



Centipede systematics: progress and problems*

GREGORY D. EDGECOMBE

Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

**In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. Zootaxa, 1668, 1–766.*

Table of contents

Abstract	327
Introduction	328
Advances in the past 25 years	328
Cladistic analysis: morphology	328
Cladistic analysis: DNA sequences	328
ChiloBase: a web-based catalogue	330
Palaeontology	330
Taxonomic breakthroughs in the four large centipede orders	331
Scutigermorpha	331
Lithobiomorpha	331
Scolopendromorpha	333
Geophilomorpha	333
Ongoing problems	335
Conflict between different kinds of molecular data	335
Species delimitation	336
Geophilomorph phylogeny	336
Microanatomy and phylogeny: effecting a synthesis	336
Acknowledgments	338
References	338

Abstract

Breakthroughs in centipede systematics over the past 25 years have included: a stable morphology-based cladogram for ordinal interrelationships that is largely congruent with well-sampled nuclear ribosomal genes; the discovery of mid Palaeozoic crown-group fossils, including Silurian-Devonian stem-group Scutigermorpha and an extinct order in the Middle Devonian; and, a web-based catalogue of all centipede species globally. Challenges include species delimitation in several groups, conflict between different kinds of molecular data (nuclear coding genes versus ribosomal genes), the inter-familial relationships and classification of the Geophilomorpha in particular, and effecting a synthesis between microanatomical studies of selected ‘model’ species and dense taxonomic sampling in numerical phylogenetic analyses.

Key words: Chilopoda, phylogeny, taxonomy

Introduction

Centipedes are enjoying a renaissance of study in terms of what their segmental variation means in the context of arthropod bodyplan development. The genetic basis of segment formation (Kettle et al. 2003; Chipman et al. 2004a, b) and segment identity (Hughes & Kaufman 2002), as well as the relationship between intraspecific variation in segment numbers and geographic distribution (Arthur & Chipman 2005), are among the questions that put centipedes near the forefront of arthropod segmentation and tagmosis research. Concurrently, phylogenetic relationships within the Chilopoda as well as broader arthropod studies focused on the position of myriapods are active fields of both morphological and molecular research, generating phylogenetic hypotheses that underpin higher-level taxonomy (Edgecombe & Giribet 2007).

Despite the burst of research on centipede segmentation, developmental genetics, phylogeny, and ultrastructure, taxonomic work on Chilopoda is conducted by only about 20 active specialists worldwide, and by any measure basic descriptive taxonomy of centipedes is less intensely practiced now than in the early or mid 20th century. For the purpose of carving taxonomic research on centipedes into historical slices, I have chosen the early 1980s as a dividing point. This coincides with the publication of J.G.E. Lewis' (1981) seminal review, *The Biology of Centipedes*, which included a summary of taxonomic work to that point, as well as R.L. Hoffman's (1982) widely-used synoptic classification of Chilopoda. As such, major developments of the past 25 years are the focus of this review.

Advances in the past 25 years

Cladistic analysis: morphology

As has been the case in systematics generally, the past 25 years have witnessed an agreement by centipede workers that taxonomy should reflect phylogenetic relationships. Earlier classifications of Chilopoda—e.g., the Anamorpha-Epimorpha split advocated by Haase (1881) and Attems (1926)—admitted groupings diagnosed on the basis of shared primitive characters such as anamorphic development. The relationships between the five extant orders of Chilopoda entered the era of explicit cladistic argumentation via Dohle's (1985) defence of the Notostigmophora-Pleurostigmophora split [endorsed by Verhoeff (1902-1925) and Fahlander (1938), among others, in the pre-cladistic era], as well as a sister group relationship between Craterostigmomorpha and Epimorpha (Fig. 1A). A more detailed analysis that drew the same phylogenetic conclusions was made by Borucki (1996). The focus of these studies was the interrelationships of the five extant centipede orders more so than relationships within those orders. A prevalent theme of the 1980s and 1990s studies was a groundpattern approach to estimating the basal condition for the orders.

Numerical parsimony analyses that sample major groups by coding the observed character state in a range of exemplar taxa that are also sampled for molecular sequences corroborate the earlier, non-numerical cladograms (Edgecombe et al. 1999; Edgecombe & Giribet 2004; Giribet & Edgecombe 2006). The classification of chilopod orders depicted in Fig. 1A is relatively uncontested from the perspective of morphology apart from the inverted topology defended by Ax (1999), an arrangement made possible by excluding much of the relevant character data.

Cladistic analysis: DNA sequences

DNA sequence data applied to centipede systematics have principally involved nuclear ribosomal and nuclear protein-encoding genes, with lesser focus on mitochondrial and segment polarity gene sequences.

The first study to sample all five extant orders of centipedes for sequence data, using fragments of the small (18S) and large (28S) nuclear ribosomal subunits (Giribet et al. 1999), retrieved a cladogram for 12 species that is congruent with the morphological hypothesis in Fig. 1A. This scheme was also retrieved using the same markers when the taxonomic sample was trebled and different analytical methods were employed (mul-

tiple alignments versus Direct Optimization) (Edgecombe et al. 1999). An augmentation of that sample to include 70 terminals corroborated Fig. 1A for morphology as well as for combined morphology and nuclear ribosomal genes, but including mitochondrial genes yielded a novel topology with *Craterostigma* more closely allied to Geophilomorpha than to Scolopendromorpha (Edgecombe & Giribet 2004) (Fig. 1B).

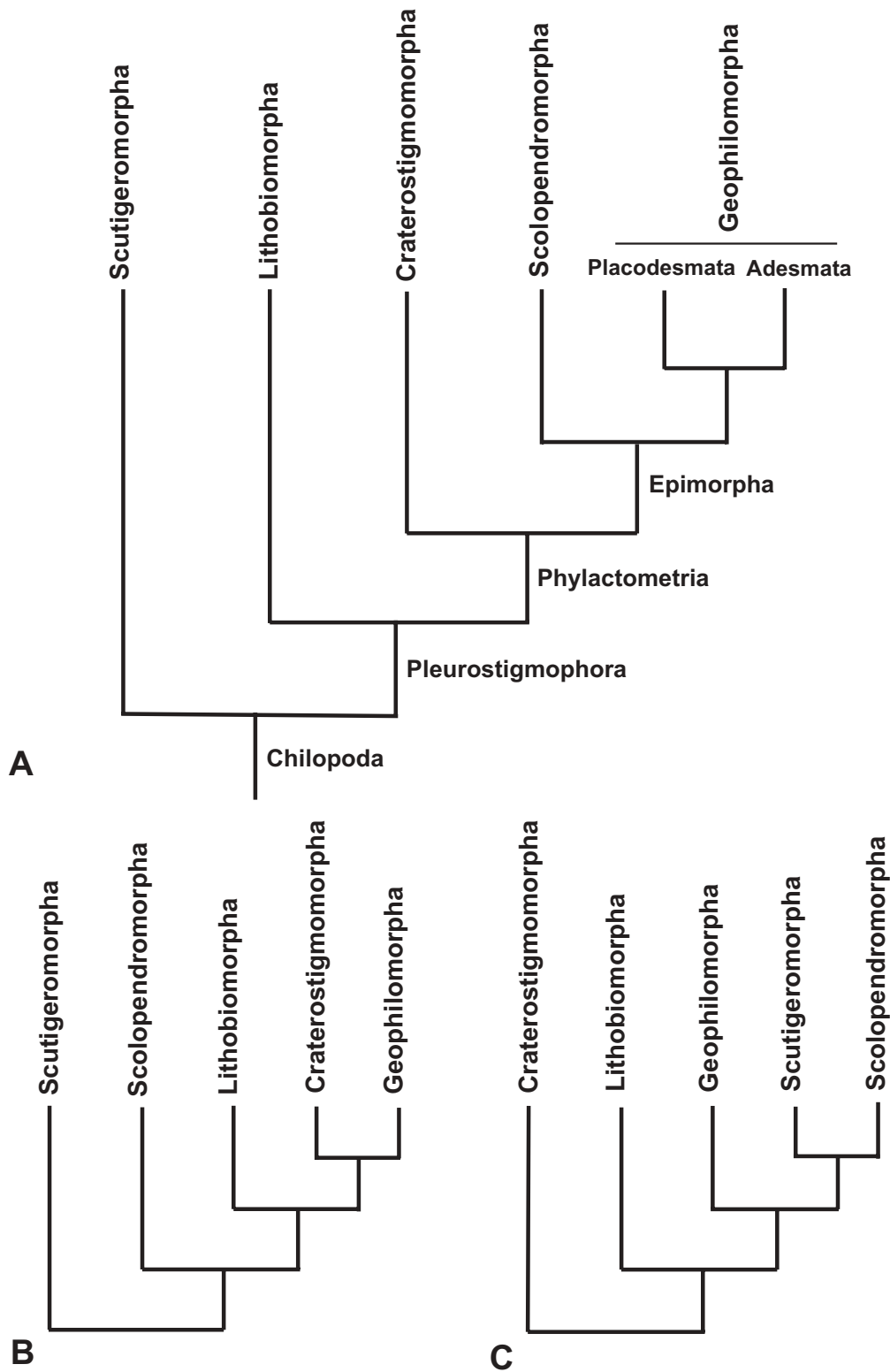


FIGURE 1. A, Cladogram of ordinal interrelationships of Chilopoda based on morphology and combined analysis of morphology and the small and large nuclear ribosomal subunits 18S and 28S rRNA (Edgecombe & Giribet 2004); B, molecular cladogram of Edgecombe & Giribet (2004); C, alternative cladogram based on three nuclear coding genes (Regier et al. 2005) and combined analysis of seven genes and morphology (Giribet & Edgecombe 2006).

Phylogenetic analyses of nuclear coding genes commenced with a survey of elongation factor-1 α sequences for five species representing four orders, yielding morphologically anomalous groupings (Shultz & Regier 1997). Expanding the taxonomic sample to 11 species and adding RNA polymerase II sequences, analysis under parsimony and maximum likelihood frameworks retrieved Epimorpha but was otherwise incongruent with morphology (Regier & Shultz 2001). A 27 species centipede sample that added a third gene, elongation factor-2, and employed parsimony and Bayesian inference generally retrieved monophyly of the four large chilopod orders but produced the enigmatic scheme of relationships shown in Fig. 1C (Regier et al. 2005).

Sequences of *engrailed* have been surveyed for eight centipede species that include all orders except for Scutigermorpha (Bastianello & Minelli 2001). Rooted on Lithobiomorpha, a *Craterostigma* + Scolopendromorpha group (to the exclusion of Geophilomorpha) conflicts with the Epimorpha hypothesis.

Taking it as a given that congruence with morphological data is a desirable property of molecular analyses, to date, nuclear ribosomal genes have provided more congruent signal than other molecular data sources for deep centipede phylogenetics. This may be an effect of denser taxon sampling for these markers than for other available genes.

ChiloBase: a web-based catalogue

An electronic catalogue of centipedes of the world, ChiloBase, went online in April 2006 (<http://chilobase.bio.unipd.it/docs/chilobase.php>). This project, supported by the Global Biodiversity Information Facility, was developed collaboratively by 10 centipede taxonomists. ChiloBase provides bibliographic data for all genus- and species-group taxa of centipedes, synonymies, type localities, geographic distributions, and identifies the most recent taxonomic scrutiny. The site will be updated at regular intervals.

ChiloBase stands as the state of the art in terms of known global species diversity of Chilopoda, drawing on over 4700 published taxonomic references. In the current (April 2006) version, 3493 valid species-group taxa are recognised from a total of 5112 named species and subspecies (i.e., 1619 synonyms).

Palaeontology

Twenty years ago, the fossil record of Chilopoda extended no further back than the Upper Carboniferous, ca 300 million years ago. Carboniferous fossils are confidently assigned to Scutigermorpha and Scolopendromorpha (Mundel 1979). Several remarkable discoveries have pushed the history of centipedes back to the Silurian and Devonian, among the earliest diverse terrestrial arthropod assemblages.

The description of an extinct order of Chilopoda, Devonobiomorpha, was necessary to accommodate the Middle Devonian species *Devonobius delta* Shear & Bonamo, 1988. Though its trunk is incompletely known, this species from the Gilboa deposits of New York is preserved in fine detail, like other arthropods extracted from maceration samples. Although *Devonobius* has been allied with *Craterostigma* (Borucki 1996), most evidence favors a closer relation to the Epimorpha (Shear & Bonamo 1988; Edgecombe & Giribet 2004).

Even earlier records of centipedes are provided by latest Silurian and Lower/Middle Devonian occurrences of Scutigermorpha in Britain and the eastern United States, all of which have been assigned to the genus *Crussolum* (Shear et al. 1998). This material includes antennae, maxillipedes and trunk legs (see Anderson & Trewin 2003 for specimens from Lower Devonian chert from Scotland). The lack of some characters shared by all extant Scutigermorpha (e.g., tarsal papillae; four elongate spine bristles on the forcipular coxa) indicates that *Crussolum* is a stem-group scutigermorph.

Descriptions of Upper Jurassic Geophilomorpha (Schweigert & Dietl 1997) and Lower Cretaceous Scutigeromorpha (Wilson 2001) and Scolopendromorpha (Wilson 2003) attest to the modern aspect of Mesozoic chilopods. The latter appear to represent members of the extant families Scutigeridae and Scolopendridae. Likewise a geophilomorph from Upper Cretaceous (Cenomanian) amber in France belongs to the Geophilidae or Schendylidae (Edgecombe, Minelli & Bonato submitted).

Taxonomic breakthroughs in the four large centipede orders

Scutigeromorpha

The taxonomy of Scutigeromorpha received intense scrutiny in the 1970s in a series of papers by M. Würmli, notably a seminal review of taxonomic characters (Würmli 1974), but only a few publications have dealt with this group since the late 1970s. An over-riding theme of Würmli's revisionary works has been extensive synonymy at the species level (see discussion below), with the conclusion that scutigeromorph species are morphologically variable and for the most part geographically widespread, and synonymy overtook the pace of describing new species.

A serious limitation of much taxonomic work on scutigeromorphs has been establishment of species based on a paucity of material, which impedes an understanding of variability within and between populations and limits the utility of many species as meaningful biogeographic data. This need not be the case. An instructive example from Australia is provided by *Pilbarascutigera incola* (Verhoeff, 1925). This species was erected (as a member of *Allothereua*) based on three specimens from the Kimberley region in northwestern Australia. A pitfall trapping program in the Pilbara region, to the southwest of the type locality, by several Australian government and non-government agencies in 2000-2006 amassed more than 800 specimens of this species from many sites (Edgecombe & Barrow 2007). Acquiring this kind of sample size (more than 100 specimens in one set of traps) required large traps—buckets used for trapping reptiles - maintained for a period of up to six months. Longer term pitfall surveys should be a standard protocol for obtaining adequate material for describing scutigeromorph species in arid regions.

The higher-level taxonomy of Scutigeromorpha has been informed by new characters from the preoral chamber (Koch & Edgecombe 2006), and combined morphological and multiple-marker molecular analyses (Edgecombe & Giribet 2006). A three-family arrangement of the order recognizes two families as species-poor, Afro-Malagasy (Scutigerinidae) and Neotropical-Afrotropical (Pselliodidae) endemics, and a third family (Scutigeridae) is more broadly cosmopolitan and contains most of global species diversity. This (old) classification is compatible with the (new) phylogenetic analyses.

Traditionally employed characters in scutigeromorph taxonomy, such as the distribution of spines, bristles and hairs on the tergal plates, are conducive to examination by scanning electron microscopy (Fig. 2). As an example, Figure 2 highlights similarities between the New Guinea genus *Ballonema* Verhoeff, 1904 and Indo-Australian *Parascutigera* Verhoeff, 1904, with respect to having a pair of elongate spines at the base of each bristle (Stachelborste), a complete lack of large unpaired spines associated with the bristles, and elongate, tapering, variably hair-like spicula. Originally classified together in Ballonemini (Verhoeff 1904), *Ballonema* was subsequently transferred to Scutigerinae (Verhoeff 1925). Molecular data conclusively nest *Parascutigera* within the Thereuoneminae (Edgecombe & Giribet 2006), and *Ballonema* appears likely to group with it there.

Lithobiomorpha

Lithobiomorpha is usually classified as two families, the principally Northern Hemisphere Lithobiidae (974 species in ChiloBase) and the principally Southern Hemisphere Henicopidae (122 species). The latter (sensu Eason 1992) is sometimes viewed as separate families Anopsobiidae and Henicopidae (Farzalieva et al. 2004).

In the last major review of lithobiid taxonomy, Eason (1992) divided the Lithobiidae into four subfamilies, Lithobiinae, Ethopolyinae, Pseudolithobiinae and Pterygoterginae. The Lithobiinae is probably paraphyletic (leftovers after small groups are removed), whereas the Ethopolyinae is very likely monophyletic; Pterygoterginae is monotypic, and Pseudolithobiinae is composed of a few species sharing coxal pores on legs 11–15 and female gonopods that are homoplastic in shape with certain American species formerly classified as a family Gosibiidae (=Lithobiinae fide Eason 1992). Eason (1992), following Matic (1973), conceived of Pseudolithobiinae as having a disjunct distribution in the western United States (*Pseudolithobius*) and Turkey (*Osellaebius*), but the Turkish genus has since been synonymised with *Ottobius* Chamberlin, 1952, and the monophyly of Pseudolithobiinae questioned (Zapparoli 1993).

Species-level work on Lithobiidae has benefitted from modern restudy of old type material (e.g., a series of papers by Eason in the 1970s revising types of Fanzago and Fedrizzi, C.L. Koch and L. Koch, Newport, Pocock, Stuxberg and Verhoeff), allowing modern keys to be made for the some broad geographic regions, such as northwest Europe (Eason 1982). Important regional monographs have documented and revised the centipedes in general or lithobiids in particular from Turkey (Zapparoli 1994, 1999, among others), Greece (Zapparoli 2002), and the former U.S.S.R. (Zalesskaja 1978); recent taxonomic descriptions of lithobiids from China (e.g., Ma et al. 2007) are a welcome addition. Morphometric approaches have productively been applied to some species-delimitation problems in Lithobiidae (Pilz et al. 2007). Though much revisionary and descriptive work remains to be done, the classification of lithobiids at the generic and higher levels is an even more daunting challenge. For example, within the species-rich genus *Lithobius*, the existing subgeneric framework relies on combinations of characters of antennal segment numbers and maxillipede dentition that delimit geographically more or less coherent groups (Eason 1992) but the monophyly of these groups, such as *Sigibius*, *Monotarsobius*, *Chinobius* and *Ezembius*, would be usefully tested with new character data, such as DNA sequences. Whether certain Nearctic groupings established by Chamberlin but generally dismissed by later workers as members of Lithobiinae (e.g., Gosibiidae and Watobiidae) are in fact useful monophyletic groups is another promising avenue of study. Indeed the taxonomy of North and Central American lithobiids is wide open, although it will require careful consideration of types for the myriad species erected by Chamberlin over a span of 60 years.

The systematics of the much smaller lithobiomorph family, the Henicopidae, has been reassessed in a series of cladistic analyses using combined morphological and molecular data (e.g., Edgecombe et al. 2002; Edgecombe & Giribet 2003). These analyses were undertaken in conjunction with taxonomic description of the Henicopidae of Australia, as well as descriptive or revisionary work on related Southern Hemisphere henicopids (see references in Hollington & Edgecombe 2004). Some of the protocols employed in the systematics of Australian henicopids could prove useful in other geographic regions or for other centipede groups. For example, a previously undescribed species, *Henicops washpoolensis*, was based on 2000 specimens from ca 300 sites, most sites sampled by a two-month pitfall survey spanning much of northeastern New South Wales (Edgecombe & Hollington 2005). This regional survey allowed sites to be identified for re-collection for DNA sequencing, sampling a putative morphospecies across much of its geographic range. In the case of *Henicops washpoolensis*, sequences for 28S rRNA and 16S rRNA were obtained for 24 individuals from eight populations (Edgecombe et al. 2006). Cladistic analysis of morphological and molecular data for those specimens allowed a phylogenetic test of the monophyly of a morphospecies. The Gondwanan henicopid studies found scanning electron microscopy to be a useful taxonomic tool, and this approach has since been increasingly applied to other chilopod groups (e.g., Pilz et al. 2007 for Lithobiidae; Edgecombe & Barrow 2007 for Scutigerae) (Fig. 2).

The taxonomic framework for Henicopidae after these studies is in many respects still compatible with the classic scheme of Attems (1928). The two most contentious groups are those with disjunct biogeographic distributions. Anopsobiinae has most of its species diversity in Gondwana but has five monotypic Northern Hemisphere genera, and Zygethobiini has a trans-Pacific distribution including three Nearctic genera and two

Oriental genera. The morphologically-defined Anopsobiinae and Zygethobiini are both non-monophyletic under most analytical conditions for molecular data (Edgecombe & Giribet 2003) and the former is weakened by new morphological characters (Koch & Edgecombe 2007).

Within the mostly Southern Hemisphere Henicopini, the greatest existing challenge for taxonomists is an understanding of the most species-rich, geographically widespread genus, *Lamyctes*, especially in tropical Africa and South America. The validity of many of the ca 60 named species (at least 17 of which have already been placed in subjective synonymy) cannot be established with the existing descriptions, and new field sampling and exhaustive museum surveys, in conjunction with molecular analyses, are needed.

Scolopendromorpha

Although markedly at odds with some earlier schemes, Attems' (1930) monograph remained the standard for scolopendromorph classification until the 1990s, from which point several challenges have come forth.

The most basic disagreement with Attems two-family (Cryptopidae versus Scolopendridae) arrangement involves a view that "Cryptopidae" is a non-monophyletic grouping of blind taxa that have lost their ocelli multiple times. Schileyko (1992) initially rejected "Cryptopidae" in favour of a classification that instead weighted 21- versus 23-legged states as the fundamental basis for scolopendromorph classification. Subsequent phylogenetic analyses at the generic-level (Schileyko & Pavlinov 1997) reinforced non-monophyly of a blind scolopendromorph grouping. The notion that trunk leg number could be employed in classification without homoplasy (Schileyko 1992) is emphatically refuted by the discovery that 21 versus 23 trunk segments are variable at a very restricted taxonomic level in the scolopendrine *Scolopendropsis* (Schileyko 2006).

A three-family classification of Scolopendromorpha by Shelley (2002) used trunk leg number to distinguish Scolopocryptopidae (23-legged) from Cryptopidae (21-legged), while retaining Scolopendridae for taxa with ocelli. Along with the geographically widespread clades Newportiinae and Scolopocryptopinae, two geographically-restricted clades composed of a few species each have been established within Scolopocryptopidae—the Kethopinae for two genera in the western United States (Shelley 2002) and Ectonocryptopinae for two species in Mexico (Shelley & Mercurio 2005). Restudy of the Chinese *Mimops orientalis* (Kraepelin) led to its removal from the Cryptopinae and establishment of a new monotypic family, Mimopidae Lewis, 2006.

A few monographic revisionary works have made important contributions to understanding species diversity and distributions as well as classification of Scolopendromorpha in various parts of the world. These include the Plutoniuminae of Europe and North America (Shelley 1997), the entire North American scolopendromorph fauna (Shelley 2002), the scolopendromorphs of the former Soviet Union (Zalesskaja & Schileyko 1991), and the Scolopendridae of Australia (see references to nine papers on Australian scolopendrids by L.E. Koch cited by Koch & Colless 1986). Extensive taxonomic work in India is summarized in a check list of Indian scolopendromorphs (Khanna 2001). Taxonomic description of scolopendromorphs can hopefully be facilitated by a standardisation of descriptive terminology (Lewis et al. 2005).

Within the large, species-rich genera of Scolopendridae, considerable progress has been made in analyzing variation in taxonomic characters in *Otostigmus* (Lewis 2000), which has allowed numerous nominal species to be placed in synonymy (see e.g., Lewis 2002 for Indo-Australian diversity). The ca 70 species of *Cormocephalus* have recently been reorganized into nine informal species groups (Schileyko & Stagl 2004), though these would be profitably tested by cladistic analysis using a larger suite of characters. For *Scolopendra*, species-level revision is aided by the availability of a catalogue of New World species (Shelley 2006). In the same geographic region, the taxonomy of the large Neotropical genus *Newportia* has been advanced by a comprehensive species-level revision and generation of a key (Schileyko & Minelli 1998).

Geophilomorpha

Useful reviews of taxonomic characters employed in the Geophilomorpha and techniques for examining specimens were provided by Foddai et al. (2002).

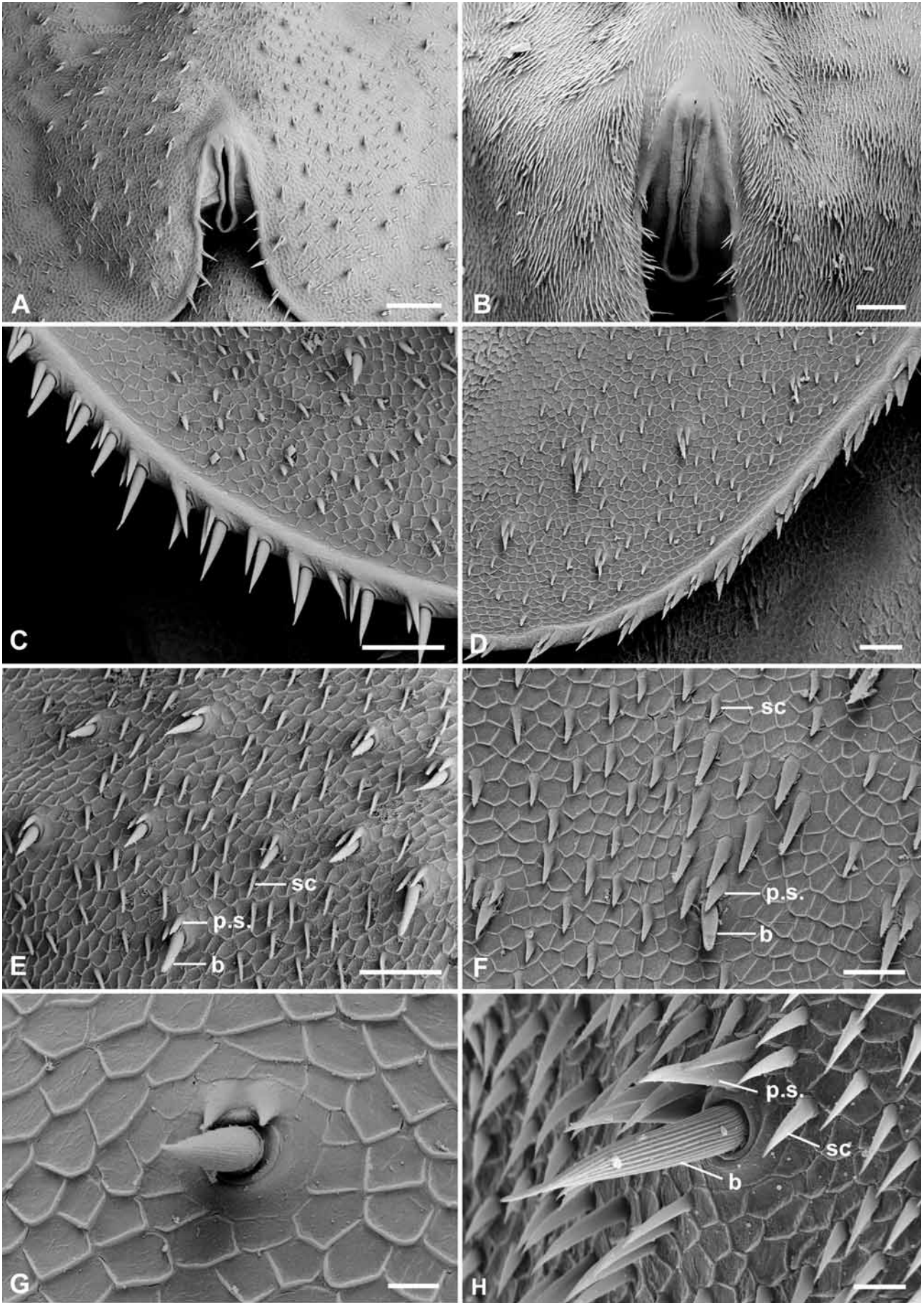


FIGURE 2. Tergal prominences as taxonomic characters in Scutigermorpha. Scanning electron micrographs. A, C, E, *Ballonema gracilipes* Verhoeff, 1904. Tergal plate 6. A, stoma saddles and spiracle, scale 100 µm; C, margin, scale 50 µm; E, left stoma saddle, scale 50 µm. B, H, *Parascutigera festiva* Ribaut, 1923. B, stoma saddles and spiracle of tergal plate 5, scale 100 µm; H, bristle on tergal plate 1, scale 10 µm. D, F, G, *Parascutigera* cf. *P. sphinx* Verhoeff, 1925. D, margin of tergal plate 6, scale 50 µm; F, tergal plate 5, scale 30 µm; G, bristle on tergal plate 1, scale 10 µm. Abbreviations: b, bristle (Stachelborste); p.s., paired spines at bristle base; sc, spicula.

Taxonomic work on geophilomorphs in the past 25 years has especially concentrated on Schendylidae, Geophilidae and Mecistocephalidae. Exemplary descriptions of schendylids and geophilids by L.A. Pereira, A. Minelli and colleagues have especially focused on temperate and tropical South America (e.g., Pereira et al. 1995, 2000). These data have contributed to a better understanding of Neotropical biogeography (Pereira et al. 1997) and the likely ages of various geophilomorph taxa in that region, in total including nearly one-third of global diversity of the order. The 320 species-group taxa of Geophilomorpha from Central and South America have been catalogued (Foddai et al. 2000).

Monographic revision of Mecistocephalidae has included a comprehensive assessment of species diversity in India (Bonato & Minelli 2004) and Japan and Taiwan (Uliana et al. 2007). Within *Mecistocephalus*, studies of variation have allowed traditional taxonomic characters to be reassessed and new diagnostic characters identified (Bonato & Minelli 2004). Mecistocephalidae is the best understood geophilomorph group in terms of phylogeny, with detailed cladistic analysis of the family as a whole (Bonato et al. 2003) and the subfamily Arrupinae in particular (Foddai et al. 2003). Three monophyletic subfamilies, Arrupinae, Dicellyphilinae and Mecistocephalinae, are employed in a revised classification.

Concerning higher-level taxonomy of Geophilomorpha, the deepest division within the order proposed by Verhoeff (1908 in Verhoeff 1902–1925), a separation of mecistocephalids (=Placodesmata) from all remaining geophilomorphs (=Adesmata), has found new support. Maternal brooding behaviour (Bonato & Minelli 2002) as well as DNA sequence analyses and large insertions in 18S rRNA (Edgecombe et al. 1999; Edgecombe & Giribet 2004) identify plesiomorphic character states in Placodesmata/Mecistocephalidae relative to Adesmata. This basal split is also retrieved in morphological cladistic analyses (Foddai & Minelli 2001; Edgecombe & Giribet 2004).

Ongoing problems

Conflict between different kinds of molecular data

Deeper chilopod interrelationships can be considered very well established from the perspective of morphology – new studies of individual organ systems such as eye ultrastructure (Müller & Rosenberg 2006 and references therein) and the circulatory system (Wirkner & Pass 2002) corroborate and strengthen the cladogram in Fig. 1A. As noted above, the same or nearly identical scheme of ordinal interrelationships is retrieved by analyses of nuclear ribosomal genes. This indicates that there is no necessary conflict between molecules and morphology *per se* with respect to centipede systematics.

Conflict is, however, identified between different classes of sequence data. Analysed under a range of protocols, trees generated using nuclear protein encoding genes surveyed by Regier et al. (2005) yield a topology (Fig. 1C) that is markedly incongruent with morphology, notably with respect to a basal position of *Craetostigmus* in the Chilopoda and a putative sister group relationship between Scutigermorpha and Scolopendromorpha. The signal from the Regier et al. data comes to the fore when those data are combined with other molecular and morphological characters (Giribet & Edgecombe 2006). Whether this situation persists with denser taxonomic sampling or inclusion of further markers must be examined.

Species delimitation

An insightful review of problems involved in identifying scolopendromorphs at the species level by Lewis (2003) explored sources of individual variability that have not always been perceived or appreciated by earlier workers (see also Lewis 2000; Bonato & Minelli 2004 for Geophilomorpha). These include sexual dimorphism, ontogenetic variation, wear on spines, and difference in size in different parts of a species' distribution. Determining the morphological limits of species remains problematic in several groups of chilopods, notably scutigermorphs and scolopendromorphs, and the problem has been compounded by taxonomic practice. A long period of fine splitting at the species-level by the early 20th century workers such as K.W. Verhoeff and R.V. Chamberlin was followed by extensive synonymy in the later 20th century when a polymorphic species concept took hold. Extreme examples from the Scutigermorpha include *Thereuopoda longicornis* (Fabricius, 1793), which has been assigned 26 junior subjective synonyms (Würmli 1979), with the result that the species is considered to range from India to Japan and Australia, and *Sphendononema guildingii* (Newport, 1844), with 22 subjective synonyms (Würmli 1978) that subsume a distribution from Mexico to Paraguay.

It may prove that the extreme polymorphic species concept masks real diversity, and some of the nominal species currently in synonymy may be resurrected. DNA sequences are likely to play a role in evaluating the status of geographically widespread species. An obvious example is *Scolopendra morsitans*, which is recorded from all inhabited continents throughout the tropical and warm temperate parts of the world (Shelley et al. 2005). Shelley et al. (2005) make a sound case for parts of the distribution that are likely to be non-synanthropic, e.g., much of Africa and Australia (see Koch 1983 for the extensive distribution in the latter), parts that are likely to be introductions (records from tropical islands and the New World tropics), and parts that are likely to be misidentifications (e.g., Europe and most records in the Middle East). Molecular phylogeographic studies of widespread species like *Scolopendra morsitans* and *Scutigera coleoptrata* (11 junior subjective synonyms fide Würmli 1977) are needed.

The best documented case of genetic methods being employed in the identification of a cryptic centipede species involves *Geophilus* in Britain, wherein a new species, *G. easoni*, was separated from *G. carpophagus* using electrophoresis together with morphology (trunk segment counts, body size, labral dentition, coxal pore numbers, pigmentation) (Arthur et al. 2001).

Geophilomorph phylogeny

The morphology-based phylogeny of Geophilomorpha by Foddai & Minelli (2001) was a much-welcomed first step in unravelling relationships within this largest of chilopod orders. It remains the only geophilomorph phylogeny that includes exemplars of all 14 or 15 currently recognised families. The most densely sampled molecular analysis to date (Edgecombe & Giribet 2004) included members of just eight families. Molecular data are especially needed for the Eriphantidae, Eucratonychidae, Gonibregmatidae, Macronicophilidae and Neogeophilidae, most of which are not collected with regular frequency.

The available morphological data display sensitivity to analytical methods, notably *a posteriori* reweighting. Equally weighted versus reweighted analyses (Foddai & Minelli 2001) differ with respect to the position of *Macronicophilus*, the nominate genus in a re-established monogeneric family (Pereira et al. 2000), and whether Himantariidae is more closely related to Oryidae and Gonibregmatidae or to Ballophilidae and Schendylidae. Geophilidae s.l. is evidently a paraphyletic group in need of reclassification. Although additional morphological analyses will no doubt contribute to resolving these issues, an exhaustively sampled molecular survey is the obvious next step in retrieving a tree that can serve as a basis for geophilomorph familial and superfamilial taxonomy.

Microanatomy and phylogeny: effecting a synthesis

Detailed microanatomical studies are a major focus of research on chilopod morphology, permitting homology statements to be founded based on detailed, precise character descriptions. Studies of particular

organ systems using transmission electron microscopy have allowed new ultrastructural data from, among many possible examples, the eyes (Müller & Meyer-Rochow 2006; Müller & Rosenberg 2006) and anal organs (Rosenberg et al. 2006) to be productively applied to phylogenetic questions.

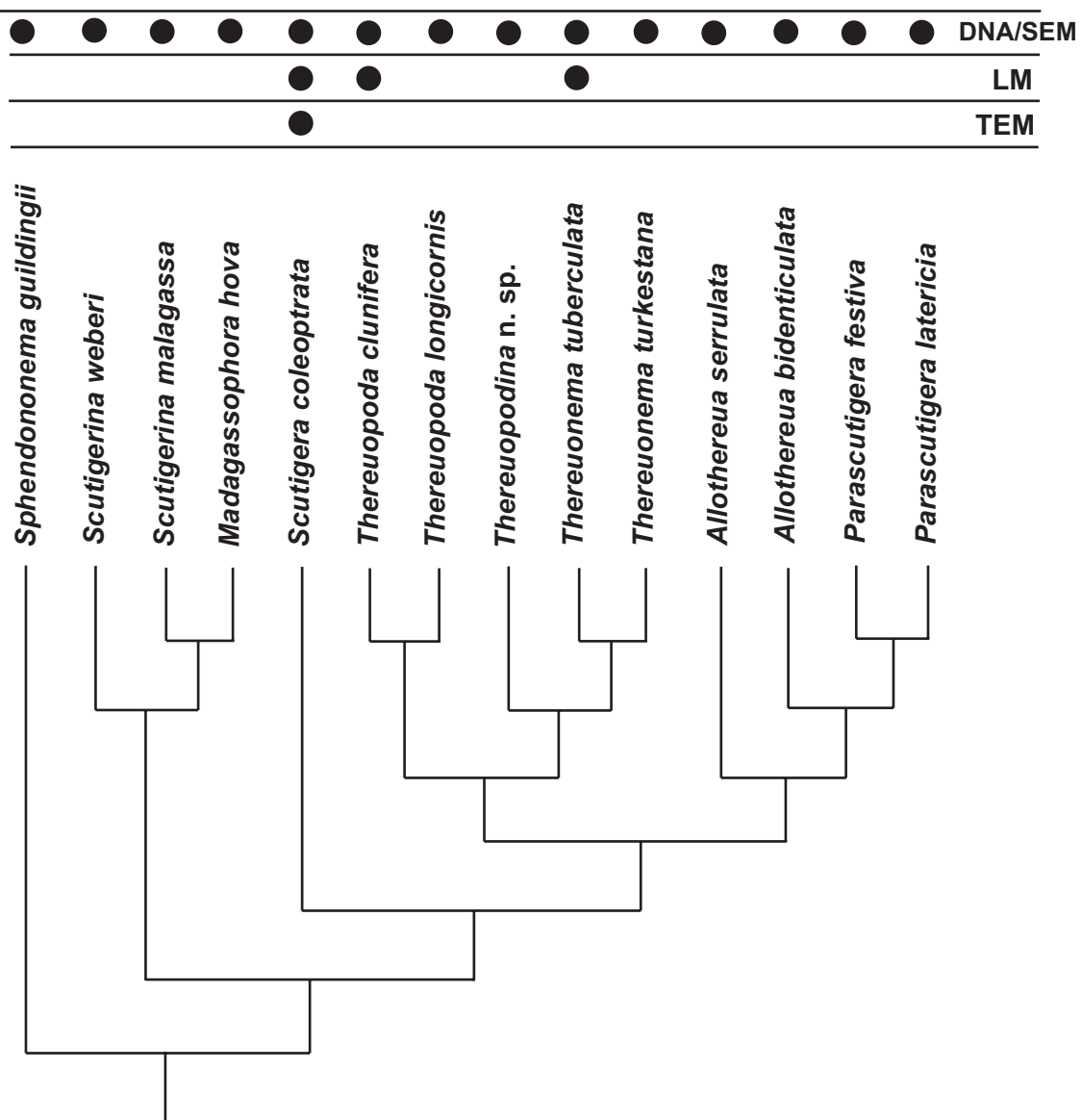


FIGURE 3. Relationships between Scutigeraomorpha sampled for DNA sequence data (Edgecombe & Giribet 2006), indicating sampling for scanning (SEM) and transmission (TEM) electron microscopy and light microscopy (LM) / histology.

For practical reasons, the taxonomic sampling in microanatomical studies is limited, generally involving detailed descriptions of single or few species within each of the major chilopod groups and as such these data are informative for questions involving relationships between chilopod orders but are generally neutral on taxonomic problems at finer levels, even between families. The taxonomic sampling design is thus markedly different from studies using DNA sequence data and external morphology, which aim to cover the tree via dense taxonomic sampling (Fig. 3). Currently the only solution to marrying these two sampling strategies is to restrict codings for the TEM characters to those ‘model species’ that have been surveyed (e.g., *Scutigera coleoptrata* alone within the Scutigeraomorpha). To some extent, these sampling strategies can be bridged by

light microscopic studies of anatomy examined via histological sections (e.g., fine structure of the preoral chamber: Koch & Edgecombe 2006, 2007) and broader SEM survey of structures that have been studied in fewer species by TEM (e.g., maxillary organ: Hilken & Rosenberg 2006).

Acknowledgments

I thank W.A. Shear for inviting this contribution, a referee for comments on the manuscript, and Sue Lindsay (Australian Museum) for operating the SEM for images in Fig. 2.

References

- Anderson L.I. & Trewin, N.H. (2003) An Early Devonian arthropod fauna from the Windyfield Cherts, Aberdeenshire, Scotland. *Palaeontology*, 46, 457–509.
- Arthur, W. & Chipman, A.D. (2005) How does arthropod segment number evolve? – some clues from centipedes. *Evolution & Development*, 7, 600–607.
- Arthur, W., Foddai, D., Kettle, C., Lewis, J.G.E., Luczynski, M. & Minelli, A. (2001) Analysis of segment number and enzyme variation in a centipede reveals a cryptic species, *Geophilus easoni* sp. nov., and raises questions about speciation. *Biological Journal of the Linnean Society*, 74, 489–99.
- Attems, C. (1926) Chilopoda. In: Kükenthal, W. & Krumbach, T. (Eds), *Handbuch der Zoologie, 4 (Myriapoda)*. Walter de Gruyter, Berlin, pp. 239–402.
- Attems, C. (1928) The Myriapoda of South Africa. *Annals of the South African Museum*, 26, 1–431.
- Attems, C. (1930) Myriapoda 2. Scolopendromorpha. In: Schulze, F.E. & Kükenthal, W. (Eds), *Das Tierreich*, 54. Walter de Gruyter, Berlin, pp. 1–308.
- Ax, P. (1999) *Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik*. Gustav Fischer, Stuttgart.
- Bastianello, A. & Minelli, A. (2001) engrailed sequences from four centipede orders: strong sequence conservation, duplications and phylogeny. *Development Genes Evolution*, 211, 620–623.
- Bonato, L., Foddai, D. & Minelli, A. (2003) Evolutionary trends and patterns in centipede segment number based on a cladistic analysis of Mecistocephalidae (Chilopoda: Geophilomorpha). *Systematic Entomology*, 28, 539–579.
- Bonato, L. & Minelli, A. (2002) Parental care in *Dicellogophilus carniolensis* (C. L. Koch, 1847): new behavioural evidence with implications for the higher phylogeny of centipedes (Chilopoda). *Zoologischer Anzeiger*, 241, 193–198.
- Bonato, L. & Minelli, A. (2004) The centipede genus *Mecistocephalus* Newport 1843 in the Indian Peninsula (Chilopoda Geophilomorpha Mecistocephalidae). *Tropical Zoology*, 17, 15–63.
- Borucki, H. (1996) Evolution und phylogenetisches System der Chilopoda (Mandibulata, Tracheata). *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg*, 35, 95–226.
- Chipman, A.D., Arthur, W. & Akam, M. (2004a) Early development and segment formation in the centipede, *Strigamia maritima*. *Evolution & Development*, 6, 78–89.
- Chipman, A.D., Arthur, W. & Akam, M. (2004b) A double segment periodicity underlies segment generation in centipede development. *Current Biology*, 14, 1250–1255.
- Dohle, W. (1985) Phylogenetic pathways in the Chilopoda. *Bijdragen tot de Dierkunde*, 55, 55–66.
- Eason, E.H. (1982) A review of the north-west European species of Lithobiomorpha with a revised key to their identification. *Zoological Journal of the Linnean Society*, 74, 9–33.
- Eason, E.H. (1992) On the taxonomy and geographical distribution of the Lithobiomorpha. *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck Supplement*, 10, 1–9.
- Edgecombe, G.D. & Barrow, L. (2007) A new genus of scutigered centipedes (Chilopoda), from Western Australia, with new characters for morphological phylogenetics of Scutigerozoa. *Zootaxa*, 1409, 23–50.
- Edgecombe, G.D., Colgan, D.J. & Sharkey, D. (2006) Phylogeny and biogeography of the Australasian centipede *Henicops* (Chilopoda: Lithobiomorpha): a combined morphological and molecular approach. *Insect Systematics & Evolution*, 37, 241–256.
- Edgecombe, G.D. & Giribet, G. (2003) Relationships of Henicopidae (Chilopoda: Lithobiomorpha): New molecular data, classification and biogeography. *African Invertebrates*, 44, 13–38.
- 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. (2006) A century later – a total evidence re-evaluation of the phylogeny of scutigero-

- morph centipedes (Myriapoda, Chilopoda). *Invertebrate Systematics*, 20, 503–525.
- Edgecombe, G.D. & Giribet, G. (2007) Evolutionary biology of centipedes (Myriapoda: Chilopoda). *Annual Reviews of Entomology*, 52, 151–170.
- Edgecombe, G.D., Giribet, G. & Wheeler, W.C. (1999) Phylogeny of Chilopoda: Combining 18S and 28S rRNA sequences and morphology. *Boletín de la Sociedad Entomológica Aragonesa*, 26, 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. & Hollington, L.M. (2005) Morphology and relationships of a new species of *Henicops* (Chilopoda: Lithobiomorpha) from New South Wales and Queensland, Australia. *Zootaxa*, 961, 1–20.
- Edgecombe, G.D., Minelli, A. & Bonato, L. (submitted). A geophilomorph centipede (Chilopoda) from La Buzinie amber (Late Cretaceous: Cenomanian), SW France. *Geodiversitas*.
- Fahlander, K. (1938) Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. *Zoologische Beiträge von Uppsala*, 17, 1–148.
- Farzaliyeva, G. Sh., Zalesskaja, N.T. & Edgecombe, G.D. (2004) A new genus and species of lithobiomorph centipede (Chilopoda, Lithobiomorpha, Anopsobiidae) from eastern Kazakhstan. *Arthropoda Selecta*, 13, 219–224.
- Foddai, D., Bonato, L., Pereira, L.A. & Minelli, A. 2003. Phylogeny and systematics of the Arrupinae (Chilopoda Geophilomorpha Mecistocephalidae) with the description of a new dwarfed species. *Journal of Natural History*, 37, 1247–1267.
- Foddai, D. & Minelli, A. (2001) Phylogeny of geophilomorph centipedes: old wisdom and new insights from morphology. *Fragmenta Faunistica*, 43, 61–71.
- Foddai, D., Minelli, A. & Pereira, L.A. (2002). Geophilomorpha. In: Adis, J. (Ed), *Amazonian Arachnida and Myriapoda*. PENSOF: Sofia, Moscow, pp. 459–474.
- Foddai, D., Pereira, L.A. & Minelli, A. (2000) A catalogue of the geophilomorph centipedes (Chilopoda) from central and South America including Mexico. *Amazoniana*, 16, 59–185.
- Giribet, G., Carranza, S., Riutort, M., Baguñà, 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, 215–22.
- 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.
- Haase, E. (1881) Beitrag zur Phylogenie und Ontogenie der Chilopoden. *Zeitschrift für Entomologie*, 8, 93–115.
- Hilken, G. & Rosenberg J. (2006) Ultrastructure of the maxillary organ of *Scutigera coleoptrata* (Chilopoda, Notostigmophora): description of a multifunctional head organ. *Journal of Morphology*, 267, 152–65.
- Hoffman, R.L. (1982) Chilopoda. In: Parker, S.P. (Ed), *Synopsis and Classification of Living Organisms*. McGraw Hill, New York, pp. 681–688.
- Hollington, L.M. & Edgecombe, G.D. (2004) Two new species of the henicopid centipede *Henicops* (Chilopoda: Lithobiomorpha) from Queensland and Victoria, with revision of species from Western Australia and a synoptic classification of Henicopidae. *Records of the Australian Museum*, 56, 1–28.
- Hughes, C.L. & Kaufman, T.C. (2002) Exploring the myriapod body plan: expression patterns of the ten Hox genes in a centipede. *Development*, 129, 1225–1238.
- Kettle, C., Johnstone, J., Jowett, T., Arthur, H. & Arthur, W. (2003) The pattern of segment formation, as revealed by *engrailed* expression, in a centipede with a variable number of segments. *Evolution & Development*, 5, 198–207.
- Khanna, V. (2001) A check-list of the Indian species of the centipedes (Chilopoda : Scolopendromorpha). *Annals of Forestry*, 9, 199–219.
- Koch, L.E. (1983) Morphological characters of Australian scolopendrid centipedes, and the taxonomy and distribution of *Scolopendra morsitans* L. (Chilopoda : Scolopendridae : Scolopendrinae). *Australian Journal of Zoology*, 31, 79–91.
- Koch, L.E. & Colless, D.H. (1986) Numerical taxonomy of Australian species of nine genera of scolopendrid centipedes (Chilopoda : Scolopendridae). *Australian Journal of Zoology*, 34, 87–105.
- Koch, M. & Edgecombe, G.D. (2006) The peristomatic structures in Scutigeraomorpha (Chilopoda): a comparative study, with new characters for higher-level systematics. *Zoomorphology*, 125, 187–207.
- Koch, M. & Edgecombe, G.D. (2007) The peristomatic structures of Lithobiomorpha (Myriapoda, Chilopoda): comparative morphology and phylogenetic significance. *Journal of Morphology*, in press.
- Lewis, J.G.E. (1981) *The Biology of Centipedes*. Cambridge University Press, Cambridge.
- Lewis, J.G.E. (2000) Variation in three centipede species of the genus *Otostigmus* and its bearing on species discrimination (Chilopoda; Scolopendromorpha; Scolopendridae). *Journal of Natural History*, 34, 433–448.
- Lewis, J.G.E. (2002) A re-examination of 11 species of *Otostigmus* from the Indo-Australian region described by R. V. Chamberlin based on type specimens in the collections of the Museum of Comparative Zoology, Harvard (Chilopoda; Scolopendromorpha; Scolopendridae). *Journal of Natural History*, 36, 1687–1706.
- Lewis J.G.E. (2003) The problems involved in the characterisation of scolopendromorph species (Chilopoda: Scolopen-

- dromorpha). *African Invertebrates*, 44, 61–69.
- Lewis, J.G.E. (2006) On the scolopendromorph centipede genus *Mimops* Kraepelin, 1903, with a description of a new family (Chilopoda: Scolopendromorpha). *Journal of Natural History*, 40, 1231–1239.
- Lewis, J.G.E., Edgecombe, G.D. & Shelley, R.M. (2005) A proposed standardised terminology for the external taxonomic characters of the Scolopendromorpha (Chilopoda). *Fragmenta Faunistica*, 48, 1–8.
- Ma H.-G., Song D.-X. & Zhu M.-S. (2007) A new genus and two new species of lithobiid centipedes (Chilopoda: Lithobiomorpha) from China. *Zootaxa*, 1460, 25–34.
- Matic, Z. (1973) Pseudolithobiidae fam. nov.: una nuova famiglia dell'ordine Lithobiomorpha (Chilopoda, Anamorpha). *Fragmenta entomologica*, 9, 135–142.
- Müller, C.H.G. & Meyer-Rochow, B. (2006) 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.
- Mundel P. (1979) The centipedes (Chilopoda) of the Mazon Creek. In: Nitecki, M. (Ed), *Mazon Creek Fossils*. Academic Press, New York, pp. 361–378.
- Pereira, L.A., Foddai, D. & Minelli, A. (1997) Zoogeographical aspects of Neotropical Geophilomorpha (Chilopoda). *Entomologica scandinavica Supplement*, 51, 77–86.
- Pereira, L.A., Foddai, D. & Minelli, A. (2000) New taxa of Neotropical Geophilomorpha (Chilopoda). *Amazoniana*, 16, 1–57.
- Pereira, L.A., Minelli, A. & Barbieri, F. (1995) Description of nine new centipede species from Amazonia and related matters on Neotropical geophilomorphs (Chilopoda: Geophilomorpha). *Amazoniana*, 13, 325–416.
- Pilz, C., Melzer, R.R. & Spelda, J. (2007). Morphometrics and SEM analysis of the species pair *Lithobius mutabilis* L. Koch, 1862 and *L. glacialis* Verhoeff, 1937 (Chilopoda: Lithobiomorpha). *Organisms, Diversity & Evolution*, 8.
- 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, 147–58.
- Rosenberg, J., Müller, C.H.G. & Hilken, G. (2006) Ultrastructural organization of the anal organ in the anal capsule of *Craterostigma tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). *Journal of Morphology*, 267, 265–272.
- Schileyko, A.A. (1992) Scolopenders of Viet-Nam and some aspects of the system of Scolopendromorpha (Chilopoda Epimorpha). Part 1. *Arthropoda Selecta*, 1, 5–19.
- Schileyko, A.A. (2006) Redescription of *Scolopendropsis bahiensis* (Brandt, 1841), the relations between *Scolopendropsis* and *Rhoda*, and notes on some characters used in scolopendromorph taxonomy (Chilopoda: Scolopendromorpha). *Arthropoda Selecta*, 15, 9–17.
- Schileyko, A.A. & Minelli, A. (1998) On the genus *Newportia* Gervais, 1847 (Chilopoda: Scolopendromorpha: Newportiidae). *Arthropoda Selecta*, 7, 265–299.
- Schileyko, A.A. & Pavlinov, I.J. (1997) A cladistic analysis of the order Scolopendromorpha (Chilopoda). *Entomologica scandinavica Supplement*, 51, 33–40.
- Schileyko, A.A. & Stagl, V. (2004) The collection of scolopendromorph Centipedes (Chilopoda) in the Natural History Museum in Vienna: a critical re-evaluation of former taxonomic identifications. *Annalen des Naturhistorisches Museum in Wien*, 105B, 67–137.
- Schweigert, V.G. & Dietl, 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. & 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) Centipede legs (Arthropoda, Chilopoda, Scutigermorpha) from the Silurian and Devonian of Britain and the Devonian of North America. *American Museum Novitates*, 3231, 1–16.
- Shelley, R.M. (1997) The Holarctic centipede subfamily Plutoniminiinae (Chilopoda: Scolopendromorpha: Cryptopidae) (Nomen Correctum Ex Subfamily Plutoniniinae Bollman, 1893). *Brimleyana*, 24, 51–113.
- Shelley, R.M. (2002) A synopsis of the North American centipedes of the order Scolopendromorpha (Chilopoda). *Virginia Museum of Natural History Memoir*, 5, 1–108.
- Shelley, R.M. (2006) A chronological catalog of the New World species of *Scolopendra* L., 1758 (Chilopoda: Scolopendromorpha: Scolopendridae). *Zootaxa*, 1253, 1–50.
- Shelley, R.M., Edwards, G.B. & Chagas, Jr., A. (2005) Introduction of the centipede *Scolopendra morsitans* L., 1758, into northeastern Florida and the first authentic North American record, and a review of its global occurrences. *Entomological News*, 116, 39–58.

- Shelley, R.M. & Mercurio, R. (2005) *Ectonocryptoides quadrimeropus*, a new centipede genus and species from Jalisco, Mexico; proposal of Ectonocryptopinae, analysis of subfamilial relationships, and a key to subfamilies and genera of the Scolopocryptopidae (Scolopendromorpha). *Zootaxa*, 1094, 25–40.
- Shultz, J.W. & Regier, J.C. (1997) Progress toward a molecular phylogeny of the centipede orders (Chilopoda). *Entomologica Scandinavica Supplement* 51, 25–32.
- Uliana, M., Bonato, L. & Minelli, A. (2007) The Mecistocephalidae of the Japanese and Taiwanese islands (Chilopoda: Geophilomorpha). *Zootaxa*, 1396, 1–84.
- 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. (1904) Ueber Gattungen der Spinnenasseln (Scutigeneriden). *Sitzungs-Berichte der Gesellschaft naturforschender Freunde zu Berlin*, 1904, 245–285.
- Verhoeff, K.W. (1925) Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913. 39. Chilopoda. *Arkiv för Zoologi*, 26A, 1–62.
- 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.
- Wirkner, C.S. & Pass, G. (2002) The circulatory system in Chilopoda: functional morphology and phylogenetic aspects. *Acta Zoologica*, 83, 193–202.
- Würmli, M. (1974) Systematic criteria in the Scutigermorpha. In: Blower, J.G. (Ed), *Myriapoda. Symposia of the Zoological Society of London*, 32. Academic Press, London, pp. 89–98.
- Würmli, M. (1977) Zur Systematik der Gattung *Scutigera*. *Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg*, 20, 123–131.
- Würmli, M. (1978) Synopsis der neotropischen Psellioididae (Chilopoda: Scutigermorpha). *Studies on Neotropical Fauna and Environment*, 13, 135–142.
- Würmli, M. (1979) Taxonomic problems in the genus *Thereuopoda* (Chilopoda Scutigermorpha: Scutigeridae): the role of postmaturational moultings. In: Camatini, M. (Ed), *Myriapod Biology*. Academic Press, London, pp. 39–48.
- Zalesskaja, N.T. (1978) *Identification key to the lithobiomorph centipedes of the USSR*. Nauka, Moscow, pp. 1–211.
- Zalesskaja, N.T. & Schileyko, A.A. (1991) *The scolopendromorph centipedes (Chilopoda, Scolopendromorpha)*. Nauka, Moscow, pp. 1–110.
- Zapparoli, M. (1993) Chilopodi di Turchia. III. Sulla identità di *Ottobius hopanus* Chamberlin, 1952 e *Osellaebius anatolicus* Matic, 1973 (Chilopoda, Lithobiomorpha). *Fragmenta entomologica*, 25, 1–9.
- Zapparoli, M. (1994) Chilopodi di Turchia. IV. Specie del genere *Lithobius* Leach, 1814 s.str. (Chilopoda, Lithobiomorpha). *Fragmenta entomologica*, 25, 175–256.
- Zapparoli, M. (1999) The present knowledge of the centipede fauna of Anatolia (Chilopoda). *Biogeographia*, 20, 106–177.
- Zapparoli, M. (2002) A catalogue of the centipedes from Greece (Chilopoda). *Fragmenta entomologica*, 34, 1–146.

