A phylogenetic analysis of the arachnid orders based on morphological characters

JEFFREY W. SHULTZ*

Department of Entomology, University of Maryland, College Park, MD 20742, USA

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Morphological evidence for resolving relationships among arachnid orders was surveyed and assembled in a matrix comprising 59 euchelicerate genera (41 extant, 18 fossil) and 202 binary and unordered multistate characters. Parsimony analysis of extant genera recovered a monophyletic Arachnida with the topology (Palpigradi (Acaromorpha (Tetrapulmonata (Haplocnemata, Stomothecata nom. nov.))), with Acaromorpha containing Ricinulei and Acari, Tetrapulmonata containing Araneae and Pedipalpi (Amblypygi, Uropygi), Haplocnemata (Pseudoscorpiones, Solifugae) and Stomothecata (Scorpiones, Opiliones). However, nodal support and results from exploratory implied weights analysis indicated that relationships among the five clades were effectively unresolved. Analysis of extant and fossil genera recovered a clade, Pantetrapulmonata nom nov., with the topology (Trigonotarbida (Araneae (Haptopoda (Pedipalpi)))). Arachnida was recovered as monophyletic with the internal relationships (Stomothecata (Palpigradi, Acaromorpha (Haplocnemata, Pantetrapulmonata))). Nodal support and exploratory implied weights indicated that relationships among these five clades were effectively unresolved. Thus, some interordinal relationships were strongly and/or consistently supported by morphology, but arachnid phylogeny is unresolved at its deepest levels. Alternative hypotheses proposed in the recent literature were evaluated by constraining analyses to recover hypothesized clades, an exercise that often resulted in the collapse of otherwise well-supported clades. These results suggest that attempts to resolve specific nodes based on individual characters, lists of similarities, evolutionary scenarios, etc., are problematic, as they ignore broader impacts on homoplasy and analytical effects on non-target nodes. © 2007 The Linnean Society of London, Zoological Journal of the Linnean Society, 2007, 150, 221–265.

ADDITIONAL KEYWORDS: Arachnida – fossil – morphology – phylogeny – systematics

INTRODUCTION

Despite an ever-increasing reliance on molecular sequence data for phylogeny reconstruction and evolutionary inference, morphological characters remain an important source of phylogenetic signal (both alone and in combination with molecular data) and are essential for reconstructing and exploring patterns in organismal evolution. Construction and maintenance of digital databases of structural information are essential if morphology and the results of morphological analyses are to remain useful. In the present work, I define, homologize and code morphological and other non-molecular characters that vary among orders and major intraordinal groups of arachnids. The results are summarized in a taxon-by-character matrix, and the phylogenetic signal within the matrix is explored using parsimony-based analyses. This research clarifies the strengths and weaknesses of current understanding of arachnid phylogeny and highlights several aspects of phylogenetic practice that may impede progress in the evolutionary morphology and phylogeny of Arachnida.

Several interordinal relationships within Arachnida can be considered well established. The monophyly of Arachnida itself is well supported by morphological characters, although some palaeontologists continue a long tradition of placing scorpions outside arachnids with Eurypterida (e.g. Dunlop & Braddy, 2001). Thelyphonida and Schizomida include the tailed whipscorpions and form an undisputed monophyletic group, Uropygi s.l. (= Camarostomata). Recent work indicates that Amblypygi, or whipspiders, is the sister group to Uropygi s.l. (Shear et al., 1987; Shultz, 1990, 1999; Giribet et al., 2002; but see Alberti, 2005) and together form the clade Pedipalpi. Earlier studies

*E-mail: jshultz@umd.edu
tended to favour a sister-group relationship between Amblypygi and Araneae, the spiders (e.g. Platnick & Gertsch, 1976; Weygoldt & Paulus, 1979), but this was based on a few similarities that do not appear to be synapomorphic (Shultz, 1990, 1999; present study). Araneae and Pedipalpi form a well-supported clade, with the fossil order Trigonotarbida being its likely sister group. Pseudoscorpiones and Solifugae, or sun-spiders, are often united within a clade, Haplocnemata (= Apatellata) (Weygoldt & Paulus, 1979; Van der Hammen, 1989; Shultz, 1990; Wheeler & Hayashi, 1998; Giribet et al., 2002; but see Alberti & Peretti, 2002).

Some interordinal relationships are often recovered in phylogenetic analyses but are supported by relatively few characters. These include Dromopoda (Opiliones + Scorpiones + Haplocnemata), Megoperculata (= Palpigradi + Tetrapulmonata) and Acaromorpha (Ricinulei + Acari) (Shultz, 1990; Wheeler & Hayashi, 1998; Giribet et al., 2002). The status of Acaromorpha is further complicated by substantial morphological divergence within and between the two principal lineages of Acari (i.e. Anactinotrichida and Acariformes) (Lindquist, 1984), which has led some workers to suggest that Acari is diphyletic (Van der Hammen, 1989).

Relationships among Palpigradi, Tetrapulmonata, Acaromorpha, Haplocnemata, Opiliones and Scorpiones are effectively unresolved, as is the placement of several fossil taxa (e.g. Haptopoda).

Results from the present analysis (Fig. 1) essentially affirm this characterization of our current understanding of arachnid phylogeny based on morphology and other non-molecular characters but also offer new proposals and evaluate alternative interpretations that have emerged in the last 17 years, i.e. since my previous attempt to resolve arachnid phylogeny (Shultz, 1990). Specifically, parsimony-based analyses corroborate the monophyly of Arachnida as well as Uropygi, Pedipalpi, Haplocnemata and Acaromorpha. The data also support more recent proposals, including the monophyly of Opiliones and Scorpiones (= Stomothecata nom. nov.) (Shultz, 2000) and Pantetrapulmonata nom. nov. with an internal structure anticipated by Dunlop (1999, 2002c); i.e. (Trigonotarbida (Araneae (Haptopoda, Pedipalpi))). However, relationships among Palpigradi, Acaromorpha, Haplocnemata, Stomothecata and Pantetrapulmonata are effectively unresolved. These results indicate that morphology offers important phylogenetic information, but it is not yet sufficient to resolve relationships at the deepest levels within Arachnida.

**METHODS**

**TERMINAL TAXA**

The study was based on 59 euchelicerate genera (41 extant, 18 fossil), with most represented by one species (detailed below), coded for 202 binary and unordered multistate characters (Table 1, Appendix).

*Xiphosura* (horseshoe crabs): The xiphosurans are an ancient (Silurian–Recent) aquatic lineage with its greatest diversity occurring in the fossil record. It comprises two main groups, Synziphosurida (Silurian–Devonian: ~ ten genera) and Xiphosurida (Carboniferous–Recent: ~14 genera). Synziphosurids are probably paraphyletic and retain plesiomorphic features, such as a ten-segmented opisthosoma with three segmented metasoma (Anderson & Selden, 1997). They were represented in the matrix by *Weinbergina opitzi*, one of the few fossil xiphosurans with preserved appendages (Moore, Briggs & Bartels, 2005), and a more typically preserved synziphosurid, *Limuloidea limuloides*. Extant xiphosurans (three genera, four spp.) were represented by the intensively studied Atlantic horseshoe crab, *Limulus polyphemus*, and an Asian horseshoe crab, *Carcinoscorpius rotundicauda*, with supplemental information drawn from another Asian species, *Tachypleus tridentatus*.

*Eurypterida* (sea scorpions): A diverse (> 60 genera) aquatic group of fossil euchelicerates that ranged from...
Table 1. Data matrix comprising 59 euchelicerata genera and 202 binary and unordered multistate characters. Fossil taxa are indicated by an asterisk. Ambiguity codes: A = [345], B = [12], C = [02], D = [34], E = [01]

| Weinbergina*  | 00010-0?11 | 0?????0?? | 0?111-???? | 0????-?? | 0????-?? | 0????0000 | 0????-?? | 00-0?1201 | 0????-?? | 0????-?? |
| Limuloides*   | 00010-0?11 | 0????11?? | 0?111-???? | 0????-?? | 0????-?? | 0????0000 | 0????-?? | 00-0?1201 | 0????-?? | 0????-?? |
| Euproops*     | 00010-0?11 | 0????11?? | 0?111-???? | 0????-?? | 0????-?? | 0????0000 | 0????-?? | 00-0?1201 | 0????-?? | 0????-?? |
| Limulus       | 10010-0?11 | 0000-0?10 | 0000-0000 | 00-0?10 | 00000000 | 10?710100 | 0100010021 |
| Tachypeus     | 10010-0?11 | 0000-0?10 | 0000-0000 | 00-0?10 | 00000000 | 10?710100 | 0100010021 |
| Baltoeurypterus* | 0000-0?11 | 0000-0?10 | 0000-0000 | 00-0?10 | 00000000 | 10?710100 | 0100010021 |
| Styylonurus*  | 0000-0?11 | 0000-0?10 | 0000-0000 | 00-0?10 | 00000000 | 10?710100 | 0100010021 |
| Chasmataspis* | 0000-0?11 | 0000-0?10 | 0000-0000 | 00-0?10 | 00000000 | 10?710100 | 0100010021 |
| Diplaspis*    | 0000-0?11 | 0000-0?10 | 0000-0000 | 00-0?10 | 00000000 | 10?710100 | 0100010021 |
| Prokoenienia  | 0000110000 | 00000000 | 00000000 | 00-0?10 | 00000000 | 1000000001 | 1000000002 |
| Eukenenia     | 0000110000 | 00000000 | 00000000 | 00-0?10 | 00000000 | 1000000001 | 1000000002 |
| Plesiosiro*   | 00110-0?00 | 00000000 | 00000000 | 00-0?10 | 00000000 | 1000000001 | 1000000002 |

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the Ordovician to the Permian (Tollerton, 1989). Phylogenetic relationships among the eurypterids have not been rigorously addressed (but see Beall & Labandeira, 1990). However, members of Stylonuroidea appear to be plesiomorphic in retaining relatively unspecialized legs and were represented by *Stylonurus* (e.g. Clarke & Ruedemann, 1912; Waterston, 1979). In the remaining eurypterids, the last leg is paddle-like (Tollerton, 1989). The non-stylonuroid eurypterids were represented in the matrix by the well-preserved and well-studied *Baltoeurypterus tetragonophthalmus*, especially as described by Selden (1981).

**Chasmataspidida**: Members of this fossil aquatic group (Ordovician–Devonian: six genera) have a four-segmented mesosoma and a nine-segmented metasoma (Dunlop, Poschmann & Anderson, 2001; Dunlop, Anderson & Braddy, 2004; Dunlop, 2002a). Three genera were included: *Chasmataspis* from the monotypic family Chasmataspidae as well as *Diploaspis* and *Octoberaspis* from Diploaspidae.

**Haptopoda**: This is a fossil terrestrial group (Carboniferous) containing one known species, *Plesiosiro madeleyi*. The known specimens have been re-examined by Dunlop (1999).

**Palpigradi**: The extant palpigrades (two families, six genera, ~50 spp.) (Harvey, 2002) are a poorly studied group of small-bodied terrestrial (some semi-aquatic) arachnids. The two most well-studied genera, *Eukoenenia* (Eukoeneniidae), especially *E. mirabilis*, and *Prokoenenia* (Prokoeneniidae), especially *P. wheeleri*, were included in the matrix. The one known fossil species, *Paleokoenenia mordax*, is relatively recent (Pliocene?) and, to the extent known, is fairly similar to extant palpigrades (Rowland & Sissom, 1980). It was not included in the analysis.

**Trigonotarbida**: This is a fossil terrestrial order (Upper Silurian to Lower Permian; ~ten families, ~50 spp.). The genera coded here were drawn from two Lower Devonian Lagerstatten: Gilboarachne from the Gilboa Formation (New York) (Shear et al., 1987) and

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**Table 1. Continued**

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Palaeocharinus from the Rhynie Chert (Scotland) (Dunlop, 1994; Fayers, Dunlop & Trewin, 2004).

Araneae (spiders): This is a very large order (110 families, ~3600 genera, ~39 000 extant spp.) (Platnick, 2005) represented here by one genus from each of the three principal extant lineages (Platnick & Gertsch, 1976; Coddington & Levi, 1991; Coddington, 2005): Liphistius (Mesothele), Aphonopelma (Mygalomorphae) and Hypochilus (Araneomorphae). The sample is small with respect to known diversity, but the basal phylogeny and relevant groundplan states of the order are well established and states derived from the represented taxa are consistent with them.

Amblypygi (whispiders): This is a small extant terrestrial order (five families, 17 genera, 136 spp.) (Harvey, 2002) and was represented in the matrix by two fairly well-studied genera, Charinus and Phrynus. Charinus retains several features that appear to be plesiomorphic for the order (e.g. adult pedal pulvilli, coxal glands associated with leg 3, eversible vesicles). Weygoldt (1996) has examined the phylogeny of the order and has provided an important summary of morphology and general biology (Weygoldt, 2000).

Thelyphonida or Uropygi s.s. (whipscorpions, vinegaroons): Extant whipscorpions (16 genera, 106 spp.) (Harvey, 2002) were represented here by one well-studied species, Mastigoproctus giganteus, although additional information was drawn from Typopeltis and Thelyphonus. The morphology of the group is highly conserved; there have been no modern studies of intraordinal phylogeny. A controversial fossil species from the late Carboniferous, Proschizomus (Dunlop & Horrocks, 1995/1996), was also included but less well-preserved Carboniferous forms were not.

Schizomida: This small order (two extant families, ~34 genera, ~200 spp.) (Harvey, 2002) is widely regarded as the sister group of Thelyphonida. The taxon sample included one representative from each extant family, Protoschizomus (Protoschizomidae) and Stenochrus (Hubbardiidae), especially S. portoricensis. There are three recent (Pliocene?) fossil species, all from the same locality; these were not included here.

Ricinulei: The extant ricinuleids (three genera, 55 spp.) (Harvey, 2002) were represented by two genera, Cryptocellus and Ricinoides. Detailed studies of gross cuticular anatomy and post-embryonic development are available for a representative of each genus (Cryptocellus: Pittard & Mitchell, 1972; Ricinoides: Legg, 1976) and some information on internal anatomy is available for Ricinoides (Millot, 1945), and this has been extrapolated to Cryptocellus in the matrix. There are two basic fossil types (Selden, 1992), one resembling modern taxa and another with a unique opisthosoma that superficially resembles the closed elytra of a beetle (i.e. curculioids). Two fossils from the former group were included, Terpsicroton and Poliochera, as they are reasonably well preserved and show important characters (e.g. two pairs of eyes or evidence of opisthosomal diplosegmentation) not expressed in extant forms. No curculioid ricinuleids were included, as they appear to offer no additional information relevant to resolving ordinal relationships.

Opilioacariformes (= Opilioacarida, Notostigmata): The opilioacariform mites (nine genera, 20 spp.) (Harvey, 2002) are generally regarded as plesiomorphic Acari and are fairly conserved in their morphology. The group was represented by two species, Neocarus texanus and Siamacarus withi. N. texanus has a typical opilioacariform morphology, and its external anatomy has been particularly well studied (e.g. Van der Hammen, 1989; Klompen, 2000). S. withi differs from most other opilioacariforms in having trichobothria and three rather than two pairs of lateral eyes (the latter also in Paracaracars), features that are potentially significant for assessing ordinal relationships. Some information on internal morphology of Opilioacarus was taken from With (1904) and extrapolated to Neocaracars and Siamacars.

Parasitiformes: This large group of mites comprises three clades, Holothryrida, Ixodida (ticks) and Mesostigmata (= Gamasida). Holothryrida (three families, five genera, <30 spp.) (Walter & Proctor, 1999) was represented here by two species, Australothyridus occlulus and Allothyridus constrictus. Ixodids (three families, 22 genera, ~860 spp.) (Kierans & Robbins, 1999) were represented by Amblyomma and Argas, and mesostigmatids (~70 families, ~10 000 spp.) were represented by Glypholaspis confusa.

Acariformes (= Actinotrichida): This is a very large, diverse group of mites that includes the Endostigmata, Sarcoptiformes and Prostigmata. Endostigmata is an apparently paraphyletic assemblage of ~ten families. A morphologically generalized species, Alycus rosus (Bimickaeliidae), was included here, with character states extracted largely from Van der Hammen (1989). Sarcoptiformes (~200 families) is effectively synonymous with Oribatida, with Astigmata being a large, derived ‘oribatid’ clade (Norton, 1998; Maraun et al., 2004). The group was represented by an early divergent, plesiomorphic genus, Palaeacarus (Palaeosomata), and a more derived and well-studied genus, Archozetes (especially A. longisetus and A. magnus). The Prostigmata (~120 families, ~7000 spp.) (Walter & Proctor, 1999) was represented by two genera, Allothrombium and Microacarus.
**Solifugae** (= Solpugida) (sun spiders): The order is small (~1000 spp.), but the absence of modern phylogenetic treatments precludes meaningful estimates of genera and families (Harvey, 2002). The taxon sample included two genera, one from the New World, Eremoscosta, and one from the Old World, Galeodes.

**Opiliones** (harvestmen): Extant harvestmen (~25 families, ~500 genera, ~6000 spp.) are divided into two suborders, Cyphopthalmi and Phalangida. Cyphopthalmids were represented here by *Chileogovea oedipus* (Petallidae), which is currently under study by the author, and *Cyphophthamus duricorius* (Sironidae), which is probably the most well-studied member of the suborder (e.g. Janczyk, 1956). Phalangida includes three major groups, Laniatores, Eupnoi and Dysnoi, but there is disagreement as to whether Dysnoi is the sister group to Laniatores or to Eupnoi (Shultz & Regier, 2001; Giribet et al., 2002). Laniatores was represented by *Sclerobunus* and *Gonyleptes* and Eupnoi by *Leiobunum* and Caddo.

**Scorpiones** (scorpions): The extant scorpions (16 families, 155 genera, 1279 spp.) (Pet et al., 2000) were represented by three taxa, *Centruroides vittatus* (Buthidae), *Hadrurus arizonensis* (Iuridae) and *Heterometrus spinifer* (Scorpionidae). Buthidae is widely regarded as the sister group to other extant lineages, and similarities among the represented terminals are likely to be ground plan features of extant scorpions generally. The morphology of fossil scorpions is substantially more diverse (Kjellesvig-Waering, 1986), but their phylogenetic relationships are unclear (but see Jeram, 1998). The fossil taxa used in this study (*Proscorpius*, *Stoermeroscorpio*, *Paleoscorpius*, *Prearcturus*) were chosen for quality of preservation and/or presence of a phylogenetically significant constellation of characters.

**Character coding**

Most character states were determined from direct observation, the primary literature and authoritative reviews. In some cases, states were assigned to terminals based on observations from related species, as noted in the Appendix. In the matrix, state ‘?’ indicates that the character is inapplicable because the taxon lacks a more general character. For example, if a taxon lacks eyes, then special features of the eyes (number, position, retinal configuration, etc.) are inapplicable to that taxon. A ‘?’ indicates that the state is unknown or uncertain. An entry with multiple states (e.g. 0/1, 3/4/5) should be treated as an ambiguity code, not a polymorphism; it indicates that two or more interpretations of homology are applicable and that assignment was established analytically by character concordance. Although ‘?’ and ‘0/1' are analytically identical when applied to binary characters, they provide information about the empirical status of the character state in specific taxa. Characters are cited throughout the text as italicized numbers in parentheses and are discussed in the Appendix.

**Phylogenetic analysis**

Phylogenetic analysis of the full data matrix was performed using the program Tree Tree Analysis using New Technologies (TNT), ver. 1 (Goloboff, Farris & Nixon, 2000) using ‘traditional’ search based on 1000 replicates using TBR branch swapping. Results were compared to those obtaining using the ratchet algorithm (Nixon, 1999) to determine any difference due to analytical approach. Nodal support for the minimal-length topology was evaluated by bootstrap (Felsenstein, 1985) and Bremer support (Bremer, 1994). Bootstrap analysis was conducted in TNT and based on 1000 pseudoreplicates each analysed by ten random-addition replicates using TBR branch swapping. A nexus file containing the resulting 1000 trees was imported into PAUP* ver. 10 (Swofford, 2002) to obtain bootstrap frequencies. Bremer support was determined in TNT by constraining specific nodes in the minimal-length topology and then determining the shortest tree that did not recover the specified clade. The difference in length between the unconstrained and constrained minimal-length trees is the Bremer support. The effect of homoplasy on results was explored by conducting implied weights analysis (Goloboff, 1993) in TNT. Six analyses were conducted, each with constant of concavity (k) set to a different integer value of 1–6, where 1 is weighted most severely against homoplasious characters. Each implied weights analysis was conducted using ‘traditional’ search based on 1000 replicates using TBR branch swapping. The same procedures were used in analysing a matrix that included only extant taxa. However, characters rendered uninformative by removal of fossil taxa (i.e. 49, 98, 99, 100, 113, 114, 125, 161) were excluded prior to analysis.
Comparisons of alternative hypotheses

Phylogenetic hypotheses proposed in the recent literature were also evaluated, including those that attempted to resolve arachnid phylogeny completely (Fig. 2), their hypothesized subclades (Fig. 3) and hypotheses that proposed only specific nodes (Figs. 3, 4). The fully resolved topologies of Weygoldt & Paulus (1979), Van der Hammen (1989), Shultz (1990), Wheeler & Hayashi (1998) and Giribet et al. (2002) were compared with the optimal topology using the Templeton test (Templeton, 1983) as implemented in PAUP*®. Internal relationships of multisampled orders were constrained to match those of the optimal topology, unless the original authors explicitly favoured an alternative. Node-specific hypotheses were evaluated by determining the frequency with which the node was recovered in bootstrap analysis. They were also evaluated by constraining parsimony analysis in TNT to recover the shortest tree containing each specific node and then assessing the effect on relative tree length and overall resolution, taking note of effects on otherwise stable or well-supported clades. The entire matrix was used to assess the two cases where node-specific hypotheses involved fossil taxa (Fig. 4).

Results

Extant taxa

Unweighted analysis of extant taxa produced two minimal-length trees (length 383, CI 0.57) (Fig. 5A) with conflicts limited to relationships within Pseudoscorpiones. Multiply sampled orders were recovered as monophyletic with high nodal support as measured by bootstrap percentage (BP > 80), except Acari (BP 30). There were few well-supported interordinal groups, except Uropygi (BP 100), Pedipalpi (BP 100), Tetrapulmonata (BP 93) and Arachnida/Xiphosura (BP 100). All other interordinal relationships were recovered with BP less than 60.

Results from implied weights analysis (IWA) indicated a significant effect of homoplasy on resolution of the deepest interordinal relationships in Arachnida, although Stomothecata, Haplocnemata, Acaromorpha, Cryptognomae, Pantetrarapulmonata, Tetrapulmonata, Schizotarsata, Pedipalpi and Uropygi were recovered under all values of k. IWA with k = 1 (7 trees, best score = 56.75) recovered Megoperculata and Micrura, with Micrura being the sister group to Haplocnemata. Stomothecata was not recovered in the strict consensus (Fig. 6B). With k = 2 (3 trees, best score = 42.43), IWA recovered the topology shown in Fig. 6C, with Palpigradi being the sister group to all other arachnids. The strict consensus topologies reconstructed using k = 3–6 were identical to those obtained with k = 2 (k = 3, 3 trees, best score = 34.19; k = 4, 3 trees, best score = 28.74; k = 5, 3 trees, best score = 24.83; k = 6, 3 trees, best score = 21.88).

Comparisons of alternative hypotheses

The hypothesis of Weygoldt & Paulus (1979) (Fig. 2) was 398 steps (15 steps longer than the unconstrained minimal-length tree), Van der Hammen (1989) was 400 steps (17 steps longer), Shultz (1990) was 399 steps (six steps longer), Wheeler & Hayashi (1998) was 391 steps (eight steps longer) and Giribet et al. (2002) was 394 steps (11 steps longer). Templeton tests conducted at the 0.05 significance level rejected the hypothesis of no difference between the optimal topology and those of Weygoldt & Paulus (P = 0.0002), Van der Hammen (P = 0.0011), Wheeler & Hayashi (P = 0.0018) and Giribet et al. (P = 0.0343). The Shultz topology was not significantly different (P = 0.1444) from the optimal topology.
Figure 2. Fully resolved phylogenetic hypotheses of extant euchelicerate groups proposed in the recent literature. Note the similarity in the topologies of the parsimony-based analyses by Shultz (1990), Wheeler & Hayashi (1998) and Giribet et al. (2002). The Giribet et al. topology is based on neontological data (morphology and molecules) and the original ‘ROOT’ may be an artefact from use of the highly divergent pycnogonids as an outgroup.
Figure 3. Consensus trees produced by parsimony analysis of neontological data constrained to produce relationships proposed in the recent literature. The constrained (target) node is indicated by a black dot and the taxa encompassed by the constraint are enclosed in a box. Numbers below each tree represent the number of minimal-length constrained trees, length of minimal-length trees, difference in the length of the unconstrained minimal-length tree and the constrained minimal-length tree, and percentage unconstrained bootstrap trees in which the target node was recovered, respectively. These trees indicate the effect on branch length imposed by specific hypotheses and impact of constraining target nodes on non-target nodes.
Results from analyses of node-specific hypotheses are summarized in Figures 3, 4. In most cases, proposed relationships were recovered in fewer than 5% of bootstrap pseudoreplicates. The notable exceptions were Rostrosomata (25%), Cryptognomae (24%) and Megoperculata (28%), and the strict-consensus constrained minimal-length tree for each was only one step longer than the unconstrained optimal tree. In most cases, constrained topologies did not add many steps; most were less than five steps longer and none was greater than 14 steps longer than the unconstrained minimal-length tree. It is noteworthy, however, that even constrained nodes that impose relatively few extra steps sometimes supported improbable relationships or eliminated clades that were well supported or stable in the unconstrained analysis. Specific examples and their implications are discussed below.

DISCUSSION

RECENT ISSUES IN ARACHNID PHYLOGENY

Available morphological evidence consistently resolves some interordinal relationships and fails to resolve others (Fig. 1). Continued progress depends on the ability of arachnologists to discover new characters and to assess the evidence critically. While reviewing the recent arachnological literature, several aspects of phylogenetic practice emerged that seemed counterproductive to both the perception and the actual rate of progress toward resolving arachnid phylogeny. Some of these are summarized here, with specific examples given in the remainder of the Discussion and in the Appendix.

There is a tendency to portray arachnid ordinal phylogeny as more poorly resolved and contentious than is actually the case (Coddington et al., 2004). Phylogenetic hypotheses generated during different historical periods and using differing standards of evidence are often cited as examples of current disagreement (e.g. Selden, 1993; Dunlop, 1996; Selden & Dunlop, 1998; Wheeler & Hayashi, 1998). In fact, recent parsimony-based analyses of morphology have tended to converge on topologies with internal structures congruent with those found here (e.g. Shultz, 1990; Wheeler & Hayashi, 1998; Giribet et al., 2002) (Fig. 2). Arachnid phylogeny is not fully resolved, especially at its deepest levels (Fig. 1), but this does not mean that all aspects of arachnid phylogeny are controversial or poorly supported by the available evidence.

Matrices are sometimes constructed by uncritical ‘recycling’ of erroneous or problematic characters based on diverse, secondary sources (Jenner, 2001). Conclusions derived from mixtures of valid, invalid, speculative and redundant characters are sometimes portrayed as the phylogenetic signal provided by morphology. Data recycling can perpetuate errors (see 13, 20, 39, 52, 136, 140, 144, 152, 169, 171–174), legitimize speculations (see 13, 32, 63, 95) or create duplicate or non-independent characters (see 13, 30, 70, 77, 172). The ‘lateral organ’ is a notable example. Yoshikura (1975) equated the embryonic/early postembryonic ‘lateral organs’ of Amblypygi, Thelyphonida and Solifugae with the dissimilar ‘lateral organ’ of Xiphosura but failed to note the very similar Claripède organ of Acariformes (see 173, 174). This coding was recycled by Wheeler & Hayashi (1998) and then by Giribet et al. (2002). Error is probably inevitable when assembling a large matrix from morphology, including the one presented here, but this can be minimized by making original observations and by consulting primary sources.

Some workers advocate weighting characters a priori on the basis of structural or functional complexity (e.g. Kraus, 1998; Dunlop & Braddy, 2001) and dismiss phylogenetic conclusions derived from equal-weights parsimony. In short, these workers criticize parsimony for emphasizing data quantity over data quality. This criticism ignores the intense debate in systematic biology that eventually led to widespread adoption of
Figure 5. Results from analysis of neontological data. A, minimal-length topology. Numbers below internodes are bootstrap percentages/Bremer support values. B, parsimony tree produced by implied weights with $k = 1$. C, parsimony tree produced by implied weights with $k = 2$. Parsimony trees produced by implied weights with $k = 3$–6 are identical to topology A. For B and C, relationships within terminal clades are the same as those shown in A.
Figure 6. Results from analysis of the full data matrix. A, minimal-length topology. Numbers below internodes are bootstrap percentages/Bremer support values. B, parsimony tree produced by implied weights with $k = 1$. C, parsimony tree produced by implied weights with $k = 2$. Parsimony trees produced by implied weights with $k = 3–6$ are identical to topology C. For B and C, relationships within terminal clades are the same as those shown in A.

parsimony and, instead, advocates a return to the speculative and subjective approaches of the late 19th and early 20th century that once threatened the scientific legitimacy of the discipline (Bowler, 1996). Furthermore, it misrepresents the properties of parsimony-based analyses. Specifically, characters with functional significance are readily encompassed by parsimony analyses and, in fact, characters derived from locomotor systems (e.g. 46–94) have played an important role in developing current ideas about arachnid phylogeny (e.g. Shultz, 1989, 1991). In addition, ‘complex characters’ can be viewed as composites of several characters, such that morphological complexity is effectively weighted by the number of independent ‘subcharacters’ it contains. For example, the ‘sucking stomach’ once considered a synapomorphy of Labellata (= Araneae + Amblypygi; Fig. 3) is coded here as a composite of three characters (199–201). The Labellata hypothesis was not corroborated in the present analysis (Figs 1, 3–5) and, in fact, was highly disfavoured (Fig. 3), but this result cannot be dismissed as a failure to acknowledge the complexity of the character.

Some workers support specific (target) clades with one or more similarities without exploring the impact on overall homoplasy or relationships among non-target clades. Each character offers its own phylogenetic hypothesis, which may or may not be consistent with relationships implied by other characters. It is exceedingly rare for all characters to be perfectly compatible in the phylogenetic hypotheses they support, and criteria such as parsimony have been developed to discover those hypotheses that minimize the conflicting phylogenetic signals of different characters. Even though character conflict (homoplasy) is a virtually inescapable phenomenon in comparative biology, it is not uncommon for workers to discover one or more characters and to promote their phylogenetic implications over alternative hypotheses, even those that otherwise appear to be well supported. This approach may have value in highlighting new data and perspectives but accomplishes this by promoting the erroneous impression that all aspects of arachnid phylogeny are so tenuous that a single character can falsify even well-supported hypotheses. Several examples of this approach have appeared in the recent arachnological literature.

For example, Alberti & Peretti (2002) argued that aflagellate spermatozoa (163) are a compelling synapomorphy for a Solifugae + Acari clade and dismissed some of the characters that support Solifugae + Pseudoscorpiones as having ‘debatable value.’ Yet, their proposal rejects two hypotheses that are consistently recovered in recent phylogenetic analyses: that is, Haplocnemata (= Solifugae + Pseudoscorpiones) and Acaromorpha (= Acari + Rinocnemata) (Figs 1, 2). Rejection of Haplocnemata would require its presumed synapomorphies to be reinterpreted as homoplasies, including features of the chelicerae (18, 19, 20), preoral chamber (13, 32), legs (12, 48) and respiratory system (126). The same reason applies to Acaromorpha and its synapomorphies. It is noteworthy that a Solifugae + Acari clade was recovered in the present analysis in fewer than 5% of bootstrap pseudoreplicates and that analyses constrained to recover this clade were five steps longer than the minimal-length tree and favoured a problematic clade uniting Rinocnemata and Pseudoscorpiones (Fig. 3).

In another example, Dunlop (1996) proposed a close relationship between Trigonotarbidae and Rinocnemata based on two-segmented chelicerae (18), prosoma–opisthosoma coupling mechanism (96), diplotergites (100, 101) and longitudinally divided opisthosomal tergites (115). However, phylogenetic analyses constrained to recover this relationship required eight additional steps, eliminated support for Acari and necessarily rejected Acaromorpha and forced its synapomorphies to be reinterpreted as homoplasies. Alberti (2005) proposed an interesting hypothesis for the evolution of male gonads in tetrapulmonates (153) but chose to accept Labellata (= Araneae + Amblypygi) in developing his argument over the much more well-supported Pedipalpi (= Amblypygi + Uropygi) (Shultz, 1999), a phylogenetic reconfiguration that was recovered here in fewer than 5% of bootstrap pseudoreplicates, increased tree length by a minimum of 14 steps and resulted in the collapse of Stomothecata and Haplocnemata (Fig. 3). Many other examples can be cited.

Promoting or defending a specific phylogenetic hypothesis via lists of compatible synapomorphies is a common but problematic approach. By restricting attention to the states of specific characters at one or two target nodes, one can easily overlook the unintended impact of the hypothesis on phylogenetic signal elsewhere and its effect on non-target clades. A node supported by a long list of synapomorphies may seem convincing taken in isolation but may become less acceptable when its full phylogenetic implications are explored.

**SUMMARY OF INTERORDINAL ARACHNID CLADES RECOVERED IN THIS ANALYSIS**

*Arachnida* Lamarck, 1801

Analyses consistently recovered Arachnida as a monophyletic group with high bootstrap support (Figs 1, 4, 5). Possible synapomorphies include the loss of the carapacial pleural doublure (9), cardiac lobe (10), pedal gnathobases (52) and moveable endites (53) and the gain of aerial respiration (120) and an anteriorly or anteroventrally directed mouth (185). Some traditional synapomorphies, such as slit sensilla (142) and
fluid feeding (184), may have appeared later in arachnid evolution, but this can only be decided once the internal phylogeny of Arachnida has been determined.

Some workers regard many proposed arachnid synapomorphies as adaptations to terrestrial life and thereby link the hypothesis of arachnid monophyly to the hypothesis of a single ancestral aquatic-to-terrestrial transition and arachnid polyphyly to multiple transitions (e.g. Selden & Jeram, 1989; Dunlop, 1997; Dunlop & Webster, 1999; Dunlop & Braddy, 2001). This line of reasoning, the existence of apparently aquatic scorpions in the fossil record (Kjellesvig-Waering, 1986; Jeram, 1998) and the inference that terrestrialization occurred late in scorpion evolution, these workers conclude that character states supporting arachnid monophyly are actually convergences and do not necessarily support arachnid monophyly.

However, this approach to assessing phylogenetic hypotheses is founded on overly simplistic assumptions, such as the ability of the investigator to discriminate unerringly between characters that exist exclusively in aquatic organisms (including fossils) from those that occur exclusively in terrestrial organisms. There also appears to be an assumption that homoplasy can be generated through parallelism (i.e. multiple aquatic-to-terrestrial events) but not through terrestrial-to-aquatic reversals. Furthermore, an assumed dichotomy between exclusively aquatic and terrestrial life histories in ancestral arachnids is simplistic, as illustrated by the amphibious life cycles of basal vertebrates and pterygote hexapods. In fact, these examples demonstrate that there is no necessary inconsistency in basing a hypothesis of arachnid monophyly on the derived terrestrial features of an amphibious ancestor whose descendants then completed terrestrialization once or several times independently or even returned to a fully aquatic existence. Workers who link the frequency and direction of aquatic–terrestrial transitions to the assessment of arachnid phylogeny do so by endowing themselves with substantially greater insight than seems prudent, by ignoring the huge gaps in our understanding of early arachnid evolution, and by denying to arachnids the evolutionary complexity known to exist in other groups.

Several palaeontologists have been particularly active during the past decade in proposing new characters with the stated goal of removing Scorpiones from Arachnida and erecting a Scorpiones + Eurypterida clade (Braddy & Dunlop, 1997; Dunlop & Braddy, 1997; Dunlop, 1998; Braddy et al., 1999; Dunlop & Webster, 1999). Dunlop & Braddy (2001) recently summarized this evidence and conducted a parsimony-based analysis of Xiphosura, Eurypterida, Scorpiones, Opiliones and Tetrapulmonata (but not Haplocnemata, Acaromorpha or Palpigradi) using 33 morphological characters. Their analysis produced a topology congruent with those generated here (Figs 1, 5, 6), including recovery of Stomothecata (= Scorpiones + Opiliones). However, they rejected this result as a product of ‘empirical cladistics’ because it gives the same weight to prosomal characters that support arachnid monophyly and to selected opisthosomal characters that support their favoured Eurypterida + Scorpiones clade, namely, a five-segmented metasoma (116), suppression of opisthosomal tergite 1 (95), loss of lamellate respiratory organs on the postgenital somite (122), Kiemenplatten (125), loss of respiratory lamellae on the genital segment (121) and a ‘non-staining’ exocuticle (but see Grainge & Pearson, 1966 for evidence of this in Opiliones; see Appendix for comments on the other characters).

A Eurypterida + Scorpiones clade was not favoured in the present analysis (Fig. 6); the strict consensus of minimal-length trees constrained to recover this clade (Fig. 4) is nine steps longer than the tree recovered by analysis without this constraint. It is also noteworthy that Opiliones was consistently reconstructed as the sister group to Eurypterida + Scorpiones in the minimal-length constrained trees, a provocative result that was probably unintended and unanticipated by supporters of the Eurypterida + Scorpiones. Given that Dunlop & Braddy (2001) reject equal weights parsimony as an arbiter of phylogenetic hypotheses, they would presumably dismiss these results as irrelevant to their argument, just as they dismissed their own parsimony-based results. However, if the Eurypterida + Scorpiones hypothesis is to be credible it must be open to evaluation and potential falsification using objective criteria, and the subjective or intuitive a priori weighting of characters advocated by Dunlop & Braddy clearly does not qualify. At present, it is unclear how one would objectively evaluate Dunlop & Braddy’s proposal with criteria compatible with those used in its original formulation. For now, the Eurypterida + Scorpiones concept advocated by Dunlop & Braddy may persist outside the mainstream of modern systematic practice, but it is increasingly problematic within it.

Stomothecata nom. nov.
Opiliones and Scorpiones were consistently recovered as a monophyletic group. The proposed name acknowledges a unique preoral chamber, the stomotheca, formed by coxapophyses of the palp and leg 1 (50), often with an auxiliary role played by the coxapophysis of leg 2 (51). In addition, the epistome appears to have been modified for adduction of the palpal coxae. The lateral walls of the epistome are fused to the medial surfaces of the palpal coxae, and the epistomal lumen is spanned by a transverse muscle (188), which
apparently adducts the palpal coxae thereby constricting the stomotheal chamber. Scorpions and opilions are also unique in having a pair of large epistomal arms projecting rearward into the prosoma and attaching to the endosternite (189). The epistomal arms provide attachment sites for pharyngeal dilator muscles (196) and extrinsic muscles of anterior proso- mal appendages (e.g. 37). The chelicera is equipped with a muscle that arises on the carapace and inserts on the ventral margin of the second cheliceral article (23). There is an anteriorly placed genital opening (155).

Several notable similarities were found while reviewing the literature, but information from other arachnid groups was considered too incomplete to allow them to be included in the matrix. For example, both orders have apparent haemocytotopic organs associated with major nerves of the anterior opisthosoma. These are termed suponeural organs in scorpions (Farley, 1999) and perineural organs in opilions (Kästner, 1935). Haemocytes develop in the cardiac wall in spiders (Seitz, 1972) and perhaps amblypygids (Weygoldt, 2000), but haemocytotopic organs are unknown in most other arachnid groups. Germ cells differentiate very early during embryogenesis in both scorpions and opilions relative to spiders (Moritz, 1957; Anderson, 1973). Additional research is required to determine the phylogenetic utility of these characters.

**Haplocnemata Börner, 1904**

Several workers recognize a close phylogenetic relationship between Pseudoscorpiones and Solifugae (Weygoldt & Paulus, 1979; Van der Hammen, 1989; Shultz, 1990; Wheeler & Hayashi, 1998; Giribet et al., 2002), and this was consistently recovered in the present analysis. Haplocnemata is supported by several synapomorphies, including (i) a feeding complex formed by two-segmented chelicerae (18) with a ventrolateral intrinsic articulation (19) and, perhaps, a dorsolateral articulation with the carapace (20), and (ii) a rostrosoma (32), a preoral apparatus formed by an anteriorly projecting epistome affixed dorsally to enlarged palpal coxae and bordered by lateral palpal projections. The epistome forms the dorsal component of a ‘beak’ with the ventral part formed by a midventral sternapophysis (13) fused between the palpal coxae. The locomotor apparatus consists of coxae that meet along the ventral midline (12), elongate femur-like patellae (48) and an apotele in the adult modified as an eversible empodium or pulvillus (92). The respiratory system is formed entirely (Pseudo-scorpiones) or in part (Solifugae) by paired tracheal stigmata opening on opisthosomal somites 3 and 4 (126).

**Acaromorpha Dubinin, 1957**

A clade comprising Ricinulei and Acari is consistently recovered in the present analysis. It is united here by two unique and seven homoplasious synapomorphies. These include a gnathosoma (31) defined, in part, by medial fusion of the palpal coxae (30), although presence of a gnathosoma in Ricinulei is debatable, as discussed in the Appendix. Acaromorphs also have a unique post-embryonic development consisting of a hexapodal larva and up to three octopodal nymphal instars (176). The pedal patella–tibia joints are formed by a bicondylar dorsal hinge rather than a single mid-dorsal condyle (69), all postcheliceral segmental ganglia are unified in the subesophageal ganglion (130), and a postcerebral pharynx is absent (192). The group is also tentatively united by presence of differentiated pedal basi- and telofemora (63, 64) and the absence of a ventral (sternal) pharyngeal dilator muscle (199), but these may be synapomorphies erroneously reconstructed as a synapomorphies.

The internal phylogenetic structure of Acaromorpha is controversial, with many recent workers favouring a monophyletic Acari (Weygoldt & Paulus, 1979; Shultz, 1990; argued most thoroughly by Lindquist, 1984) and others advocating a diphyletic Acari, with Acariformes being the sister group to Cryptognomae (= Ricinulei + Anactinotrichida) (especially Van der Hammen, 1979, 1989) (Fig. 3). Acari was recovered as monophyletic when fossils were excluded (Fig. 2), but not when they were included (Fig. 3). A ‘mite-centred’ survey of arachnid characters may be needed if morphology is to offer a compelling solution to the internal phylogeny of Acari and its placement within Arachnida. These issues are not resolved by the present analysis.

**Pantetrapulmonata nom. nov.**

Pantetrapulmonata includes the extinct orders Trigonotarbida, Haptopoda and the extant orders Araneae, Amblypygi, Schizomida and Thelyphonida. The clade is united by cheliceral structure (18, 19), a megoper- culum (106), booklings on the genital and first post-genital somites (121, 122) and enlargement of the epipharyngeal sclerite (192). It is important to note, however, that most of these characters were coded as uncertain in Plesiosiro (Haptopoda). Aside from the placement of Haptopoda, the monophyly of Trigono- tarbida and the extant orders was anticipated by Shear et al. (1987) and is generally regarded as a monophyletic group.

**Tetrapulmonata Shultz, 1990**

Tetrapulmonata was originally proposed on the basis of neontological analyses and encompassed Araneae,
Amblypygi, Schizomida and Thelyphonida (Shultz, 1990) and was also recovered here in analysis of neontological data (Fig. 5). However, results from analysis of all taxa required that the Tetrapulmonata concept be expanded to include the fossil order Haptopoda. Features uniting this group are problematic, however, as many states in Haptopoda were coded as uncertain.

Schizotarsata nom. nov.
Haptopoda and Pedipalpi (= Amblypygi + Schizomida + Thelyphonida) are united here in a group named for possession of divided pedal telotarsi (84). Synapomorphies include a pointed anterior carapacial margin (3) and elongation of leg 1 (46). As already noted, the placement of Haptopoda should probably be regarded as tentative because the state of many characters in this group was coded as unknown. The placement of Haptopoda as the sister group to Pedipalpi was anticipated by Dunlop (1999, 2002c).

Pedipalpi Börner, 1904
Pedipalpi encompasses Amblypygi and Uropygi (= Thelyphonida + Schizomida). Although widely recognized in the past, Pedipalpi was set aside in the mid-20th century in favour of Labellata (= Amblypygi + Araneae) based largely on the presumed synapomorphies of a narrow prosoma–opisthosoma juncture (97) and sucking stomach (199–201). The situation began to reverse when Shear et al. (1987) again highlighted similarities of Amblypygi and Uropygi, such as raptorial palps (35) and antenniform leg 1 (46). Shultz (1989, 1990, 1999) subsequently described numerous derived similarities, including asymmetrical flexor muscles at the pedal femur–patella joint (70), three telotarsomeroses on legs 2–4 (85), and modification of the palpal coxae to provide support for extrinsic pharyngeal muscles (197). Pedipalpi has emerged as one of the most well-supported interordinal relationships in Arachnida.

Uropygi Thorell, 1882
Uropygi has long been accepted as a monophyletic union of Thelyphonida and Schizomida. Synapomorphies include a unique mating behaviour (159), fused palpal coxae (30), 2-1-1-1 arrangement of tibial trichobothria (144), posterior defensive glands (102), elongated patella of leg 1 (68) and many others.

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REFERENCES


Pocock RI. 1893. On some points in the morphology of the Arachnida (s.s.), with notes on the classification of the group. Annals and Magazine of Natural History, Series 6 11: 1–19.


Sitnikova LG. 1978. The main evolutionary trends of the

Snodgrass RE. 1948. The feeding organs of Arachnida, including mites and ticks. Smithsonian Miscellaneous Collections 110 (10): 1–94.


APPENDIX

Each character used in this analysis is numbered, defined and cross-referenced with characters used in four previous studies that are abbreviated in brackets, specifically: WP = Weygoldt & Paulus (1979), S = Shultz (1990), WH = Wheeler & Hayashi (1998), GEWB = Giribet et al. (2002). Descriptions include corrections of errors, discussions of controversies or ambiguities, and justifications for state assignments to ‘problem’ taxa.
PROSOMA

1. Dorsal sclerite formed by fusion of the prosomal carapace, the dorsal portion of the first opisthosomal somite and the dorsomedial (axial) portion of the second opisthosomal somite: 0, absent; 1, present. State 1 is present in extant xiphosurids and close fossil relatives (Scholl, 1977; Anderson & Selden, 1997; Shultz, 2001). The fossil record suggests that this structure originated with the disappearance of the already reduced first opisthosomal tergite (= microtergite) and axial portion of the second opisthosomal tergite (Anderson & Selden, 1997). Similar structures are present in the already reduced first opisthosomal tergite (= microtergite) and axial portion of the second opisthosomal tergite (Anderson & Selden, 1997).

2. Single dorsal sclerite covering entire dorsal surface of body, no lines indicating original segmentation: 0, absent; 1, present. State 1 occurs throughout Holothyrida (Acari) (Van der Hammen, 1989) and in many Mesostigmata (Alberti & Coons, 1999), including Glypholaspis (Van der Hammen, 1989).

3. Anterior end of dorsal prosoma with median marginal or submarginal pointed process: 0, absent; 1, present. State 1 occurs throughout Schizomida (Protoschizomus, Stenochorus: Reddell & Cokendolpher, 1995; Thelyphonida (Rowland & Cooke, 1973; Shultz, unpubl. obs.; Protoschizomus: Dunlop & Horrocks, 1995/1996); Amblypygi (Charinus: Millo, 1949b; Phrynus: Shultz, 1999); and Plesiosiuro (Dunlop, 1999). Citing a figure in Rowland & Cooke (1973), Dunlop & Horrocks assumed that the anterior process was limited to ‘hypoctonid’ thelyphonids and united them with Protoschizomus and Schizomida. If valid, this would make Thelyphonida paraphyletic. However, the doubtful monophyly of ‘hypoctonids’ (Haupt & Song, 1996) and widespread presence of a submarginal anterior process in Pedi-palpi weaken this proposal (Harvey, 2002).

4. Ophthalmic ridges: pair of longitudinal crests intersecting or passing near the region of the lateral eyes or comparable region where lateral eyes are absent: 0, absent; 1, present. State 1 is present throughout Xiphosura (Anderson & Selden, 1997). Similar structures are present in Plesi-oistro (Dunlop, 1999) and ‘non-hypoctonid’ Thelyphonida (Mastigoproctus: Rowland & Cooke, 1973). Dunlop (2002a) described apparent ophthalmic ridges in the chasmataspidid Octoberaspis, but these were not observed in Diploaspis (Dunlop et al., 2001), either due to absence or inadequate preservation of specimens, nor in Chasmataspis (Dunlop et al., 2004).

5. Carapace with demarcations (e.g. grooves, sclerites, phragmata) between pro-, meso- or metapeltidial: 0, absent; 1, present. [S 1, WH 48, GEWB 29] State 1 is present in extant Scorpiones, Cyphophthalmi (Hansen & Sørensen, 1904) and many Palpatores (Opiliones), including Caddo and Leiobunum, and most Pseudoscorpiones (Chamberlin, 1931). Giribet et al. (2002) coded this character as absent in Cyphophthalmi (Opiliones), but a transverse procurred groove is present throughout the group (Hansen & Sørensen, 1904) and represents the meso-metapeltidial border, as indicated by attachment of the dorsal endosternal suspensor of postoral somite VI in Chileogovea oedipus and Siro exilis (Shultz, unpubl. observ). Kjellesvig-Waering (1986) did not explicitly describe such grooves in fossil scorpions, although he illustrated corresponding structures in Prearcturus, Archaeophonus, Archaeoctonus, Palaeophonus and other Palaeozoic scorpions (Kjellesvig-Waering, 1986: figs 14A, 21E, 27D, 59) (coded as uncertain here) but not in Proscorpius (contra Giribet et al., 2002). Distinct carapacial sclerites are present throughout Palpigradi, Schizomida and Solifugae (6).

The condition in Acari is controversial but is coded here as State 1. Van der Hammen (1989) considered the tergal region of the leg-bearing somites (postoral somites III–VI), or podosoma, to be reduced and replaced by posterior migration of the aspidosoma (i.e. tergal region assumed to be associated with appendages of the gnathosoma) and anterior migration of the opisthosomal tergal region to form the hysterosoma. The dorsal proterosomal and hysterosomal elements meet at a transverse sejugal furrow that continues laterally and passes ventrally between the coxae of legs 2 and 3. According to this scheme, the prosoma–opisthosoma border is expressed as the disjugal furrow, which passes from the ventral posterior margin of the podosoma anterodorsally to join the dorsal part of the sejugal furrow. Based on the arrangement of setae and slit sensilla (= lyrifissures), Van der Hammen (1989) interpreted the region above coxae 3 and 4 (i.e. region C = as a fusion of the dorsal parts of the first two opisthosomal somites (= postoral somites VII and VIII) in early divergent Anactinotrichida (i.e. Opilioacariformes) and Acariformes (e.g. Alycus). These interpretations have been followed by many acarologists, although its speculative aspects are widely acknowledged (Evans, 1992; Alberti & Coons, 1999).

From the standpoint of a general arachnologist, the Van der Hammen system seems unnecessarily complicated; it appears to have been formulated to explain broad morphological themes in Oribatida but was then extrapolated to other mites. A more conservative ‘arachnological’ scheme adopted here equates the podosoma with the pars cephalica (= propeltidium) of the arachnid prosoma and region C with the pars thoracica (= mesopeltidium + metapeltidium). In fact, the earliest and most recent treatments of Opilioacariformes (With, 1904; Klompen, 2000) reached similar conclusions. This interpretation is also consistent with evidence from Acariformes. For example, the region dorsal to the coxa of legs 3 and 4 in Alycus is as readily
explained by the persistence of primitive prosomal tergal elements as by the supposition that these disappeared and were replaced by two opisthosomal elements. Furthermore, several diverse lineages of basally divergent Acariformes display features that do not fit readily within the Grandjean–Van der Hammen system but seem to correspond to the cephalica/thoracica division of the prosoma. They have a sejugal furrow that may have demarcated the cephalica/thoracica border and a postpedal furrow that appears to represent the prosoma–opisthosoma junction; there is no disjugal furrow. Examples include palaeosomate (especially aphelacarid) and pediculocelid Oribatida, alicorhagiid and micropsammid ‘Endeostigmata’ and paratydeid Prostigmata (Alberti & Coons, 1999: fig. 42). This organization may be synapomorphic for Acariformes but could be a convergence brought about by selection for enhanced flexibility.

6. Carapace with distinct pro-, meso- or metapeltidial sclerites: 0, absent; 1, present; -, inapplicable due to absence of pro-, meso- or metapeltidial demarcations (5).

State 1 occurs throughout Palpigradi, Schizomida and Solifugae. It also appears sporadically within Opiliones (e.g. *Leiobunum flavum*: Shultz, unpubl. observ.) and Pseudoscorpiones (e.g. *Pseudochiridium*) (Chamberlin, 1931).

7. Sejugal furrow: circumferential zone of body flexibility that passes between the coxae of legs 2 and 3: 0, absent; 1, present.

State 1 is probably synapomorphic for Acariformes, as it occurs in most ‘endeostigmatids’, including Alycus (Van der Hammen, 1989), and is variously developed throughout Sarcoptiformes (Alberti & Coons, 1999). It is probably the primitive condition for Prostigmata but is either absent or weakly expressed in representatives included here. See 5 for alternative morphological interpretations of this body region in Acari.

8. Prosomal ozopores: 0, absent; 1, present [WH 46, GEWB 12]

State 1 occurs throughout Opiliones and Holothyrida (Van der Hammen, 1989).

9. Carapacial pleural doublure: 0, absent; 1, present. [WP 12, S 2, WH 49, GEWB 27]

A carapacial pleural doublure occurs throughout Xiphosura (Størmer, 1944), Eurypterida (Clarke & Ruedemann, 1912; Selden, 1981) and Chasmataspiddida (Dunlop et al., 2001, 2004; Dunlop, 2002a) and is absent in all known Arachnida.

10. Cardiac lobe: a longitudinal axial elevation of the carapace: 0, absent; 1, present.

State 1 occurs throughout Xiphosura (Anderson & Selden, 1997) and Eurypterida (Clarke & Ruedemann, 1912; Selden, 1981). Carapaces are not preserved sufficiently to determine this condition in the chasmataspidids *Diploaspis* (Dunlop et al., 2001) and *Octoberaspis* (Dunlop, 2002a) but an apparent cardiac lobe occurs in the *Chasmataspis* (Dunlop et al., 2004). A cardiac lobe is absent in Arachnida.

11. Moveable cucullus: 0, absent; 1, present [WP 54, GEWB 22]

State 1 is a synapomorphy of Ricinulei (Selden, 1992).

12. Medial intercoxal ‘sternal’ region: 0, all pedal coxae separated medially; 1, anterior pedal coxae abutting medially, posterior coxae separated; 2, anterior pedal coxae separated medially, posterior coxae abutting; 3, all pedal coxae abutting medially; 4, epimera: coxae undifferentiated medially from ventral body wall [S ∼3, WH ∼50, GEWB ∼17]

Proosomal sternites appear to be those portions of the ventral body wall not occupied by coxae. Despite early attempts to assess metamerism of the ventral prosoma (protosternum, deutosternum, tritosternum, etc.) (Börner, 1902a; Millot, 1949a), no apparent morphological features, such as borders of sclerites or muscle attachments, reliably demarcate the ventral body wall of one somite from that of an adjacent somite. Thus, coding schemes that focus on describing metamic components of the sternum region are problematic. Shultz (1990) attempted to code the shape of the entire intercoxal region and subsequent workers have adopted this approach. All pedal coxae are separated medially in *Plesiosiro* (Dunlop, 1999), Palpigradi (Roewer, 1934), Araneae (Millot, 1949c), Amblypygi (Weygoldt, 2000) and many Acari, including Opilioacariformes, Holothyrida, Mesostigmata, Ixodida, Alycus and many Prostigmata (Van der Hammen, 1989; Evans, 1992; Alberti & Coons, 1999). The anterior coxae are separated in extant Thelyphonida, Schizomida (Hansen & Sørensen, 1905; Millot, 1949e) and Ricinulei (Pittard & Mitchell, 1972; Legg, 1976). The coxae are fused to the ventral body wall in Sarcoptiformes (Van der Hammen, 1989; Evans, 1992).

Interpreting this character is complicated for the anterior coxae of Scorpiones and Opiliones and all coxae in Xiphosura and Eurypterida due to the presence of coxapophyses, endites and/or gnathobases, which form components of the preoral chambers in these groups. Thus, coxae may abut medially when these structures are considered part of the coxae but are separate medially if these structures are ignored. As coxapophyses etc. are here coded as separate characters (50–53), I have chosen to code this character as if these structures did not exist. Consequently, phalangid Opiliones are coded as having all coxae separated (Pocock, 1902; Hansen & Sørensen, 1904). Fossil scorpions also show substantial variation in this character. All pairs of pedal coxae in *Palaeoscorpius* abut medially but also have gnathobases (Jeram, 1998), and this condition is coded here as uncertain. A sternum separates all pairs of pedal coxae medially in...
Proscorpius and Stoemeroscorpio (State 0) and Pre-
archurus approximates modern scorpions (State 1)
(Kjellesvig-Waering, 1986; Jeram, 1998). The coxal
bases of Eurypterida and Xiphosura are separated by
a small sternite, the endostoma (Selden, 1981; Shultz,
2001).

13. Postoral sternapophysis (=tritosternum, labium):
a cuticular evagination of the ventral body wall pos-
teriorly adjacent to the palpal coxae forming the pos-
terior border of the preoral chamber in some taxa or
placed posteriorly by fusion of the palpal coxae in
others: 0, absent; 1, present. [S = 10, WH = 56, GEWB
19 = 33]

State 1 is present throughout Palpigradi, Araneae,
Amblypygi (Snodgrass, 1948), Schizomida (Hansen &
Sørensen, 1905; Van der Hammen, 1989), Thely-
phonida (Van der Hammen, 1989), extant Ricinulei
Sørensen, 1905; Van der Hammen, 1989), Thely-
phonida (Van der Hammen, 1989), extant Ricinulei
(1989), Holothyrida (Van der Hammen, 1989),Mesos-
tigmata (Van der Hammen, 1989; Alberti & Coons,
1999). Allothyrus constrictus is the only holothyrid mite
to have sternalophyses. An apparent sternapophysis has
been described in a palaeocharinid trigonotarbid (Dunlop,
1994). Giribet et al. (2002) miscoded Ixodida and Acariformes as hav-
ing a labium (=tritosternum). The lophognath of
pseudoscorpions (Chamberlin, 1931) and labium of
Solifugae (Roewer, 1934) also appear to be sternapo-
phies that have been incorporated into the ro-
stroma (32). The labium of phalangid Opiliones
(Pocock, 1902; Hansen & Sørensen, 1904) is a ster-
napophysis but is associated with leg 1 rather the
pedipalp (Winkler, 1957). A small anterior sclerite in
the fossil scorpions Proscorpius, Waeringoscorpio and
Labriscorpio has been interpreted as a labium homol-
ogous with the sternapophyses of other arachnids
(Weygoldt, 1998), despite absence of any indication of
the relationship of this sclerite to the mouth and pos-
ible alternative interpretations (e.g. 16). Giribet et al.
coded this sclerite as a sternapophysis, but the char-
acter is coded here as uncertain in fossil scorpions.

14. Channels on the body surface linking openings of
coxal organs to preoral chamber: 0, absent; 1, present.
Van der Hammen (1989) described bilaterally paired
cuticular tracts (‘taenidia’) connecting orifices of coxal
organs to the preoral chamber in some arachnids and/
or a ventromedian groove (= intercoxal or subcapitular
gutter) that leads, in turn, to the preoral chamber in
other taxa. Taenidia and intercoxal gutters are present
in Opilioacariformes (Van der Hammen, 1989), Holothyrida (Van der Hammen, 1989), Mesos-
tigmata (Glytholapias: Van der Hammen, 1989),
Ricinulei (Pittard & Mitchell, 1972; Van der Hammen,
1989), Araneae (Heptathela, Aphonopelma, Hypochi-
lus: Shultz, unpubl. observ.; also Porrhothele (Mygal-
omorphae, Dipluridae): Butt & Taylor, 1991; Segestria
(Araneomorphae, Segestriidae): Van der Hammen,
1989), Amblypygi (Van der Hammen, 1989), Schizo-
mida (Stenochirus: Shultz, unpubl. observ.; unidenti-
fied Hubbardianae: Van der Hammen, 1989); and
Thelyphonida (Mastigoproctus: Shultz, unpubl. observ.;
also Tetrabalius: Van der Hammen, 1989). The conduction of large volumes of fluid from orifices of the
coxal organs to the preoral chamber has been observed
in the mygalomorph spider Porrhothele (Dipluridae)
(Butt & Taylor, 1991) and Mastigoproctus (Thely-
phonida) (Shultz, unpubl. observ.). The podocephalic
canal (15) is present in Acariformes (Acari) (Lindquist,
1984) and appears to have evolved as an invaginated
supracoxal channel (Grandjean, 1938; G. Alberti in
Evans, 1992). Van der Hammen (1982) could not dis-
cern with certainty whether a channel exists in
Eukoenenia (Palpigradi), but none has been reported
by previous authors and they have not been observed
by the present author; Palpigradi is coded as having
State 0.

15. Podocephalic canal: cuticular channel and/or
duct draining multiple glands and opening near
mouthparts: 0, absent; 1, present; -, inapplicable due to
absence of channel (14).

State 1 occurs throughout Acariformes (Acari)
(Lindquist, 1984).

16. Heavily sclerotized suboral sclerite serving, in
part, as basal pivot point for coxae of appendages of
postoral somites II–IV (=arachnid palp and legs 1 and
2): 0, absent; 1, present.

The sclerite forms the posterior wall of the true mouth
and is heavily sclerotized in extant scorpions. It is not
visible externally due to the tightly fitting coxae of the
anterior prosomal appendages (Shultz, 2007) It may
correspond to the so-called labium (Weygoldt, 1998) or
labrum (Kjellesvig-Waering, 1986) of certain fossil
scorpions (see 13).

17. Genal angles: 0, rounded; 1, pointed.

Anderson & Selden (1997) originally coded a pointed
genal angle and genal spine as separate characters,
but they are combined here. State 1 is present in many
Xiphosura (Anderson & Selden, 1997) and Chas-
mataspidida (Dunlop et al., 2001, 2004; Dunlop,
2002a).

APPENDAGES OF POSTORAL SOMITE I: CHELICERAE

18. Cheliceral segmentation: 0, three articles; 1, two
articles [WP = 25 +42, WH = 15, GEWB = 44]

State 0 is present in extant Xiphosura, Eurypterida
(Clarke & Ruedemann, 1912; Selden, 1981), Palpi-
gradi (Roewer, 1934), Opiliones (Hansen & Sørensen,
1904), Scorpiones (Hjelle, 1990) and throughout non-
acariform Acari (Evans, 1992). State 1 is present
throughout known Trigonotarbida, Araneae, Ambly-
pygii, Thelyphonida, Schizomida, Pseudoscorpiones
and Solifugae. Acariform mites have two unambigu-
ous cheliceral articles but may have a reduced third article (Van der Hammen, 1989; Evans, 1992); acariform mites are thus coded as uncertain. Chelicerae are not known or their condition is unclear in several fossil taxa, including Xiphosura, Chasmataspida (Dunlop et al., 2001, 2004; Dunlop, 2002a), Ricinulei (Selden, 1992), Plesiosiro (Dunlop, 1999), Proschizomus (Dunlop & Horrocks, 1995/1996) and the fossil scorpions Praeracturus and Palaeoscorpius (Kjellesvig-Waering, 1986). Kjellesvig-Waering (1986) consistently interpreted chelicerae of fossil scorpions as having four articles, but this is probably a misinterpretation of the basal article (see also Stockwell, 1989). The basal article in extant scorpions consists of a distal collar of cuticle and a large proximal process, but the state of the chelicerae is unclear in several fossil scorpions represented here (Kjellesvig-Waering, 1986). State 1 is present in Xiphosura (Shultz, 2001), extant Scorpiones (Millot & Vachon, 1949), Opiliones (Hansen & Sørensen, 1904), Palpigradi (Börner, 1904; Millot, 1949d), Ricinulei (Pittard & Mitchell, 1972; Legg, 1976) and Eurypterida, including Baltoeurypterus (Selden, 1981) and Stylonurus (Clarke & Ruedemann, 1912). State 0 is present in the fossil scorpions Proscorpius and Stoermerscorpio but the state of the chelicerae is unclear in the other fossil scorpions represented here (Kjellesvig-Waering, 1986). State 1 is present in Trigonotarbida (Shear et al., 1987), mygalomorph Araneae, Amblypygi, Schizomida and Thelyphoniida (Weygoldt & Paulus, 1979). State 2 is present in Pseudoscorpiones (Chamberlin, 1931) and Solifugae (Roewer, 1934) and appears to be a groundplan feature for all major groups of mites (e.g. Van der Hammen, 1989; Alberti & Coons, 1999). The difference between the orthognathy of mygalomorph Araneae and ‘plagiognathy’ mesothelae (Liphistius, Heptathela) and palaeocribellate Araneae (Hypochilus) (Kraus & Kraus, 1993) is small compared with the variation that occurs throughout arachnids, and plagiognathy is coded as State 1 here.

State 2 appears to be a unique synapomorphy of Opiliones (Shultz, 2000).

19. Terminal cheliceral joint: 0, laterally placed bicondylar hinge; 1, dorsally placed bicondylar hinge; 2, centrally placed bicondylar hinge. [WP 25 + 42, S 11 + 12, WH 15, GEWB 44]

State 0 is present in Xiphosura (Shultz, 2001), extant Scorpiones (Millot & Vachon, 1949), Opiliones (Hansen & Sørensen, 1904), Palpigradi (Börner, 1904; Millot, 1949d), Ricinulei (Pittard & Mitchell, 1972; Legg, 1976) and Eurypterida, including Baltoeurypterus (Selden, 1981) and Stylonurus (Clarke & Ruedemann, 1912). State 0 is present in the fossil scorpions Proscorpius and Stoermerscorpio but the state of the chelicerae is unclear in the other fossil scorpions represented here (Kjellesvig-Waering, 1986). State 1 is present in Trigonotarbida (Shear et al., 1987), mygalomorph Araneae, Amblypygi, Schizomida and Thelyphoniida (Weygoldt & Paulus, 1979). State 2 is present in Pseudoscorpiones (Chamberlin, 1931) and Solifugae (Roewer, 1934) and appears to be a groundplan feature for all major groups of mites (e.g. Van der Hammen, 1989; Alberti & Coons, 1999). The difference between the orthognathy of mygalomorph Araneae and ‘plagiognathy’ mesothelae (Liphistius, Heptathela) and palaeocribellate Araneae (Hypochilus) (Kraus & Kraus, 1993) is small compared with the variation that occurs throughout arachnids, and plagiognathy is coded as State 1 here.

State 2 appears to be a unique synapomorphy of Opiliones (Shultz, 2000).

20. Chelicera articulating with carapace at anterolateral pivot: 0, absent; 1, present [S 13, WH 57, GEWB 45]

State 1 occurs in Solifugae (Roewer, 1934) and Pseudoscorpiones, except Chthonioidea and Feaelloidea (Chamberlin, 1931). Giribet et al. (2002) coded the character as present in Pseudoscorpiones.

21. Chelicera pivoting on dorsal protuberance of epistome: 0, absent; 1, present.

State 1 appears to be a unique synapomorphy of Opiliones (Shultz, 2000).

22. Extrinsic cheliceral muscle arising on carapace and inserting on dorsal margin of nonbasal cheliceral article: 0, absent; 1, present. (Note: Characters 22 and 23 refer to two different muscles.)

State 1 is known only in extant Scorpiones (Lankester, Benham & Beck, 1885; Vyas, 1970, 1974; Shultz, 2007) but may occur in acariform mites if their chelicerae are composed of three rather than two articles (Evans, 1992) (see 18). Acariformes are coded as uncertain.

23. Extrinsic cheliceral muscle arising on carapace and inserting on ventral margin of nonbasal cheliceral article: 0, absent; 1, present [GEWB 252] (Note: Characters 22 and 23 refer to two different muscles.)

State 1 is known only in extant Scorpiones (Lankester et al., 1885; Vyas, 1970, 1974; Shultz, 2007), some mesostigmatid Acari (Evans, 1992) and representative Opiliones, particularly Leiobunum (Shultz, 2000), Chilieogovea and Gonyleptes (Shultz, unpubl. observ.). The status of the character in other opiliones is not yet known. The character was originally defined as an extrinsic muscle inserting on the second segment of three-segmented chelicerae (Shultz, 2000; Giribet et al., 2002), but it has been redefined here to make it applicable to arachnids with two-segmented chelicerae.

24. Extrinsic cheliceral muscles attaching to epistome: 0, absent; 1, present.

State 1 is known only in extant Scorpiones (Lankester et al., 1885; Vyas, 1970, 1974; Shultz, 2007) but may occur in Prostigmata, if the sigmoid piece to which the cheliceral protractors attach (Evans, 1992) is a modification of the epistome.

25. Lateral tergocheliceral muscle with three heads: 0, absent; 1, present; -, coded only for extant tetraplomatoes and the palpigrade Eukoenenia, homology is unclear in other taxa [GEWB 230]

State 1 is present in Pedipalpi (Shultz, 1999).

26. Cheliceral silk glands: 0, absent; 1, present [GEWB 47]

State 1 is a unique synapomorphy of Pseudoscorpiones (Chamberlin, 1931). The silk gland of spider mites (e.g. Tetranychus) are associated with the pedipalps (Evans, 1992).

27. Cheliceral venom glands: 0, absent; 1, present [WP 34, WH 40, GEWB 46]

State 1 appears to be a unique synapomorphy of Araneae (Platnick & Gertsch, 1976).

28. Cheliceral serrula interior and exterior: 0, absent; 1, present.

State 1 is a unique synapomorphy of Pseudoscorpiones (Chamberlin, 1931; Harvey, 1992).

29. Cheliceral 'flagellum' in male: 0, absent; 1, present [GEWB 48]
State 1 is a unique synapomorphy of Solifugae (Roewer, 1934).

APPENDAGES OF POSTORAL SOMITE II: LEG 1 IN NONARACHNIDS AND PALP IN ARACHNIDS

30. Palpal coxae fused ventromedially and forming posterior wall of preoral chamber: 0, absent; 1, present [WP 27, S 18, WH 17 = 62, GEWB 33 + 63]
State 1 occurs in Schizomida, Thelyphonida, Acari and Ricinulei.

31. Gnathosoma: 0, absent; 1, present; -, inapplicable, palpal coxae not fused (30) [WP 56, S 19, WH –63, GEWB –36 + 37]
The gnathosoma is a functional complex comprising an epistome attached to the dorsal surface of medially fused palpal coxae (= infra- or subcapitulum) (see 30), the chelicerae and, in some taxa, a supracheliceral tectum. These components are tightly integrated and move in unison relative to the body. The gnathosoma has traditionally been considered a feature of Acari. However, Van der Hammen (1989) argued that a gnathosoma is present in Ricinulei, and this interpretation has received wide acceptance (e.g. Lindquist, 1984). However, it is not clear that the relationship of the chelicerae and subcapitulum is as intimate in Ricinulei as in Acari, and the ricinuleid subcapitulum does not appear to be as moveable. In fact, the ‘subcapitulum’ in Ricinulei is similar in many respects to the condition in Schizomida and Thelyphonida (Hansen & Sørensen, 1904), which has never been regarded as a gnathosoma. Consequently, I have coded the condition of Ricinulei as uncertain.

32. Rostrosoma: long, narrow, subcylindrical epistome projecting anteriorly with base fixed to dorsal surface of palpal coxae, bordered laterally by lobes projecting from palpal coxae; ventral wall of preoral chamber formed by anterior element of prosoma (sternapophysis): 0, absent; 1, present [S 15, WH 59, GEWB 20 + 36]
State 1 is present in Pseudoscorpiones and Solifugae (Chamberlin, 1931; Roeuer, 1934; Van der Hammen, 1989). Dunlop (2000) attempted to homologize components of the rostrosoma and gnathosoma (31), an argument accepted by Giribet et al. (2002). However, fusion of the palpal coxae (30) apparently evolved independently in the two structures. Coxal fusion in the gnathosoma is complete ventrally and excludes the suboral sternapophysis (13), while fusion is incomplete ventrally in the rostrosoma and incorporates the sternapophysis. Unlike the gnathosoma, the rostrosoma is largely immobile and cheliceral movement is not coupled with that of the palpal coxae.

33. Rutella/corniculi: hypertrophied setae modified as mouthparts located on the anterior processes of the palpal coxae: 0, absent; 1, present [GEWB 39]
State 1 occurs in the anactinotrichid groups Opilioacariformes, Holothyrida and Mesostigmata but not Xodoidea (Van der Hammen, 1989). It also occurs in Sarcoptiformes (Evans, 1992) and certain endostigmats (e.g. Alycus: Van der Hammen, 1989) but not in Prostigmata. Comparable structures are unknown in other chelicerate groups.

34. Terminal segments specially modified in adult male as a clasper used to engage the female: 0, absent; 1, present.
State 1 is known only in extant Xiphosura (Yamasaki, Makio & Saito, 1988).

35. Robust, raptorial: 0, absent; 1, present [S 17, WH 61, GEWB –59, 97]
State 1 is present in Amblypygi, Thelyphonida and Schizomida (Shear et al., 1987) and in Laniatores (Opiliones).

36. Orientation of robust, raptorial appendage: 0, operating in subtransverse plane; 1, operating in subvertical plane; -, inapplicable, coded only for Pedipalpi.
State 0 is present in extant Thelyphonida and most Amblypygi, and State 1 is present in Schizomida (Cokendolpher & Reddell, 1992) and in the basally divergent amblypygid Paracharon caecus (Weygoldt, 2000). The orientation of the pedipalps in the fossil Proschizomus is uncertain (Dunlop & Horrocks, 1995/1996).

37. Extrinsic muscle attaching to epistome: 0, absent; 1, present.
State 1 occurs in Chileogovea and Siro (Opiliones, Cyphophthalmi) and extant Scorpionides (Vyas, 1970; Shultz, 2007).

38. Muscle originating and inserting within coxa: 0, absent; 1, present [GEWB –292]
State 1 occurs in Amblypygi (Phrynus: Shultz, 1999: Phrynichus: Börner, 1904), Thelyphonida (Mastigoproctus: Shultz, 1993; Thelyphonus: Börner, 1904) and Schizomida (Stenochrus: Shultz, unpubl. observ.)
There are two intracoxal muscles in amblypygids and thelyphonids, the one coded here and another that is serially homologous with a muscle in the pedal coxae (54).

39. Tarsus and/or tibia with venom glands: 0, absent; 1, present [GEWB 64]
State 1 is known only from extant Pseudoscorpiones, except the superfamilies Chthonioidea and Faellioidea (Chamberlin, 1931; Harvey, 1992). Giribet et al. (2002) coded this character as present for Pseudoscorpiones.

40. Tarsal grooming organ: 0, absent; 1, present [GEWB 98]
State 1 is a unique synapomorphy of Amblypygi (Delle Cave, 1975; Weygoldt, 2000).

41. Scorpionoid chela: a large, well-developed chela formed by tibia (manus + fixed finger) and tarsus (moveable finger): 0, absent; 1, present [S 16, WH 60, GEWB 62]
State 1 occurs throughout Scorpiones and Pseudoscorpiones.

42. Modified in male as copulatory organ: 0, absent; 1, present [WP 35, WH 39, GEWB 67]

State 1 appears to be a unique synapomorphy of Araneae (Platnick & Gertsch, 1976).

43. Apotele: 0, apparently absent, not differentiated externally from penultimate article; 1, present [GEWB 69]

The apotele exists as a structure (i.e. dactyl, claw, empodium) differentiated from the tibiotarsus, tarsus or telotarsus and is typically associated with a pair of antagonistic muscles. The apotele occurs as a distinct structure in Xiphosura (Snodgrass, 1948), Eurypterida (Clarke & Ruedemann, 1912), Schizomida (Cokendolpher & Reddell, 1992), Araneae (Foelix, 1996), early divergent Amblypygi (Charinus: Weygoldt, 2000; not Phrynus: Shultz, 1999), Anactinotrichida (Camin, Clark & Bourdeau, 1956; Lindquist, 1984), Ricinulei (Pittard & Mitchell, 1972; Legg, 1976) and Solifugae (Roewer, 1934). Giribet et al. (2002) coded Solifugae as not having a palpal apotele, but it is present as an adhesive organ (45). Dunlop (1999) reconstructed Haptoptoda as having a palpal claw but notes in his description that the distal ends were not preserved in the known specimens.

44. Apotele (claw), position: 0, terminal; 1, subterminal; -, inapplicable, coded only for taxa with a distinct apotele (43).

State 1 occurs in Parasitiformes (Acari) (Evans, 1992).

45. Terminal adhesive organ: 0, absent; 1, present; -, inapplicable, due to lack of an apotele (43) [GEWB 66]

State 1 is a unique synapomorphy of Solifugae (Roewer, 1934).

APPENDAGES OF POSTORAL SOMITES III–VI: LEGS 2–5 IN NON-ARACHNIDS AND LEGS 1–4 IN ARACHNIDS

46. Appendage III (=arachnid leg 1) extremely elongate, antenniform: 0, absent; 1, present [WP ~24 + 32, S 20, WH 14, GEWB ~84]

State 1 occurs in Amblypygi, Thelyphonida, Schizomida (Shear et al., 1987) and Opiliones (van der Hammen, 1987). State 1 is approximated in Solifugae as having a palpal apotele, but it is present as an adhesive organ (45). Dunlop (1999) reconstructed Haptoptoda as having a palpal claw but notes in his description that the distal ends were not preserved in the known specimens.

47. Appendage V (=arachnid leg 3) of male specialized for sperm transfer: 0, absent; 1, present [WP 55, GEWB 94]

State 1 is known only from extant Ricinulei.

48. Appendages V and VI (=arachnid legs 3 and 4) with femur shorter than patella and with principal site of flexion/extension at patella-tibia joint ('apatellite' condition sensu Van der Hammen, 1989): 0, absent; 1, present [S 25, GEWB 86]

APPENDAGES OF POSTORAL SOMITES III–VI: COXA AND BODY–COXA JOINT

50. Appendage III (=arachnid leg 1) with coxapophysis forming floor or wall of preoral chamber: 0, absent; 1, present [S ~14, WH ~58]

State 1 occurs in Opiliones (Hansen & Sørensen, 1904) and higher scorpions (Jeram, 1998). A lobe is present on the coxa of leg 1 in the fossil scorpion Prearcturus and, perhaps, Stoerneroscorpio, and is coded here as a coxapophysis. Coxapophysis of leg 1, together with the epistome and coxapophysis of the palp, form a unique preoral chamber, the stomotheca. Weygoldt (1998) and Dunlop & Braddy (2001) reject the homology of coxapophyses and stomothecae in Opiliones and Scorpiones, because these structures are not apparent in fossils of those scorpions thought to have been aquatic. However, the coxapophyses in Opiliones are formed largely from soft cuticular ‘lips’ and similar structures in fossil scorpions would probably not have been preserved.

51. Appendage IV (=arachnid leg 2) with coxapophysis: 0, absent; 1, present [S ~23, WH ~66, GEWB 78]

State 1 occurs in all appropriately preserved Eurypterida, including Baltoeurypterus (Selden, 1981) and Stylosurus (Clarke & Ruedemann, 1912), extant Xiphosura on appendages II–VI and apparently Proscorpius on appendage III (=arachnid leg 1) (Kjesbye-Waering, 1986; Jeram, 1998; contra Giribet et al., 2002). Fossilized appendages with gnathobases have been found in association with Chasmataspis (Chasmataspida), suggesting that they may have had State 1 (Dunlop et al., 2004).

53. Coxae of appendages III–V (=arachnid legs 1–3) with jointed, moveable endites: 0, absent; 1, present [S ~23]

State 1 occurs in extant Xiphosura (Manton, 1964; Shultz, 2001) and in adequately preserved eurypterids (Clarke & Ruedemann, 1912) (Baltoeurypterus: Selden, 1981).
54. Intracoxal muscle: a muscle arising on anterior wall of coxa and inserting on posterior wall: 0, absent; 1, present [GEWB 237]
State 1 occurs in Thelyphonida (Mastigoproctus: Shultz, 1993) and Amblypygi (Phryus: Shultz, 1999).
It is unclear whether the muscle operating the moveable endite (53) in extant Xiphosura (Manton, 1964; Shultz, 2001) is homologous with this muscle and is coded here as uncertain. It is not present in Stenochrus (Schizomida) (Shultz, unpubl. observ.)
55. Coxae of appendages II–VI (= arachnid palp and legs) with dorsal articulation with carapace: 0, absent; 1, present.
State 1 occurs in extant Xiphosura (Yamasaki et al., 1988).
56. Flabellum (exite) on coxa of appendage VI (= arachnid leg 4): 0, absent; 1, present [GEWB –110]
State 1 occurs in extant Xiphosura (Yamasaki et al., 1988). An apparent exite occurs on appendages associated with Chasmataspis (Chasmataspidida) (Dunlop et al., 2004).
57. Insertion process of anteromedial tergo-coxal muscle: 0, weakly developed; 1, well to extremely well developed [GEWB 238]
State 1 occurs in Thelyphonida, Schizomida and Amblypygi (Börner, 1904; Shultz, 1999).
58. Musculi laterales: enlarged lateral tergocoxal muscle with attachment shifted from coxa to adjacent pleural membrane: 0, absent; 1, present [S 22, WH 65, GEWB 242]
State 1 occurs in Araneae and Thelyphonida (Shultz, 1989).

APPENDAGES OF POSTORAL SOMITES III–VI: TROCHANTER AND COXA–TROCHANTER JOINT
59. Coxa–trochanter joint with complex posterior articulation composed of two articulating sclerites: 0, absent; 1, present [S 24, WH 67, GEWB 85]
State 1 occurs in Araneae, Amblypygi, Thelyphonida and Schizomida (Shultz, 1989).

APPENDAGES OF POSTORAL SOMITES III–VI: FEMUR AND TROCHANTER–FEMUR JOINT
60. Depressor muscle (or homologue) of trochanter-femur joint: 0, absent; 1, present [WH 42, GEWB 220]
State 0 appears to be a unique synapomorphy of Araneae (Liphistius: Shultz, 1989; Aphonopelma: Ruhland & Rathmayer, 1978; Hypochilus: present study; other examples: Clarke, 1984, 1986).
61. Trochanter–femur joint with dorsal hinge or pivot operated by flexor muscles only: 0, absent; 1, present [WH –44, GEWB –91]
State 1 occurs in Palpigradi. Other chelicerates have a bicondylar articulation and are typically equipped with antagonistic muscles (Van der Hammen, 1985; Shultz, 1989), but see 60 for an exception.
62. Superior trochanter–femur muscle (or homologue) originating broadly in femur, inserting on distal margin of trochanter: 0, absent; 1, present.
State 1 occurs in extant Xiphosura (Shultz, 1989, 2001).
63. Basifemur–telofemur joint of appendages III and IV (= arachnid legs 1 and 2) in adult: 0, absent, 1, present [S 25, WH 68, GEWB 86]
The basifemur and telofemur apparently develop as ‘sister’ articles through division of a parental article, the femur (e.g. opilioacariform, endostigmatid, palaeosomatid mites) (Coineau & Van der Hammen, 1979; Evans, 1992). A single animal can have all legs with divided or undivided femora or have some combination of the two, typically with the more posterior legs having the divided femora. Thus, anterior legs often tend to be paedomorph with respect to posterior legs. Most chelicerates have undivided femora on some or all legs, but muscles homologous with those of the basifemur–telofemur joint may still develop (66) (Shultz, 1989), suggesting that the development of cuticular and muscular components of a joint have a degree of developmental and evolutionary independence.
Undivided femora occur in most extant eucharicerates, including Xiphosura, Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Scorpiones, Opiliones, Pseudoscorpiones, higher Sarcoptiformes (Archeogzetes: Van der Hammen, 1989), many Prostigmata (Tetranychus: Evans, 1992) and throughout Parasitiformes. Divided femora occur in all legs in many early divergent Acariformes, including many Endostigmata, basally divergent Sarcoptiformes (e.g. Palaeacarus) and Prostigmata (e.g. Allothrombium, Microacarus) (Van der Hammen, 1989; Evans, 1992). Only leg 4 has basi- and telofemora in Ancylius (Van der Hammen, 1989). Baso- and telofemora occur on legs 3 and 4 in Solifugae, Ricinulei, Opilioracariiformes and Eurypterida (Clarke & Ruedemann, 1912; Selden, 1981; Shultz, 1989).
Giribet et al. (2002) coded the ‘annulus’ of certain Trigonotarbidida (Shear et al., 1987) as a basifemur, but a similar non-muscularized annulus is present in the posterior legs of extant Thelyphonida. In both cases, the condyles of the trochanter–annulus and annulus–femur joints are aligned in such a way that they perform essentially identical movements and appear not to enhance either the range or degree of leg movement. (This contrasts with the condition in the last two pairs of legs in Baltoeurypterus where condyles of the apparent trochanter-basifemur and basifemur–telofemur joints have different arrangements (Selden, 1981)). The annulus in Thelyphonida appears to function in maintaining constant volume of the tro-
chanter–femur joint by preventing ballooning of the arthrodid membrane thereby minimizing the effect of internal fluid pressure on movement.

64. Basifemur–telofemur joint of appendage V (= arachnid leg 3) in adult: 0, absent; 1, present. See 63.
65. Basifemur–telofemur joint of appendage VI (= arachnid leg 4) in adult: 0, absent; 1, present. See 63.

66. Cuticular differentiation of basifemur–telofemur joint absent, but muscles present: 0, absent; 1, present; -, inapplicable due to presence of joint (63–65).
State 1 occurs in appendages of postoral somites III–IV (= arachnid legs 1–4) in Xiphosura, Araneae, Amblypygi, Thelyphonida, Schizomida, Scorpiones and Pseudoscorpiones (Shultz, 1989).

67. Circumfemoral ring: 0, absent; 1, present.
The femora of one or more pairs of legs in anactinotrichid Acari have a basal groove or ring associated with slit sensilla. Acarologists term that portion proximal to the ring the ‘basifemur’ and that portion distal to the ring the ‘telofemur’ and they refer to the basifemur as the ‘second trochanter’ and the telofemur as the ‘femur’. Despite the confusing terminology, the basifemur discussed in 63–65 is not homologous with the ‘basifemur’ of opilioacariform and parasitiform Acari, as both a true basifemur–telofemur joint and a circumfemoral ring are present in legs 3 and 4 of Opilioacariformes (Van der Hammen, 1989).

APPENDAGES OF POSTORAL SOMITES III–VI: PATELLA AND FEMUR–PATELLA JOINT
68. Patella of appendage of postoral somite III (= arachnid leg 1) proportionally much longer than those of more posterior appendages: 0, absent; 1, present.
State 1 occurs in Thelyphonida, Schizomida (Hansen & Sørensen, 1905; Shultz, 1989) and Opilioacariformes (Van der Hammen, 1989).

69. Femur–patella joint: 0, monocondylar, several axes of movement and multifunctional muscles; 1, bicondylar hinge, one axis of movement and antagonistic muscles; 2, hinge, one axis of movement, muscles without muscular antagonists [S ~26, WH ~69, GEWB ~87]
State 0 occurs in Solifugae. State 1 occurs in Phalangida (Opiliones), Scorpiones and Pseudoscorpiones. State 2 occurs in the remaining taxa (Shultz, 1989).
70. Patellar plagula: 0, absent or with simple median attachment; 1, symmetrical, Y-shaped with long proximal stem; 2, symmetrical, U-shaped (= arcuate sclerite); 3, asymmetrical, attaching to patella only at anterior margin [S 27, WH ~70, GEWB 234 = 243]

APPENDAGES OF POSTORAL SOMITES III–VI: TIBIA AND PATELLA–TIBIA JOINT
71. Tibiae divided by one or more joints: 0, absent; 1, present.
State 1 occurs in Amblypygi (Weygoldt, 2000).
72. Patella–tibia joint: 0, monocondylar with or without CZY (73); 1, bicondylar hinge, one axis of movement, antagonistic muscles; 2, hinge, one axis of movement, muscles without muscular antagonists [S ~31, WH 74, GEWB ~92] (Shultz, 1989; Selden, Shear & Bonamo, 1991)
73. Patella–tibia joint with posterior compression zone (‘CZY’): 0, absent; 1, present; -, inapplicable due to absence of monocondylar articulation [GEWB 99]
State 1 is a unique synapomorphy of Araneae (Selden et al., 1991).
74. Patella–tibia joint of appendages III–VI (= arachnid legs 1–4) with deep-set monocondylar pivot bordered by a pair of tibial processes to which extensor muscles attach: 0, absent; 1, present; -, inapplicable due to absence of monocondylar joint (72)
State 1 occurs in extant Xiphosura (Snodgrass, 1952; Shultz, 1989), although a similar arrangement is present in the appendage III (= arachnid leg 1) in Thelyphonida (Shultz, 1993).
75. Patella–tibia joint largely immobile, specialized for autotomy: 0, absent; 1, present.
State 1 occurs throughout Amblypygi (Weygoldt, 1984, 2000).
76. Anterior femur–tibia or femoropatella–tibia (transpatellar) muscle: 0, absent; 1, present [S ~30, GEWB 222] (Shultz, 1989)
77. Proximal attachment of posterior femur–tibia or femoropatella–tibia (transpatellar) muscle: 0, muscle absent; 1, dorsal, posterior surface of femur and/or posterior surface of patella; 2, distal process of femur, muscles attach: 0, absent; 1, present; -, inapplicable due to absence of monocondylar joint [S 28, WH ~71 + 72, GEWB 235 = 244, 245] (Shultz, 1989)
78. Distal attachment of posterior femur–tibia (transpatellar) muscle: 0, posterior; 1, dorsal, acting as extensor of femur–patella joint [S ~28, WH ~71 + 72, GEWB 235 = 244, 245] (Shultz, 1989)
79. Anterior patella–tibia muscle: 0, absent; 1, present [S ~32, WH ~73, GEWB 246] (Shultz, 1989)
80. Posterior patella–tibia muscle: 0, absent; 1, present [S 33, WH 76, GEWB 248] (Shultz, 1989)
81. Patella–tibia joint spanned by elastic (‘springlike’) sclerite: 0, absent; 1, present [GEWB 107]
State 1 is a unique synapomorphy of Solifugae (Sensenig & Shultz, 2003).
APPENDAGES OF POSTORAL SOMITES III–VI: TARSUS AND TIBIA–TARSUS JOINT

82. Tarsus divided into proximal basitarsus (= metatarsus) and distal telotarsus (= distitarsus or 'tarsus'): 0, absent; 1, present.
State 0 occurs in extant Xiphosura (Shultz, 1989) and throughout Acariformes (Lindquist, 1984; Evans, 1992), in the anterior two pairs of legs in chthonioid pseudoscorpions and all legs in 'monosynphorid' pseudoscorpions, including Feaelloidea and Cheliferidea (Chamberlin, 1931). A circumtarsal ring (83) associated with slit sensilla in Parasitiformes (Acari) may represent a joint between a telotarsus and basitarsus (Evans, 1992).

83. Circumtarsal ring: 0, absent; 1, present.
State 1 is an apparent synapomorphy of Parasitiformes (Evans, 1992).

84. Telotarsus in adult with two or more tarsomeres: 0, absent; 1, present; -, inapplicable due to absence of telotarsus (82) [GEWB 71]
State 1 occurs in Schizomida, Thelyphonia, Amblypygi, Palpigradi, Ricinulei, Solifugae (Shultz, 1989), Opilioacariformes (Van der Hammen, 1989) and Pleiosiro (Dunlop, 1999).

85. Three telotarsomeres on appendages of postoral somites IV–VI (= arachnid legs 2–4): 0, absent; 1, present; -, inapplicable due to absence of telotarsus (82) or absence of telotarsomeres (84) [S 34, WH 77, GEWB 102]
State 1 occurs in Thelyphonia, Schizomida and Amblypygi (Shultz, 1989).

86. Tibia–tarsus joint spanned by well-developed elastic ('springlike') sclerite: 0, absent; 1, present [GEWB 107]
State 1 occurs in Scorpiones, phalangid Opiliones and Solifugae (Alexander, 1967; Shultz, 2000; Sensenig & Shultz, 2003). Extant Xiphosura is coded for the last prosomal appendage only (see 88).

87. Appendage of postoral somite VI (= arachnid leg 4) with ring of large, basally articulated spatulate processes at tibia-tarsus joint: 0, absent; 1, present.
State 1 occurs in extant Xiphosura (Yamasaki et al., 1998).

88. Appendages postoral somites III–V (= arachnid legs 1–3) with tibiotarsus (i.e. tibia and tarsus not differentiated): 0, absent; 1, present.
State 1 occurs in extant Xiphosura (Shultz, 1989) but not apparently in Weinbergina (Moore et al., 2005), the only synxiphosurid in which appendages are sufficiently preserved to determine the number of podomeres.

89. Ambulacrum: peduncle-like extension of the tarsus with internal condylophores and terminating distally with apotele (e.g. claws) and/or pulvillus: 0, absent; 1, present.

State 1 is present throughout Acari (Alberti & Coons, 1999).

APPENDAGES OF POSTORAL SOMITES III–VI: APOTELE AND TARSUS–APOTELE JOINT

90. Apotele of appendage III (= arachnid leg 1): 0, absent or not apparent; 1, present [GEWB 101]
State 0 occurs in Amblypygi, Thelyphonia and Schizomida (Shultz, 1999). However, the apotele is probably present but undifferentiated, because muscles that would normally insert on the apotele terminate on the end of the 'tarsus'. Dunlop (1999) reconstructed Haptopoda as lacking an apotelic claw on leg 1 but noted in the text that this was speculative. Dunlop (2002b) has reviewed apotelic diversity in Chelicerata.

91. Appendages of postoral somites III–VI (= arachnid legs) chelate with chela formed from tibiotarsus and apotele or tarsus and apotele: 0, absent; 1, present.
State 1 occurs in extant Xiphosura (Yamasaki et al., 1988). The condition appears to occur in Chasmataspis based on associated appendages (Dunlop et al., 2004), but not in Diploaspis and Octoberaspis (Dunlop et al., 2001; Dunlop, 2002a).

92. Apotele with eversible or padlike empodium (= pulvillus) in adult: 0, absent, although empodial claw may be present; 1, present [S 38, WH 81, GEWB 95]
State 1 occurs throughout Pseudoscorpiones (Chamberlin, 1931), Solifugae (Roewer, 1934), Opilioacariformes, Holothyrida, Ixodida and free-living Mesostigmata (Evans, 1992). An eversible 'pulvillus' is probably a primitive feature of Amblypygi (e.g. Charinus: Weygoldt, 2000) but is absent in higher groups (e.g. Phrynus: Weygoldt, 2000).

93. Inferior apotele muscle (= claw depressor) with tibial attachment: 0, absent; 1, present [S 35, WH 78, GEWB 249]
The character is coded for extant Xiphosura using appendage of postoral somite VI (= arachnid leg 4), as other legs lack a differentiated tibia (88). State 1 appears to occur throughout Arachnida (Shultz, 1989).

94. Inferior apotele muscle (= claw depressor) with patellar attachment: 0, absent; 1, present [S 36, WH 79, GEWB 250]
State 0 occurs in extant Xiphosura, Acari, Amblypygi, Palpigradi and Ricinulei. State 1 occurs in all other arachnids examined here (Shultz, 1989).

OPISTHOSOMA

95. Number of opisthosomal somites in adult: 0, five; 1, eight; 2, nine; 3, 10, 4, 11; 5, 12; 6, 13 [WH 33, GEWB 190]
Chasmataspids appear to have 13 opisthosomal somites (Dunlop et al., 2004). The synxiphosurans
Weinberga (Moore et al., 2005) and Limuloidea (Anderson & Selden, 1997) appear to have ten opisthosomal somites; Moore et al. (2005) found no evidence of an anterior microtergite in Weinberga as proposed by Anderson & Selden (1997). Xiphusurids appear to have nine opisthosomal somites (Scholl, 1977; Anderson & Selden, 1997; Shultz, 2001). Members of the following orders have 12 opisthosomal somites: Araneae (Millot, 1949a,c), Amblypygi (Weygoldt, 2000), Thelyphonida and Schizomida (Hansen & Sørensen, 1905) and Pseudoscorpiones (Chamberlin, 1931). Eleven somites are present in Palpigradi, Solifugae (Roewer, 1934) and Trigonotarbidia (Gilboaarchnus: Shear et al., 1987; Palaeocharinus: Fayers et al., 2004). Plesiosiro may have 11 or 12 somites (Dunlop, 1999). Justification for coding of more controversial taxa is provided below.

Scorpiones: Two principal hypotheses regarding the number of opisthosomal somites in scorpions have been advocated: a 13-somite hypothesis derived from embryological studies (Brauer, 1895; Patten, 1912; Farley, 1999, 2005) and a 12-somite hypothesis based on comparative anatomy of adults (Weygoldt & Paulus, 1979). The embryological interpretation is based on the observation of pregenital, genital and pectinal somites (each with segmental ganglia and paired limb buds) in early scorpion embryos followed by extreme reduction or loss of the pregenital somite in later embryos. According to this view, a missing pregenital somite should be added to the 12 apparent opisthosomal somites of post-embryonic scorpions to achieve a final number of 13. The anatomy-based hypothesis was introduced by Weygoldt & Paulus (1979), who advocated a literal interpretation of post-embryonic segmentation based on opisthosomal tergites. Specifically, these authors argued that the last pair of dorsal endosternal suspensor muscles of non-scorpion arachnids, especially Pedipalpi, attach to the first (= pregenital) somite, that this condition also occurs in scorpions, and that there is no reason to invoke a missing pregenital tergite. They proposed that the pectines belong to the genital somite and that functional specializations of the nervous system for pectinal function give the appearance of an extra neuromere during embryonic development.

I recently dissected the prosoma and anterior opisthosoma of the scorpions Centruroides, Hadrurus and Heterometrus and focused on the composition of the muscular diaphragm (103) that separates the haemocoelic compartments of the prosoma and opisthosoma (Shultz, 2007). The diaphragm is composed of a metameric series of axial muscles from three somites; the anterior somite corresponds to the last prosomal somite and the posterior somite corresponds to the genital somite. The middle elements insert dorsally along a tranverse tendon attached to the anterior margin of the first tergite. These observations are consistent with the embryological interpretation that a pregenital somite is present but its tergite is not expressed. It appears likely that the the pregenital somite was compressed longitudinally during the evolution of the diaphragm. I code scorpions as having 13 opisthosomal somites.

Eurypterida: The eurypterid opisthosoma is widely assumed to have 12 somites (Clarke & Ruedemann, 1912; Størmer, 1944). However, in a speculative paper on the evolutionary morphology of trilobites and chelicerates, Raw (1957) proposed that both scorpions and eurypterids have 15 opisthosomal somites. Raw assumed that scorpions have 13 apparent opisthosomal somites based on the transient pregenital somite of scorpion embryology, that scorpions and eurypterids are close relatives and should have the same number of somites, and that olenellid trilobites and chelicerates always have somites in multiples of three. Raw achieved 15 somites in scorpions by assuming the last opisthosomal somite to be a diplosomite and that the telson is a postanal somite, even though there is no evidence for either of these proposals. He attributed these features to eurypterids, as well. He also noted that the connection between the prosomal carapace and first opisthosomal tergite in Eurypterida differed structurally from the connection between adjacent opisthosomal tergites and regarded this as evidence for a reduced pregenital tergite in the prosoma–opisthosoma junction. Raw's speculations were largely forgotten until Dunlop & Webster (1999) resurrected the proposal that eurypterids have a reduced opisthosomal tergite and therefore share a unique similarity with scorpions. Unfortunately, Dunlop & Bullock treated Raw's conjecture as if it were based on empirical evidence rather than an attempt to force eurypterid morphology into a peculiar numerical system. In the absence of convincing evidence to the contrary, I have coded eurypterids as having 12 opisthosomal somites.

Ricinulei: The opisthosoma consists of a membranous pedicel (97) bearing the gonopore ventrally. The female gonopore is bordered by an anterior plate and a posterior plate. The remainder of the opisthosoma is composed of thick sclerites separated by less heavily sclerotized cuticle. The first dorsal sclerite is short and functions as part of a prosoma–opisthosoma coupling mechanism (96) that may or may not be a specialized component of the following tergite. This is followed by four tergites and sternites and a three-segmented metasoma (= ‘pygidium’). Millot (1945, 1949f) reasoned that the opisthosoma contains ten somites, with somites VII–IX incorporated into the pedicel, X–XIII expressed as tergites and sternites, and the metasoma...
comprising four somites. He did not regard the dorsal coupling sclerite as a separate tergite, and his interpretation of four rather than three metasomal somites has been rejected. Pittard & Mitchell (1972) also proposed ten opisthosomal somites, but achieved this number by regarding the dorsal coupling sclerite as a tergite of somite IX and by recognizing three metasomal somites. Legg (1976) adopted the system proposed by Pittard & Mitchell but did not regard the dorsal coupling sclerite as separate from the following tergite (X). Van der Hammen (1979, 1989) reconstructed 13 coupling sclerite as separate from the following tergite by Pittard & Mitchell but did not regard the dorsal somites. Legg (1976) adopted the system proposed by Pittard & Mitchell but did not regard the dorsal coupling sclerite as a tergite of somite IX and by recognizing three metasomal somites. Dunlop (1996) attempted to homologize the prosoma–opisthosoma coupling mechanisms of Ricinulei and Trigonotarbida, a goal that required a novel and rather forced interpretation of the dorsal sclerites. He regarded the coupling sclerite as homologous with the first opisthosomal tergite (VII) of trigonotarbid and then followed Van der Hammen’s attempt to unite Ricinulei with anactinotrichid Acari, which he also regarded as having a primitive number of 13 somites. Selden (1992) described a fossil ricinuleid, Terpsicroton, that shows two pairs of depressions on the three large premetastomal tergites, which contrasts with the single pair seen in extant species. This observation appears to corroborate the diplosomite hypothesis, but the evidence does not indicate that the tergite anterior to these is a diplosomite.

Dunlop (1996) attempted to homologize the prososoma–opisthosoma coupling mechanisms of Ricinulei and Trigonotarbida, a goal that required a novel and rather forced interpretation of the dorsal sclerites. He regarded the coupling sclerite as homologous with the first opisthosomal tergite (VII) of trigonotarbid and then followed Van der Hammen’s diplosomite hypothesis to achieve 12 somites in total. Dunlop’s scheme differs from previous systems in suggesting that the pedicel does not contain the dorsal elements of the first and second somites and is inconsistent with Mililot’s (1945) observation that the pre- and postgenital plates each have dorsoventral muscles. Here I code Ricinulei as having 12 somites. There are three metasomal somites (XVI–XVIII), three diplosomites (= six somites) (X–XV), one coupling somite (IX) and two somites in the pedicel (i.e. the genital and pregenital somites) (VII, VIII).

Opiliones: Harvestmen have nine opisthosomal somites and an anal operculum that is traditionally regarded as the tergite of a tenth somite; a tenth sternite is lacking (Hansen & Sørensen, 1904; Winkler, 1957). However, the anal operculum appears to represent a persistent embryonic telson (Moritz, 1957) and is therefore likely to be a postsegmental structure comparable with the stinger of scorpions, flagella of theylphonids, etc. (Shultz, 2000).

Acari: The number of opisthosomal somites is problematic for most mite taxa due to uncertainty about the location of the prosoma–opisthosoma boundary (5), extensive simplification or loss of metamerically arranged sclerites and muscle attachments, a paucity of developmental studies of engrailed expression and, in Acariformes, opisthosomal anamorphosis and heterochronic modification of somite number (Evans, 1992). Ixodids appear to be the exception; developmental studies indicate five somites in the opisthosoma of ticks (Evans, 1992).

Some mites retain external evidence of segmentation – metameric patterns of furrows, muscle attachments, and slit sensilla – and, with certain assumptions, the number of opisthosomal somites can be estimated. Here it is assumed that the dorsal surfaces of the last two prosomal somites are present in mites and retain their primitive association with legs 3 and 4 (contra Van der Hammen, 1989) (see 5 for justification). Given this, there appear to be 11 somites in the opisthosoma of Opilioacariformes, a conclusion also reached by other workers (e.g. With, 1904; Sitnikova, 1978; Klompen, 2000). Similar reasoning suggests that Alycus has seven opisthosomal somites, not nine as advocated by Van der Hammen (1989). Unfortunately, external evidence is ambiguous for determining the number of somites in other mite lineages and these are coded as uncertain.

96. Prosome-opisthosoma coupling mechanism: 0, absent; 1, present [GEWB –24]
The posterior margin of the carapace and the anterior margin of the first apparent opisthosomal tergite are specialized as a coupling mechanism in Ricinulei and Trigonotarbida, and Dunlop & Horrocks (1996) proposed that these are synapomorphic for the two groups. However, there is uncertainty about the homology of the anterior opisthosomal somites in Trigonotarbida and Ricinulei (95).

97. Pedicel: 0, absent; 1, aranean type; 2, ricinuleid type [WP 30, S –40, WH –20, GEWB –126]
The body narrows at or near the prosoma–opisthosoma juncture in several arachnid lineages (i.e. Solifugae, Palpigradi, Amblypygi, Araneae, Ricinulei) and this ‘waist’ has often been used as character at the interordinal level (e.g. Pocock, 1893). However, this interpretation is rejected here for being subjective and for uniting non-homologous conditions. For example, Araneae and Amblypygi are often grouped on the basis of a ‘pedicel’, yet it is a highly specialized structure in Araneae and its parts are not readily homologized with those of Amblypygi. In contrast, the condition in Amblypygi is a slightly narrower version of the highly moveable prosoma–opisthosoma juncture in Uropygi, which is not generally considered a ‘pedicel’. The pedicel in Ricinulei is also unique: a weakly sclerotized stalk containing the genital opening (Cryptocelulus: Pittard & Mitchell, 1972; Ricinoides: Legg, 1976). See 95.
98. Opisthosoma with three-segmented ‘buckler’: 0, absent; 1, present.
State 1 occurs throughout Chasmatapsidida (Dunlop, 2002a).

99. Thoracetron: consolidation of tergites of postgenital somites: 0, absent; 1, present; -, inapplicable, coded only for Xiphosura (Anderson & Selden, 1997).

100. Fusion of tergites of postoral somites VIII and IX (= opisthosomal somites 2 and 3) only: 0, absent; 1, present [GEWB 146]
State 1 appears to be a synapomorphy Trigonotarbidida (Shear et al., 1987). Rininuleids also have diplotremites (101), but these appear to encompass a different combination of somites (see 95).

101. Three diplotremites: 0, absent; present.
State 1 is a unique synapomorphy of Rininulei (Selden, 1992). See 95.

102. Paired opisthosomal defensive glands opening via ducts on either side of the anus: 0, absent; 1, present [S 46, WH 86, GEWB 122]
State 1 occurs in Thelyphonida and Schizomida (Hansen & Sørensen, 1905).

103. Muscular diaphragm separating prosomal and opisthosomal compartments, formed by dorsoventral muscles of postoral somites VI–VIII and extrinsic muscles of leg 4: 0, absent; 1, present.
State 1 is known only in extant scorpions (Lankester et al., 1885; Firstman, 1973). The diaphragm is often treated as a single structure, but recent anatomical work (Shultz, 2007) has shown that it is a composite of dorsal endosternal suspensors and extrinsic leg muscles (see 95). A diaphragm is also present in Solifugae, but it is located more posteriorly and does not appear to be homologous with that of scorpions (Roewer, 1934).

104. Opisthosomal appendicular cartilages: 0, absent; 1, present.
These cartilage-like columns of mesodermally derived tissue are associated with each opisthosomal appendage, including the chilaria, in extant Xiphosura (Patten & Hazen, 1900; Yamasaki et al., 1988; Fahrenbach, 1999; Shultz, 2001).

105. Paired appendages on ventral surface of postoral somite VII (= opisthosomal somite 1) in adult: 0, absent; 1, present [WP ~13, S 39, WH 82, GEWB 143]
State 1 is known in Weinbergina (Moore et al., 2005) and extant Xiphosura. The bilobed structure of the metastoma in certain eurypterids as well as the corresponding placement of chilaria in Xiphosura have led some workers to regard the metastoma as fused appendages of postoral somite VII (e.g. Stermer, 1955). This hypothesis is problematic given that (i) no special explanation is needed to account for bilaterally symmetrical structures in bilaterally symmetrical organisms, (ii) incorporation of the ventral part of the first opisthosomal sternite as a functional element of the prosoma is typical of arachnids and, perhaps, Euchelicerata generally, and (iii) some workers regard the metastoma as a sternite (e.g. Jeram, 1998). Thus, the metastoma is coded here as uncertain. Dunlop has proposed that the sternum of scorpions is derived from appendages citing the presence of transient limb buds in scorpion development (Brauer, 1895; Patten, 1912), but this is not compelling evidence for a persistent appendicular contribution to the sternite of the adult.

106. Megoperculum: 0, absent; 1, present [S ~41 + 42, WH ~83, GEWB 162 + 163]
State 1 occurs in Thelyphonida, Schizomida, Amblypygi, Araneae (Shultz, 1993, 1999), Trigonotarbidida (Shear et al., 1987) and probably Haptopoda (Dunlop, 1999) and Palpigradi. The megoperculum consists of appendages of opisthosomal somite 2 (= genital somite or postoral somite VIII) (Shultz, 1993, 1999; Popadić et al., 1998) that have fused medially and displaced the ventral body wall of the somite anteriorly (often represented by a small sternite to which dorsoventral muscles of postoral somite VIII attach). The megoperculum projects posteriorly to form the ventral surface of a pregenital chamber. The dorsal surface of the chamber is formed by the ventral body wall of opisthosomal somite 3 (= postoral somite IX), which serves as the ventral attachment of the paired dorsoventral muscles of that somite. The megoperculum bears booklungs (where present) and sometimes paired gonopods that are probably derived from telopodites. A similar but less developed operculum is present on the opisthosomal somite 3, which may also bear booklungs and eversible vesicles (e.g. Amblypygi) (see 111) corresponding to the booklungs and gonopods of the megoperculum (Shultz, 1999).

I contend here that a megoperculum is present in Palpigradi and that this is particularly evident in females. Specifically, a large, unpaired lobe projects posteriorly from the genital somite over the ventroanterior surface of the first postgenital somite thereby forming a pregenital chamber. The dorsoventral muscles of the genital somite attach ventrally near the anterior border of postoral somite VIII and those of postoral somite IX attach to the upper surface of the pregenital chamber (Rucker, 1901; Börner, 1902b Roewer, 1934; Millot, 1949d; Van der Hammen, 1989). Weygoldt (1998) has questioned this interpretation of Palpigradi.

107. Postgenital operculum or ‘sternite’: 0, sclerotized; 1, not sclerotized; -, inapplicable, coded only for Panterapulmonata (Platnick & Gertsch, 1976).
State 1 is present in Trigonotarbidida, Amblypygi, Thelyphonida, Schizomida and Mesothelae (Araneae) but not Opisthothelae (Araneae).

108. Genital opening of female guarded by four plates (one pregenital, one postgenital, two laterogenitals);
genital opening of male guarded by two plates: 0, absent; 1, present
This an apparent synapomorphy of Holothyrida (Acarci) (Van der Hammen, 1989).
109. Anterior margin of genital opening in male with glands secreting via fusules: 0, absent; 1, present.
State 1 occurs in Araneae as epiagastic or ‘epiandrioid’ glands (Marples, 1967) and in Palpigradi (Condé, 1991b).
110. Paired valve-like plates apparently formed from components of three somites covering triradiate genital opening: 0, absent; 1, present.
This is an apparent synapomorphy of Acariformes (Evans, 1992; Alberti & Coons, 1999)
111. Eversible ‘appendages’ on the ventral surface of postgenital somites: 0, absent; 1, present [S –43, WH –84, GEWB –127]
Paired ventral ‘appendages’ operated, in part, by haemolymph pressure occur in form of ventral sacs in certain Amblypygi (postoral somite IX) (Weygoldt, 2000) (Charinus: Millot, 1949b; not Phrynus: Shultz, 1999), prokoenenian Palpigradi (postoral somites X–XII) (Rucker, 1901; Condé, 1991a); as spinnerets in Araneae (X–XI) (Shultz, 1987); and as genital papillae in many Acariformes (Alberti & Coons, 1999), including Oribatida, many Endostigmata (Alcyus: Van der Hammen, 1989) and Prostigmata (Allothrombium: Saboori & Kamali, 2000; Microecaeculus: Evans, 1992). Eversible vesicles similar to those of amblypygids occur in fossils of the trigonotarbid Palaeocharinus (postoral somite IX) (Fayers et al., 2004). Two cuticular structures (‘genital verrucae’) occur anterior to the genital opening in Opilioacariformes, and each covers the opening to a thin-walled invaginated sac (‘genital papilla’) of unknown function (Van der Hammen, 1989). Van der Hammen proposed that it is homologous to a genital papilla of Acariformes, but Alberti & Coons (1999) have questioned this interpretation on several grounds and refer to these structures as pregenital capsules.
112. Opisthosomal silk glands and spinnerets derived from appendages on postoral somites X and XI (= opisthosomal somites 4 and 5): 0, absent; 1, present [WP 33, WH 41, GEWB 123 + 142].
State 1 is a unique synapomorphy of Araneae (Platnick & Gertsch, 1976), although potentially homologous glands and spigot-like setae occur on the ventral opisthosomal surface in Palpigradi (Millot, 1943; Condé, 1991a).
113. Opisthosomal spinnerets, location: 0, near middle of opisthosoma; 1, near posterior end of opisthosom; –, inapplicable, coded only for Araneae. (Platnick & Gertsch, 1976)
114. Anterior medial ‘spinnerets’: 0, absent; 1, present; –, inapplicable, coded only for Araneae. (Platnick & Gertsch, 1976)
115. Opisthosomal tergites divided longitudinally into one median and two lateral plates: 0, absent; 1, present [GEWB 145].
State 1 occurs in non-curculioid Ricinulei (Selden, 1992) and many Trigonotarbida (Dunlop, 1996). This feature, or something very like it (e.g. distinct opisthosomal trilobation), occurs sporadically in several euchelicerate groups, including Chasmataspis (Chasmataspida) (Dunlop et al., 2004), most fossil xiphosurans (Anderson & Selden, 1997) and a few derived Eurypterida (especially Mixopteroidea) (Tollerton, 1989).
116. Number of metasomal somites: 0, zero; 1, two; 2, three; 3, five; 4, nine [S –44, WH –85, GEWB 128, 144]
The metasoma is a preanal region comprising multiple somites that are substantially narrower than the preceding somites, or mesosoma. Metasomal somites often lack pleural membranes and take the form of sclerotized rings. State 1 occurs in Trigonotarbida. State 2 is present in synziphosurid Xiphosura (Anderson & Selden, 1997), Amblypygi, Thelyphonida, Schizomida and Ricinulei. State 3 occurs in Scorpiones and Eurypterida, and State 4 occurs in Chasmataspida.
Some workers appear to consider a five-segmented metasoma as conclusive evidence for the monophyly of a Eurypterida + Scorpiones clade (e.g. Dunlop & Braddy, 2001), presumably because the character represents a kind of tagmosis and should therefore be given substantial phylogenetic weight. However, Weygoldt (1998) has pointed out that a metasoma containing three somites is probably part of the ground plan of Euchelicerata. The known diversity of the euchelicerate metasoma indicates that this feature can in increase or decrease its segmental composition in evolution or be eliminated entirely without necessarily changing the total number of opisthosomal somites. Consequently, it is problematic to assume that the five-segmented metasoma has any special immunity to homoplasy.
117. Postanal structure (telson): 0, absent or not obviously developed; 1, present.
Postanal structures are considered non-segmental because they are modifications of the embryonic region posterior to the site of somite addition (embryonic growth zone). A well-developed postanal structure persists in adults in Xiphosura, Eurypterida, Chasmataspida, Scorpiones, Schizomida, Thelyphonida and Palpigradi. The anal operculum of Opiliones is generally considered by morphologists to be the tergite of the tenth opisthosomal or anal somite (e.g. Hansen & Sørensen, 1904), but embryological evidence (Moritz, 1957) suggests that it is derived from the postproliferative zone and thus corresponds to the telson of other chelicerates (see 95).
118. Postanal structure, shape: 0, caudal spine; 1, aculeus; 2, flagellum; 3, anal operculum; –, inapplica-
ble due to absence of postanal structure (117) [WP ×41, S ×45, WH ×24, GEWB ×121, 129 + 147].
State 0 is present in Xiphosura, Eurypterida and Chasmataspida. State 1 occurs in Scorpiones. State 2 occurs in Palpigradi, Thelyphonida and Schizomida. State 3 occurs in Opiliones (see 95, 117).

119. Specialized postanal flagellum in male (see 157–159): 0, absent; 1, present; -, inapplicable, coded only for taxa with postanal flagellum (118) [GEWB 131]
State 1 is a unique synapomorphy of Schizomida (Hansen & Sørensen, 1905; Cokendolpher & Reddell, 1992; Reddell & Cokendolpher, 1995).

**RESPIRATORY SYSTEM**

120. Respiratory medium: 0, water; 1, air.
Among the terminal taxa included, only fossil scorpions are problematic for this character. They are coded here as uncertain. Based on a study of book lung microsculpture, Scholtz & Kamenz (2006) have argued that arachnids are primitive terrestrial and pulmonary (see also Firstman, 1975) and have questioned whether any fossil scorpions were aquatic. No position on this proposal is taken here.

121. Respiratory lamellae on opisthosomal somite 2 (=genital somite, postoral somite VIII): 0, absent; 1, present [WP ×37, S ×-51, WH ×22, GEWB ×133–137]
This character encompasses book gills (=lamellae that function in water) and book lungs (=lamellae that function in air). The distinction between book gills and book lungs is accommodated here by 120 in combination with 121–124. Respiratory lamellae are present on the genital somite in Trigonotarbida, Araneae, Amblypygi, Thelyphonida and Schizomida. Petrunkevitch (1949) reconstructed *Plesiosiro* as having book lungs, but Dunlop (1999) could not corroborate this. This character was used by Dunlop & Webster (1999) to propose that Xiphosura and Scorpiones are closely related because they both lack respiratory lamellae on the genital somite. Dunlop & Braddy (2001) also argued for the placement of Eurypterida with Xiphosura and Scorpiones based, in part, on this character. At least some eurypterids may have had respiratory lamellae (e.g. Manning & Dunlop, 1995), but the only evidence of their segmental distribution is derived from one specimen (Braddy et al., 1999).

122. Respiratory lamellae on opisthosomal somite 3 (=postoral somite IX): 0, absent; 1, present [GEWB 136]
State 1 occurs in Amblypygi, Thelyphonida and Xiphosura. It is a groundplan feature of Araneae (Platnick & Gertsch, 1976) and is present in all representative taxa included here. Braddy et al. (1999) proposed the existence of respiratory lamellae on postoral somites IX–XII in Eurypterida based on evidence from one specimen. This character is coded as uncertain for the Eurypterida included here. Extant scorpions are coded here as lacking respiratory lamellae on this somite (=pectinal somite) based on the interpretation of the opisthosomal segmentation discussed in 95.

123. Respiratory lamellae on opisthosomal somites 4–6 (=postoral somites X–XII): 0, absent; 1, present.
State 1 is definitely present in extant Xiphosura and Scorpiones and may have occurred in Eurypterida.

124. Respiratory lamellae on opisthosomal somite 7 (=postoral somite XIII)
State 1 occurs in extant Xiphosura and Scorpiones only.

125. Kiemenplatten: 0, absent; 1, present.
These structures are located on the roof of opercular chambers in Eurypterida (Clarke & Ruedemann, 1912), where they take the form of ventrally projecting cones with a distinct cuticular microsculpture (Manning & Dunlop, 1995). Dunlop & Braddy (2001) inferred the existence of Kiemenplatten in all Palaeozoic scorpions based on a description and photos of one specimen of *Paraisobuthus duobicuscinatus* by Kjellesvig-Waering (1986: pls 16–18). The plates depict dark cone-like, rearward-pointing denticles distributed within a white amorphous material. The denticles appear to lack microsculpture, even though the magnifications at which the photos were taken (×90–×330) are comparable with those illustrating the cones of *Kiemenplatten* (×170–×350 in Manning & Dunlop, 1995: figs 1, 2). Given the diversity of cuticular structures present in the atria of booklungs, book gills and tracheae, the denticles appear to bear no special similarity to the cones of *Kiemenplatten*.

126. Tracheal system: 0, absent; 1, paired ventral stigmata on postoral somite VIII (=opisthosomal somite 2); 2, paired ventral stigmata on postoral somites IX and X; 3, one pair of stigmata opening near legs 3 or 4; 4, paired stigmata associated with cheleticare; 5, four pairs of stigmata on dorsal surface of opisthosoma; -, inapplicable, aquatic (120) [WP ×40, ×44, S ×52 + 53, 54, WH ×23, 45, 88, GEWB ×138, 139]
Firstman (1973) and Weygoldt & Paulus (1979) hypothesized that tracheae are homologous in all tracheate arachnids except spiders, and subsequent workers have entertained this hypothesis by including a character for the presence/absence of tracheal systems that ignores the diverse arrangement of stigmata in arachnids (e.g. Shultz, 1990; Wheeler & Hayashi, 1998; Giribet et al., 2002). However, this approach assumes that internal tracheal systems are conserved but that tracheal openings (stigmata) appear and disappear on different parts of the body with higher evolutionary frequency. Here I assume that stigmata are conserved in evolution and that differences in their anatomical placement reflect the evolution of new tracheae. State 1 occurs throughout Opiliones. State 2 occurs throughout Solifugae.
(Roewer, 1934) and Pseudoscorpiones (Chamberlin, 1931). State 3 recognizes the possible homology of stigmata in Ricinulei, Opiliaoariformes and Parasitiformes (Acari) (Lindquist, 1984; Van der Hammen, 1989). Tracheal systems are apparently absent in the groundplan of Acariformes, but Prostigmata typically have tracheae associated with the chelicerae. Tracheae derived from the posterior pair of book lungs are widespread in araneomorph Araneae, but the book lungs are retained and tracheae are absent in the most basally divergent groups (e.g. Hypochilus).

**BOX–TRUSS AXIAL MUSCLE SYSTEM (BTAMS)**

127. **Posterior oblique muscles of BTAMS of postoral somites I–VI**: 0, absent; 1, present in one or more somites.

State 0 occurs in Xiphosura, and state 1 occurs in Palpigradi, Araneae, Amblypygi, Thelyphonida and Schizomida (Shultz, 2001). The condition in Acari, Ricinulei, Opiliones and Solifugae is not known.

128. **Anterior oblique muscles of BTAMS posterior to postoral somite VI**: 0, absent; 1, present.

State 1 occurs in Xiphosura, which is probably the primitive condition based on comparison with other arthropods (Shultz, 2001). State 0 occurs in all arachnids examined thus far.

129. **Ventral attachments of posterior oblique muscles of opisthosomal BTAMS located in prosoma**: 0, absent; 1, present.

State 1 occurs in extant Xiphosura (Shultz, 2001).

130. **Endosternite fenestrate**: 0, absent; 1, present [S 8, WH 54, GEWB 35]

State 1 occurs in Thelyphonida and hubbardiid Schizomida (Firstman, 1973). The condition in protoschizomid Schizomida is not known.

131. **Suboral suspensor**: a tendon that arises from the BTAMS and inserts on the ventral surface of the oral cavity via muscle: 0, absent; 1, present.

State 1 occurs in Palpigradi (Eukoenienia: Millot, 1943), Amblypygi (Shultz, 1999) and Thelyphonida (Shultz, 1993).

132. **Perineural vascular membrane in adult**: 0, absent; 1, present [WH 28, GEWB 155]

Wheeler & Hayashi (1998) coded extant Xiphosura as unknown, although the primary source for this character (Firstman, 1973) stated that adult Limulus have a perineural vascular membrane. Within Arachnida, presence of a perineural vascular membrane is apparently correlated with the presence of tracheae (126).

133. **Ventral endosternal suspensor attaching on coxa of anteriorly adjacent somite**: 0, absent; 1, present [GEWB 239, 253]

State 1 occurs in Amblypygi (Shultz, 1999), Thelyphonida (Shultz, 1993) and Schizomida (Shultz, unpubl. observ.)

134. **Posteriormost postoral somite with a pair of dorsoventral muscles**: 0, VI; 1, VII; 2, VIII; 3, XII; 4, XIII; 5, XIV; 6, XV; 7, XVI.

Dorsoventral muscles tend to run in a continuous metameric series beginning in the prosoma. Determining the last tergite on which the muscle series ends is substantially easier than counting, especially given frequent anatomical complexities near the prosoma–opisthosoma juncture. The dorsoventral muscle series ends on postoral somite VII in Cyphophthalmi (e.g. Chileogoea) and Laniatores (Opiliones) (Shultz, unpubl. observ.), on postoral somite VII or VIII in Eupnoi (Leiobunum: Shultz, 2000, unpubl. observ.), on postoral somite XII in Palpigradi (Roewer, 1934), Solifugae (Bernard, 1896; Roewer, 1934; Millot & Vachon, 1949) and Araneae (Liphistius, Hypochilus: Millot, 1933; but segmentation reinterpreted here following Shultz, 1993, 1999), on postoral somite XIII in hubbardiid Schizomida (Cokendolpher & Reddell, 1992) and Scorpiones (Lankester et al., 1885), and on postoral somite XIV in extant Xiphosura (Shultz, 2001), Thelyphonida (Shultz, 1993), protoschizomid Schizomida (Cokendolpher & Reddell, 1992) and Amblypygi (Shultz, 1999).

Dunlop (1999) reconstructed Plesiosiro as having paired tergal apodemes ending on postoral somite XV, but his figures indicate that the series ends on postoral somite XIV. The interpretation of opisthosomal segmentation in Ricinulei coded here (95) indicates that the series ends on postoral somite XV in Torpsicroton, and this is treated as the groundplan for the order. The posteriormost dorsoventral muscles in Pseudoscorpiones occur on postoral somite XVI (Vachon, 1949).

**NERVOUS SYSTEM**

135. **Segmental ganglia**: 0, consolidated in prosoma; 1, one or more present in opisthosoma [WH 30, GEWB 210 + 216]

Adult neuromeres are exclusively prosomal in Amblypygi, liphistiomorph and araneomorph Araneae, Opiliones, Pseudoscorpiones, Ricinulei and Acari (Millot, 1949a).

136. **Dorsal median eyes**: 0, absent; 1, present [WP 14 + 47, S 50, WH ~ 7, GEWB 1]

Median eyes are a groundplan feature of Euchelicerata and are retained in extant Xiphosura, Eurypterida and occur in all arachnid orders except Palpigradi, Schizomida, Ricinulei and Pseudoscorpiones (Paulus, 1979). Median eyes are also absent in opilioacariform and parasitiform Acari (Lindquist, 1984) and perhaps the fossil whipscorpion Proschizomus (Dunlop & Hörrocks, 1995/1996). They are unknown in synziphosuran Xiphosura. Median eyes are present in a variety of basal acariform mites, including Edestostigma (but
not Alycus), Prostigmata (Microacarus) and certain oribatids (Palaeacarus) (Evans, 1992; Alberti & Coons, 1999). Giribet et al. (2002) coded all representative Acari as lacking median eyes. It is not known whether the eyes of some cyphophthalmid opilions are median or lateral; evidence from tracheal branching in Cyphophthalmus (Janczyk, 1956) suggests that they are median eyes (Shultz & Pinto da Rocha, 2007) and presence of a tapetum in Stylocellus is consistent with lateral eyes (Shear, 1993).

137. Retinula cells of dorsal median eyes: 0, organized into closed rhabdoms; 1, organized into network of rhabdomeres; 2, disorganized; -, inapplicable due to absence of median eyes (136) [GEWB −3]

State 0 is present in Scorpiones, Thelyphonida and Amblypygi, State 1 is present in Solifugae and Araneae; state 2 is present in Xiphosura (Paulus, 1979). The retinula cells of median eyes have been studied in several prostigmatid Acariformes and are organized in a network in some taxa and in an irregular pattern in others (Alberti & Coons, 1999). Retinulae in phalangid Opiliones have state 0 proximally and state 2 distally (Schliwa, 1979).

138. Ventral median eyes: 0, absent; 1, present.

State 1 occurs in early instars of extant Xiphosura (Paulus, 1979).

139. Lateral eyes: 0, absent; 1, present.

Lateral eyes are primitively present in Chelicerata and are absent in Palpigradi and Opiliones (Paulus, 1979). It is unclear whether the eyes of cyphophthalmid opilions are median or lateral (see 136).

140. Arrangement and number of lateral eyes: 0, compound, many; 1, five or more pairs (includes micro-lenses); 2, three primary pairs (excludes micro-lenses); 3, two pairs; 4, one pair; -, inapplicable due to absence of lateral eyes (139) [WP 13 + 18 + 38 + 44 + 52, S 49, WH 10, GEWB 4 + 5]

True compound eyes are present in Xiphosura, Euryptera, Chasmatastipida and many Palaeozoic Scorpiones. Among the anactinotrichid Acari, Opilioacariformes have two (Neocarus) or three (Siamacarus) pairs of lateral eyes (although at least one species of Siamacarus lacks eyes), the allothyrid Holothyrida and many Ixodida have a single pair of lateral lenses and the remainder apparently lack eyes (Evans, 1992). Theleyphonida was coded as ‘1/2’ to reflect five pairs of lenses comprising three pairs of primary lenses and two pairs of small accessory lenses (not simply three pairs as coded by Giribet et al., 2002). Trigonotorbida is also coded as ‘1/2’ to reflect three pairs of primary lenses and multiple small accessory lenses. Dunlop (1999) illustrated Haptopoda as having paired triads of lateral eyes but noted that there was actually no evidence of this in the fossils. The lateral eyes of fossil ricinuleids have two pairs of lenses (Selden, 1992). One pair of eyes or eyespots are present in extant Ricinulei and many Schizomida, although five genera of hubbardiid Schizomida have a pair of lenses (Reddell & Cokendolpher, 1995). State 1 is the groundplan for extant Scorpiones, and State 3 occurs in the pseudoscorpions Chthonius, Feaella, Neobisium (but State 4 in Chelifer) and Solifugae (Paulus, 1979).

141. Lateral eyes with closed rhabdoms: 0, absent; 1, present; -, inapplicable due to absence of lateral eyes (139) [WP 21, WH 12, GEWB 6]

Presence of closed rhabdoms is probably primitive for Chelicerata and is retained in extant Xiphosura and Scorpions. Retinula cells form a network of rhabdomeres in other extant chelicerates (Paulus, 1979), but these networks can differ substantially in detail. Weygoldt (1998) and other workers have given substantial weight to the network character in unifying non-scorpion arachnids, but these authors seem not to grant comparable phylogenetic significance to the analogous character of the median eyes shared by Solifugae and Araneae (137).

142. Slit sensilla: 0, absent; 1, present [WP 19, S 47, WH 11, GEWB 209]

State 1 occurs in all arachnid orders except Palpigradi (Shultz, 1990). The proposal that ‘primitive’ slit sensilla were present in Euryptera (Dunlop & Braddy, 1997) appears to be based on the over-interpretation of a comparatively large notch that occurs in Balloeu- rypterus at the terminus of the tibia (= podomere 7) (see also Edgecombe et al., 2000; Giribet et al., 2002).

The neural construction of slit sensilla, like functionally similar campaniform sensilla of hexapods, is similar to that of trichoid sensilla (Chapman, 1998; Klompen, 2000). Thus, these cuticular stress receptors may represent modified bases of sensory setae, a view supported by the replacement of setae by slit sensilla during post-embryonic development in some Opilioacariformes (Klompen, 2000).

143. Trichobothria: 0, absent; 1, present [GEWB 213]

Trichobothria are present in extant Scorpiones (Jeram, 1998), Pseudoscorpiones (Chamberlin, 1931), some endostigmatid Acari: (Alycus): Van der Hammen, 1989) and prostigmatid Acariformes, and most Oribatida (Lindquist, 1984). They occur on the ventral surface of the pedal femora in the opilioacariiform Siamacarus (Leclerc, 1989). They are also present in Araneae (Felix, 1996), Amblypygi (Weygoldt, 2000), Schizomida and Thelyphonida (Hansen & Sørensen, 1985). They are apparently absent in all non-arachnid chelicerates, Solifugae, Ricinulei, Opiliones (Reissland & Görner, 1985) and Parasitiformes (Acari) (Lindquist, 1984).

144. Tibial trichobothria with 2-1-1-1 pattern on appendages III–VI (= arachnid legs 1–4): 0, absent; 1, present; -, inapplicable due to absence of trichobothria (143) [S 48, WH 87, GEWB 88]
State 1 occurs only in Thelyphonida and Schizomida (Hansen & Sørensen, 1905). Note that Shultz (1990) erroneously described this character as a 2-2-1-1 pattern and that this error was repeated by Giribet et al. (2002) and described as 2-1-1 by Wheeler & Hayashi (1998).

145. Paired trichobothria on dorsal surface of prosoma: 0, absent; 1, present; -, inapplicable due to absence of trichobothria (143)

State 1 is an apparent synapomorphy of Acariformes and is present in all acariforms included in this study (Alberti & Coons, 1999).

146. Malleoli: 0, absent; 1, present [WP 45, GEWB 96]

State 1 is a unique synapomorphy of Solifugae (Roewer, 1934).

147. Pectines: 0, absent; 1, present [WP 20, WH 38, GEWB 120]

State 1 is a unique synapomorphy of Scorpiones.

148. Intercheliceral median organ: 0, absent; 1, present [GEWB 212]

State 1 is a unique synapomorphy of Palpigradi (Roewer, 1934).

149. Tarsal organ on appendage of postoral somite III (= arachnid leg 1) (= Haller’s organ): sensilla contained within a cuticular depression on the superior surface of the tarsus of appendage III (= arachnid leg 1): 0, absent; 1, present. [GEWB ~100]

Kломpen (2000) has noted that State 1 occurs in Opiliaoacariformes, Parasitiformes (except Mesostigmata) and Ricinulei, where it also occurs on leg 2 (Talarico et al., 2005). State 1 occurs on all legs in Araneae and, perhaps, Scorpiones (Foelix, 1985).

150. Tarsal organ on appendage of postoral somite IV (= arachnid leg 2): 0, absent; 1, present. (See 149)

**REPRODUCTION**

151. Gonads: 0, primarily prosomal; 1, primarily opisthosomal.

State 0 is limited to Xiphosura (Sekiguchi, 1988); State 1 occurs throughout Arachnida (Millot, 1949a).

152. Ladder-like opisthosomal gonads/accessory glands (see 153): 0, absent; 1, present [WH ~37, GEWB ~158]

Giribet et al. (2002) followed Wheeler & Hayashi (1998) who followed Clarke (1979) in coding gonads as reticulate (Xiphosura), ladder-like (Scorpiones, Thelyphonida, Schizomida) or ‘saccular’ (all remaining Arachnida). However, comparisons between Xiphosura and Arachnida are problematic given that the xiphosuran gonads are primarily prosomal and those of arachnids are primarily opisthosomal (151). Further, the reticulate pattern in Limulus (Xiphosura), but not other extant xiphosurans, contains a distinctly ladder-like component. The ‘saccular’ state is probably artificial, as it encompasses a wide variety of paired and unpaired structures.

153. Male gonads in two distinct parts, one producing sperm and another (tubular gland) producing a holocrine secretion similar to degenerate sperm: 0, absent; 1, present.

State 1 occurs in Thelyphonida, Schizomida and Amblypygi, although the holocrine material is produced by ventral organs in Amblypygi and dorsal organs in Thelyphonida and Schizomida (Alberti, 2005).

154. Number of gonopores: 0, two; 1, one.

Extant xiphosurans have two small genital openings on the base of the genital telopodite, and all extant arachnids have a single opening. The condition in Eurypterida is not known. Clarke & Ruedemann (1912) located a pair of openings near the base of the median organ (161) that are the outlets of the ‘horns’, but it is unclear whether these are genital ducts or accessory structures. Braddy & Dunlop (1997) have developed numerous speculations about these structures and extended their arguments far beyond the available evidence.

155. Genital opening (i.e. gonopore or gonostome) appearing to open in prosomal region (i.e. between leg coxae or anterior to posterior carapacal margin): 0, absent; 1, present [WP ~50, WH 26, GEWB 166]

The genital opening in Euchelicerata is located on postoral somite VIII (= opisthosomal somite 2), but it has shifted anterior to the posterior margin of the carapace or between the coxae of the last pair of legs in most Scorpiones (but not in Palaeoscorpius: Kjellesvig-Waering, 1986) and Opiliones. The genital opening occurs near or anterior to the last coxae in the opilioacariform and parasitiform Acari represented here. It is variable in Acariformes but is located posterior to the coxae in all representative taxa.

156. Ovipositor: 0, absent; 1, present [WP ~51, S ~60, WH ~91, GEWB ~172]

An ovipositor with a trilobed terminus is an apparent groundplan character of Oribatida (Lindquist, 1984; Alberti & Coons, 1999). An ovipositor is also present in Opilioacariformes and Opiliones (Van der Hammen, 1989).

157. Stalked spermatophore attached to substratum: 0, absent; 1, present [S 57]

State 1 occurs in Scorpiones, Pseudoscorpiones, Amblypygi, Thelyphonida and Schizomida. The mechanism of sperm transfer is unknown in Palpigradi, Opilioacariformes and Holothryridia.

158. Male turns posterior end toward female during mating behaviour: 0, absent; 1, present.

State 1 occurs in Amblypygi (Weygoldt, 2000), Thelyphonida and Schizomida (Weygoldt & Paulus, 1979).
159. Female grasps male opisthosoma during mating behaviour: 0, absent; 1, present [WP 29, S 58, WH 19, GEWB 188]
State 1 occurs in Thelyphonida and Schizomida (Weygoldt & Paulus, 1979). Evolution of this behaviour was probably facilitated by 158.

160. Penis: 0, absent; 1, present [WP ~51, GEWB 167]
State 1 is a unique synapomorphy of Opiliones. A true penis occurs in Phalangida. A clearly homologous structure is present in Cyphophthalmi (Opiliones) and apparently functions in depositing a spermatophore in the female’s genital chamber (Karaman, 2005). A true penis may occur in some mites, but it does not appear to be a groundplan feature of any major group (Evans, 1992). The ‘penis’ in Oribatida is really a spermatophore: it functions in construction of a spermatophore (Alberti & Coons, 1999).

161. Median organ: 0, absent; 1, present
State 1 occurs throughout Eurypterida (Clarke & Rue-demann, 1912) and has been observed in diplopodid Chasmataspidida (Dunlop, 2002a; also Loganamaras-pis: Tetlie & Braddy, 2004).

SPERM MORPHOLOGY

162. Nucleus with manchette of microtubules: 0, absent; 1, present [S 54, WH 89, GEWB 193]
State 1 occurs in Araneae, Amblypygi, Thelyphonida, Schizomida, Ricinulei and gonyuleptid Lani- atores (Opiliones) (Alberti, 1995; Giribet et al., 2002).

163. Axoneme: 0, absent; 1, present [WP ~49, S ~55, WH ~25, GEWB 195]
State 1 occurs in Xiphosura, Scorpiones, Cyphophthal mi (Opiliones), Pseudoscorpiones, Ricinulei, Araneae, Amblypygi, Thelyphonida and Schizomida (Alberti, 1995).

164. Coiled axoneme: 0, absent; 1, present; -, inapplicable due to absence of axoneme (163) [WP 22, S ~55, WH 13, GEWB 196]
State 1 occurs in Pseudoscorpiones, Ricinulei, Araneae, Amblypygi, Thelyphonida and Schizomida (Alberti, 1995).

165. Microtubule arrangement in axoneme: 0, 9 + 0; 1, 9 + 1; 2, 9 + 2; 3, 9 + 3; -, inapplicable due to absence of axoneme (163) [WP ~26, S ~56, WH ~16, GEWB 198] (Alberti, 1995)

166. Helical or corkscrew shaped nucleus: 0, absent; 1, present [GEWB ~204]
State 1 occurs in Araneae, Amblypygi, Thelyphonida, Schizomida and certain Scorpiones (e.g. Hadrurus) (Alberti, 1995).

167. Vacuolated-type sperm: 0, absent; 1, present [GEWB 205]
State 1 is unique to Opilioacariformes and Parasiti-formes (Acari) (Alberti, 1995).

168. Sperm aggregates: 0, absent; 1, present [GEWB 206] (Alberti, 1995)

DEVELOPMENT

169. Yolk in early embryo: 0, concentrated (centrolec-thal or telolecithal); 1, evenly distributed (isolecithal). [WH ~34, GEWB ~191]
Wheeler & Hayashi (1998) and Giribet et al. (2002) coded this character as ‘0, isolecithal or telolecithal; 1, centrolecithal’ based on information presented by Yoshikura (1975). Their coding appears to highlight separate conditions found in Scorpiones (i.e. isolecithal and telolecithal) rather than a property intrinsic to the character itself.

170. Embryonic nutrition other than yolk: 0, absent; 1, present [WP ~49]
State 1 occurs in extant Scorpiones (except buthids and chaerilids) and Pseudoscorpiones (Weygoldt, 1969).

171. Embryological growth zone: 0, initiating segment addition within prosoma; 1, initiating segment addition posterior to prosoma [GEWB ~192]
Giribet et al. (2002) followed Dunlop & Webster (1999) in stating that only Xiphosura and Scorpiones have state 0 among Chelicerata. However, the last prosomal somite develops from the growth zone in Ixodida (Anderson, 1973; Evans, 1992). A similar process apparently occurs in the acariform mites Tyrophlyphus (Sarcoptiformes, Astigmata) (Yoshikura, 1975) and Archeogozetes (Sarcoptiformes, Oribiathida) (Thomas & Telford, 1999) but not apparently in Tetranychus (Prostigmata) (Dearden, Donly & Gribi, 2002).

172. Eggs/embryos maintained in external, attached brood sac secreted by genital glands: 0, absent; 1, present [WP ~46, S 59, WH 90, GEWB 208 ~219]
State 1 occurs throughout Ambylypygi, Schizomida, Thelyphonida and Pseudoscorpiones. Giribet et al. (2002) followed Shear et al. (1987) in homologizing spinneret-derived silken egg sacs of spiders with genital-gland-derived brood sacs of Pedipalpi. However, as these structures are not homologous in secretory origin, construction or composition (Shultz, 1987), they are not regarded here as homologous. Giribet et al. (2002) miscoded the character as absent in Pseudo-scorpiones and, without justification, in Palpigradi. Female palpigrades have well-developed glands associated with postgenital somites and an array of setae, fusules and other structures (112) (Börner, 1902b; Millot, 1942; Condé, 1991a), which are consistent with some sort of brood care, and Palpigradi should therefore be coded as unknown for this character.

173. Embryonic and early postembryonic ‘lateral’ or Claparède organs associated with coxa of postoral somite IV (= arachnid leg 2): 0, absent; 1, present [WH ~31, GEWB ~211]
Bilaterally paired, rounded protuberances located between coxae of appendages of postoral somites III and IV (arachnid legs 1 and 2) in prelarval and larval instars appear to be a primitive feature of Acariformes (Lindquist, 1984; Evans, 1992; Alberti & Coons, 1999). It is known to be derived embryologically from the coxa of leg 2 in the oribatid *Archegozetes* (Thomas & Telford, 1999). Structures apparently homologous with the acariform Claparède organ are present in embryonic Amblypygi (Weygoldt, 2000) and Thelyphonida (Yoshikura, 1975) and in embryonic and early post-embryonic stages of Solifugae (Roewer, 1934), where they are termed lateral organs. The so-called 'lateral organ' of embryonic *Xiphosura* (174) occurs on the lateral surface of the carapace and does not appear to be homologous with the coxa-associated structures sharing their name. In fact, the xiphosuran lateral organ develops even when the coxa of postoral somite IV has been excised (Sekiguchi, 1988). In contrast, Wheeler & Hayashi (1998) and Giribet et al. (2002) followed Yoshikura (1975) in regarding all 'lateral organs' as homologous and in miscoding this character as absent in Acariformes. Van der Hammen (1989) suggested that the sternal verrucae of Opilioacariformes are homologous with the Claparède organ, but it differs in gross structure and ontogenetic timing. 174. Embryonic lateral organ associated with carapace: 0, absent; 1, present [WH = 31, GEWB = 211] State 1 is known only from embryonic stages of extant *Xiphosura* (Yoshikura, 1975). In contrast to previous interpretations, this feature does not appear to be homologous with the 'lateral' or Claparède organ of certain arachnids (173).

175. Live birth: 0, absent; 1, present.
State 1 occurs in extant Scorpiones and has evolved several times in a few mites (Evans, 1992).


177. Hexapodal prelarva: 0, absent; 1, present [S = 61, WH 47] State 1 occurs in Opilioacariformes (Neocaracaridae; Klompen, 2000) and many Acariformes (Evans, 1992).

**EXCRETORY/OSMOREGULATORY SYSTEM**

178. Malpighian tubules: 0, absent; 1, present [WP 17, S = 62, WH 9, GEWB 153] State 1 occurs in all major arachnid groups except Palpigradi, Pseudoscorpiones, Opiliones, Oribatida (Sarcoptiformes) and Prostigmata. Within Acari, State 1 occurs in all major anactinotrichid lineages (Opilioacariformes, Holothyrida, Mesostigmata, Ixodida), and similar structures are present in certain Astigmata (Evans, 1992; Alberti & Coons, 1999).

179. Dorsomedian excretory organ: 0, absent; 1, present.
This is a specialized excretory/osmoregulatory organ formed by the postventriculus and proctodeum in Prostigmata (Alberti & Coons, 1999).

180. Adult coxal organ opening on or near coxa of appendage III (= arachnid leg 1): 0, absent, 1, present [S = 64, WH 93, GEWB 90] State 1 occurs throughout Acari (Evans, 1992; Alberti & Coons, 1999), Ricinulei (Pittard & Mitchell, 1972; Legg, 1976), Palpigradi (Millot, 1942), Araneae, Amblypygi, Thelyphonida and Schizomida (Buxton, 1913, 1917). There is evidence that the second ‘ozo pore’ of gonyleptids (Opiliones, Laniatores) (Hara & Gnaspini, 2003) is a persistent opening to the coxal organ associated with leg 1 (Sørensen, 1879), which also occurs in embryonic *Phalangium* (Opiliones, Eupnoi) (Moritz, 1959).

181. Adult coxal organ opening on or near coxa of appendage V (= arachnid leg 3): 0, absent; 1, present [S = 63, WH 92, GEWB 89] State 1 occurs in extant *Xiphosura* (Yamasaki et al., 1988), Scorpiones, mygalomorph (Buxton, 1913, 1917) and mesothele Araneae (*Liphistius*: J. Millot in Bristowe, 1932). State 1 occurs in basal Amblypygi (Charon, Charinus: Buxton, 1913, 1917) but degenerates prior to the adult stage in higher groups (*Phrynus*: Weygoldt, 2000). Adequately preserved eurypterids show a small submarginal opening on the coxa of appendage V (*Baltoeurypterus*: Selden, 1981; also *Eurypterus*, *Hughmilleria*: Clarke & Ruedemann, 1912) and this is interpreted here as the opening to a coxal organ. Giribet et al. (2002) coded this character as uncertain for Eurypterida.

182. Adult coxal organ opening on coxa of appendage II (= arachnid palp): 0, absent; 1, present [GEWB 65] Buxton (1913, 1917) noted that the coxal organ of Solifugae opens on the prolateral surface of the palpal coxa. The proximal end of the duct leading to the orifice is associated with glands and, apparently, the glandular secretion and/or coxal fluid serve as saliva (Alberti, 1979) (see also 14, 15).

183. Genital papillae: 0, absent; 1, present; -, inapplicable, coded only for those taxa with eversible 'appendages' (111). The genital papillae are associated with the genital opening in postlarval *Acariformes* (Evans, 1992; Alberti & Coons, 1999). These structures are probably serially homologous with the prosomal Claparède organ (173), and both structures probably function in water and ion regulation.

**DIGESTIVE SYSTEM**

184. Ingestion: 0, solid food; 1, primarily liquid food, with or without preoral digestion [WP = 16, WH = 8, GEWB = 218]
Extant xiphosurans ingest solid food, and members of most extant arachnid orders ingest fluids. Opiliones and Acari are the principal exceptions. The phalangid Opiliones ingest solids, but Shultz (2000, unpubl. observ.) has shown that the precerebral pharyngeal apparatus of Cyphophthalmi is very similar to that of the fluid-feeding Scorpiones and differs substantially from phalangid Opiliones. Examination of gut contents of the cyphophthalmids Siro acaroides, S. exilis and Chilegovea eodipus have failed to reveal solid particles typically found in the guts of phalangids (Shultz, unpubl. observ.); the character is coded as unknown for Cyphophthalmi. Within Acari, consumption of particles has been documented in Opilioacariformes (Neocarid: Van der Hammen, 1989; unidentified: Walter & Proctor, 1998), Holothryrida, non-parasitic Sarcoptiformes (Evans, 1992; Walter & Proctor, 1998; Alberti & Coons, 1999) and many endo-stigmatids, including the nematophagous Alycus roseus (Walter, 1988).

185. Mouth: 0, directed posteroventrally; 1, directed anteroventrally [S 9, WH 55, GEWB 28] State 1 occurs throughout Arachnida (Shultz, 1990).

186. Oral cavity dilated by muscles arising from coxae and constricted by large circular sphincter: 0, absent; 1, present. State 1 occurs in extant Xiphosura (Manton, 1964; Scholl, 1977; Shultz, 2001).

187. Palate plate: 0, absent; 1, present [GEWB 159] State 1 is a unique synapomorphy of Araneae (Dunlop, 1994).

188. Lateral walls of epistome broadly fused to medial walls of palpal coxae, opposite sides connected by well-developed transverse epistomal muscle: 0, absent; 1, present. State 1 occurs throughout Opiliones and Scorpiones (Shultz, 2000; unpubl. observ.).

189. Epistome with a pair of lateral arms that projects posteriorly into the prosoma on either side of the pharynx: 0, absent; 1, present. State 1 occurs in Scorpioidea, Palpigrada and Opiliones (Shultz, 2000).

190. Epistome with four pairs of suspensor muscles attaching to the carapace: 0, absent; 1, present. State 1 occurs in extant Scorpiones (Lankester et al., 1885; Vyas, 1970; Shultz, unpubl. observ.) and apparently in Solifugae (Roewer, 1934).

191. Intercheliceral epipharyngeal sclerite: 0, absent; 1, present. [GEWB 31] State 1 occurs in Palpigradi (Börner, 1904), Trigonotarbida (Palaeocharina: Dunlop, 1994), Araneae (Firstman, 1954; Marples, 1983), Amblypygi (Milot, 1949b; Shultz, 1999), Schizomida (Milot, 1949e), Thelyphonida (Milot, 1949e; Shultz, 1993) and Phalangida (Opiliones) (Shultz, 2000; unpubl. observ.)


193. Dorsal dilator muscle of precerebral pharynx attaching to intercheliceral septum or associated epipharyngeal sclerite (191): 0, absent; 1, present. State 1 occurs in Palpigradi (Milot, 1943), Araneae (Marples, 1983), Amblypygi, Schizomida and Thelyphonida (Milot, 1949e; Shultz, 1993, 1999). Extremely fine muscles have been documented in some Scorpiones (Shultz, 2007) and in Leiobunum (Opiliones) (Shultz, 2000). Lankester et al. (1885) reported a muscle in Limulus that would appear to correspond to this muscle, but the muscle does not exist (Manton, 1964; Shultz, 2001).

194. Dorsal dilator muscle of precerebral pharynx attaching to dorsal surface of prosoma: 0, absent; 1, present. [GEWB 228] State 1 occurs in Palpigradi (Roewer, 1934) and most Araneae (Palmgren, 1978; Aphonopelma: Firstman, 1973) but not in Heptathela (coded as Liphistius) or Hypochilus (Marples, 1983).

195. Lateral dilator muscle of precerebral pharynx attaching to endosternite: 0, absent; 1, present. [GEWB 226] State 1 is a unique feature of Araneae (Marples, 1983).

196. Lateral dilator muscle of precerebral pharynx attaching to lateral surface of epistomal processes: 0, absent; 1, present. [GEWB 38] State 1 occurs in Scorpioidea and Opiliones (Shultz, 2000).

197. Lateral dilator muscle of precerebral pharynx attaching to medial process of coxa of appendage II (= arachnid palp): 0, absent; 1, present. [GEWB 226] State 1 occurs in Amblypygi, Thelyphonida and Schizomida (Börner, 1904; Shultz, 1993, 1999).

198. Dilator muscle of precerebral pharynx and/or preoral cavity attaching to ventral surface of prosoma: 0, absent; 1, present. [GEWB 227] State 1 occurs in extant Xiphosura (Manton, 1964; Shultz, 2001), Araneae (Marples, 1983), Palpigradi (Milot, 1943) and Solifugae (Roewer, 1934).

199. Postcerebral pharynx: 0, absent; 1, present. [WP 31–31, S –5, WH –21, GEWB 154] The cuticle-lined foregut passes through the central nervous system in many arthropods. That portion posterior to the CNS is here termed the postcerebral pharynx, regardless of the details of its morphology or functional specialization. A substantial postcerebral pharynx is known in extant Xiphosura (Lankester...
et al., 1885; Manton, 1964; Yamasaki et al., 1988), Scorpiones (Centruroides, Hadrurus, Heterometrus: Shultz, 2007; also Androctonus: Abd el-Wahab, 1952), Solifugae (Millot & Vachon, 1949), Araneae, Amblypygi, Thelyphonida and Schizomida (Millot, 1949a–e; Shultz, 1993). Weygoldt & Paulus (1979) applied the term ‘postcerebral pharynx’ only to the ‘sucking stomach’ of Araneae and Amblypygi, but the sucking stomach is here regarded as a complex of three characters, 199–201.

200. Dilator muscle of postcerebral pharynx attaching to endosternite: 0, absent; 1, present; -, inapplicable due to absence of postcerebral pharynx (199). State 1 occurs in extant Xiphosura (Lankester et al., 1885; Manton, 1964; Shultz, 2001), Scorpiones (Centruroides, Hadrurus, Heterometrus: Shultz, 2007; also Androctonus: Abd el-Wahab, 1952), Araneae (Firstman, 1954; Palmgren, 1978), Amblypygi (Millot, 1949b; Shultz, 1999) and apparently the palpigrade Prokoenenia wheeleri (Rucker, 1901) but not in Eukoenenia mirabilis (Millot, 1943; contra Börner, 1904).

201. Dilator muscle of postcerebral pharynx attaching to dorsal surface of prosoma: 0, absent; 1, present; -, inapplicable due to absence of postcerebral pharynx (199). State 1 occurs throughout Araneae (Millot, 1949c; Firstman, 1954; Palmgren, 1978) and Amblypygi (Charinus: Millot, 1949b; Phrynus: Shultz, 1999).

202. Crop and gizzard: 0, absent; 1, present; -, inapplicable due to absence of postcerebral pharynx (199). State 1 occurs in extant Xiphosura (Sekiguchi, 1988) but not in extant Arachnida.