoda). In: Minelli, A. (Ed.), *Proceedings of the 7th International Congress of Myriapodology*. E.J. Brill, Leiden, pp. 69–79.
- Dohle, W., 1997. Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship. In: Fortey, R.A., Thomas, R.H. (Eds.), *Arthropod relationships*. Chapman and Hall, London, pp. 306–315.
- Dohle, W., 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name Tetraconata for the monophyletic unit Crustacea + Hexapoda. In: Deuve, T. (Ed.), *Origin of the Hexapoda*. *Annales de la Société Entomologique de France (N.S.)* 37, pp. 85–103.
- Donovan, S.K., Veltkamp, C.J., 1994. Unusual preservation of late Quaternary millipedes from Jamaica. *Lethaia* 27, 355–362.
- Dove, H., Stollewerk, A., 2004. Comparative analysis of neurogenesis in the myriapod *Glomeris marginata* (Diplopoda) suggests more similarities to chelicerates than to insects. *Development* 130, 2161–2171.
- Duncan, I.J., Briggs, D.E.G., Archer, M., 1998. Three-dimensionally mineralized insects and millipedes from the Tertiary of Riversleigh, Queensland, Australia. *Palaeontology* 41, 835–851.
- Dzik, J., 1975. Results of the Polish-Mongolian paleontological expeditions—Part VI. Spiroboloid millipedes from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeontologica Polonica* 33, 17–24.
- Dzik, J., 1981. An early Triassic millipede from Siberia and its evolutionary significance. *Neues Jahrbuch der Geologie und Paläontologie Monatshefte* 7, 395–404.
- Edgecombe, G.D., 2004. Morphological data, extant Myriapoda, and the myriapod stem-group. *Contributions to Zoology* 73, 207–252.
- Edgecombe, G.D., 2010. Arthropod phylogeny: an overview from the perspectives of morphology, molecular data and the fossil record. *Arthropod Structure & Development* 39 (2–3), 74–87.
- Edgecombe, G.D., Giribet, G., 2002. Myriapod phylogeny and the relationships of Chilopoda. In: Llorente Bousquets, J., Morrone, J.J. (Eds.), *Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una Síntesis de su Conocimiento*. *Prensas de Ciencias*, Vol. III. Universidad Nacional Autónoma de México, pp. 143–168.
- Edgecombe, G.D., Giribet, G., 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome c oxidase subunit I) to the phylogeny of centipedes (Myriapoda, Chilopoda): an analysis of morphology and four molecular loci. *Journal of Zoological Systematics and Evolutionary Research* 42, 89–134.
- Edgecombe, G.D., Giribet, G., Wheeler, W.C., 1999. Phylogeny of Chilopoda: Combining 18S and 28S rRNA sequences and morphology. In: Melic, A., de Haro, J.J., Mendez, M., Ribera, I. (Eds.), *Evolución y Filogenia de Arthropoda*. *Boletín de la Sociedad Entomológica Aragonesa* 26, pp. 293–331.
- Edgecombe, G.D., Giribet, G., Wheeler, W.C., 2002. Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci. *Systematic Entomology* 27, 31–64.
- Edgecombe, G.D., Minelli, A., Bonato, L., 2009. A geophilomorph centipede (Chilopoda) from La Buzinie amber (Late Cretaceous: Cenomanian), SW France. *Geodiversitas* 31, 29–39.
- Engel, H., 1984. Phylogeny of millipedes: a cladistic analysis. *Zeitschrift für Zoologie, Systematik und Evolutionsforschung* 22, 8–26.
- Engel, H., Dohle, W., Blower, J.G., 1993. Anamorphosis in millipedes (Diplopoda) – the present state of knowledge, with some developmental and phylogenetic considerations. *Zoological Journal of the Linnean Society* 109, 103–234.
- Fayers, S.R., Trewin, N.H., 2003. A review of the palaeoenvironments and biota of the Windyfield chert. *Transactions of the Royal Society of Edinburgh. Earth Sciences* 94, 325–339.
- Fayers, S.R., Trewin, N.H., 2005. A hexapod from the early Devonian Windyfield Chert, Rhynie, Scotland. *Palaeontology* 48, 1117–1130.
- Gai, Y.-H., Song, D.-X., Sun, H.-Y., Zhou, K.-Y., 2006. Myriapod monophyly and relationships among myriapod classes based on nearly complete 28S and 18S rDNA sequences. *Zoological Science* 23, 1101–1108.
- Gai, Y., Song, D., Sun, H., Yang, Q., Zhou, K., 2008. The complete mitochondrial genome of *Symphylella* sp. (Myriapoda: Symphyla): extensive gene order rearrangement and evidence in favour of Progoneata. *Molecular Phylogenetics and Evolution* 48, 103–111.
- Giribet, G., Edgecombe, G.D., 2006. Conflict between data sets and phylogeny of centipedes: an analysis based on seven genes and morphology. *Proceedings of the Royal Society B* 273, 531–538.
- Giribet, G., Carranza, S., Riutort, M., Baguña, J., Ribera, C., 1999. Internal phylogeny of the Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. *Philosophical Transactions of the Royal Society of London* 354, 215–222.
- Giribet, G., Richter, S., Edgecombe, G.D., Wheeler, W.C., 2005. The position of crustaceans within Arthropoda – evidence from nine molecular loci and morphology. In: Koenemann, S., Jenner, R. (Eds.), *Crustacea and Arthropod Relationships*. *Crustacean Issues* 16, pp. 307–352.
- Hahn, G., Hahn, R., Brauckmann, C., 1986. Zur Kenntnis von *Arthropleura* (Myriapoda; Ober-Karbon). *Geologica et Palaeontologica* 20, 125–137.
- Hannibal, J.T., 1981. Giant millipedes of the Coal Age. *The Explorer* 23, 15–17.
- Hannibal, J.T., 1984. Pill millipedes from the Coal Age. *Bulletin of the Field Museum* 55, 12–16.
- Hannibal, J.T., 1987. Remains of *Arthropleura*, a gigantic myriapod arthropod, from the Pennsylvanian of Ohio and Pennsylvania. *Kirtlandia* 50, 1–10.
- Hannibal, J.T., 1995. Modified legs (clasp appendages?) of Carboniferous euphoberid millipedes (Diplopoda: Euphoberiida). *Journal of Paleontology* 69, 932–938.
- Hannibal, J.T., 2000. Hexecontasoma, a new helminthomorph millipede (Hexecontasomatidae, n. fam.) from the Mazon Creek, Illinois, fauna (Carboniferous, North America). *Fragmenta Faunistica* 43 (Suppl.), 19–35.
- Hannibal, J.T., 2006. Millipedes (Diplopoda) from the Fort Sill fissures (Lower Permian) of southwestern Oklahoma: rare examples of Permian millipedes and of fossil millipedes from a Paleozoic fissure fill. *Geological Society of America Abstracts with Programs* 38, 553.
- Hannibal, J.T., Feldmann, R.M., 1981. Systematics and functional morphology of oniscomorph millipedes (Arthropoda: Diplopoda) from the Carboniferous of North America. *Journal of Paleontology* 55, 730–746.
- Hannibal, J.T., Feldmann, R.M., 1988. Millipedes from late Paleozoic limestones at Hamilton, Kansas. *Kansas Geological Society Guidebooks Series* 6, 1–23.
- Hannibal, J.T., Krzemiński, W., 2005. A palaeosomatid millipede (Archipolypoda: Palaeosomatida) from the Carboniferous (Namurian A) of Silesia, Poland. *Polish Journal of Entomology* 74, 205–217.
- Hannibal, J.T., Lerner, A.J., Zeigler, K.E., Lucas, S.G., 2004. A juliform millipede from the Upper Pennsylvanian (Virgilian) Bursum Formation, Carrizo Arroyo, of central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 25, 211–213.
- Harvey, T.H.P., Butterfield, N.J., 2008. Sophisticated particle-feeding in a large Early Cambrian crustacean. *Nature* 452, 868–871.
- Harzsch, S., 2004. Phylogenetic comparison of serotonin-immunoreactive neurons in representatives of the Chilopoda, Diplopoda, and Chelicerata: implications for arthropod relationships. *Journal of Morphology* 259, 198–213.
- Harzsch, S., Müller, C.H.G., Wolf, H., 2005. From variable to constant cell numbers: cellular characteristics of the arthropod nervous system argue against a sister-group relationship of Chelicerata and “Myriapoda” but favour the Mandibulata concept. *Development Genes and Evolution* 215, 53–68.
- Hembree, D.I., 2009. Neoichnology of burrowing millipedes: linking modern burrow morphology, organism behavior, and sediment properties to interpret continental ichnofossils. *Palaios* 24, 425–439.

- Hilken, G., 1997. Tracheal systems in Chilopoda: a comparison under phylogenetic aspects. *Entomologica Scandinavica Supplement* 51, 49–60.
- Hilken, G., Kraus, O., 1994. Struktur und Homologie der Komponenten des Gnathochilarium der Chilognatha (Tracheata, Diplopoda). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 34, 33–50.
- Hoffman, R.L., 1963. New genera and species of Upper Paleozoic Diplopoda. *Journal of Paleontology* 37, 267–174.
- Hoffman, R.L., 1969. Myriapoda, exclusive of Insecta. R572–R606. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part R, Vol. 2*. Geological Society of America and University of Kansas Press, Lawrence, KS.
- Jell, P.A., 1983. An Early Jurassic millipede from the Evergreen Formation in Queensland. *Alcheringa* 7, 195–199.
- Johnson, E.W., Briggs, D.E.G., Suthren, R.J., Wright, J.L., Tuncliffe, S.P., 1994. Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District. *Geological Magazine* 131, 395–406.
- Kadner, D., Stollewerk, A., 2004. Neurogenesis in the chilopod *Lithobius forficatus* suggests more similarities to chelicerates than to insects. *Development. Genes & Evolution* 214, 367–379.
- Klass, K.-D., Kristensen, N.-P., 2001. The ground plan and affinities of hexapods: recent progress and open problems. *Annales de la Société entomologique de France NS* 37, 265–298.
- Kluge, N.J., 1999. Mitos en Sistemática y principios de Nomenclatura Zoológica, in: Melic, A., de Haro, J.J., Mendez, M., Ribera, I. (Eds.), *Evolución y Filogenide Arthropoda*. Boletín de la Sociedad Entomológica Aragonesa 26, pp. 347–331.
- Koch, M., 2003. Monophyly of the Myriapoda? Reliability of current arguments, in: Hamer, M. (Ed.), *Proceedings of the 12th International Congress of Myriapodology*. African Invertebrates 44, pp. 137–153.
- Kraus, O., 1974. On the morphology of Paleozoic diplopods. *Symposia of the Zoological Society of London* 32, 13–22.
- Kraus, O., 1997. Phylogenetic relationships between higher taxa of tracheate arthropods. In: Fortey, R.A., Thomas, R.H. (Eds.), *Arthropod Relationships*. Systematics Association Special Volume 55. Chapman & Hall, London, pp. 295–303.
- Kraus, O., 2001. 'Myriapoda' and the ancestry of the Hexapoda, in: Deuve, T. (Ed.), *Origin of the Hexapoda*. Annales de la Société Entomologique de France, Nouvelle Série 37, pp. 105–127.
- Kraus, O., 2005. On the structure and biology of *Arthropleura* species (Atelocerata, Diplopoda; Upper Carboniferous/Lower Permian). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 41, 5–23.
- Kraus, O., Brauckman, C., 2003. Fossil giants and surviving dwarfs. *Arthropleurida and Pselaphognatha* (Atelocerata, Diplopoda): characters, phylogenetic relationships and construction. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 40, 5–50.
- Kusche, K., Hembach, A., Hagner-Holler, S., Gebauer, W., Burmester, T., 2003. Complete subunit sequences, structure and evolution of the 6 x 6-mer hemocyanin from the common house centipede, *Scutigera coleoptrata*. *European Journal of Biochemistry* 270, 2860–2868.
- Loesel, R., Nüssel, D.R., Strausfeld, N.J., 2002. Common design in a unique midline neuropil in the brains of arthropods. *Arthropod Structure & Development* 31, 77–91.
- Lucas, S.G., Lerner, A.J., Hannibal, J.T., Hunt, A.P., Schneider, J.W., 2005. Trackway of a giant *Arthropleura* from the Upper Pennsylvanian of El Cobre Canyon, New Mexico, Geology of the Chama Basin. *New Mexico Geological Society, 56th Field Conference Guidebook*, pp. 279–282.
- MacNaughton, R.B., Dole, J.M., Dalrymple, R.W., Braddy, S.J., Briggs, D.E.G., Lukie, T.E., 2002. First steps on land: arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology* 30, 391–394.
- Mallatt, J.M., Giribet, G., 2006. Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. *Molecular Phylogenetics and Evolution* 40, 772–794.
- Mallatt, J.M., Garey, J.R., Shultz, J.W., 2004. Ecdysozoan phylogeny and Bayesian inference: first use of nearly complete 28S and 18S rRNA gene sequences to classify the arthropods and their kin. *Molecular Phylogenetics and Evolution* 31, 178–191.
- Manton, S.M., 1964. Mandibular mechanisms and the evolution of arthropods. *Philosophical Transactions of the Royal Society of London B* 247, 1–183.
- Martill, D.M., Barker, M.J., 1998. A new centipede (Arthropoda, Chilopoda) from the Crato Formation (Lower Cretaceous, Aptian) of N.E. Brazil. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 207, 395–404.
- Martino, R.L., Greb, S.F., 2009. Terrestrial arthropod *Arthropleura* from the Upper Carboniferous of Kentucky. *Journal of Paleontology* 83, 140–146.
- Mayer, G., Whittington, P.M., 2009. Velvet worm development links myriapods with chelicerates. *Proceedings of the Royal Society B* 276, 3571–3579.
- Müller, C.H.G., Meyer-Rochow, V.B., 2006a. Fine structural description of the lateral ocellus of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha) and phylogenetic considerations. *Journal of Morphology* 267, 850–865.
- Müller, C.H.G., Meyer-Rochow, V.B., 2006b. Fine structural organization of the lateral ocelli in two species of *Scolopendra* (Chilopoda: Pleurostigmophora): an evolutionary evaluation. *Zoomorphology* 125, 13–26.
- Müller, C.H.G., Rosenberg, J., 2006. Homology of lateral ocelli in the Pleurostigmophora? New evidence from the retinal fine structure in some lithobiomorph species (Chilopoda: Lithobiidae). *Norwegian Journal of Entomology* 53, 165–186.
- Müller, C.H.G., Sombke, A., Rosenberg, J., 2007. The fine structure of the eyes of some bristly millipedes (Penicillata, Diplopoda): additional support for the homology of mandibulate ommatidia. *Arthropod Structure and Development* 36, 463–476.
- Mundel, P., 1979. The centipedes (Chilopoda) of the Mazon Creek. In: Nitecki, M.H. (Ed.), *Mazon Creek Fossils*. Academic Press, New York, pp. 361–378.
- Negrisoló, E., Minelli, A., Valle, G., 2004. The mitochondrial genome of the house centipede *Scutigera* and the monophyly versus paraphyly of Myriapoda. *Molecular Biology and Evolution* 21, 770–780.
- Nguyen Duy-Jacquemin, M., Azar, D., 2004. The oldest records of Polyxenida (Myriapoda, Diplopoda): new discoveries from the Cretaceous ambers of Lebanon and France. *Geodiversitas* 26, 631–641.
- Peñalver, E., 1998. Rubielos de Mora y Ribesalbes: dos yacimientos españoles del Neógeno con insectos fósiles. *Cidaris* 13–14, 17–29.
- Pierce, W.D., 1946. Fossil arthropods of California. 5a. A crystallized millipede from volcanic rock from a well (cont.). *Southern California Academy of Sciences Bulletin* 44, 1–3.
- Pierce, W.D., 1951. Fossil arthropods of California. 13. A progress report on the Rancho la Brea asphaltum studies. *Southern California Academy of Sciences Bulletin* 46, 136–143.
- Pierce, W.D., 1957. Insects, in: Ladd, H.S. (Ed.), *Treatise on Marine Ecology and Paleocology, Vol. 2, Paleocology*. Geological Society of America Memoir 67, pp. 943–952.
- Podsiadlowski, L., Kohlhagen, H., Koch, M., 2007. The complete mitochondrial genome of *Scutigera caudata* (Myriapoda: Symphyla) and the phylogenetic position of the Symphyla. *Molecular Phylogenetics and Evolution* 45, 251–260.
- Poinar, G.O., Edwards, C.A., 1995. First description of a fossil symphylan, *Scutigera dominica* sp. n. (Scutigereillidae, Symphyla) in Dominican amber. *Experientia* 51, 391–393.
- Prunescu, C.C., 1965. Contribution à l'étude de l'évolution des Chilopodes. *Revue Roumaine de Biologie. Zoologie* 10, 89–102.
- Racheboeuf, P.R., Hannibal, J.T., Vannier, J., 2004. A new species of the diplopod *Amynylsypes* (Oniscomorpha) from the Stephanian lagstätte of Montceau-les-Mines, France. *Journal of Paleontology* 78, 221–229.
- Regier, J.C., Shultz, J.W., 2001. A phylogenetic analysis of Myriapoda (Arthropoda) using two nuclear protein-encoding genes. *Zoological Journal of the Linnean Society* 132, 469–486.
- Regier, J.C., Wilson, H.M., Shultz, J.W., 2005. Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. *Molecular Phylogenetics and Evolution* 34, 147–158.
- Regier, J.C., Shultz, J.W., Ganley, A.R.D., Hussey, A., Shi, D., Ball, B., Zwick, A., Stajich, J.E., Cummings, M.P., Martin, J.W., Cunningham, C.W., 2008. Resolving arthropod phylogeny: exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequences. *Systematic Biology* 57, 920–938.
- Retallack, G.J., 2001. *Scoyenia* burrows from Ordovician paleosols of the Juniata Formation in Pennsylvania. *Palaeontology* 44, 209–235.
- Rota-Stabelli, O., Telford, M.J., 2008. A multi criterion approach for the selection of optimal outgroups in phylogeny: recovering some support for Mandibulata over Myriochelata using mitogenomics. *Molecular Phylogenetics and Evolution* 48, 103–111.
- Santiago-Blay, J.A., Poinar, G.O., 1992. Millipedes from the Dominican amber, with the description of two new species (Diplopoda, Siphonophoridae) of *Siphonophora*. *Annals of the Entomological Society of America* 85, 363–369.
- Scheller, U., Wunderlich, J., 2001. First description of a fossil Pauropod *Eopauropus balticus* n. gen. n. sp. (Pauropoda, Pauropodidae), in Baltic amber. *Mitteilungen des Geologisch-paläontologischen Instituts und Museum. Universität Hamburg* 85, 221–227.
- Scheller, U., Wunderlich, J., 2004. Two fossil symphylan species, *Scutigera baltica* n. sp., *Hanseniella baltica* n. sp. (Tracheata, Scutigereillidae), in Baltic amber. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 351, 1–11.
- Scholtz, G., Edgecombe, G.D., 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Development, Genes and Evolution* 216, 395–415.
- Schweigert, V.G., Diel, G., 1997. Ein fossiler Hundertfüßler (Chilopoda, Geophilida) aus dem Nusplinger Plattenkalk (Oberjura, Südwestdeutschland). *Stuttgarter Beiträge zur Naturkunde B (Geologie und Paläontologie)* 254, 1–11.
- Shear, W.A., 1981. Two fossil millipedes from the Dominican amber (Diplopoda: Chytodesmidae, Siphonophoridae). *Myriapodologica* 8, 51–54.
- Shear, W.A., 1994. Myriapodous arthropods from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh. Earth Sciences* 84, 309–316.
- Shear, W.A., 1997. The fossil record and evolution of the Myriapoda. In: Fortey, R.A., Thomas, R.H. (Eds.), *Arthropod Relationships*. Systematics Association Special Volume 55. Chapman & Hall, London, pp. 211–219.
- Shear, W.A., 2008. Spinnerets in the millipede order Polydesmida, and the phylogenetic significance of spinnerets in millipedes (Diplopoda). *International Journal of Myriapodology* 2, 123–146.
- Shear, W.A., Bonamo, P.M., 1988. Devonobiomorpha, a new order of centipedes (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. *American Museum Novitates* 2927, 1–30.
- Shear, W.A., Jeram, A.J., Selden, P.A., 1998. Centiped legs (Arthropoda, Chilopoda, Scutigereomorpha) from the Silurian and Devonian of Britain and the Devonian of North America. *American Museum Novitates* 3231, 1–16.
- Shear, W.A., Selden, P.A., Gall, J.-C., 2009. Millipedes from the Grès à Voltzia, Triassic of France, with comments on Mesozoic millipedes (Diplopoda: Helminthomorpha: Eugnatha). *International Journal of Myriapodology* 3, 7–19.

- Shelley, R.M., 2003. A revised, annotated, family-level classification of the Diplopoda. *Arthropoda Selecta* 11, 187–207.
- Shinohara, K., 1970. On the phylogeny of Chilopoda. *Proceedings of the Japanese Society of Systematic Zoology* 65, 35–42.
- Sierwald, P., Bond, J.E., 2007. Current status of the myriapod Class Diplopoda (millipedes): taxonomic diversity and phylogeny. *Annual Review of Entomology* 52, 401–420.
- Sierwald, P., Shear, W.A., Shelley, R.M., Bond, J.E., 2003. Millipede phylogeny revisited in the light of the enigmatic order Siphoniulida. *Journal of Zoological Systematics and Evolutionary Research* 41, 87–99.
- Stollewerk, A., Chipman, A., 2006. Neurogenesis in myriapods and chelicerates and its importance for understanding arthropod relationships. *Integrative and Comparative Biology* 46, 195–206.
- Strausfeld, N.J., 1998. Crustacean - insect relationships: the use of brain characters to derive phylogeny amongst segmented invertebrates. *Brain, Behavior and Evolution* 52, 186–206.
- Strausfeld, N.J., Strausfeld, C.M., Loesel, R., Rowell, D., Stowe, S., 2006. Arthropod phylogeny: onychophoran brain organization suggests an archaic relationship with a chelicerate stem lineage. *Proceedings of the Royal Society B* 273, 1857–1866.
- Ungerer, P., Scholtz, G., 2008. Filling the gap between identified neuroblasts and neurons in crustaceans adds new support for Tetraconata. *Proceedings of the Royal Society B* 275, 369–376.
- Verhoeff, K.W., 1902–1925. Chilopoda. In: Bronn, H.G. (Ed.), *Klassen und Ordnungen des Tierreichs*, 5, Abteilung 2, Buch 1. C.F. Winter'sche Verlagshandlung, Leipzig, pp. 1–725.
- Verhoeff, K.W., 1928. Klasse Diplopoda I. In: Bronn, H.G. (Ed.), *Klassen und Ordnungen des Tierreichs*, 5, Abteilung 2, Buch 2. Akademische Verlagshandlung, Leipzig, pp. 1–1071.
- von Reumont, B.M., Meusemann, K., Szucsich, N.U., Dell'Amplio, E., Gowri-Shakar, V., Bartel, D., Simon, S., Letsch, H.O., Stocsits, R.R., Luan, Y.-X., Wägele, J.W., Pass, G., Hadrys, H., Misof, B., 2009. Can comprehensive background knowledge be incorporated into substitution models to improve phylogenetic analyses? A case study on major arthropod relationships. *BMC Evolutionary Biology* 2009 (9), 119.
- Willmann, R., 2003. Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. *Verhandlungen des Westdeutschen Entomologentags* 2001, 1–64.
- Wilson, H.M., 2001. First Mesozoic scutigermorph centipede, from the Lower Cretaceous of Brazil. *Palaeontology* 44, 489–495.
- Wilson, H.M., 2003. A new scolopendromorph centipede (Myriapoda: Chilopoda) from the Lower Cretaceous (Aptian) of Brazil. *Journal of Paleontology* 77, 73–77.
- Wilson, H.M., 2005a. A new genus of archipolypodan millipede from Coseley lagerstätte, Upper Carboniferous, UK. *Palaeontology* 48, 1097–1100.
- Wilson, H.M., 2005b. *Zosterogrammida*, a new order of millipedes from the Middle Silurian of Scotland and the Upper Carboniferous of Euramerica. *Palaeontology* 48, 1101–1110.
- Wilson, H.M., 2006a. Juliformian millipedes from the Lower Devonian of Euramerica: implications for the timing of millipede cladogenesis in the Paleozoic. *Journal of Paleontology* 80, 638–649.
- Wilson, H.M., 2006b. Aggregation behavior in juvenile millipedes from the Upper Carboniferous of Mazon Creek, Illinois. *Palaeontology* 49, 733–740.
- Wilson, H.M., Shear, W.A., 2000. *Microdecemplicida*, a new order of minute Arthroplopleurideans (Arthropoda, Myriapoda) from the Devonian of New York State, USA. *Transactions of the Royal Society of Edinburgh. Earth Sciences* 90, 351–375.
- Wilson, H.M., Anderson, L.I., 2004. Morphology and taxonomy of Paleozoic millipedes (Diplopoda: Chilognatha: Archipolypoda) from Scotland. *Journal of Paleontology* 78, 169–184.
- Wilson, H.M., Hannibal, J.T., 2005. Taxonomy and trunk-ring architecture of plerurojulid millipedes (Diplopoda: Chilognatha: Plerurojulida) from the Pennsylvanian of Europe and North America. *Journal of Paleontology* 79, 1105–1119.
- Wilson, H.M., Briggs, D.E.G., Mikulic, D.G., Klussendorf, J., 2004. Affinities of the Lower Silurian Waukesha 'myriapod'. *Geological Society of America, Abstracts with Program* 36, Annual Meeting, Denver, CO, p. 542.
- Wilson, H.M., Daeschler, E.B., Desbiens, S., 2005. New flat-backed archipolypodan millipedes from the Upper Devonian of North America. *Journal of Paleontology* 79, 718–744.
- Wirkner, C.S., Pass, G., 2002. The circulatory system in Chilopoda: functional morphology and phylogenetic aspects. *Acta Zoologica* 83, 193–202.