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MYRIAPOD PHYLOGENY AND THE RELATIONSHIPS OF CHILOPODA

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Resumen. Estudios recientes han propuesto que los Myriapoda constituyen un grupo monofilético, parafilético en relación con los Hexapoda, o incluso polifilético. Algunos caracteres morfológicos compartidos por los Chilopoda y los Progoneata son sinapomorfías potenciales de los Myriapoda. La monofilia de Myriapoda es más robusta cuando los hexápodos se unen con los crustáceos (las supuestas sinapomorfías de Atelocerata unen a los miriápodos). El análisis de la filogenia interna de los Chilopoda (ciempiés) basada en la combinación de secuencias de rRNA 18S y 28S y morfología soportan la monofilia de todos los órdenes, incluyendo a Lithobiomorpha, y de los clados supraordinales Pleurostigmophora, Epimorpha y *Craterostigmus* + Epimorpha. Los datos moleculares y morfológicos coinciden en la división de Lithobiomorpha en Lithobiidae y Henicopidae (= Anopsobiinae + Henicopinae), en la parafilia de las 'Cryptopidae' en relación con las Scolopendridae, y en la división de los Geophilomorpha en Adesmata y Placodesmata.

INTRODUCTION

The relationships of myriapods are central to most questions in higher-level arthropod phylogeny. Many current controversies in arthropod systematics, such or whether insects are most closely related to crustaceans (Paulus, 2000; Dohle, 2001) or whether the mandibulate arthropods are a clade (Wägele, 1993; Scholtz *et al*., 1998), are fundamentally affected by the status of Myriapoda.

Four monophyletic groups (classes according to many classifications) have traditionally been united as Myriapoda, namely Chilopoda (centipedes), Symphyla, Pauropoda, and Diplopoda (millipedes). The monophyly of Myriapoda, however, has long been questioned. Pocock (1893: 275) stated that "the so-called group of Myriapoda is an unnatural assemblage of beings", a view maintained by Snodgrass (1952: 4), who asserted "modern zoologists do not generally recognize the myriapods as a natural group". Dohle (1980) provided an authoritative review of the question "Sind die Myriapoden eine monophyletische Gruppe?" ["Are myriapods a monophyletic group?"], concluding that myriapod monophyly was dubious, though some contemporary workers (Boudreaux, 1979b) argued in defense of Myriapoda. The twenty years since Dohle's review have witnessed significant contributions on the higher-level systematics of major myriapod taxa, notably the two most diverse classes, Diplopoda (Enghoff, 1984, 1990) and Chilopoda (Borucki, 1996; Edgecombe *et al*., 1999). Molecular sequencing as well as mitochondrial gene order data have provided novel sources of information bearing on myriapod phylogeny and the status of Myriapoda in the context of arthropod interrelationships (Giribet & Ribera, 2000; Regier & Shultz, 2001). As well, many classical characters have been reinvestigated (*e.g*., tracheae; Hilken, 1998; Klass & Kristensen, 2001), and in some cases homology can be appraised with reference to gene expression patterns (Popadic *et al*., 1998; Scholtz *et al*., 1998). The present contribution reviews the major controversies in the higher-level phylogeny of myriapods. This review is followed by a parsimony analysis of relationships within Chilopoda, based on morphological and molecular sequence data.

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THE STATUS OF MYRIAPODA: AN OVERVIEW

Myriapoda have been interpreted by various authors in recent literature as either monophyletic, paraphyletic or polyphyletic. These competing concepts are briefly reviewed herein, including a historical perspective (Fig. 6.1).

Myriapoda as a monophyletic group. Manton's (1964) survey of mandibular structure and function concluded that Myriapoda are monophyletic. In particular, she identified the role of the cephalic endoskeleton (the anterior tentorial apodemes) in the abduction of the mandible as a feature unique to myriapods. Students of sperm ultrastructure (Baccetti *et al.*, 1979; Jamieson, 1987) have likewise regarded Myriapoda as monophyletic, based principally on the absence (inferred loss) of a filamentous rod, the so-called perforatorium, in the acrosome. Boudreaux (1979a) diagnosed Myriapoda as a clade composed of the sister groups Collifera (= Pauropoda + Diplopoda) and Atelopoda (= Symphyla + Chilopoda), citing numerous characters in his diagnosis (Fig. 6.1F). Myriapod monophyly was endorsed by Ax (1999) based on the absence of median eyes and the structure of the lateral ocelli (Fig. 6.1G).

Analyses based on molecular sequence data have generally resolved Myriapoda as monophyletic. The first molecular studies using more than one myriapod class analyzed ribosomal sequence data for Chilopoda and Diplopoda. These studies consistently found monophyly of Chilopoda + Diplopoda relative to other arthropods (Wheeler *et al.*, 1993; Friedrich & Tautz, 1995; Giribet & Ribera, 1998; Wheeler, 1998a, b); however, the picture gets more complicated when ribosomal sequences of several myriapods, including Symphyla and Pauropoda, are involved (Giribet & Ribera, 2000). Non-ribosomal sequence data, especially elongation factor-1a (EF-1a) and RNA polymerase II (Pol II), have added corroboration to the monophyly of Myriapoda (Regier & Shultz, 1997, 1998, 2001; Shultz & Regier, 2000), although no pauropods were used in those studies. Sequence data for Pauropoda have only been published recently for Histone H3 and for the small nuclear rRNA U2 (Colgan *et al.*, 1998; Edgecombe *et al.*, 2000), as well as for the 18S rRNA and 28S rRNA

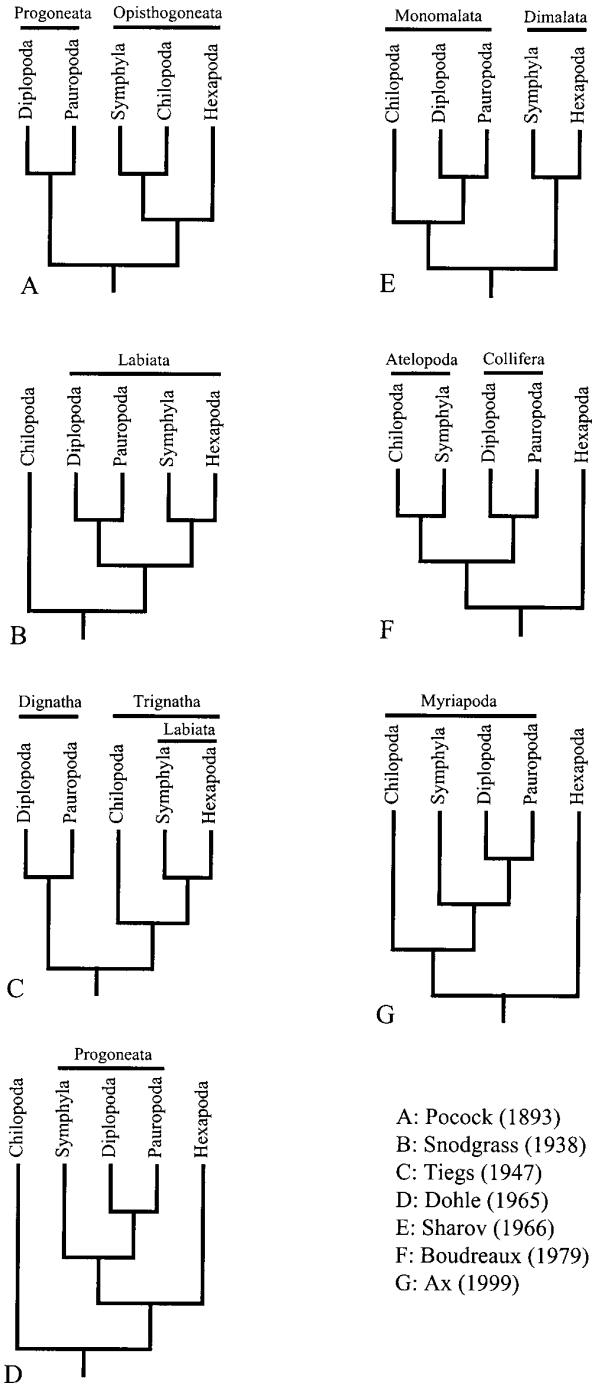

Fig. 6.1. Alternative hypotheses of relationships between the four myriapod classes in the context of Atelocerata (= Tracheata). Trees A-E resolve "Myriapoda" as paraphyletic with respect to Hexapoda; trees F-G resolve Myriapoda as monophyletic. Authors introducing or endorsing each hypothesis are indicated in the lower right.

loci (Giribet & Ribera, 2000), although the aberrant pauropod sequences did not contribute much to the stability in myriapod relationships.

Myriapoda as a paraphyletic group. Hypotheses of myriapod paraphyly have involved the Atelocerata (= Tracheata) hypothesis, *i.e.*, some clade within Myriapoda is more closely related to Hexapoda than to other myriapods (Fig. 6.1A-E). Pocock (1893) divided the Atelocerata into Opisthogoneata (Chilopoda + Symphyla + Hexapoda) and Progoneata (Pauropoda + Diplopoda) based on the position of the gonopore (Fig. 6.1A). Pocock's classification implied that 'Myriapoda' are paraphyletic if the opisthogoneate and progoneate groups are both themselves monophyletic (the former being especially doubtful). Snodgrass (1938) alternatively considered Symphyla to be the sister group of Hexapoda, Pauropoda + Diplopoda to be sister to this clade, and Chilopoda to be sister to all other atelocerates (Fig. 6.1B). Sharov (1966) favoured another pattern of myriapod paraphyly, with Chilopoda as the sister group of Dignatha Tiegs 1947 (= Pauropoda + Diplopoda), and Symphyla as the sister group of Hexapoda (Fig. 6.1E). The chilopod-pauropod-diplopod group was named Monomalata by Sharov. This group was defended based on a single pair of jaws (the mandible being the sole masticatory limb) and having the first maxilla forming the posterior wall of the preoral chamber. The symphylan-insect group, named Dimalata by Sharov (1966), was united based on having the first maxilla acquiring a function of mastication and the second maxilla forming an underlip (labium).

In recent years, myriapod paraphyly has been most forcefully advocated by Kraus & Kraus (1994, 1996; Kraus, 1998, 2001). As argued earlier by Dohle (1965, 1980), Kraus and Kraus regard Dignatha as the sister group of Symphyla, these taxa together comprising the Progoneata (Fig. 6.1D). Progoneata is considered to be sister group of Hexapoda, forming the taxon Labiophora, of which Chilopoda is resolved as the sister group. The character evidence for this labiophoran group is discussed below.

Myriapoda as a polyphyletic group. An analysis of 100 brain characters by Strausfeld (1998) represented Myriapoda by two taxa, *Orthoporus ornatus* (Diplopoda) and *Lithobius variegatus* (Chilopoda). Parsimony analysis resolved the diplopod as sister group to Onychophora, whereas the chilopod united with a hexapod-crustacean clade. Strausfeld did not publish his character matrix or the list of apomorphies that support the diplopod-onychophoran clade, so evaluation of this hypothesis is not possible. As well, no Symphyla or Pauropoda were included in the analysis.

FIRMLY ESTABLISHED CLADES WITHIN MYRIAPODA

The monophyly of the four main myriapod groups (Chilopoda, Symphyla, Pauropoda and Diplopoda) is considered uncontroversial. In the following section we cite characters that provide evidence for the monophyly of these taxa, and then briefly summarize the evidence for two well-supported groupings, Dignatha and Progoneata (Fig. 6.2).

Chilopoda. Synapomorphies of Chilopoda include: an egg tooth on the embryonic cuticle of the second maxilla; the appendage of the first postcephalic segment modified as a maxillipede housing a poison gland; trunk legs with a ring-like trochanter lacking mobility at the joint with the prefemur; and a spiral ridge on the nucleus of the spermatozoan (Dohle, 1985; Kraus, 1998; Edgecombe *et al.*, 2000).

Symphyla. Synapomorphies of Symphyla are: a single pair of tracheal stigmata on the lateral sides of the head capsule; absence of eyes; labium with distal sensory cones; female spermathecae formed by paired lateral pockets in the mouth cavity; an unpaired genital opening; paired terminal spinnerets; and anal segment with a pair of large sense calicles (trichobothria), each with a long sensory seta (Scheller, 1982; Kraus, 1998; Ax, 1999).

Pauropoda. Pauropod synapomorphies are: antennae branching, with a special sensory organ, the globulus; paired pseudoculi on lateral sides of the head capsule; exsertile vesicles on the ventral side of the first postcephalic segment; and trichobothria at margins of the tergites (Dohle, 1998; Kraus, 1998).

Diplopoda. Diplopod monophyly is supported by: body segments fused into diplosegments; antenna with eight articles, the distal article bearing apical sensory cones (primitively four cones); and

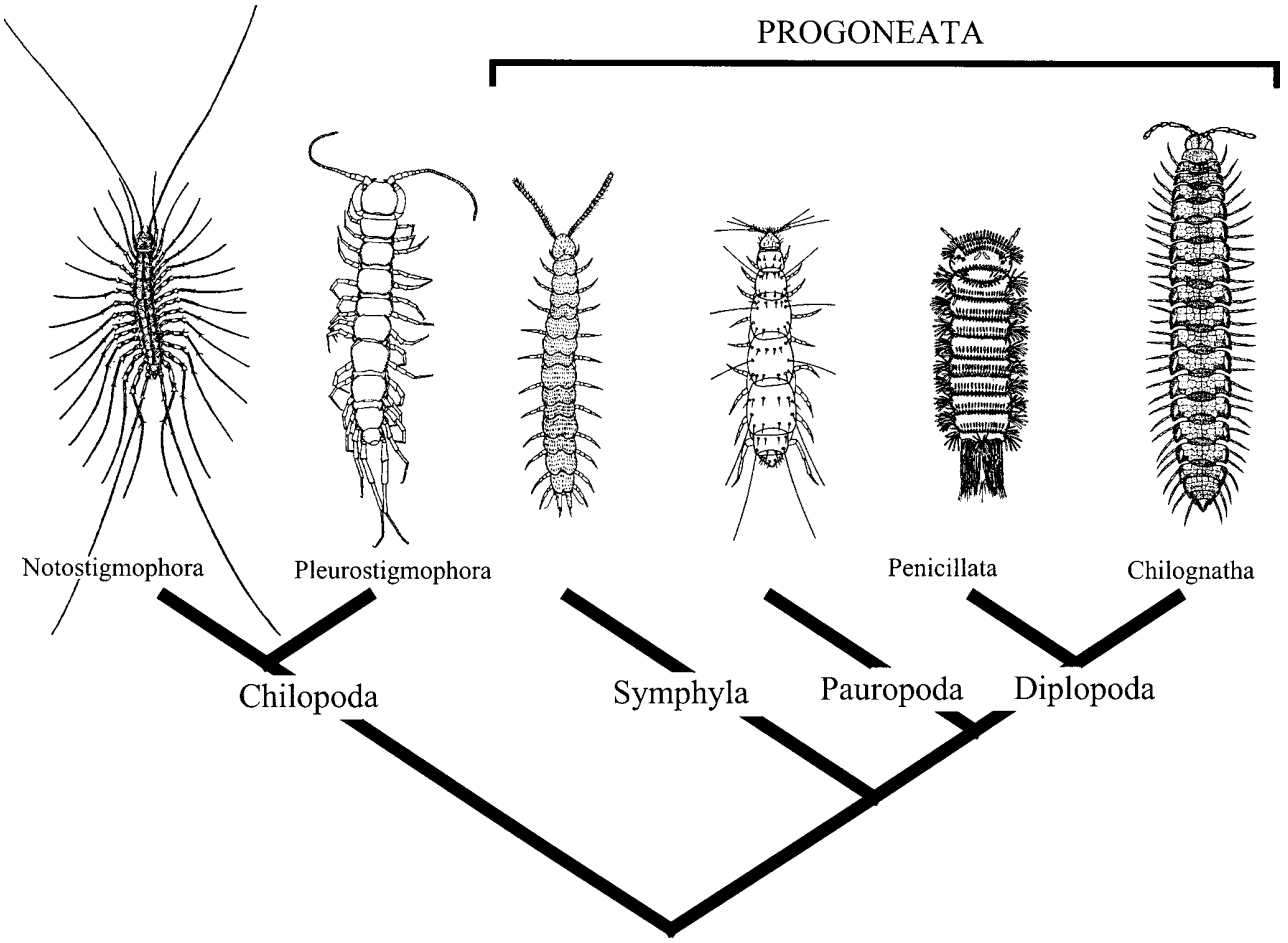

Fig. 6.2. Relationships within Myriapoda based on morphological evidence and showing exemplar organisms (Progoneata following Dohle, 1980, 1998). Illustrations sourced as follows: Notostigmophora (Snodgrass, 1952); Pleurostigmophora (Eason, 1964); and Penicillata, Chilognatha, Symphyla and Pauropoda (Eisenbeis & Wichard, 1985).

aflagellate spermatozoa (Enghoff, 1984). Within Diplopoda, a sister group relationship between Penicillata and Chilognatha (Fig. 6.2) has been endorsed by most workers since Pocock (1887), and is defended in those studies that have used explicit cladistic argumentation (*e.g.*, Enghoff, 1984; Wilson & Shear, 2000).

Dignatha. Dohle (1980, 1998) appropriately cited the union of Pauropoda and Diplopoda as a strongly supported monophyletic group. The reader is referred to Dohle's (1980) discussion and illustration of the characters that unite pauropods and diplopods. Synapomorphies of Dignatha include: limbless first trunk segment (collum); vas deferens opening on the tip of conical penes (inferred basal state for Diplopoda based on similarity of penes of Penicillata with those of Pauropoda; modified within various lineages of Chilognatha); sternal spiracles at bases of walking legs which open into a tracheal pouch giving rise to an apodeme (present only in Hexamerocerata within Pauropoda); motionless pupoid stage, pupoid encased in embryonic cuticle; and first free-living juvenile with three pairs of legs (Enghoff *et al.*, 1993).

Progoneata. Dohle (1980, 1998) regarded a sister group relationship between Symphyla and Dignatha (= Progoneata) as having reasonable support, and this clade has been endorsed by other morphologists (Kraus, 1998; Edgecombe *et al.*, 2000). Again, we refer the reader to Dohle (1980)

for documentation of the following synapomorphies of Progoneata: gonopore situated behind second pair of trunk legs; midgut developing within the yolk, the lumen being devoid of yolk; cephalic fat body developing from vitellophages in yolk (versus from walls of mesodermal somites in Chilopoda and Hexapoda); sternal apodemata; and trichobothria with a basal bulb. Trichobothria have distinctive modifications in polyxenid millipedes, pauropods and symphylans, notably a hair that forms a basal bulb (Haupt, 1979). Despite the variable position of such trichobothria on the body (on the anal segment in symphylans, on the tergites in pauropods, on the head in polyxenids), the basal bulb is a plausible synapomorphy of Progoneata. This hypothesis, however, forces a loss of trichobothria in chilognathan millipedes (Enghoff, 1984).

In addition to the above characters, polyxenid diplopods, symphylans and pauropods share a single median, mound-shaped germarium on the floor of the ovary (Yahata & Makioka, 1994, 1997). This contrasts with the usual arthropod germarium, either an elongate zone in the ventral or lateral wall of the ovary, or an apical position in the egg tube. Anderson (1973) additionally defended the monophyly of Progoneata based on the gonoduct arising as a secondary ectodermal ingrowth (versus a mesodermal coelomoduct in Chilopoda, the inferred plesiomorphic state). Absence of palps on the first maxilla has been cited as a progoneate synapomorphy (Kraus & Kraus, 1994; Kraus, 1998; Ax, 1999), but Shear (1998) indicated that palps are present in Penicillata within Diplopoda.

SYNAPOMORPHIES OF MYRIAPODA?

Dohle (1998) regarded myriapod monophyly as unsubstantiated, because putative synapomorphies of the group involve absences *("I conclude that no positive character can be found in favour of the Myriapoda")*. In the following section we review the supposedly reductive characters shared by myriapods, and marshal positive evidence for myriapod monophyly. Additional characters that earlier workers had employed to define Myriapoda (homonymy of the trunk and diplosegmentation) are soundly criticized by Dohle (1980) and are not further considered.

Absence characters

Absence of median eyes. Median eyes with protocerebral innervation are present in euchelicerates, pycnogonids, crustaceans, and hexapods, and are widely regarded as a synapomorphy for Euarthropoda (Paulus, 1979). All myriapods lack organs of the median eye complex. Monophyly of euarthropod clades such as Mandibulata forces this absence of median eyes in myriapods to be interpreted as a loss. Dohle (1997, 1998) differed from Ax (1999) in dismissing the value of absence features such as this in phylogenetic inference. The alternative interpretation, that the absence of median eyes in myriapods is primitive, resolves Myriapoda basally within Euarthropoda.

Absence of scolopidia. Scolopidia are specialized mechanoreceptive sensilla, known from various groups of insects and crustaceans but not occurring in myriapods. Under the Atelocerata hypothesis, the absence of scolopidia in myriapods was interpreted as an apomorphic state (loss) (Paulus, 1986). However, the character can be reassessed under the Pancrustacea model, with the absence of scolopidia in myriapods being plesiomorphic, and their presence being a possible synapomorphy for insects and crustaceans.

Absence of a perforatorium in the acrosomal complex of the sperm. A bilayered acrosome is regarded as a plesiomorphic state for arthropods. Myriapod sperm lack a filamentous actin perforatorium in the acrosome, this 'monolayered' acrosome being cited as a synapomorphy for Myriapoda (Baccetti & Dallai, 1978; Jamieson, 1987).

Presence characters

Hypopharynx supported by fultural sclerites that bear the head apodemes. Fulturae are represented in Myriapoda by paired hypopharyngeal processes that are fused with parts of the anterior tentorial apodemes (Kluge, 1999; Bitsch & Bitsch, 2000). Snodgrass (1952) cited similarities of fultural sclerites of the hypopharynx as a "strong point in evidence of a relationship" between Diplopoda, Pauropoda and Chilopoda. In each case the fulturae support the apodemes that give rise to mandibular adductor muscles. The hypopharnygeal fulturae of Myriapoda can be considered as a character independent of the style of mandibular adbuction by movements of the tentorium (see below); one

character involves the topological relationships of the hypopharynx, fulturae and apodemes, whilst the other involves movements of the apodemes relative to the mandible. Symphyla possess the head apodemes that serve as the attachments of the mandibular adductors, but lack fultural sclerites (Snodgrass, 1952). Fultural sclerites thus do not provide an unambiguous synapomorphy of Myriapoda, but the probability of their homology between Chilopoda and Dignatha suggests that they are a basal synapomorphy for myriapods. Snodgrass interpreted the fultural plates as the premandibular sternal sclerites of Myriapoda, and noted the absence of corresponding plates in Crustacea and Insecta.

Mandible with musculated gnathal lobe, flexor (anterior dorsal muscle) arising dorsally on the cranium. The significance of jointed mandibles in myriapods has generated considerable discussion. Staniczek (2000) criticized the arguments of Kraus & Kraus (1996), Kraus (1998) and Kukalová-Peck (1998) that hexapods have segmented ('telognathic') mandibles, and concluded that gnathobasic mandibles are general for Mandibulata. According to Staniczek (2000: 176), this implies "a secondary subdivision of the mandible in the myriapod lineages", mirroring the conclusion of Lauterbach (1972) that myriapod mandibles are secondarily subdivided gnathobases. Regardless of the status of 'telognathy' in hexapods, the structural differentiation of myriapod mandibles can be characterised with apparently apomorphic details. Chilopoda resemble Diplopoda and Symphyla in having the gnathal lobe of the mandible musculated by a large flexor that arises on the dorsal surface of the cranium (Snodgrass, 1950, 1952). In contrast, the dorsal mandibular muscles of hexapods and crustaceans do not serve as gnathal lobe flexors. Kluge (1999) argued in defence of myriapod monophyly based on division of the mandible into two movably jointed sclerites (*i.e*., gnathal lobe and base), with the anterior dorsal muscle serving as an adductor. Exceptions to this musculation of the gnathal lobe within Myriapoda, *e.g*., the single-piece mandible of tetramerocerate pauropods, must be regarded as reversals if the similarities are homologous. Hüther's (1968) description of the mandible of Hexamerocerata (see Kraus & Kraus, 1994: Figs. 16, 17) suggests that a movable, articulated gnathal lobe is plesiomorphic for Pauropoda.

'*Swinging tentorium*'. As noted above, Manton (1964) reinstated Myriapoda as a monophyletic group based on a common pattern of mobility of the anterior tentorial apodemes that is confined to chilopods, diplopods, pauropods and symphylans. Movement of the tentorial apodemes serves to abduct the mandibles. Boudreaux (1979a: 105) regarded these tentorial movements, in concert with the mandibular musculation described above, as "an outstanding specialization in myriapods that is unique and more than any suggests that myriapods form a natural assembly".

Pectinate (comb) lamellae on mandibular gnathal lobe. In addition to the musculation of the gnathal lobe of the mandible, structural details of the gnathal lobe present apparent homologies between Diplopoda and Chilopoda. The comb-lobe of diplopods consists of two to about a dozen comb- or rakelike rows of slender lamellae (see Enghoff, 1979 for julids; Ishii, 1988, for polyxenids; Ishii & Tamura, 1996 for polydesmids; Köhler & Alberti, 1990 for several orders; Fig. 6.3A,B herein for Sphaerotheriida and Penicillata, respectively). The comb-lobe lies distal to the molar plate. The corresponding positions on the gnathal lobe of Chilopoda are occupied by the pectinate lamellae and dentate lamina, respectively. A differentiation of the gnathal lobe into pectinate and dentate laminae appears to be general (*i.e.,* optimise basally) for Myriapoda. The morphology of the pectinate lamellae (pl. in Fig. 6.3) in particular presents detailed similarity between diplopods (Fig. 6.3A,B) and chilopods (Fig. 6.3C-F). In Scutigeromorpha (Fig. 6.3C) and Scolopendromorpha (Fig. 6.3D-F), the pectinate lamina is composed of multiple rows of hyaline combs that are individually embedded in soft tissue, as is the case for the comb-lamellae of Diplopoda. In Scolopendromorpha, the number of combs is as few as three in some 'criptoids' to as many as 11 in scolopendrids. Even in some Geophilomorpha (Mecistocephalidae, Himantaridae, Oryidae), the pectinate lamellae consist of multiple combs, such that multiple comb lamellae can be regarded as the general condition for Chilopoda. No homologue of the comb lamellae of diplopods and chilopods is present in insects (see, *e.g*., Staniczek, 2000), and a comparable comb-

like series of lamellae is likewise lacking in Crustacea. Homology between the comb lamellae of chilopods and diplopods is suggested by their identical position on the gnathal lobe, similar structure, the same orientations of the lamellae, their hyaline composition, and comparable numbers of elements. The "lamellenartige Chitinstruktur des Pharynx oder der Mandibel", shown

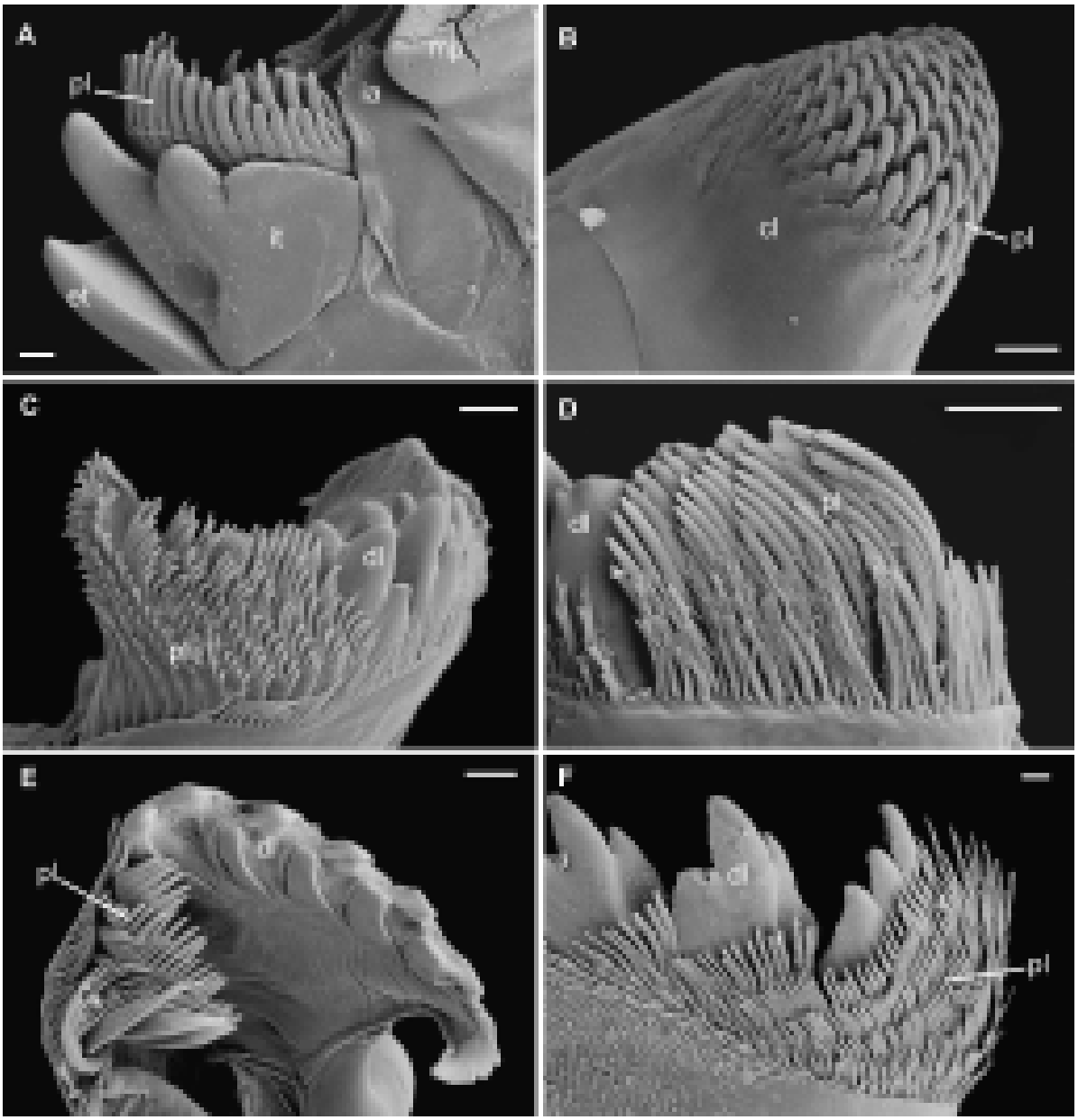

Fig. 6.3. Scanning electron micrographs of the mandibular gnathal lobe in Diplopoda (A, B) and Chilopoda (C-F), showing pectinate (comb) lamellae. A, *Epicyliosoma* sp. [Sphaerotheriida]. B, *Unixenus mjobergi* [Penicillata]. C, *Parascutigera* sp. [Scutigeromorpha]. D, *Cryptops spinipes* [Scolopendromorpha]. E, *Cryptops australis* [Scolopendromorpha]. F, *Ethmostigmus rubripes* [Scolopendromorpha]. Scale bars 50 µm except B, 10 µm. Abbreviations as follows: cl, comb lobe; dl, dentate lamina; et, external tooth; ia, intermediate area; it, internal tooth; mp, molar plate; pl, pectinate lamellae.

by Hüther (1968: fig. 8) in the hexamerocerate pauropod *Rosettauropus*, is situated in the appropriate position for comb lamellae, whereas it is not readily interpreted as part of the hypopharynx. The possibility that multiple rows of comb lamellae are a synapomorphy of Myriapoda must be seriously considered.

Lateral eye developed as stemmata with rhabdom composed of multilayered retinular cells. Myriapod lateral eyes possess a rhabdom composed of two (Scutigeromorpha and Polyxenida) or many (Pleurostigmophora and Chilognatha) layers of retinular cells. Paulus (1986) considered the layering of the rhabdom as a probable synapomorphy for Myriapoda, noting a similar construction only in the larval eyes of certain insects. The homology of this layering is weakened by the variability displayed. *i.e.,* a precise correspondence in numbers of retinular cell layers is not observed. Ax (1999) cited the absence ('loss') of a crystalline cone, secretion of the lenses of the ocelli from a multicellular layer of epidermis cells, and the multilayered retinular cells as an apomorphic character complex for Myriapoda. Ax's interpretation of the absence of a crystalline cone as a loss is dependent on the monophyly of Mandibulata and Atelocerata.

IMPLICATIONS OF A CRUSTACEAN-HEXAPOD SISTER GROUP RELATIONSHIP

Many recent workers have abandoned the Atelocerata hypothesis, instead regarding hexapods as more closely related to crustaceans than to myriapods. The hexapod-crustacean clade has been named Pancrustacea (Zrzavý & Štys, 1997). Evidence for pancrustacean monophyly has emerged from numerous anatomical and neurological systems, including: ommatidial structure, including the cellular composition of the crystalline cone and retinula as well as the chiasmata between the optic neuropils (Paulus, 1979; Nilsson & Osorio, 1998); details of early differentiating neurons (Whitington *et al*., 1991, 1993); ganglion formation via neuroblasts (Gerberding, 1997); *Engrailed* expression in the segmental mesoderm (Zrzavý & Štys, 1995); presence of a fan-shaped body in the brain (Strausfeld, 1998); and mitochondrial gene order data (Boore *et al*., 1995, 1998). Dohle (2001) reviewed evidence in favour of Pancrustacea. A hexapod-crustacean clade has likewise been recovered in analyses of elongation factor-1 alpha and the large subunit of RNA polymerase II sequences (Shultz & Regier, 2000), as well as in some analyses of combined molecular data using mainly 18S rRNA sequences (Wheeler *et al*., 1993; Friedrich & Tautz, 1995; Giribet *et al*., 1996; Giribet & Ribera, 1998) (though it is ambiguous with more comprehensive taxonomic sampling: Giribet & Ribera, 2000).

Under the Pancrustacea hypothesis, the classical 'synapomorphies' of Atelocerata are instead interpreted as convergences related to terrestrial habits in both myriapods and hexapods (Averof & Akam, 1995). This reinterpretation carries the important consequence that these characters must be considered as potential synapomorphies of Myriapoda, a point appreciated by Paulus (2000). Denying the status of these characters as synapomorphies for Myriapoda, in the complete absence of rival hypotheses of relationships for Chilopoda and Progoneata, is problematic. 'Atelocerate' characters that remain as potential synapomorphies of Myriapoda are the following:

Limbless intercalary segment. The postantennal (intercalary) segment in hexapods and myriapods has, at most, transient expression of a limb bud.

Pretarsal segment of leg with a single muscle, a depressor. The absence of a pretarsal levator was cited by Snodgrass (1952) as a unique feature of the myriapod-hexapod assemblage, in contrast to paired pretarsal muscles in Crustacea.

Anterior tentorial apodemes. Snodgrass (1950) regarded the head apodemes of Myriapoda as homologous with the anterior tentorial arms of Insecta, in which they likewise arise as cuticular (ectodermal) invaginations. Bitsch & Bitsch (2000), Koch (2000) and Klass & Kristensen (2001) cited probable homology of these structures, though the morphological details of myriapods are in need of more detailed observations. Homology of the varied tentorial structures in Hexapoda is controversial. Bitsch & Bitsch (2000) regarded the fulcrotentorium of Protura as non-homologous with the true tentorium of Insecta, and interpreted the endoskeletal formations of Collembola and Diplura to be a complex endosternite composed of connective fibres rather than a cuticular tentorium. Koch (2000), in contrast, endorsed homology be-

tween the anterior tentorial apodemes of Collembola, Diplura, and Insecta, citing common points of origin, for example, identical sclerotic connections with the labrum. Even if the cuticular tentorium of insects is non-homologous with that of myriapods, the presence of anterior tentorial apodemes is ubiquitous in Myriapoda and cannot be easily dismissed as a possible synapomorphy, particularly in light of shared movements of the tentorium in mandibular abduction (see 'Swinging tentorium' above).

Postantennal (Tömösváry) organs. Protocerebral Tömösváry organs are present in Chilopoda (Scutigeromorpha, Lithobiomorpha, and Craterostigmomorpha; absent in Epimorpha *s. str.*) (Minelli, 1993), Symphyla (Haupt, 1971), Pauropoda (Haupt, 1973), and Diplopoda (but lacking in Juliformia) (Enghoff, 1990). Their homology, and especially homology with the postantennal organs of Collembola and Protura, has been variably defended (Bitsch & Bitsch, 1998) or questioned (Bourgo in, 1996).

Malpighian tubules. Myriapods share a single pair of Malpighian tubules at the juncture between the midgut and the hindgut. Some chilopods have one or a small pair of supernumerary Malpighian tubules (Prunescu & Prunescu, 1996). The homology of Malpighian tubules in hexapods and myriapods has been questioned by Dohle (1997, 1998) and Kraus (1998). In addition to uncertainties in the ectodermal status of insect Malpighian tubules (see Dohle, 1997), these organs exhibit topological differences between myriapods and hexapods, the latter having several pairs of tubules that are positioned at the anterior part of the hindgut. Whereas the status of Malpighian tubules as an atelocerate synapomorphy is problematic, homology of the single pair of similarly positioned tubules in Myriapoda is less readily dismissed.

Tracheae. The homology of tracheae between Symphyla, Dignatha, Scutigeromorpha, Pleurostigmophora, Collembola (Symphypleona), Protura (Eosentomoidea) and Diplura/Ectognatha has been rejected by several workers (Kraus & Kraus, 1994, 1996; Dohle, 1997; see Hilken, 1998 for especially thorough study). Tracheae differ substantially in their positioning, gross morphology and fine structure, and primary homology cannot be regarded as well supported. Even between the Symphyla (single pair of spiracles on the head), Dignatha (spiracles at bases of legs, opening into tracheal pouches), Scutigeromorpha (dorsal spiracle opening into tracheal lungs), and Pleurostigmophora (pleural spiracles), homology of tracheae is problematic and we are sceptical of the value of this character as a myriapod synapomorphy.

CHALLENGES TO THE LABIOPHORA HYPOTHESIS

The Labiophora hypothesis (Progoneata as the sister taxon to Hexapoda) conflicts with the characters that support myriapod monophyly, and also conflicts with the characters that support Hexapoda + Crustacea. We might thus investigate whether Labiophora is based on well-founded homologies. Kraus & Kraus (1994, 1996) and Kraus (1998, 2001) defended Labiophora based on the purported synapomorphies discussed in the following section. As argued below, the homology of each of these characters is problematic.

Maxillary plate (basal parts of second maxilla or labium medially merged, bordering side of mouth cavity). Kraus & Kraus (1994) cited this morphology as a synapomorphy for Labiophora. They contrasted it with the situation in chilopods, in which the first maxillae border the mouth. Some earlier workers (*e.g.*, Sharov, 1966) had regarded chilopods, pauropods, and diplopods as sharing a first maxillary border of the mouth. Kraus & Kraus' (1994, 1996) argument is dependent on their interpretation that the diplopod and pauropod gnathochilarium is composed of two pairs of appendages, first and second maxillae, a theory developed earlier by Verhoeff, and upheld by Kraus and Kraus based on external morphology. Dohle (1998), however, presented counterarguments, including the complete lack of limbs on the second maxillary segment in diplopod embryos, innervation by a single pair of ganglia, and muscles being those of a single segment. Dohle (1998) concluded that the lower lip of Dignatha is composed of the appendages of the first maxillary segment and the intervening sternite alone. Scholtz *et al.* (1998) strengthened Dohle's interpretation by showing the lack of *Distal-less* expression on the postmaxillary segment in diplopods. As such, a role of

the second maxilla in forming the lower lip in Dignatha requires more conclusive documentation.

Coxal vesicles. Dohle (1980) reviewed the distribution of coxal vesicles (or eversible sacs) in myriapods and hexapods. He noted that they have variable positions in different progoneate and hexapod taxa, and questioned whether they provide sound evidence for a monophyletic group. Despite Dohle's reservation, Kraus & Kraus (1994) listed coxal vesicles together with styli as a synapomorphy uniting progoneates and hexapods. Moura & Christoffersen (1996) cited a stylus and eversible vesicles as an atelocerate synapomorphy, but their absence in Chilopoda makes this hypothesis unacceptable. Within Myriapoda, coxal vesicles are confined to Symphyla, some groups within Diplopoda, and probably Pauropoda (see comments below). In addition to their scattered systematic distribution, the homology of 'coxal vesicles' between progoneates and hexapods is brought into doubt by different origins of these structures. Matsuda (1976) distinguished between eversible sacs of appendicular nature and those that have extra-appendicular origins. The former include the single pair of sacs at the end of the *Ventraltubus* on the first abdominal segment in Ellipura, as well as the vesicles of Diplura, which arise from the appendicular *Anlagen* of the abdominal segments (Ikeda & Machida, 1998). In contrast, the vesicles of Symphyla arise on the 'ventral organs' associated with ganglion formation (Tiegs, 1940, 1945), these being segmental thickenings of the embryonic ventral ectoderm. Although Tiegs (1947) regarded a pair of organs of the collum of pauropods (Edgecombe *et al*., 2000: fig. 2F) as vesicles, this homology is contentious, with Kraus & Kraus (1994) suggesting instead that they are vestigial appendages.

Styli. Styli have a close association with coxal vesicles/eversible sacs in some myriapod and hexapod taxa, for example Symphyla and Diplura; however, styli and vesicles do not covary phylogenetically (Ellipura, for example, possess vesicles but lack styli). As such they may be regarded as separate characters (*cf.* Dohle, 1980) rather than a single, obligately-linked feature (Kraus & Kraus, 1994). Evidence for styli in chilopods is weak, the only evidence being the description (Heymons, 1901) of a coxal spur on embryonic appendages of *Scolopendra*, which has been upheld as being in a position comparable to the coxal stylus of machiloids (Matsuda, 1976). Styli are absent in pauropods and diplopods, and may not be present at the basal node for Insecta (palaeontological arguments summarised by Ax, 1999), so the status of this feature as a synapomorphy of Labiophora is challenged.

Superlinguae. Kraus & Kraus (1994) cited Dohle's (1980) argument that presence of hypopharyngeal superlinguae may be a synapomorphy for Labiophora, though they cautioned that details of structure and function were insufficiently known to defend the use of this character. This caution is well placed. The possibility of homology between superlinguae and the paragnaths of Crustacea (Crampton, 1921; Snodgrass, 1952; Bitsch & Bitsch, 2000) requires scrutiny. Walossek & Müller (1998) indicate that paragnaths originate on the mandibular sternite. Tiegs (1940) considered the superlinguae of Symphyla to likewise develop on the mandibular sternum, and to have mandibular innervation. The median apical lobes of the gnathochilarium of pauropods arise from the mandibular segment (Tiegs, 1947; Snodgrass, 1952), and are thus considered homologous with superlinguae. Even if the superlinguae of progoneates and basal hexapods pass a test of primary homology, the possibility of homology with paragnaths in Crustacea allows that they may be symplesiomorphic for Mandibulata rather than a synapomorphy for Labiophora.

In summary, the proposed synapomorphies of Labiophora are questionable on their own intrinsic basis. Even if this were not so, they could be overturned on the basis of parsimony, because a larger body of evidence supports the monophyly of clades (Myriapoda and Pancrustacea) that are incompatible with Labiophora.

CLADISTIC ANALYSIS OF CHILOPODA

Of the four major myriapod clades, Chilopoda have attracted the most attention in terms of their internal phylogeny. A fundamental controversy concerns whether the basal split within Chilopoda is between Anamorpha and Epimorpha or between Scutigeromorpha (=Notostigmophora) and

Pleurostigmophora (see Dohle, 1985 for a historical review). The Anamorpha concept has recently been resurrected in a modified form by Ax (1999). In contrast, nearly all other contemporary workers have supported the Pleurostigmophora concept *(e.g.,* Prunescu, 1965, 1996; Shinohara, 1970; Dohle, 1985; Shear & Bonamo, 1988; Borucki, 1996; see Edgecombe *et al.* 1999: fig. 1 for a summary of competing hypotheses of ordinal interrelationships).

Chilopod phylogeny has traditionally been the domain of morphologists, but molecular sequence data have recently been applied to the problem. Shultz & Regier (1997) analyzed elongation factor-1 alpha sequences for five chilopod species representing four orders, the resultant phylogeny being at odds with morphological hypotheses. More thorough sampling was undertaken by Giribet *et al.* (1999) in an analysis of complete 18S rRNA sequences and the D3 region of 28S rRNA. This study surveyed 12 species representing the five extant orders of Chilopoda. The most parsimonious cladograms of Giribet *et al.* (1999) endorsed the Pleurostigmophora clade, as well as supporting a sister group relationship between *Craterostigmus* and Epimorpha *s.str*. Giribet *et al.* (1999) were able to defend the monophyly of all orders of Chilopoda except Lithobiomorpha, which was resolved as paraphyletic based on three exemplars of the family Lithobiidae. Regier & Shultz (2001) included 11 species of Chilopoda in their analysis of myriapod phylogeny based on elongation factor-1 alpha and the large subunit of RNA polymerase II. These data identify Epimorpha *s.str*. as a clade, with Scutigeromorpha (sampled only for *Scutigera*) its sister group. In parsimony analyses, *Craterostigmus* is sister group to all other Chilopoda, whereas their preferred maximum likelihood tree identifies Lithobiomorpha as sister group to other Chilopoda.

More comprehensive taxonomic sampling, along with a morphological dataset for the same set of terminals as used in molecular analysis, was employed by Edgecombe *et al.* (1999). Their study analysed the internal phylogeny of Chilopoda based on 117 morphological characters, 18S rRNA sequences for 38 chilopod taxa, and sequences of the D3 region of the 28S rRNA for 34 chilopods. The morphology dataset used in a new analysis in the present study is modified from that presented by Edgecombe *et al.* (1999). We have revized several codings, these changes being indicated in the character list presented in Appendix 6.1. Nineteen new morphological characters are added (described as characters 118-136 in Appendix 6.1), largely based on new analyses on Lithobiomorpha (Edgecombe *et al.* 2001) and Geophilomorpha (Foddai & Minelli, 2000). A total of 136 characters is now employed (see Appendix 6.3 for codings). As well, we have included additional taxa within Lithobiomorpha based on new sequences studied by Edgecombe *et al.* (2001). The lithobiid *Bothropolys multidentatus* and the henicopids *Esastigmatobius japonicus* and *Lamyctinus coeculus* are added to the taxonomic sample. In the current analysis, *Lithobius obscurus* replaces the partial sequence of *Lithobius forficatus* (Friedrich & Tautz, 1995), such that all sequences analysed herein were generated by the authors. On this basis, we have not included the 18S sequence of the mecistocephalid *Nodocephalus doii*. GenBank accession codes for 18S and 28S rRNA sequences are shown in Appendix 6.2, together with taxonomy of all species used in molecular and morphological analyses.

METHODS

Methods of DNA isolation, amplification and sequencing are as detailed by Edgecombe *et al.* (1999, 2001).

The morphological data set consists of 136 characters (Appendices 6.1 and 6.3). Most characters were treated as unordered (non-additive); instances where ordering was specified (characters 33 and 44) are justified in Edgecombe *et al.* (1999). The morphological data matrix was analysed using a heuristic search strategy implemented in the parsimony analysis program NONA (Goloboff, 1998). This search strategy consisted of 1,000 replicates of random addition sequence using tbr (tree bisection and reconnection) branch swapping and retaining a maximum of 10 trees per replicate. The results where then submitted to branch swapping again without specifying the number of maximum trees to retain, so all trees of every minimum-tree length island could be obtained (commands: hold10000;hold/10;mul*1000;max*). More efficient swappers were not required due to the clear

structure of our morphological data set. Approximate Bremer support (bs) values (Bremer, 1988) up to four extra steps were calculated (hold1000; bs3).

Molecular data partitions were analyzed independently and in combination using the Direct Optimization method (Wheeler, 1996) implemented in the computer program POY (Wheeler & Gladstein, 2000), following the methodology described in our previous work (Edgecombe *et al*., 1999, 2001). The 18S rRNA partition was split into 33 fragments (see Giribet, 2001 for a justification) from which three hypervariable fragments were excluded from the analysis. The D3 fragment of the 28S rRNA partition was split into three fragments, with one hypervariable fragment excluded. In our previous study of chilopod relationships we undertook an exploratory analysis of 12 parameter sets (following Wheeler, 1995), and compared two methods of optimization, direct optimization (Wheeler, 1996) and fixed-states optimization (Wheeler, 1999; see also Wheeler, 2001). On the basis of character congruence, we favoured the direct optimization method for the study of chilopod relationships (Edgecombe *et al*., 1999). Since the current data set is very similar to that explored by Edgecombe *et al.* (1999), we have sacrificed exploring multiple parameters in favour of much more aggressive searches in four parameters (Appendix 6.4). We have thus analyzed for simple parameter sets that were the optimal and immediate suboptimal parameters in our previous study. The combined analyses of all sources of data were also performed in POY.

The POY analyses (for independent partitions as well as for the combined analysis) were run in a cluster of 256 pentium III processors of 500 MHz (65,536 Mb of RAM) connected in parallel using pvm software and the parallel version of POY (-parallel -jobspernode 2 -controllers 32). Each analysis started from the best of 10 "quick" random addition sequence builds (-multibuild 10 -buildspr -buildtbr -approxbuild -buildmaxtrees 2), followed by spr and tbr branch swapping holding one cladogram per round of spr (-sprmaxtrees 1) and tbr (-tbrmaxtrees 1). Two rounds of tree fusing (Goloboff, 1999) (-treefuse -fuselimit 10-fusemingroup 5) and tree drifting (Goloboff, 1999) (-numdriftchanges 30 -driftspr -numdriftspr 10 -drifttbr -numdrifttbr 10) swapping on suboptimal cladograms (-slop 5 -checkslop 10) were used to make more aggressive searches; holding up to five cladograms per round (-maxtrees 5) and using the command -fitchtrees which saves the most diverse cladograms that can be found for each island. This search strategy was repeated a minimum of ten times and then up to 100 times, or until minimum cladogram-length is hit three times (-random 100 -stopat 3 -minstop 10). The option -multirandom was in effect, which does one complete replication in each processor instead of parallelising every search. This strategy tries to increase the chances of finding minimum length cladograms. The parameter sets were specified through stepmatrices (-molecularmatrix "name"). Other commands in effect were -noleading -norandomizeoutgroup. Bremer support values were estimated using the heuristics procedure implemented in POY (-bremer -constrain "filename" -topology "treetopology -in -parenthetical -notation").

Character congruence was used to choose the combined analysis that minimized incongruence among partitions measured by the Incongruence Length Difference (ILD) metrics (Mickevich & Farris, 1981; Farris *et al*., 1995). Character congruence is used as an optimality criterion to choose our 'best' cladogram, the cladogram that minimises conflict among all the data.

The root for the chilopod cladogram is placed between Scutigeromorpha and Pleurostigmophora (Fig. 6.2). As well as conforming to most investigators' hypothesis of chilopod phylogeny, this position recognises the basal split within Chilopoda when 18S and 28S sequence data were analysed with diplopod and hexapod outgroups by Edgecombe *et al.* (1999, fig. 2). Scutigeromorpha is likewise resolved as sister group of Pleurostigmophora when eight broadly-sampled molecular markers are combined with morphological data for all major arthropod groups (Giribet *et al*., unpublished).

RESULTS

Morphological analysis. Ten minimal length trees of 212 steps (consistency index 0.75, retention index 0.94) combine to yield the strict consensus in figure 6.4. Resolution of orders within Pleurostigmophora is as in the Prunescu-Dohle cladogram.

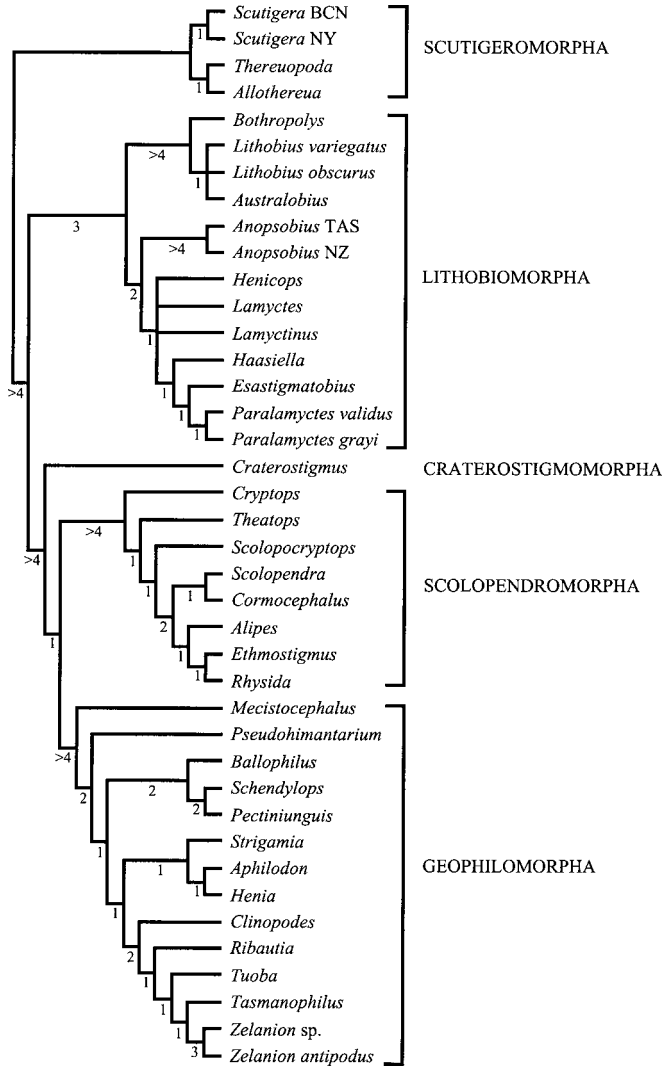

Fig. 6.4. Strict consensus of 10 shortest cladograms (length 212) for Chilopoda based on morphological data in Appendix 6.1.

Clades with Bremer support values of four or more include Epimorpha *s.str*., as well as the clade uniting Epimorpha with *Craterostigmus*. Monophyly of Geophilomorpha and Scolopendromorpha (bs = 4+) is more strongly supported than Lithobiomorpha (bs = 3). Nevertheless, Lithobiomorpha is resolved as a clade supported by several unambiguous synapomorphies (see Edgecombe *et al*., 1999 for discussion).

Internal phylogeny of Lithobiomorpha conforms to Eason's (1992) classification in the monophyly of Lithobiidae, Lithobiinae, Henicopidae, Anopsobiinae and Henicopinae. The traditional grouping Henicopini is non-monophyletic because *Esastigmatobius* (Tribe Zygethobiini) nests within the group, as detailed by Edgecombe *et al.* (2001).

Scolopendromorpha is resolved with the traditional groupings of Scolopendridae divided into Scolopendrinae (= *Scolopendra* + *Cormocephalus*) and Otostigminae (= *Alipes* (*Ethmostigmus* + *Rhysida*)). "Cryptopidae", however, comprises a paraphyletic grade, with *Cryptops*, *Theatops* and *Scolopocryptops* each successively more closely allied to Scolopendridae.

Within Geophilomorpha, Mecistocephalidae (*Mecistocephalus*) is resolved as sister group to all other taxa (bs = 2), corresponding to Verhoeff's (1908 in Verhoeff, 1902-1925) division of Geophilomorpha into Placodesmata and Adesmata. Foddai & Minelli (2000) obtained this same basal split within Geophilomorpha after successive weighting of their morphological characters. Prunescu (1967) also considered Mecistocephalidae to be the most primitive geophilomorphs on the basis of their large, lobate dorsal and ventral accesory glands in the female genital system. The relationships of the non-mecistocephalid geophilomorphs are resolved with Himantariidae (*Pseudohimantarium*) as sister group to the remaining families. Within that large clade, Ballophilidae and Schendylidae are united, and together are sister to a clade that corresponds to Geophilidae *sensu* Attems (1929). Most relationships within this clade are weakly supported (most collapse with a single extra step added to the tree).

Molecular analysis. The parameter set that minimizes incongruence (Appendix 6.4) corresponds with an equal weight of all transformations (gaps, transversion/transitions, and morphology), and this is chosen as our best hypothesis. Twelve cladograms of minimal length (1661 steps) for the combined 18S and 28S rRNA data (Fig. 6.5) identify the orders Scutigeromorpha, Lithobiomorpha (bs = 5), Scolopendromorpha (bs = 2), and Geophilomorpha (bs = 7) as clades. As for the morphological data, the monophyly of Epimorpha *s.str*. is endorsed (bs = 5). The position of *Craterostigmus* is ambiguous, being resolved as either sister group to Lithobiomorpha or as sister group to all other Pleurostigmophora. The former position has been proposed by some morphologists (*e.g.*, Lewis, 1981;

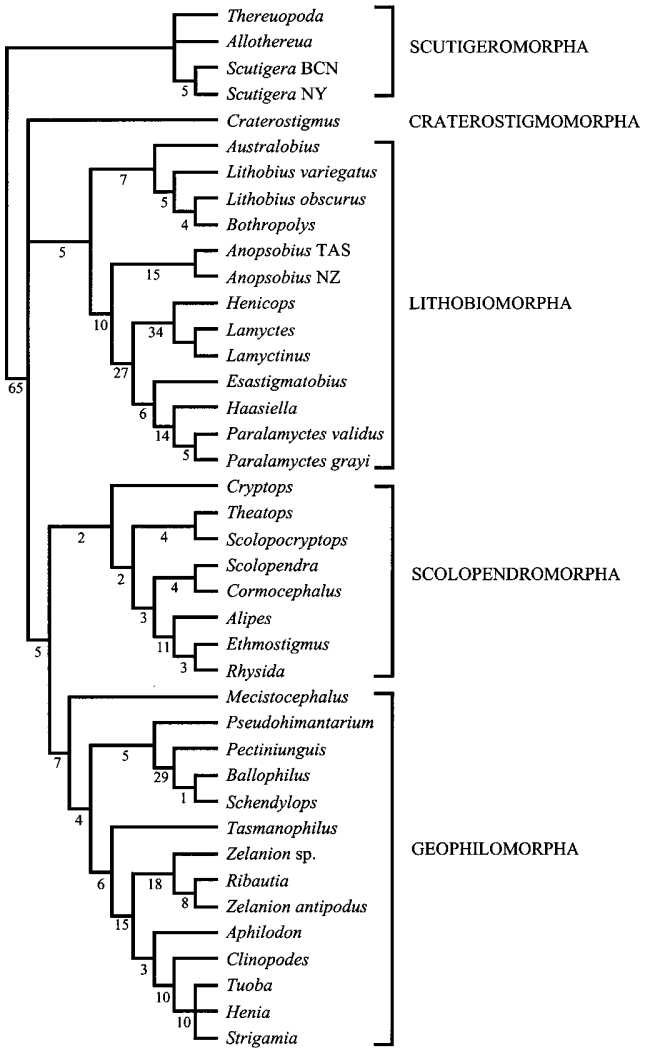

Fig. 6.5. Strict consensus of 12 shortest cladograms (length 1661) for Chilopoda based on combined 18S and 28S rRNA sequence data for parameter set 111.

Hoffman, 1982), whereas the latter resolution is novel. Neither of these resolutions is, however, supported by combination with morphological data (see "Combined analysis" below).

Higher-level relationships within Lithobiomorpha are highly congruent with the morphological hypothesis. Monophyly of Lithobiidae and Henicopidae are both supported by the molecular data, the latter being especially strong (bs = 10). The molecular data on their own resolve Ethopolyinae (*Bothropolys*) within a paraphyletic Lithobiinae (*i.e.,* grade including *Australobius* and *Lithobius* species). The higher-level systematics of Henicopidae are resolved with Anopsobiinae (bs = 15) as sister group to Henicopinae (bs = 27), as for the morphological data. Placement of Zygethobiini (*Esastigmatobius*) within Henicopini, more closely allied to *Paralamyctes* than to a well-defined clade composed of *Henicops*, *Lamyctes* and *Lamyctinus* (bs = 34), is a common feature of the molecular and morphological data partitions.

Relationships of the five genera of Scolopendridae are identical between the molecular and morphological cladograms. Both partitions further agree in resolving *Cryptops* as the most basal lineage in Scolopendromorpha, *i.e.,* with 'Cryptopidae' paraphyletic. The sequence data on their own differ from morphology in uniting the 'cryptopid' taxa *Theatops* and *Scolopocryptops* as a clade. This union of Plutoniuminae and Scolopocryptopinae has more support (bs = 4) than does the morphological evidence that splits them (bs = 1).

Molecular data are congruent with morphology in splitting Geophilomorpha into Placodesmata and Adesmata. The morphologically-defined ballophilid-schendylid clade is also strongly corroborated (bs = 29) by the molecular data, though its closest relative is Himantariidae (rather than the latter being the basal lineage within the non-mecistocephalid Geophilomorpha). A relationship between himantariids and ballophilids + schendylids was discussed by Foddai & Minelli (2000) based on morphological characters. As for the morphological dataset, the molecular data resolve the clade corresponding to Geophilidae *sensu* Attems (1929). The topology within this group differs substantially between the two data partitions, which may reflect the weak Bremer support for the clades resolved by the morphological data.

Combined analysis. Analyzed simultaneously, morphological and sequence data yield six equally-shortest cladograms (length 1893; Fig. 6.7) for parameter set 111 (ILD 0.019). The split between Scutigeromorpha and Pleurostigmophora is strongly supported (bs = 86; note that this value is the combined support for the branch leading to the Scutigeromorpha plus the value for the branch leading to the Pleurostigmophora). Ordinal and supraordinal relationships, in order of increasing support, are as follows: *Craterostigmus* + Epimorpha *s.str*. (bs = 5), Lithobiomorpha (bs = 7), Epimorpha *s.str*. (bs = 10), Scolopendromorpha (bs = 13), and Geophilomorpha (bs = 19).

Relationships within Scutigeromorpha conform to the morphological cladogram (*Scutigera* excluded from a clade composed of *Allothereua* and *Thereuopoda*). The combined cladogram is entirely congruent with the molecular cladogram with respect to phylogeny of Lithobiomorpha, the only difference being one less resolved node within Lithobiidae when the data are combined. Strongly supported clades within Lithobiomorpha (all having Bremer support values of at least 10) include Lithobiidae, Henicopidae, Anopsobiinae, Henicopinae, a *Henicops* + *Lamyctes* + *Lamyctinus* clade, and *Paralamyctes* (including *Haasiella*).

Resolution within Scolopendromorpha is as for the molecular data. The node splitting 'Cryptopidae' is strongly supported (bs = 10). Within Geophilomorpha, the topology is also entirely congruent with the molecular-only partition. The only differences concern the status of Schendylidae relative to Ballophilidae (being ambiguous for the combined data) and enhanced resolution within a clade composed of *Tuoba*, *Strigamia* and *Henia*. The best supported clades within Geophilomorpha are Ballophilidae + Schendylidae (bs = 31), Chilenophilidae (bs = 20), and a group that unites Geophilidae *sensu* Attems (1929) to the exclusion of *Tasmanophilus* (bs = 17).

SUMMARY

The best supported hypothesis of chilopod ordinal interrelationships is summarized in figure 6.6. Phylogeny of pleurostigmophoran orders is as

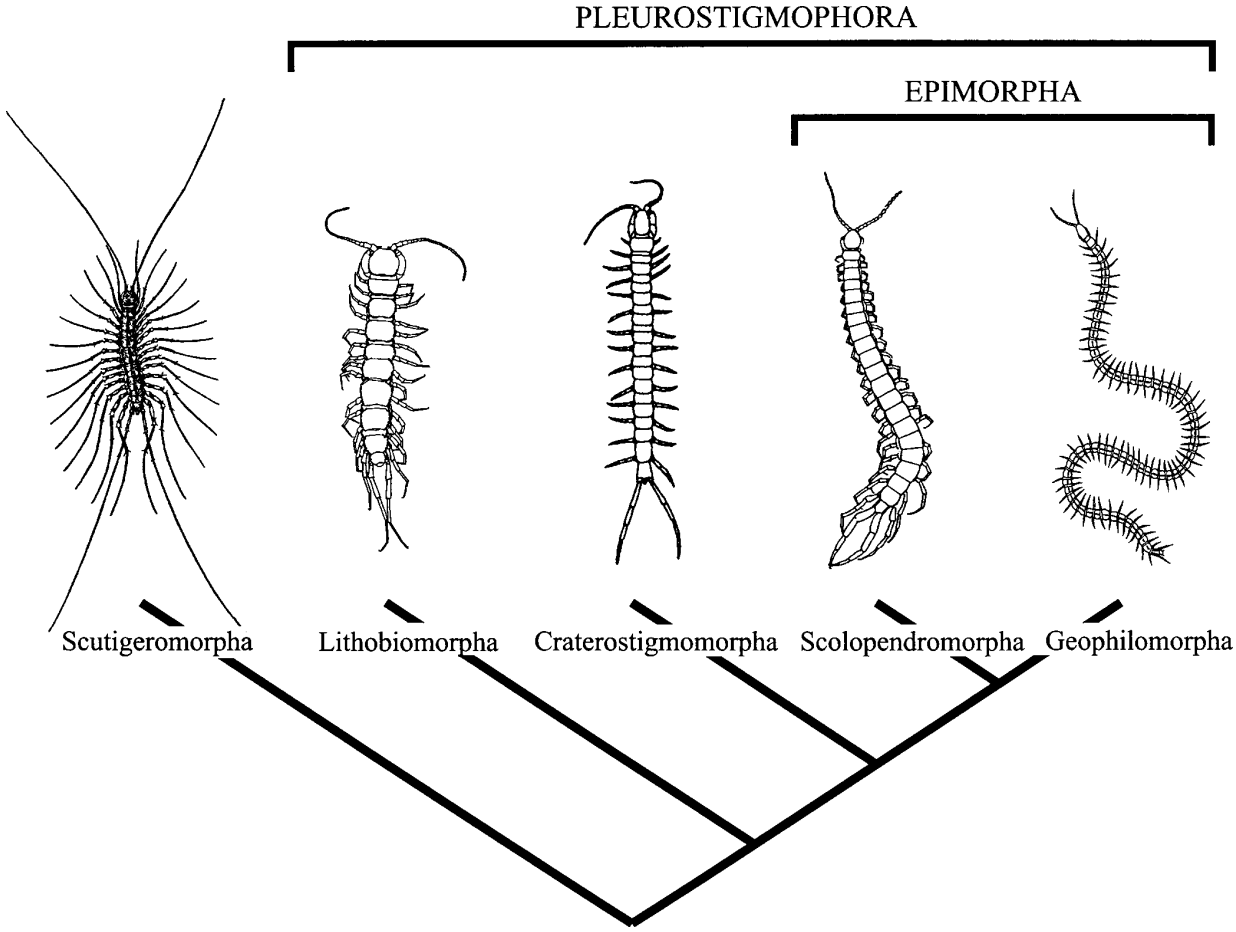

Fig. 6.6. Summary cladogram of relationships of chilopod orders (simplified from Fig. 6.7), showing exemplar organisms. Illustrations sourced as follows: Scutigeromorpha (Snodgrass, 1952); Lithobiomorpha and Scolopendromorpha (Eason, 1964); Craterostigmomorpha (Mesibov, 1986); and Geophilomorpha (Eisenbeis & Wichard, 1985).

defended by Prunescu (1965, 1996), Shinohara (1970), Dohle (1985), Shear & Bonamo (1988) and Borucki (1996) based on morphological evidence, and by Giribet *et al.* (1999) based on 18S and 28S rRNA sequence data.

Monophyly of the ordinal groups Scutigeromorpha, Lithobiomorpha, Scolopendromorpha and Geophilomorpha, as well as the union of the last two orders as Epimorpha *s.str.*, have independent support from morphological (Fig. 6.4) as well as molecular (Fig. 6.5) data analyses. Each of these groups is robust in a simultaneous analysis regime, having a Bremer support of at least 5 when all data are combined, and all are stable to parameter change (see discussion below). Probably the most contentious of these findings is the support for Lithobiomorpha. Previous authors (Dohle, 1985; Borucki, 1996) indicated that synapomorphies for Lithobiomorpha are few in number and more ambiguous than those defending the other chilopod orders, whereas Prunescu (1996) explicitly rejected the monophyly of Lithobiomorpha. Lithobiomorph paraphyly according to Prunescu involves Henicopidae as a basal grade within Pleurostigmophora, with the resolution (Anopsobiinae (Henicopinae + Lithobiidae) (*Craterostigmus* + Epimorpha *s.str.*))). The present study, which includes additional taxa within Henicopidae, agrees with our previous analysis (Edgecombe *et al.*, 1999) in supporting the monophyly of Henicopidae (=Anopsobiinae + Henicopinae) as sister group of Lithobiidae. This result is found with both data partitions (morphological and molecular) analysed separately as well as in combination. Morphological synapomorphies for Lithobiomorpha and Henicopidae are discussed by Edgecombe *et al.* (1999).

In order to add an additional test of the stability of the phylogenetic hypothesis here presented, we explored eight parameter sets with gap values of 1, 2, 4, and 8, and transversion/transition values of 1, 2, 4, and infinity (transversion parsimony) (specific parameter sets are 111, 121, 141, 110, 211, 221, 241, 210). The strict consensus of all the trees obtained under these eight parameter sets for all molecular and morphological data resolves all the orders as monophyletic, as are the supraordinal groups Pleurostigmophora, Epimorpha *s.str.* and the latter group united with *Craterostigmus*. Infraordinal groupings obtained under all of these parameter sets include Lithobiidae, Henicopidae, Anopsobiinae, Henicopinae, Scolopendridae, (Ballophilidae + Schendylidae), Geophilidae *sensu* Attems, 1929, and Chilenophilidae. We therefore regard these results as stable in that they are not parameter-dependent. Stability, in the sense applied here, should be a desirable property of phylogenetic hypotheses. Stability is also achieved in several internal nodes, especially within the Scolopendridae, in which all parameters and every single analysis performed retrieves the same topology (Figs. 6.4-7).

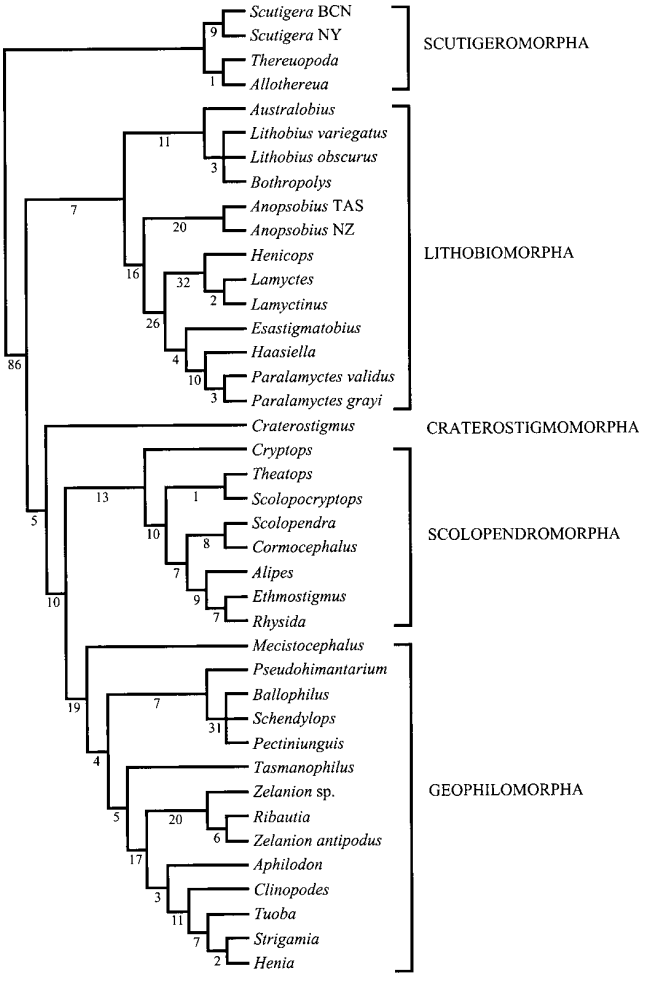

Fig. 6.7. Strict consensus of six shortest cladograms (length 1893) for Chilopoda based on combination of morphology and 18S and 28S rRNA sequences for parameter set 111.

The much-debated position of *Craterostigmus* (Manton, 1965; Shear & Bonamo, 1988; Dohle, 1990; Borucki, 1996) is one of the few areas of incongruence between the morphological and molecular data partitions as concerns high-level relationships. Simultaneous analyses (Fig. 6.6) favours the morphological resolution (Fig. 6.4) as sister to Epimorpha *s.str*. rather than as sister to Lithobiomorpha or to all other Pleurostigmorpha (Fig. 6.5).

The resolution of 'Cryptopidae' as paraphyletic (a basal grade of Scolopendromorpha) in morphological (Fig. 6.4), molecular (Fig. 6.5), and combined (Fig. 6.7) analyses conforms to a view developed by Schileyko (1996) and Schileyko & Pavlinov (1997) that this group is non-monophyletic.

A fundamental division of Geophilomorpha into Placodesmata and Adesmata *sensu* Verhoeff is a component of morphological (Fig. 6.4), molecular (Fig. 6.5), and combined (Fig. 6.7) analyses. This systematic scheme is endorsed by other morphologists (Prunescu, 1967; Foddai & Minelli, 2000; Minelli *et al*., 2000). Morphological features such as the acquisition of sternal pores and intraspecific variability in the number of trunk legs are optimised as synapomorphies of non-mecistocephalid geophilo-morphs, and correlate with an insertion in the 18S rRNA sequence of up to 300 bp documented by Edgecombe *et al*. (1999: Table 4).

The present study demonstrates that the phylogeny of Chilopoda is resolved with a high degree of congruence using morphological and 18S and 28S rRNA sequence data. More importantly, a high degree of congruence, resulting in a more robust and stable classification of the Chilopoda, is achieved by combining different sources of information. These results should suffice to encourage total evidence analyses in other myriapod groups.

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APPENDIX 6.1.

Morphological characters used for the phylogenetic analysis of the Chilopoda. Characters 1-117 are described by Edgecombe *et al.* (1999); comments have been introduced when coding changes or newly available data require discussion.

1. Egg tooth on embryonic cuticle of second maxilla: (0) absent; (1) present.
2. Segment addition in ontogeny: (0) hemianamorphic; (1) reduced hemianamorphosis (one anamorphic stage); (2) epimorphic.
3. Brood care: (0) absent; (1) female bends ventrally around eggs; (2) female bends dorsally around eggs.
4. Sclerotized bridge between antennae: (0) present; (1) absent.
5. Antenna composed of 14 articles: (0) absent; (1) present.
6. Flattened head capsule: (0) head capsule domed; (1) flattened, with head bent posterior to the clypeus.
7. Transverse cephalic suture: (0) absent; (1) present (frontal line or frontal sulcus); (2) present, divided near lateral margin into anterior and posterior branches (antennocellar suture of Crabill, 1960b). Edgecombe *et al.* (1999) coded an ecdysial complex of transverse and antenocellar sutures (state 2 above) as shared by *Craterostigmus* and Lithobiomorpha. Here we add state 1 to code for a frontal line in some Geophilomorpha.
8. Lateral margin of head shield interrupted at anterior limit of marginal ridge: (0) not interrupted; (1) interrupted.
9. Swinging tentorium (abduction of mandible achieved by movements of the anterior tentorial arms): (0) present; (1) absent.
10. Fenestrated plate composed of fused transverse tendons of mandibular, first maxillary and second maxillary segments: (0) absent; (1) present.
11. Lateral eye: (0) cluster of ocelli; (1) pseudofacetted; (2) absent; (3) single ocellus.
12. Four ocelli in rhomboid cluster: (0) absent (larger number of ocelli); (1) present.
13. Mandibular glands: (0) restricted to hypopharyngeal region; (1) extended back into trunk.
14. First maxillary gland: (0) present; (1) absent.
15. First vesicular gland: (0) absent; (1) present.
16. Second vesicular gland: (0) absent; (1) present.
17. Labrum divided into five sclerites (small median sclerite and pair of alae, each transversely divided into anterior and posterior halves): (0) side pieces of labrum undivided; (1) labral division present.
18. Transverse, fimbriate labral midpiece: (0) absent; (1) present.
19. Labrum divided into superior and inferior lamellae, with teeth on superior lamella directed anteriorly: (0) absent; (1) present.
20. Single transverse seta projecting medially from labral side piece: (0) absent; (1) present.
21. Side piece of labrum incised medially: (0) not incised; (1) incised.
22. Side pieces of labrum bearing numerous strong, medially directed teeth: (0) absent; (1) present.
23. Dentate lamellae on mandible: (0) present; (1) absent.
24. First maxilla with basal joint of telopodite fused on inner side to coxal projection: (0) telopodite distinctly demarcated, not fused; (1) inner part of telopodite fused to adjacent part of coxa.
25. Median suture on first maxillary coxosternite: (0) coxae medially coalesced, separated by median suture; (1) coxae fused, without median suture.
26. Sternite of first maxilla: (0) small, wedge-shaped or absent (coxosternum with median suture); (1) large, bell-shaped sternite.
27. Lappet on basal article of first maxillary telopod: (0) absent; (1) present. Edgecombe *et al.* (1999) coded for two pairs of lateral lobes (lappets) on the first maxilla. The character is now defined more precisely as the presence of a lappet on the basal article of the telopod.
28. Telopodite of first maxilla indistinctly segmented, only slightly longer than and resembling median coxal projections: (0) absent (telopodite segmented, longer than and differentiated from coxal projection); (1) present.
29. Plumose setae on coxal projection of first maxilla: (0) absent; (1) present.
30. Maxillary organ: (0) absent; (1) present.
31. Maxillary nephridia: (0) fused; (1) absent.
32. Coxae of second maxilla fused: (0) coxae separate; (1) coxae fused.
33. Metameric pores on second maxillary coxosternum: (0) minute opening of second maxillary gland medial to coxosternite; (1) enlarged opening of second maxillary gland ("metameric pore") incorporated in medial part of coxosternite; (2) metameric pore on lateral part of coxosternite. ORDERED.
34. Opening of coxal gland (metameric pore) on second maxilla surrounded by a thickened rim, opening towards the median side: (0) absent; (1) present.
35. Form of second maxillary telopod: (0) slender, leg-like, with elongate prefemur/femur; (1) short, stout.
36. Trochanter on second maxilla: (0) present; (1) absent.
37. Plumose setae on inner surface of tarsus of second maxillary telopod: (0) absent (simple setae); (1) plumose setae present.
38. Claw of second maxillary telopod pectinate: (0) non-pectinate; (1) pectinate. A new character (character 129) accommodates the absence/presence of a claw on the second maxilla. The present character, which codes for one variant in claw morphology, is coded only for those taxa that possess a

claw. The pectinate claw of ballophilids and schendylids is comparably developed in *Scolopocryptops*.
39. Maxillipede fang and poison gland: (0) absent; (1) present.
40. Pleurite of maxillipede segment arching over coxosternite: (0) absent (small pleurite); (1) pleurite arching over coxosternum, discontinuous medially; (2) pleurite arching over coxosternum, continuous ventromedially.
41. Maxillipede tooth plate (anteriorly projecting, serrate endite on coxosternite): (0) absent; (1) present.
42. Teeth on dental edge of maxillipede coxosternite reduced to small knobs: (0) large angular teeth; (1) small sclerotized teeth.
43. Porodont on maxillipede coxosternite: (0) absent; (1) present. Edgecombe *et al.* (1999) coded absence of a porodont in *Anopsobius* and Henicopinae. However, the "pseudoporodont" in certain henicopids (see Edgecombe *et al.* 2001: *Anopsobius*, *Lamyctes*, *Lamyctinus*) appears to be homologous, and we have recoded this character accordingly.
44. Coxosternite of maxillipede sclerotised in midline: (0) coxae separated medially, with sternite present in adult; (1) coxosternal plates meeting medially, with flexible hinge; (2) coxosternal plates meeting medially, hinge sclerotised and non-functional. ORDERED.
45. Coxosternite of maxillipede deeply embedded into cuticle above second trunk segment: (0) not embedded; (1) deeply embedded.
46. Tarsungulum on maxillipede: (0) separate tarsus and pretarsus; (1) tarsus and pretarsus fused.
47. Basal node on maxillipede tarsus/tarsungulum: (0) absent; (1) present.
48. First and fourth articles of maxillipede articulated: (0) absent; (1) present.
49. Course of coxopleural suture on maxillipede: (0) oblique to margin of head (converging posteriorly); (1) parallel to margin of head.
50. Tergite of maxillipede segment : (0) separate tergite; (1) separate tergite lacking, fused to next posterior segment.
51. Width of maxillipede tergite: (0) of similar width to head shield and T1; (1) much narrower than head shield and T1, with maxillipede pleurite strongly developed dorsally and coxopleural suture terminating dorsally.
52. Number of post-cephalic leg-bearing segments: (0) maxillipedes + 15; (1) maxillipedes + 21; (2) maxillipedes + 23; (3) >27.
53. "Special heterotergy" (alternating long and short tergites, with reversal of lengths between seventh and eighth walking leg-bearing segments): (0) absent; (1) present.
54. Tergite 1 overlaps head shield: (0) absent; (1) present.
55. Single large tergal plate over trunk segments 7-9: (0) separate tergites; (1) single tergite.
56. Paramedian sutures on tergum: (0) absent; (1) present.
57. Intercalary sclerites: (0) absent or weakly sclerotised; (1) small intercalary tergites (pretergites) and sternites; (2) strongly developed intercalary tergites and sternites.
58. Tergite margination: (0) absent or on last tergite only; (1) on most or all tergites.
59. Tergal spines associated with bristles, aligned longitudinally on midline: (0) absent; (1) present.
60. Pleuron filled with small pleurites: (0) absent; (1) present.
61. Sternal pore areas/sternal glands: (0) absent; (1) present. Edgecombe *et al.* (1999) coded for the presence of sternal pores within *Aphilodon* (see Verhoeff, 1937). Here we employ a more strict exemplar coding to recognise the absence of sternal pores in *A. weberi*.
62. Suture in cuticular ring around sternal pores: (0) absent; (1) present.
63. Definition of sternal pore area: (0) diffuse, outline of sternal pore area variably shaped; (1) outline of sternal pore area well-defined, circular or elongated.
64. First genital sternite of male divided longitudinally: (0) undivided; (1) divided.
65. Leg pentagonal in cross-section, with marginal spines on the angles: (0) absent; (1) present.
66. Proliferation of silk-spinning telopodal glands on posterior legs: (0) absent; (1) present. Previous coding of this character (Edgecombe *et al.*, 1999) extrapolated its presence in *Lithobius* and *Lamyctes* (Blower, 1952; Minelli, 1993) across Lithobiinae and Henicopini; however, telopodal glands are sparse in some other Lithobiomorpha (e.g., *Lithobius variegatus variegatus*: Zapparoli, 1997, Appendix 2). Coding is here restricted to those taxa that have a concentration of telopodal glands (e.g., Minelli, 1993: fig. 8).
67. Socketed spurs D/V, a/m/p in a whorl on distal extremities of podomeres: (0) absent; (1) present.
68. Tibial spurs (tooth-like process distally on most tibiae): (0) absent; (1) present.
69. Bipartite division of tarsi of anterior series of trunk legs: (0) absent; (1) present.
70. Tarsi divided into many joints: (0) tarsi undivided or bisegmented; (1) tarsus flagelliform, with many joints.
71. Tarsal spurs: (0) absent; (1) present.
72. Protarsi with pair of terminal spines: (0) absent; (1) present.
73. Tarsal pegs: (0) absent; (1) present.
74. Prefemur of anal leg with a single strong ventral spine: (0) absent; (1) present.
75. Anal leg coxopleural process: (0) absent; (1) present.
76. Coxopleurites on anal legs: (0) coxa and pleurites fused as short coxopleurite; (1) elongate coxopleurite.
77. Anal leg trochanter: (0) present; (1) minute or absent.
78. Anal leg prefemoral process: (0) absent; (1) present.
79. Anal leg lacking claw: (0) claw present; (1) claw absent.
80. Longitudinal muscles: (0) united sternal and lateral longitudinal muscles; (1) separate sternal and lateral longitudinal muscles, with separate segmental tendons.
81. Position of tracheae/spiracles: (0) pleural; (1) dorsal opening on tergum, with special tracheal lungs.
82. Anisostigmophory: (0) absent (spiracles present on all trunk segments from second pedigerous segment); (1) present (spiracles associated with long tergites only).
83. Longitudinal and transverse connections between segmental tracheal branches: (0) absent; (1) present. For details of tracheae (characters 83, 86, 87 and 90), Edgecombe *et al.* (1999) extrapolated interpretations by Hilken (1997, 1998) as ordinal-level groundpatterns. Here we restrict these codings to genera that have been examined in detail (Manton, 1965; Pereira & Coscaron, 1976; Lewis, 1981; Hilken, 1997, 1998), and add *Pseudohimantarium* based on *Himantarium* (Hilken, 1998). *Cryptops* and *Cormocephalus* are coded based on the presence of a transverse connection (summarized by Lewis, 1981).

84. Spiracle on first pedigerous trunk segment: (0) present; (1) absent.
85. Ten spiracles: (0) absent; (1) present (spiracles on trunk segments 3, 5, 7, 8, 10, 12, 14, 16, 18, 20).
86. Chiasmata: (0) absent; (1) present.
87. Spiracle muscles: (0) absent; (1) present.
88. Spiracle with atrium divided by flapped valves: (0) valves absent; (1) valves present.
89. Cribriform spiracles with humps: (0) absent; (1) present.
90. Taenidia: (0) helically arranged; (1) absent, tracheae strengthened by network of chitin fibres.
91. Haemocyanin: (0) absent; (1) present. The respiratory protein haemocyanin has been considered an autapomorphy for Scutigeromorpha (Hilken, 1998). Structurally similar haemocyanin has since been reported in Diplopoda (Spirostreptida: *Spirostreptus*) (Jaenicke *et al*., 1999).
92. Foregut with differentiated gizzard; inner wall of gizzard with spinose processes: (0) absent; (1) present.
93. Asymmetry of oviducts: (0) left and right ducts symmetrical; (1) left duct rudimentary or absent.
94. Accessory ventral glands of ovary: (0) present; (1) absent.
95. Unpaired median testis: (0) symmetrically paired testis; (1) one testis minute, undifferentiated; (2) unpaired testis.
96. Testes differentiated into macrotestis with ampulla and microtestis: (0) present; (1) absent.
97. Lateral testicular vesicles linked by a central, posteriorly extended deferens duct: (0) absent; (1) present.
98. Testicular vesicles spindle shaped: (0) absent; (1) present.
99. Number of testicular vesicles: (0) one pair; (1) two or more pairs.
100. Asymmetry of ejaculatory ducts: (0) left and right ducts symmetrically developed; (1) left duct rudimentary or absent.
101. Female gonopod used to manipulate single eggs: (0) absent; (1) present.
102. Female gonopod segmentation: (0) three articles and claw, with basal articles of gonopod pair separated; (1) two articles, the proximal article of each gonopod pair partly joined, the distal article a spine; (2) single segment.
103. Female gonopod with basal article bearing spines (macrosetae) and terminal article with a broad claw: (0) absent; (1) present.
104. Claw of female gonopod fused with the apical article: (0) claw separate; (1) claw fused.
105. Segmentation of male gonopod on first genital segment: (0) four segments; (1) two segments; (2) single segment, rudimentary.
106. Male gonopod on second genital segment: (0) present; (1) absent.
107. Anal organs: (0) absent; (1) present through ontogeny; (2) present only in juveniles.
108. Coxal organs: (0) absent; (1) present.
109. Serial distribution of coxal organs: (0) on last four pairs of legs; (1) on last two pairs of legs; (2) on last pair of legs only.
110. Arrangement of coxal pores: (0) few pores in linear row; (1) numerous small pores scattered over coxopleure or large pore field; (2) one or two large pores opening to expanded coxal organ; (3) rosette of coxal organs opening into pit, without external pores.
111. Spermatophore web: (0) absent; (1) present.
112. Bean-shaped spermatophore with tough, multi-layered wall: (0) absent; (1) present.
113. Ventral invagination in spermatophore: (0) absent; (1) present.
114. Sperm dimorphism: (0) absent; (1) microsperm and macrosperm present.
115. Spiral ridge on nucleus: (0) absent; (1) present.
116. Centriole of sperm with elongate, tongue-shaped capitulum and rim around acetabulum formed by posterior end of nucleus: (0) absent (connecting piece with sessile acetabulum); (1) present.
117. Tömösváry organs: (0) present; (1) absent.

NEW CHARACTERS

118. Peripatoid and foetoid stadia guarded by mother: (0) absent; (1) present. Character 3 identifies brooding of the eggs and larvae in *Craterostigmus* and Epimorpha *s.str*. The latter group shares more detailed similarity (Dohle, 1985) in that the first two postembryonic stages (peripatoid and foetoid) are inactive, whereas the 12-legged larval stage of *Craterostigmus* is active.
119. Shaft organ on antennal scape: (0) absent; (1) present. The *Schaftorgan* (Fuhrmann, 1922) opening on the basal antennal segment (scape) is distinctive for Scutigeromorpha (see Lewis, 1981: figs. 80, 89).
120. Median furrow on head shield: (0) absent; (1) deep and continuous between anterior margin of head and transverse suture (Edgecombe, 2001; Edgecombe *et al*., 2001; character 8).
121. Clypeal area: (0) absent; (1) present. Clypeal areas are clearly delimited areas on the clypeus in which reticulation is much subdued or absent and pigmentation is suppressed. Among taxa coded here, clypeal areas are present in *Ribautia*, *Tuoba*, *Zelanion* and *Tasmanophilus*. *Schendylops pampeanus* was described and illustrated with a clypeal area (Pereira & Coscarón, 1976).
122. Labrum fused to clypeus: (0) unfused; (1) fused. Among geophilomorphs in this study, fusion of the labrum and clypeus is coded by Foddai & Minelli (2000: character 17) in *Aphilodon*, *Ballophilus*, *Schendylops* and *Pectiniunguis*.
123. Mandible composed of two sclerites (lamina condylifera only sclerite differentiated from flank of mandible: (0) absent; (1) present. Borucki (1996: 203) considered that the presence of only two sclerites in the mandible could potentially be an autapomorphy for Lithobiomorpha. All lithobiomorphs have the lamina condylifera (*sensu* Crabill, 1960a: fig. 1) as the only sclerite differentiated on the mandible. *Craterostigmus* shares this two-part structure of the mandible (Borucki, 1996, fig. 11).
124. Type of aciculae/pectinate lamellae on mandible: (0) comb-like; (1) pinnules or barbs splaying from both sides of acicula; (2) simple. "Aciculae" (Chamberlin, 1912) in Lithobiomorpha refers to the "sickle-shaped setae" (Attems, 1928), "sickle bristles" (Crabill, 1960a) or "Mandibelborsten" (Borucki, 1996) of the pectinate lamella of the mandible. Edgecombe *et al*. (2001: character 22) documented variation in acicular morphology in lithobiomorphs (including states 1 and 2 above). *Craterostigmus* has two rows of short barbs along each acicula. Homology with the bipinnulate condition in Lithobiomorpha is probable, since some lithobiids and henicopids like-

wise have the usually blunt pinnules modified as barbs. The aciculae of Lithobiomorpha and *Craterostigmus* are homologised with the pectinate lamellae of Epimorpha *s.str*. (Fig. 6.3D-F) and Scutigeromorpha (Fig. 6.3C), which have a comb-like structure (state 0).

125. Fringe of branching bristles on mandible: (0) extends along entire gnathal margin, skirting aciculae; (1) terminates at aciculae (see Edgecombe *et al*., 2001: character 23 for Lithobiomorpha). In some non-lithobiomorphs *(e.g*., Cryptopidae, Scutigeromorpha), the homologous fringe of bristles can be identified (Fig. 6.3D), and the character coded. A homologous fringe cannot be specified in Geophilomorpha.

126. Ventral bristles in fringe on mandible with a wide base: (0) absent; (1) present (Edgecombe *et al*. 2001: character 24). In most henicopids and in lithobiids, the branching bristles on the ventral half of the mandibular fringe have narrow bases. In Anopsobiinae (*Anopsobius*) and in Zygethobiini (*Esastigmatobius*), these bristles are flattened and widened at their bases. These basal parts lack pectinations, whereas the bristles are branching along their lengths in other lithobiomorphs.

127. Differentiation of branching bristles on mandible: (0) gradual change in branching structure of bristles along fringe; (1) abrupt transition between simple bristles and plumose bristles (Edgecombe *et al*., 2001: character 25).

128. Number of teeth in dentate lamella of mandible: (0) three; (1) four/five; (2) undivided dentate lamella. Number of mandibular teeth is generally conservative within orders (three teeth in Scutigeromorpha, Craterostigmomorpha and in Schendylidae within Geophilomorpha; four and five teeth alternating on opposite sides of the mandible in Lithobiomorpha and Scolopendromorpha). Himantariids and ballophilids have an undivided dentate lamella.

129. Termination of telopod of second maxilla: (0) simple (no claw or seta); (1) claw; (2) seta. Scutigeromorpha differ from other chilopods in the lack of a second maxillary claw. Foddai & Minelli (2000: character 28) grouped dignathodontids and aphilodontids based on a "modified claw" of the second maxillary telopod. A possible homology is expressed more precisely by characterizing the termination of the telopod as a seta (state 2) rather than a claw (state 1). A setose termination is present in *Aphilodon* (long, slender seta) and *Henia* (small seta arising from a tubercle).

130. *Dornenkamm* on maxillipede tarsus: (0) absent; (1) present. Borucki (1996: fig. 68) documented a dense band of slender spines (*Dornenkamm*) along the inner edge of the maxillipede tarsus in Scutigeromorpha. These are not present in other chilopods.

131. Poison calyx displaced posteriorly: (0) poison calyx contained within maxillipede telopodite; (1) poison gland extends back into trunk. As was first observed by Verhoeff (1937), Dignathodontidae (*Henia*) and Aphilodontidae share a posteriorly displaced poison gland (Crabill in Lewis, 1981). Codings for most geophilomorph genera are given by Foddai & Minelli (2000: character 42).

132. Chitinous lines: (0) absent; (1) present. Many geophilomorphs have a pair of lines of chitinous thickening on the ventral surface of the maxillipede coxosternite (Foddai & Minelli, 2000: character 31). These lines run from the posterior border of the coxosternite towards the condyle at the base of the trochanterofemur.

133. Carpophagus pit/fossa on anterior margin of sternites, carpophagus peg on posterior margin: (0) absent; (1) present. Coding is restricted to the carpophagus structures of geophilids (*i.e.,* fossae on the posterior part of the sternites in some himantariids are not coded as homologous). These structures are present in *Clinopodes poseidonis* (Lewis, 1963) and *Tuoba sydneyensis* (Jones, 1998), and are weakly developed in *Tasmanophilus*.

134. Intraspecific variability in number of leg pairs: (0) constant number of leg pairs; (1) variable number of leg pairs. Mecistocephalids are the only geophilomorphs with fixed specific leg counts (Foddai & Minelli, 2000: character 57). In this respect they resemble all non-geophilomorph chilopods.

135. Antennal and leg regeneration: (0) present; (1) absent. Minelli *et al.* (2000) summarized regeneration data for chilopods. Legs are regenerated after autotomy in Scutigeromorpha and Lithobiomorpha; the anal leg is shed in a number of scolopendromorphs, but other trunk legs are not known to be regenerated. Minelli *et al.* (2000) dismissed supposed instances of regeneration in Geophilomorpha, and concluded that neither antennae nor legs were shed. We have used evidence for autotomy as a proxy for other evidence for regeneration, *i.e.,* scoring all geophilomorphs as without leg/antennal regeneration, scoring all scutigeromorphs and lithobiomorphs for autotomy.

136. Female gonopod on first genital segment: (0) absent; (1) present. Edgecombe *et al.* (1999) coded for variation in the gonopods of Chilopoda, scoring *Craterostigmus* and Scolopendromorpha as inapplicable for these characters (101-105) because gonopods are absent in both sexes. This absence is now added as a character.

APPENDIX 6.2.

Taxonomic categories and molecular data used, with GenBank accession codes. Molecular data are extracted from studies of Giribet *et al.* (1999) and Edgecombe *et al.* (1999, 2001).

Order Scutigeromorpha		
Family Scutigeridae		
Scutigera coleoptrata BCN	AF000772	AF000779
Scutigera coleoptrata NY	AF173238	AF173269
Thereuopoda clunifera	AF173239	AF173270
Allothereua maculata	AF173240	AF173271
Order Lithobiomorpha		
Family Lithobiidae		
Lithobius variegatus rubriceps	AF000773	AF000780
Lithobius obscurus	AF334271	AF334292
Australobius scabrior	AF173241	AF173272
Bothropolys multidentatus	AF334272	AF334293
Family Henicopidae		
Anopsobius n. sp.	AF173247	AF173273
Anopsobius neozelanicus	AF173248	AF173274
Henicops maculatus	AF173245	AF173275
Lamyctes emarginatus	AF173244	AF173276
Lamyctinus coeculus	AF334275	AF334296
Esastigmatobius japonicus	AF334291	
Paralamyctes (*Thingathinga*) *grayi*	AF173242	AF173277
Paralamyctes (*T.*) *validus*	AF173243	AF173278
Paralamyctes (*Haasiella*) *trailli*	AF173246	AF173279

Order Craterostigmomorpha		
Family Craterostigmidae		
Craterostigmus tasmanianus	AF000774	AF000781
Order Scolopendromorpha		
'Family Cryptopidae'		
Cryptops trisulcatus	AF000775	AF000783
Theatops erythrocephala	AF000776	AF000784
Scolopocryptops nigridus	AF173253	AF173284
Family Scolopendridae		
Scolopendra cingulata	U29493	AF000782
Cormocephalus monteithi	AF173249	AF173280
Alipes crotalus	AF173251	AF173283
Ethmostigmus rubripes	AF173250	AF173281
Rhysida nuda	AF173252	AF173282
Order Geophilomorpha		
Family Mecistocephalidae		
Mecistocephalus sp.	AF173254	AF173285
Family Himantariidae		
Pseudohimantarium mediterraneum	AF000778	AF000786
Family Ballophilidae		
Ballophilus australiae	AF173258	AF173291
Family Schendylidae		
Pectiniunguis argentinensis	AF173256	AF173293
Schendylops pampeanus	AF173257	AF173292
Family Geophilidae		
Clinopodes cf. *poseidonis*	AF000777	AF000785
Tasmanophilus sp.	AF173259	AF173286
Tuoba sydneyensis	AF173260	
Family Aphilodontidae		
Aphilodon weberi	AF173264	AF173289
Family Linotaeniidae		
Strigamia maritima	AF173265	AF173290
Family Dignathodontidae		
Henia (*Chaetechelyne*) *vesuviana*	AF173255	
Family Chilenophilidae		
Zelanion antipodus	AF173261	
Zelanion sp.	AF173262	AF173288
Ribautia n. sp.	AF173263	AF173287

APPENDIX 6.3.

Morphological character codings. -: inapplicability; ?: missing data. Acronyms in parentheses refer to the epithets used in the cladograms (Figs. 6.4-7).

Scutigera coleoptrata [Barcelona, Spain] (BCN)
1000000-11 1-01110000 0000000001 0000000-10 0-000000?0 0010100000 0—0100011 0110000000 1100000001 1000000—0 110-2000?? 0001100010 0000???001 000001

Scutigera coleoptrata [New York, USA] (NY)
1000000-11 1-01110000 0000000001 0000000-10 0-000000?0 0010100000 0—0100011 0110000000 1100000001 1000000—0 110-2000?? 0001100010 0000???001 000001

Thereuopoda clunifera
?000000-11 1-01110000 0000000001 0000000-10 0-000000?0 0010100010 0—0100011 0010000000 11?00??00? 1????????? 110-2000?? 000???0010 0000???001 000001

Allothereua maculata
?000000-11 1-????0000 0000000001 0000000-10 0-000000?0 0010100010 0—0100011 0010000000 11?00??00? 1???000—0 110-2000?? ??????0?10 0000???001 000001

Lithobius variegatus rubriceps
1000012100 0010000001 1000000010 0100011010 0011010?0 0010000100 0—0011010 0000000000 0101000000 0000210—0 1011212100 ?001110000 0011000110 000001

Lithobius obscurus
1000012100 0010000001 1000000010 0100011010 0011010?0 0010000100 0—0011010 0000000000 0101000000 0000210—0 1011212100 1001110000 0011000110 000001

Australobius scabrior
?000012100 00????0001 1000000010 0100011010 0011010?0 0010000100 0—0011010 0000000000 01?10??00? 0????????? 1011212100 ??????0000 0011000110 000001

Bothropolys multidentatus
?000012000 00????0001 1000000010 0100011010 0011010?0 0010000100 0—0011010 0000000000 01?10??00? 0????????? 1011212100 ??????0000 0011000110 000001

Anopsobius n.sp. (TAS)
?000012000 2-????0001 0000000000 0100011012 0011010?0 0010000100 0—0000100 0001100000 01?10??00? 0????????? 1010011110 ??????0?01 0011110110 000001

Anopsobius neozelanicus (NZ)
?000012000 2-????0001 0000000000 0100011012 0011010?0 0010000100 0—0000100 0001100000 01?10??00? 0?00100—0 1010011110 ??????0?01 0011110110 000001

Esastigmatobius japonicus
?000012000 3-????0001 0001010000 0100011012 0101010?0 0010000100 0—00001?0 0000000000 01?00??00? 0?00210—0 1010011100 ??????0001 0011010110 000001

Henicops maculatus
?000012000 3-????0001 0001000000 0100011012 0001010?0 0010000100 0—1000110 0000000000 01?00??00? 0????????? 1010011100 ??????0000 0011001110 000001

Lamyctes emarginatus
?000012000 3-????0001 0001000000 0100011012 0011010?0 0010000100 0—1000100 0000000000 01?00??00? 0????????? 1010011100 ??????0000 0011001110 000001

Lamyctinus coeculus
?000012000 2-????0001 0001000000 0100011012 0011010?0 0010000100 0—?000100 0000000000 01?00??00? 0????????? 1010??1100 ??????0000 0011001110 000001

Paralamyctes (*Thingathinga*) *grayi*
?000012000 3-????0001 0001010000 0100011012 0101010?0 0010000100 0—0000110 0000000000 01?00??00? 00???????? 1010011100 ??????0?01 0012000110 000001

Paralamyctes (*Thingathinga*) *validus*
?000012000 3-????0001 0001010000 0100011012 0101010?0 0010000100 0—0000110 0000000000 01?00??00? 0????????? 1010011100 ??????0?01 0012000110 000001

Paralamyctes (*Haasiella*) *trailli*
?000012000 3-????0001 0001010000 0100011012 0001010?0 0010000100 0—0000100 0000000000 01?00??00? 0????????? 1010011100 ??????0?01 0011000110 000001

Craterostigmus tasmanianus
?110012-00 3-10010000 0000000000 1100010011 1-02110000 0010001000 0—0000000 1000010001 0101000000 0000211010

——1112? ??????0000 0011???010 000000
Scolopendra cingulata
1210010-00 0110010000 0000000000 1100010011 1-02110101 0110011100 0—0000010 1000111101 0111001100 0111211111 ——10121 1111101100 0000000110 000000
Cormocephalus monteithi
1210010-00 0110010000 0000000000 1100010011 1-02110101 0111011100 0—0000010 0000111101 011100?10? 0???211111 ——10121 111???1?00 0000000110 000000
Ethmostigmus rubripes
?210010-00 0110010000 0000000000 1100010011 1-02110101 0111011100 0—0000010 1000111001 01?11??01? 0111211111 ——10121 ?111101?00 0000000110 000000
Rhysida nuda
?2?0010-00 01????0000 0000000000 1100010011 1-02110101 0111011100 0—0000010 1000111001 01?11??01? 0???21111? ——10121 ?11???1?00 0000000110 000000
Alipes crotalus
?2?0010-00 01????0000 0000000000 1100010011 1-02110101 0111011100 0—0000010 1000111001 01?10??01? 0????????? ——10121 ??????1?00 0000000110 000000
Cryptops trisulcatus
1210010-00 2-10010000 0000000000 1100010011 0-02110101 0110012000 0—0000000 0000011001 0111001000 0111211111 ——10121 ?101101100 0000000110 000000
Theatops erythocephala
?2?0010-00 2-????0000 0000000000 1100010011 1-02110101 0110012000 0—0000000 1000111001 01?10??00? 0?01211111 ——10121 ??????1?00 0000000110 000000
Scolopocryptops nigridius
?2?0010000 2-????0000 0000000000 1100010111 0-02110101 0210011100 0—0000000 1000111001 01?10??00? 01???????? ——10121 ??????1?00 0000000110 000000
Mecistocephalus sp.
?2?1111-10 2-10001000 0010000100 1120010011 0-021101?0 1300012001 0—0000000 0000010011 00?10??00? 0?00211100 020?111121 ??????1100 0000———10 000011
Pseudohimantarium mediterraneum mediterraneum
?2?1111-10 2-????0000 010000?000 1110110011 0-02110100 0300012001 1110000000 0000010011 0011010000 0?00211100 020?110121 ???0111?00 0000—210 010111
Clinopodes cf. *poseidonis*
1221110-10 2-10000100 00101?0000 1110110011 0-02110100 0300012001 1000000000 0000010001 001101?00? 0?00211100 020?111123 1000111100 0000———10 011111
Tuoba sydneyensis
?2?1110-10 2-????0100 00101?1000 1110110011 0-02111100 0300012001 1000000000 0000010001 00?10??00? 0????????? 020?111123 ??????1?00 1000———10 011111
Tasmanophilus sp.
?221111-10 2-????0100 00101?1000 1110110011 0-02111100 0300012001 0—0000000 0000010001 00?10??00? 0????????? 020?111121 ??????1?00 1000———10 011111
Ribautia sp.
?2?1110-10 2-????0100 00101?0000 1110110011 0-02111110 0300012001 1000000000 0000010001 00?10??00? 0????????? 020?111121 ??????1?00 1000———10 010111
Zelanion sp.
?221111-10 2-10000000 0010101000 1111110011 0-02111110 0300012001 0—0000000 0000010001 00?10??00? 0?00?????? 020?111121 ???01?1?00 1000———10 000111
Zelanion antipodus
?2?1111-10 2-10000000 0010101000 1111110011 0-02111110 0300012001 0—0000000 0000010001 00?10??00? 0?00?????? 020?111121 ???01?1?00 1000———10 000111
Aphilodon weberi
?2?1110-10 2-????0000 00101?0000 1110110-11 0-02110100 0300002001 0-00000000 0000010001 00?10??00? 0????????? 020?111121 ??????1?00 0100———20 100111
Strigamia maritima
?221110-10 2-10000010 00101?0000 1110110011 0-02111100 0300002001 1000000000 0000010001 001101000? 0000211100 020?111121 ???01?1100 0000———10 000111
Henia (*Chaetechelyne*) *vesuviana*
?2?1110-10 2-????001? ??101?0000 1110110-11 0-02110100 0300002001 1110000000 00000100(01)1 00?101?00? 0????????? 020?111121 ???01?1?00 0000———20 110111
Ballophilus australiae
?2?1110-10 2-????0000 00001?0000 1110110111 0-02110100 0300002001 1000000000 0000010011 00?10??00? 0????????? 020?111122 ??????1?00 0100—210 000111
Schendylops pampeanus
?2?1110-10 2-????0000 01001?0000 1110110111 0-02110100 0300012001 1000000000 0000010011 001101?00? 0????????? 020?110122 ??????1?00 1100—010 000111
Pectiniunguis argentinensis
?2?1110-10 2-????0000 01001?0000 1110110111 0-02110100 0300012001 1000000000 0000010011 001101?00? 0????????? 020?110122 ??????1?00 1100—010 000111

APPENDIX 6.4.

Tree lengths for independent partitions: 18S (18S rRNA), 28S (28S rRNA), MOR (morphology), MOL (molecular: 18S + 28S rRNA), TOT (combined analysis MOR + MOL) at different parameter sets (PAR) and ILDs for combined analyses of all data (ILD). ILD number in italics reflects minimum incongruence among datasets. PAR indicates ratio gap-cost: transversion-cost: transition-cost (i.e. 110 indicates a gap: transversion ratio of 1, and a transversion: transition ratio of infinity [gap cost = 1; transversion cost = 1; transition cost = 0]; 121 indicates a gap: transversion ratio of 1, and a transversion: transition ratio of 2 [gap cost = 2; transversion cost = 2; transition cost = 1]).

PAR	18S	28S	MOR	MOL	TOT	ILD
111	1395	250	212	1661	1893	0.0190
121	2039	373	424	2435	2900	0.0221
141	3281	595	848	3932	4870	0.0300
110	621	110	212	744	980	0.0378