

A phylogenetic analysis of the arachnid orders based on morphological characters

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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 (Trigonotarbitida (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). The Lyphonida 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

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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 sunspiders, 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), Megopericulata (= 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, *Limuloides 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

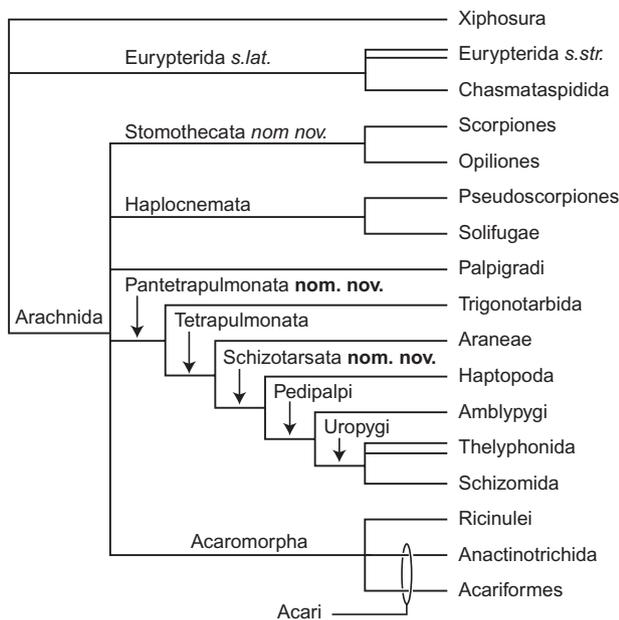


Figure 1. Cladogram summarizing results from analysis of major euchelicerate lineages generated by parsimony analysis of 59 genera and 202 non-molecular characters. Only those relationships that were well supported by bootstrap analysis or consistently recovered in sensitivity analysis are depicted; deepest relationships within Arachnida are effectively unresolved.

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]

<i>Weinbergina</i> *							
00010-0?11	0?????0???	????-?????	?????-????	?????0?00?	???????????	???????????	
???????????	?1?0-?0001	0???300000	0?????-???	?-?1210-0	?????-?????	???????????	
???????????	???????????	???????????	???????????	???????????	???????????	??	
<i>Limuloides</i> *							
00010-0?11	0?????1???	????-?????	?????-????	???????????	???????????	???????????	
???????????	???????????	???300000	0?????-???	?-?1210-0	?????-?????	???????????	
???????????	???????????	???????????	???????????	???????????	???????????	??	
<i>Euproops</i> *							
00010-0?11	0?????1???	????-?????	?????-????	???????????	???????????	???????????	
???????????	???????????	???200010	0?????-???	?-?1010-0	?????-?????	?????1????	
???????????	???????????	???????????	???????????	???????????	???????????	??	
<i>Limulus</i>							
10010-0011	0000-01000	0000-00000	-0010-0000	0010000000	011?110001	0100010021	
0001011011	000--01101	1000200010	000110-000	00-?0010-0	01110-0110	0106112110	
100--00000	0000000000	0010200000	0001000000	10-0010000	0-00000111	01	
<i>Tachypleus</i>							
10010-0011	0000-01000	0000-00000	-0010-0000	0010000000	011?110001	0100010021	
0001011011	000--01101	1000200010	000110-000	00-?0010-0	01110-0110	0106112110	
100--00000	0000000000	0010000000	0001000000	10-0010000	0-00000111	01	
<i>Baltoeurypterus</i> *							
00000-0?11	000?000000	0??-?????	-0000-???	0010000010	011?000?0?	0?011-0020	
00000?????	?100-00001	00??5000-0	0????0-0?	?0-?0310-0	??01-?????	?????1?010	
??-00000	????0?????	1?????????	???????????	1????0?0???	0-?????????	??	
<i>Stylonurus</i> *							
00000-0?11	000?000000	????-?????	-0?00-???	001000000?	01??000?0?	0?011-00?0	
0??00?????	?1?0-?0001	00??5000-0	0????0-0??	?0-?0310-0	??01-?????	?????1?010	
?????000??	????0?????	1?????????	???????????	???????????	???????????	??	
<i>Chasmataspis</i> *							
00000-0?11	0?????1???	????-?????	?????-????	???????????	?1?????????	???????????	
???????????	?????????0?	1??6?01-0	0?????-???	?-?1410-0	?00?-?????	?????1?1?	
?????0?????	????0?????	???????????	???????????	???????????	???????????	??	
<i>Diploaspis</i> *							
000?0-0?1?	0?????1???	????-?????	?????-????	?????????1?	???????????	???????????	
???????????	?????0001	0??6?01-0	0?????-???	?-?0410-0	?00?-?????	?????1?1?	
???????????	????0?????	???????????	???????????	???????????	???????????	??	
<i>Octoberaspis</i> *							
00?10-0?1?	0?????1???	????-?????	?????-????	?????????1?	???????????	???????????	
???????????	?????0?0?	??6?01-0	0?????-???	?-?0410-0	?00?-?????	?????1?1?	
???????????	????0?????	1?????????	???????????	???????????	???????????	??	
<i>Prokoenenia</i>							
0000110000	0010-00000	0000?00000	-0000-???	00100?0000	0000000?01	1000000020	
00000110??	0101000001	001?4000-0	000001-010	10-?021201	0000001?0?	?10310-00-	
-010000100	100100???	000--000??	????????001	0001100000	1011000111	00	
<i>Eukoenenia</i>							
0000110000	0010-00000	0000000000	-0000-0000	00100?0000	0000000001	1000000020	
00000?1011	0101000001	00104000-0	000001-010	00--021201	0000001?00	110310-00-	
-010000100	100100???	000--000??	????????001	0001100000	101100010-	--	
<i>Plesiosiro</i> *							
00110-0?00	00?????????	????-?????	-????-????	0??????000	000?0?0???	?000?0?0??	
0???????????	?1?10?00??	0??A?00-0	0??01?0?0	?0--00?--1	???????????	?????1????	
?????00???	????0?????	0?????????	???????????	???????????	???????????	??	

Table 1. Continued

*Palaeocharinus**

00000-0000 001??00110 0??????000 -0?00-??00 001?00?000 000?000?0? 0?000?002?
 02--0????? ?100-?0001 0???4100-1 0???0100?0 10--110--1 110000???? ????1?01B
 ?1???000?? ????0????? 0????????? ?????????? ?????1?0??? 11???????? ??

*Gilboarachne**

00000-0000 00????00110 ???????000 -0?00-??00 00????0?000 000?000?0? 0?????002?
 02--0????? ?100-?0001 0???4100-1 0???0100?0 ?0--110--1 110000???? ????1?01B
 ?1???000?? ????0????? 0????????? ?????????? ?????????? ?????????? ??

Liphistius

00000-0000 0011000110 0000001000 -0000-0000 0110000000 0000000110 0000010022
 0010011011 0100-00001 00115010-0 0000010010 1101000--1 1100001000 0003011012
 0110000011 1001000000 0111310000 1000000101 1001101000 1110100111 10

Aphonopelma

00000-0000 0011000110 0000001000 -0000-0000 0110000000 0000000110 0000010022
 0010011011 0100-00001 00115010-0 0000011010 1110000--1 1100001000 0003111012
 0110000011 1001000000 0111310000 1000000101 1001101000 1011100111 10

Hypochilus

00000-0000 0011000110 0000001000 -0000-0000 0110000000 0000000110 0000010022
 0010011011 0100-00001 00115010-0 0000011010 1110000--1 1100001000 0003011012
 0110000011 1001000000 0111310000 1000000101 ?001101000 1110100111 10

Charinus

00100-0000 0011000110 0000100000 -000100?01 0010010000 000?001011 0000010023
 1000101011 0101100000 01105000-0 0000010000 10--020--1 1100001000 1015010012
 01100000?? 1011001100 0111310000 1110000101 1001100000 1110001011 10

Phrynus

00100-0000 0011000110 0000100000 -000100101 0000-10000 0001001011 0000010023
 1000101011 0101100000 00105000-0 0000010000 00--020--1 1100001000 1015010012
 01100000?? 1011001100 0111310000 1110000101 00-1100000 1110001011 10

Stenochrus

0010110000 0211000110 0000?00001 0000110100 0010010000 0000001?11 0000010123
 0000001011 0101100000 00115000-0 0100010000 00--021211 1000001001 ?01410-014
 ?111000000 1111001110 0111310000 11?0000101 00-1100000 11100010?0 00

Protoschizomus

0010110000 0211000110 0000?00001 000011?000 0010010000 000?00??11 00000?0123
 00000????? 0101100000 001?5000-0 0100010000 00--021211 100000100? ?0?5?0-00-
 -111000000 11?1001110 0111310000 11?0000101 00-1100000 1??00010?0 00

Mastigoproctus

00110-0000 0211000110 0000100001 0000100100 000--10000 0001001111 0000010123
 0000001011 0101100000 00115000-0 0100010000 00--021201 1100001001 101511001B
 0111000000 1111001110 0111310000 1110000101 00-1100000 1110001010 00

*Proschizomus**

00100-0?00 02????001?? ??????????1 00??1?????0 00???10000 000??0???? ???? ??????
 ?????????? ????1?00?? 0???5000-0 0???0100?0 ?0--0212?1 ??0???????? ??????????
 ??????00???? ????0????? 0????????? ?????????? ?????????? ?????????? ??

*Terpsicroton**

00000-0?00 1?????0??? ????-????? ????0-????? 0?????0?000 000??0???? ??011??0??
 ?????????? ???????0?? 0???51?0-0 1???00-??? ??--120--1 ??0???????? ??5?0-?13
 ??????00???? ?????????? 0????????? ?????????? ?????????? ?????????? ??

*Poliocera**

00000-0?00 1?????0??? ????-????? ????0-????? 0?????0?000 000??0???? ??011??0??
 ?????????? ???????0?? 0???51?0-0 1???00-??? ??--120--1 ??0???????? ??5?0-?13
 ??????00???? ?????????? 0????????? ?????????? ?????????? ?????????? ??

Table 1. Continued

<i>Cryptocellus</i>						
00000-0000	1211000100	0??0-00001	?0000-0?00	0010001000	000?000001	0001100020
02--000-11	0101000001	00105120-0	100000-000	00--120--1	000003????	?1?500-014
?10-000011	1001000??0	01112000?0	?0??010101	00-1100000	0-0000000-	--
<i>Ricinoides</i>						
00000-0000	1211000100	0??0-00001	?0000-0?00	0010001000	000?000001	0001100020
02--000-11	0101000001	00105120-0	100000-000	00--120--1	000003????	?1?500-014
?10-000011	1001000??0	01112000?0	?0??010101	00-1100000	0-0000000-	--
<i>Neocarus</i>						
00001-0000	0011000020	0000-00001	10100-0?00	0010010000	000?000?01	00011?1120
02--0??0??	0101000011	011?4000-0	000000-000	00--000--1	000005????	????00-013
010--00010	100111????0	000--01000	????011101	00-0100000	0-0000000-	--
<i>Siamacarus</i>						
00001-0000	0011000020	0000-00001	1?100-0?00	0010010000	000?000?0?	0?011?112?
02--0??0??	?1010?0011	01??4000-0	000000-000	00--000--1	000005????	????00-012
?110000010	1?0111????0	0?0--?1?0?	????01?101	??-0100000	0-0????????	--
<i>Australothyrs</i>						
01000-0100	0001000020	0000-00001	10100-0?00	0011000000	000?000?0?	0?000?1020
02--0??0??	0?10-00011	01????000-0	000000-100	00--000--1	000003????	????00-014
?10--00010	100110????0	000--01000	????0?101	00-1100000	0-000?????	--
<i>Allothyrs</i>						
01000-0100	0011000020	0000-00001	10100-0?00	0011000000	000?000?0?	0?000?1020
02--0??0??	0?10-00011	01????000-0	000000-100	00--000--1	000003????	????00-00-
-10--00010	1?0110????0	0?0--?1?0?	????0?101	00-1100000	0-0????????	--
<i>Glypholaspis</i>						
01000-0000	0011000020	00?0-00001	10100-0?00	0011000000	000?000001	0000001020
02--011011	0?10-00011	0110?000-0	000000-000	00--000--1	000003????	????00-00-
-10--00000	1001100000	000--01000	?000010101	00-1100000	0-0000000-	--
<i>Amblyomma</i>						
00000-0000	0000-00020	0000-00001	10000-0?00	000--00000	000?000001	0000001020
02--011011	0?10-00011	01100000-0	000000-000	00--000--1	000003????	?1??00-014
010--00010	1001100000	000--01000	0000010101	00-1100000	0-0000000-	--
<i>Argas</i>						
00000-0000	0000-00020	0000-00001	10000-0?00	000--00000	000?000001	0000001020
02--011011	0?10-00011	00100000-0	000000-000	00--000--1	000003????	?1??00-014
010--00010	1?01100000	0?0--?1?0?	0000010101	00-1100000	0-0??0000-	--
<i>Alycus</i>						
00000?1000	0001100?20	0?00-00001	10100-0?00	000--00000	000?000001	00001?0020
02--0??011	000--00011	00101000-0	000000-001	10--000--1	000000????	????00-013
?110100000	1?0100????	0????????0?	????011??1	0010100000	0-0?????00-	--
<i>Allothrombium</i>						
0000????000	0001100?20	0?0?-00001	10000-0?00	000--00000	000?000001	00111-0020
02--011011	000--00011	0010?000-0	000000-001	10--000--1	000004????	????00-013
0110100000	1001001000	000--00000	?010011011	0011100000	0-0000000-	--
<i>Microcaeculus</i>						
0000??0000	0001100?20	0?0?-00001	10000-0?00	000--00000	000?000001	00111-0020
02--011011	000--00011	0010?000-0	000000-001	10--000--1	000004????	????012013
0110100000	1001001??0	0?0--00?00	?01001?011	001?100000	0-0000000-	--
<i>Palaeacarus</i>						
00001?1000	0401100?20	0?00-00001	10100-0?00	000--00000	000?000001	00111-0020
02--011011	000--00011	0010?000-0	000000-001	10--000--1	000000????	????01?0??
?110100000	1?01011000	0?0--?0?0?	?010011001	0010100000	0-0??0000-	--

Table 1. *Continued*

Archegozetes

00001?1000 0401100?20 0?00-00001 10100-0?00 000--00000 000?000001 0000000020
 02--011011 000--00011 0010?000-0 000000-001 10--000--1 000000???? ????00-00- -
 110100000 1001011000 000--00000 0010011001 0010100000 0-0000000- --

Cyphophthalmus

0000100100 0100-00000 10?0-00000 -0000-1000 0010000001 1000000001 0000000020
 01--010-11 0100-00001 00112000-0 000000-000 00--0013-1 000001?000 01010??0??
 ?10--00000 1001110001 001100010? ?0??000000 10-?100110 0-0001000- --

Chileogovea

0000100100 0100-00000 1010-00000 -0000-1000 0010000001 1000000001 0000000020
 01--010-11 0100-00001 00112000-0 000000-000 00--0013-1 000001?000 01010??0??
 ?10--00000 1001110001 0????00?0? ?0??000000 10-?100110 0-0001000- --

Caddo

0000100100 0000-00000 10?0-00000 -0000-?000 0010000001 1000000001 0000000010
 01--012011 0101010001 00112000-0 000000-000 00--0013-1 000001?000 010101?00-
 -10--00000 10-1110001 0????00000 ?0??000000 10-0100110 10?001000- --

Leiobunum

0000100100 0000-00000 1010-00000 -0000-0000 0010000001 1000000001 0000000010
 01--012011 0101010001 00112000-0 000000-000 00--0013-1 000001?000 010B01C00-
 -10--00000 1001110001 000--00000 1000000000 10-0100110 101001000- --

Sclerobunus

0000000100 0000-00000 10?0-00000 -0001-?000 0010000001 1000000001 0000000010
 01--012011 0101010001 00112000-0 000000-000 00--0013-1 000001?000 010001C00-
 -10--00000 1001110001 0?0--00000 1000000000 10-0100110 10?001000- --

Gonyleptes

0000000100 0000-00000 1010-00000 -0001-?000 0010000001 1000000001 0000000010
 01--012011 0101010001 00112000-0 000000-000 00--0013-1 000001?000 010001C00-
 -10--00000 1001110001 010--00000 100000000? 10-0100110 10?001000- --

Centruroides

0000100000 0100-10000 0111-00000 -0000-1000 100--00001 1000000001 0000010010
 01--012110 0100-10001 00116000-0 001000-000 00--0311-1 0011001000 0005110011
 1110001011 1101101000 0010110100 0000100100 10-1100111 0-10010011 00

Hadrurus

0000100000 0100-10000 0111-00000 -0000-1000 100--00001 1000000001 0000010010
 01--012110 0100-10001 00116000-0 001000-000 00--0311-1 0011001000 0005110011
 1110001011 1101101000 0010110111 0000100100 10-1100111 0-10010011 00

Heterometrus

0000100000 0100-10000 0111-00000 -0000-1000 100--00001 1000000001 0000010010
 01--012110 0100-10001 00116000-0 001000-000 00--0311-1 0011001000 0005110011
 1110001011 1101101000 00102?0111 0000100100 10-1100111 0-10010011 00

*Prearcturus**

0000100?00 01????0??? ?????-????0 -0?00-???? 100--00??1 000??????? ??????????
 ??????????? ??????????? ??????000-0 0????0-??? ??--0311-? ??????????? ???????????
 ??????0???? ??????????? 0?????????? ??????????? ??????????? ??????????? ??

*Palaeoscorpius**

0000?00?00 0D????0??? ?????-????0 -0?00-???? 100--0000? 0????0???? ??000?00??
 0?????????? ?1?0-?0001 0???6000-0 0????00-0?0 ??--0311-? ??????????? ??????1????
 ??????01??? ?????0????? 0?????????? ??????????? ??????????? ??????????? ??

*Stoermeroscorpio**

0000?00?00 00????000? ?????-????0 -0?00-???? 100--0000? 0????0???? ??000?00??
 0?????????? ?1?0-?0001 0???6000-0 0????00-0?0 ??--0311-? ??????????? ??????1???10
 ??????01??? ?????1????? 0?????????? ??????????? ??????????? ??????????? ??

Table 1. Continued

*Proscorpius**

0000?00?00 00????000? ????-????? -0?00-???? 100--0000? 01????0???? ??000?00??
 0????????? ?1?0-?0001 0??6000-0 0???00-0?0 ??--0311-? ?????????? ??????1??10
 ??????01??? ?????1????? 0?????????? ??????????? ??????????? ??????????? ??

Chthonius

0000100000 0310-00120 0000-10100 -1000-0000 100--00100 0000000001 0000010010
 01--012100 0E00-00001 01115000-0 000000-000 00--000--1 0000021000 01?700-013
 0110000000 1001001000 0011200011 1100000000 10-1100000 0-0000000- --

Neobisium

0000100000 0310-00121 0000-10100 -1000-0010 100--00100 0000000001 0000010010
 01--012100 0100-00001 01115000-0 000000-000 00--000--1 0000021000 01?700-013
 0110000000 1001001000 0011200011 1100000000 10-1100000 0-0000000- --

Feaella

0000100000 0310-00120 0000-10100 -1000-0000 100--00100 0000000001 0000010010
 01--012100 000--00001 01115000-0 000000-000 00--000--1 0000021000 01?700-013
 0110000000 1001001000 0011200011 1100000000 10-1100000 0-0000000- --

Chelifer

0000100000 0310-00121 0000-10100 -1000-0010 100--00100 0000000001 0000010010
 01--012100 000--00001 01115000-0 000000-000 00--000--1 0000021000 01?700-014
 0110000000 1001001000 0011200011 1100000000 10-1100000 0-0000000- --

Eremocosta

0000110000 0310-00121 0000-00010 -1000-0000 00101?0100 0000000001 00011-0000
 02--010-10 1101010001 01114000-0 000000-000 00--000--1 000002?00? ?1?31111013
 010--10000 1001000000 000--00100 1010000100 01-1100001 0-00000110 00

Galeodes

0000110000 0310-00121 0000-00010 -1000-0000 00101?0100 0000000001 00011-0000
 02--010-10 1101010001 01114000-0 000000-000 00--000--1 000002?00? ?1?31111013
 010--10000 1001000000 000--00100 1010000100 01?1100001 0-00000110 00

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 & Sisom, 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 *Lagerstätten*: *Gilboarachne* from the Gilboa Formation (New York) (Shear *et al.*, 1987) and

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* (Mesothelae), *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 (whipspiders): 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 *Paracarus*), features that are potentially significant for assessing ordinal relationships. Some information on internal morphology of *Opilioacarus* was taken from With (1904) and extrapolated to *Neocarus* and *Siamacarus*.

Parasitiformes: This large group of mites comprises three clades, Holothyrida, Ixodida (ticks) and Mesostigmata (= Gamasida). Holothyrida (three families, five genera, < 30 spp.) (Walter & Proctor, 1999) was represented here by two species, *Australothyrys ocellatus* and *Allothyrus 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 *Glyptholaspis confusa*.

Acariformes (= *Actinotrichida*): This is a very large, diverse group of mites that includes the Endeostigmata, Sarcoptiformes and Prostigmata. Endeostigmata is an apparently paraphyletic assemblage of ~ten families. A morphologically generalized species, *Alycus roseus* (Bimichaeliidae), 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, *Archezogozetes* (especially *A. longisetus* and *A. magnus*). The Prostigmata (~120 families, ~7000 spp.) (Walter & Proctor, 1999) was represented by two genera, *Allothrombium* and *Microcaeculus*.

Pseudoscorpiones: The pseudoscorpions (24 families, 425 genera, ~3200 spp.) (Harvey, 2002) were represented in the matrix by four terminal genera. *Chthonius* (Chthoniidae) was drawn from the basally divergent superfamily Chthonioidea (Harvey, 1992). *Feaella* (Feaellidae) represented the enigmatic superfamily Feaelloidea, which has an unusual combination of characters and may be an early divergent lineage close to Chthonioidea (Harvey, 1992). *Neobisium* (Neobisiidae) is morphologically intermediate between the early divergent families and the higher families represented by *Chelifer* (Cheliferidae).

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, *Eremocosta*, and one from the Old World, *Galeodes*.

Opiliones (*harvestmen*): Extant harvestmen (~25 families, ~500 genera, ~6000 spp.) are divided into two suborders, Cyphophthalmi and Phalangida. Cyphophthalmids 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 Dyspnoi, but there is disagreement as to whether Dyspnoi 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.) (Fet *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*, *Palaeoscorpius*, *Pre-arcturus*) 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 termi-

nals 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 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, although the interordinal clades Stomotheca, Haplocnemata, Acaromorpha, Tetrapulmonata, Pedipalpi and Uropygi were recovered under all values of k . IWA with $k = 1$ (1 tree, best score = 51.24) recovered Megoperculata (= Palpigradi + Tetrapulmonata) and Micrura (= Megoperculata + Acaromorpha) with Micrura being the sister group to Haplocnemata (= Pseudoscorpiones + Solifugae) and with Stomotheca (= Opiliones + Scorpiones) being the sister group to all other arachnids (Fig. 5B). With $k = 2$ (1 tree, best score = 38.07) and $k = 3$ (1 tree, best score = 30.54), Megoperculata was recovered and Stomotheca remained the sister

group to other arachnids, but the relative positions of Haplocnemata and Acaromorpha changed (Fig. 5C). IWA using $k = 4$ (1 tree, best score = 25.59), $k = 5$ (1 tree, best score = 22.05) and $k = 6$ (1 tree, best score = 19.38) recovered topologies consistent with the minimal-length topology derived from unweighted characters (Fig. 5A).

EXTANT AND FOSSIL TAXA

Unweighted analysis of extant and fossil taxa produced 18 minimal-length trees (length 426, CI 0.56) (Fig. 6A) with conflicts limited to relationships within Pseudoscorpiones, Scorpiones and Araneae. Multiply sampled orders were again recovered as monophyletic with high nodal support (BP > 80) except Acari, which was reconstructed as diphyletic with Anactinotrichida being the sister group to Ricinulei (BP 33). There were no well-supported interordinal groupings (i.e. BP > 80), except Uropygi (BP 89), Pedipalpi (BP 92) and Arachnida (BP 90).

Results from IWA indicated a significant effect of homoplasy on resolution of the deepest interordinal relationships in Arachnida, although Stomothecata, Haplocnemata, Acaromorpha, Cryptognomae, Pantetrapulmonata, 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.

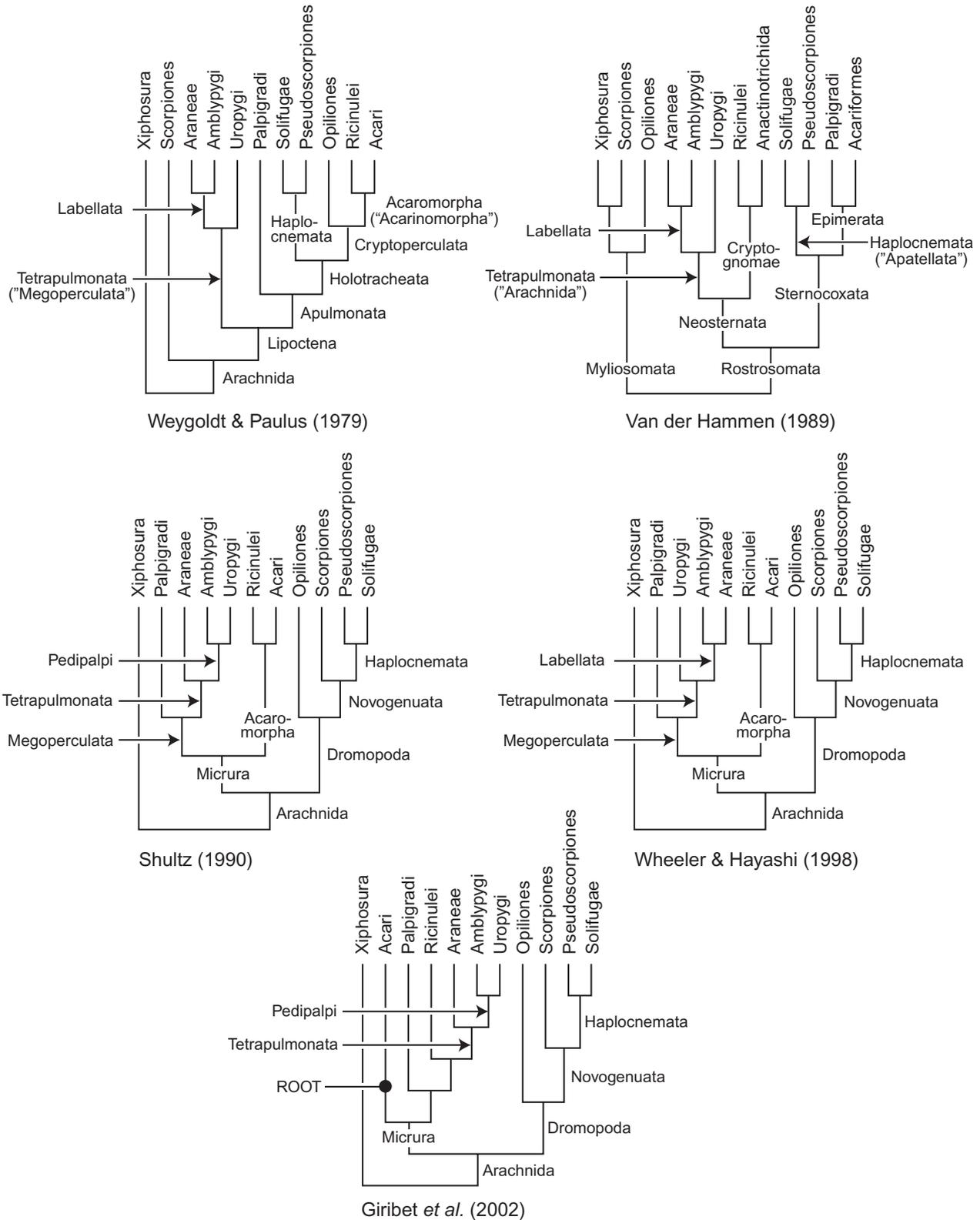


Figure 2. Fully resolved phylogenetic hypotheses of extant euchelicerate groups proposed in the recent literature. Note the similarity in the topologies of the parsimony-based analyses by Shultz (1990), Wheeler & Hayashi (1998) and Giribet *et al.* (2002). The Giribet *et al.* topology is based on neontological data (morphology and molecules) and the original 'ROOT' may be an artefact from use of the highly divergent pycnogonids as an outgroup.

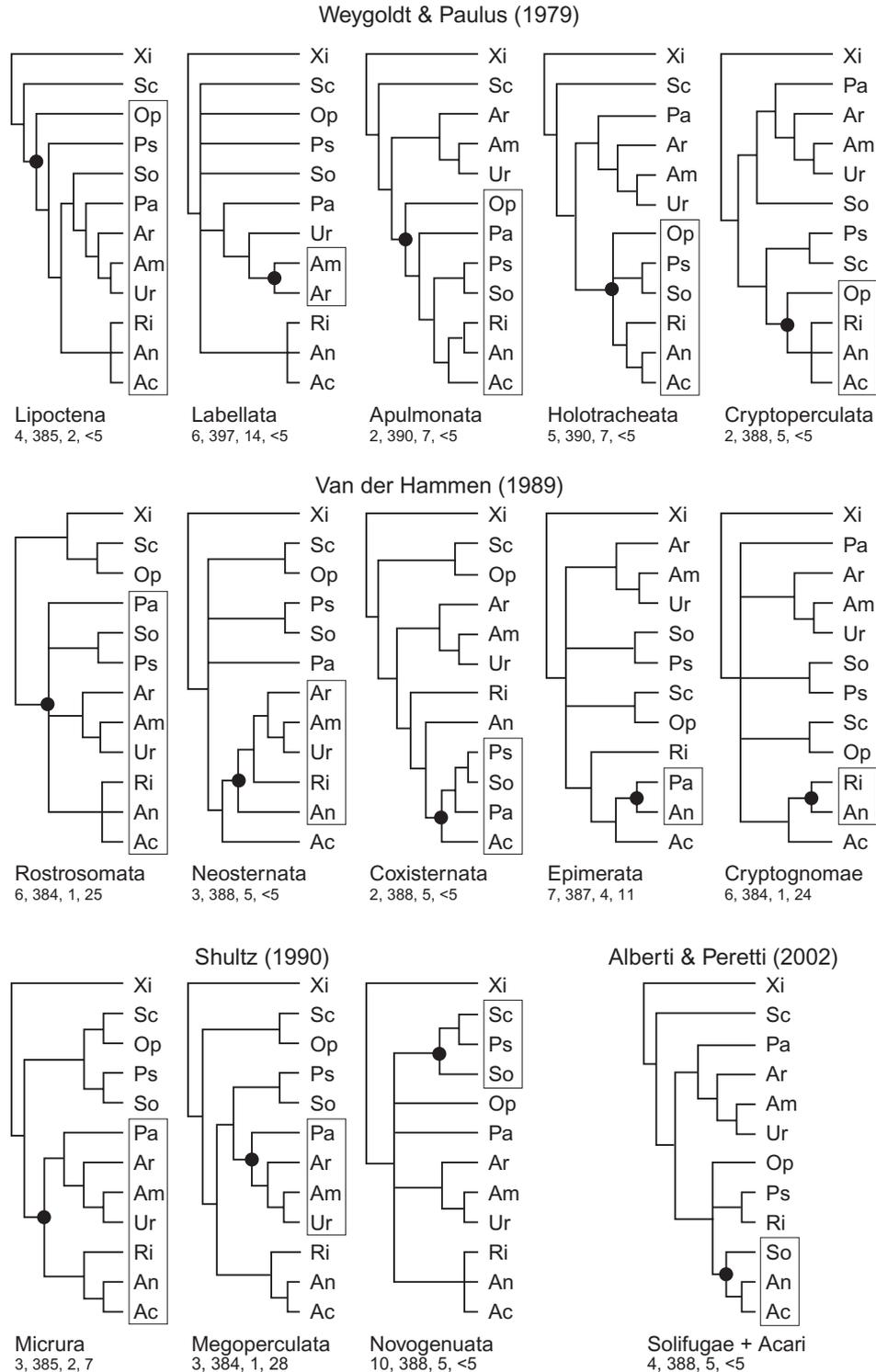


Figure 3. Consensus trees produced by parsimony analysis of neontological data constrained to produce relationships proposed in the recent literature. The constrained (target) node is indicated by a black dot and the taxa encompassed by the constraint are enclosed in a box. Numbers below each tree represent 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.

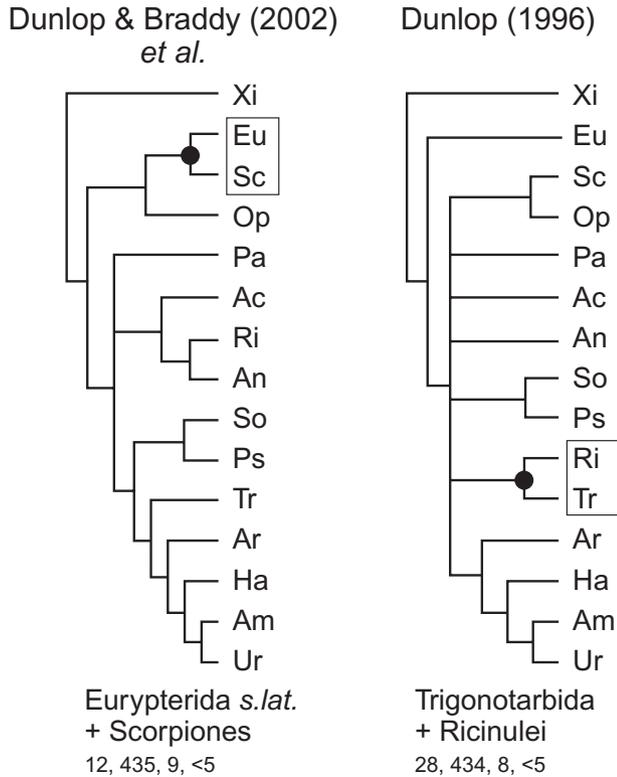


Figure 4. Consensus trees produced by parsimony analysis of the full data matrix constrained to produce relationships proposed in the recent literature. See legend to Figure 3 for details.

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 post-embryonic ‘lateral organs’ of Amblypygi, Thelyphonida and Solifugae with the dissimilar ‘lateral organ’ of Xiphosura but failed to note the very similar Claparède 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

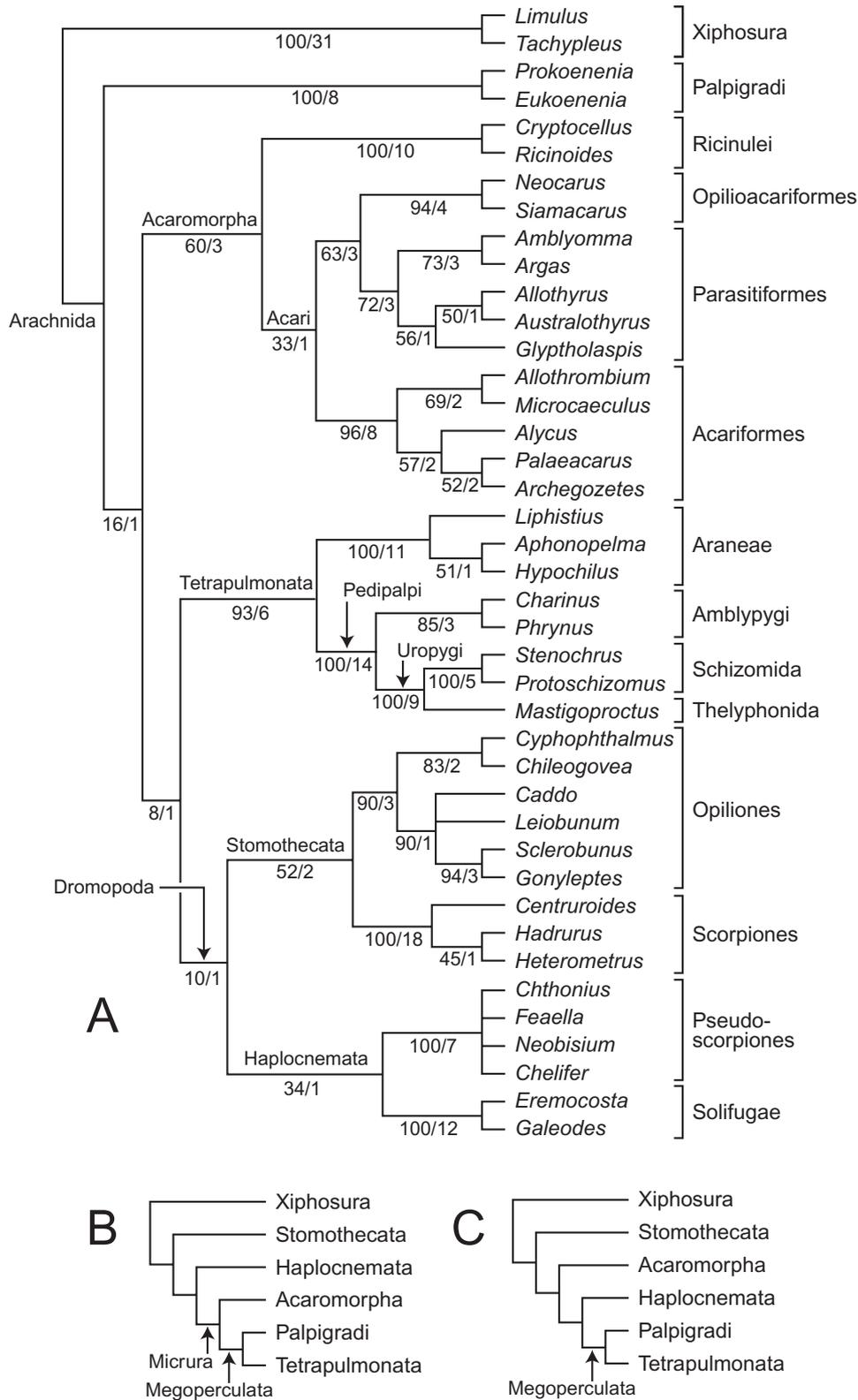


Figure 5. Results from analysis of neontological data. A, minimal-length topology. Numbers below internodes are bootstrap percentages/Bremer support values. B, parsimony tree produced by implied weights with $k = 1$. C, parsimony tree produced by implied weights with $k = 2$. Parsimony trees produced 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.

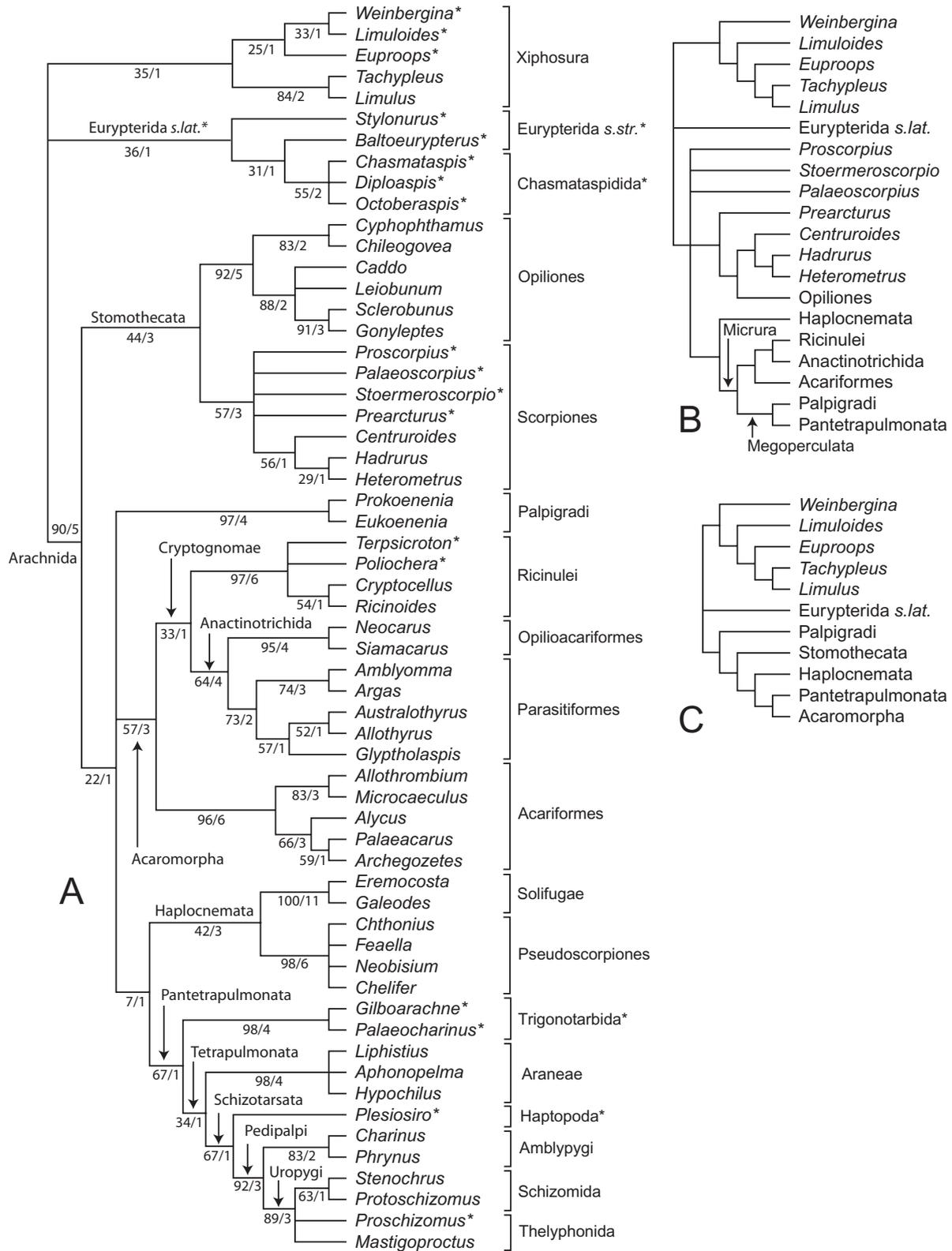


Figure 6. Results from analysis of the full data matrix. A, minimal-length topology. Numbers below internodes are bootstrap percentages/Bremer support values. B, parsimony tree produced by implied weights with $k = 1$. C, parsimony tree produced by implied weights with $k = 2$. Parsimony trees produced 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 + Ricinulei) (Figs 1, 2). Rejec-

tion 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 Ricinulei and Pseudoscorpiones (Fig. 3).

In another example, Dunlop (1996) proposed a close relationship between Trigonotarbitida and Ricinulei 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). Given 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 stomothecal 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 prosomal 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 haemocytopenic organs associated with major nerves of the anterior opisthosoma. These are termed supraneural 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 haemocytopenic 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 (Pseudoscorpiones) 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 symplesiomorphies 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 Trigonotarbita, Haptopoda and the extant orders Araneae, Amblypygi, Schizomida and Thelyphonida. The clade is united by cheliceral structure (18, 19), a megoperculum (106), booklungs 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 Trigonotarbita 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 telotarsomeres 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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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).

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 *Glyphtholaspis* (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*, *Stenochrus*: Reddell & Cokendolpher, 1995); Thelyphonida (Rowland & Cooke, 1973; Shultz, unpubl. obs.; *Proschizomus*: Dunlop & Horrocks, 1995/1996); Amblypygi (*Charinus*: Millot, 1949b; *Phrynus*: Shultz, 1999); and *Plesiosiro* (Dunlop, 1999). Citing a figure in Rowland & Cooke (1973), Dunlop & Horrocks assumed that the anterior process was limited to 'hypoc-tonid' thelyphonids and united them with *Proschizomus* and Schizomida. If valid, this would make Thelyphonida paraphyletic. However, the doubtful monophyly of 'hypoc-tonids' (Haupt & Song, 1996) and widespread presence of a submarginal anterior process in Pedipalpi 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 *Plesiosiro* (Dunlop, 1999) and 'non-hypoc-tonid' 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 metapeltidia: 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 procurved 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 Palpi-gradi, 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. Opilioacari-formes) and Acari-formes (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 propodosoma 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 Opilioacari-formes (With, 1904; Klompen, 2000) reached similar conclusions. This interpretation is also consistent with evidence from Acari-formes. 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 postpodosomal furrow that appears to represent the prosoma–opisthosoma junction; there is no disjugal furrow. Examples include palaeosomate (especially aphelacarid) and pediculochelid Oribatida, alicorhagiid and mircopsammid ‘Endeostigmata’ and paratydeid Prostigmata (Alberti & Coons, 1999: fig. 42). This organization may be symplesiomorphic 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 Holothryida (Van der Hammen, 1989).

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

A carapacal pleural doublure occurs throughout Xiphosura (Størmer, 1944), Eurypterida (Clarke & Ruedemann, 1912; Selden, 1981) and Chasmataspida (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 chasmatas-

pidids *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]*

Prosomal 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 metameric components of the sternal 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, Holothryrida, 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 *Palaeoscorpis* 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 *Stoermeroscorpio* (State 0) and *Pre-arcturus* 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 posteriorly adjacent to the palpal coxae forming the posterior border of the preoral chamber in some taxa or displaced 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), Thelyphonida (Van der Hammen, 1989), extant Ricinulei (Pittard & Mitchell, 1972; Legg, 1976), Opilioacariformes and Mesostigmata (Van der Hammen, 1989; Alberti & Coons, 1999). *Allothyrus constrictus* is the only holothyrid mite known to have sternapophyses. An apparent sternapophysis has been described in a palaeocharinid trigonotarbid (Dunlop, 1994). Giribet *et al.* (2002) miscoded Ixodida and Acariformes as having a 'labium (= tritosternum)'. The lophognath of pseudoscorpions (Chamberlin, 1931) and 'labium' of Solifugae (Roewer, 1934) also appear to be sternapophyses that have been incorporated into the rostrisoma (32). The labium of phalangid Opiliones (Pocock, 1902; Hansen & Sørensen, 1904) is a sternapophysis 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' homologous with the sternapophyses of other arachnids (Weygoldt, 1998), despite absence of any indication of the relationship of this sclerite to the mouth and possible alternative interpretations (e.g. 16). Giribet *et al.* coded this sclerite as a sternapophysis, but the character 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), Mesostigmata (*Glypholapis*: Van der Hammen, 1989), Ricinulei (Pittard & Mitchell, 1972; Van der Hammen, 1989), Araneae (*Heptathela*, *Aphonopelma*, *Hypocheilus*: Shultz, unpubl. observ.; also *Porrhothele* (Mygalomorphae, Dipluridae): Butt & Taylor, 1991; *Segestria* (Araneomorphae, Segestriidae): Van der Hammen,

1989), Amblypygi (Van der Hammen, 1989), Schizomida (*Stenochrus*: Shultz, unpubl. observ.; unidentified Hubbardiinae: 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* (Thelyphonida) (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 discern with certainty whether a channel exists in *Eukoenia* (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 Chasmataspida (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), Palpigradi (Roewer, 1934), Opiliones (Hansen & Sørensen, 1904), Scorpiones (Hjelle, 1990) and throughout non-acariform Acari (Evans, 1992). State 1 is present throughout known Trigonotarbida, Araneae, Amblypygi, 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, Chasmataspidida (Dunlop *et al.*, 2001, 2004; Dunlop, 2002a), Riciniulei (Selden, 1992), *Plesiosiro* (Dunlop, 1999), *Proschizomus* (Dunlop & Horrocks, 1995/1996) and the fossil scorpions *Praearcturus* and *Palaeoscorpis* (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, and this arrangement would probably appear as two articles in compressed specimens. In any event, there are at least three cheliceral articles in *Stoermeroscorpis* and *Proscorpius* (Kjellesvig-Waering, 1986).

19. *Terminal cheliceral joint: 0, laterally placed bicondylar hinge; 1, dorsally placed bicondylar hinge; 2, ventrally 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), Riciniulei (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 *Stoermeroscorpis* but the state of the chelicerae is unclear in the other fossil scorpions represented here (Kjellesvig-Waering, 1986). State 1 is present in Trigonotarbita (Shear *et al.*, 1987), mygalomorph Araneae, Amblypygi, Schizomida and Theylphonida (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' mesothele (*Liphistius*, *Heptathela*) and palaeo-cribellate Araneae (*Hypochilus*) (Kraus & Kraus, 1993) is small compared with the variation that occurs throughout arachnids, and plagiognathy is coded as State 1 here.

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 Fealloidea (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), *Chileogovea* and *Gonyleptes* (Shultz, unpubl. observ.). The status of the character in other opilions 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 tetrapulmonates and the palpigrade Eukoena, 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; Roewer, 1934; Van der Hammen, 1989). Dunlop (2000) attempted to homologize components of the rostrisoma 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 rostrisoma and incorporates the sternapophysis. Unlike the gnathosoma, the rostrisoma 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 Ixodida (Van der Hammen, 1989). It also occurs in Sarcoptiformes (Evans, 1992) and certain endeostigmatids (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, Makioka & 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 Scorpiones (Vyas, 1970; Shultz, 2007)

38. *Muscle originating and inserting within coxa: 0, absent; 1, present* [GEWB ~232]

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 Fealloidea (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 (Coken-dolpher & 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 Haptopoda 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 Opilioacariformes (Van der Hammen, 1989). State 1 is approximated in Solifugae, Palpigradi (Roewer, 1934) and Haptopoda (Dunlop, 1999), and it is coded as uncertain in these taxa.

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 ('apatellate' condition sensu Van der Hammen, 1989): 0, absent; 1, present* [S 25, GEWB 86]

State 1 occurs in Pseudoscorpiones and Solifugae (Shultz, 1989).

49. *Appendage VI (=arachnid leg 4) with terminus modified as flattened blade: 0, absent; 1, present*.

State 1 occurs in some Chasmataspida (*Diploapis*: Dunlop *et al.*, 2001; *Octoberaspis*: Dunlop, 2002a); uncertain in *Chasmataspis*: Dunlop *et al.*, 2004; State 0 in *Loganamaraspis*: Tetlie & Braddy, 2004) and Eurypterida, except stylonuroids (Clarke & Ruedemann, 1912; Waterston, 1979; Tollerton, 1989).

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, *Stoermeroscorpio*, 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 ~14, WH ~58, GEWB 75]

State 1 occurs in extant Scorpiones and most Opiliones, except *Dyspnoi* (Shultz, 1998).

52. *At least one pair of coxal gnathobases on appendages III–VI (=arachnid legs 1–4): 0, absent; 1, present* [S ~23, WH ~66, GEWB 78]

State 1 occurs in all appropriately preserved Eurypterida, including *Baltoeurypterus* (Selden, 1981) and *Stylonurus* (Clarke & Ruedemann, 1912), extant Xiphosura on appendages II–VI and apparently *Proscorpius* on appendage III (=arachnid leg 1) (Kjellesvig-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 tergo-coxal 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, 1999).

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, endeostigmatid, 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 paedomorphic 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 euchelicerates, including Xiphosura, Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Scorpiones, Opiliones, Pseudoscorpiones, higher Sarcoptiformes (*Archezogozetes*: 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 Endeostigmata, basally divergent Sarcoptiformes (e.g. *Palaeacarus*) and Prostigmata (e.g. *Allothrombium*, *Microcaeculus*) (Van der Hammen, 1989; Evans, 1992). Only leg 4 has basi- and telofemora in *Alycus* (Van der Hammen, 1989). Basi- and telofemora occur on legs 3 and 4 in Solifugae, Ricinulei, Opilioacariformes and Eurypterida (Clarke & Ruedemann, 1912; Selden, 1981; Shultz, 1989).

Giribet *et al.* (2002) coded the ‘annulus’ of certain Trigonotarbida (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 away 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 arthroal 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, flexor 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]*

State 1 occurs in extant Xiphosura (Shultz, 1989). State 2 occurs in Araneae (Manton, 1958; Ruhland &

Rathmayer, 1978; Clarke, 1986; Shultz, 1989). State 3 occurs in Amblypygi, Thelyphonida and Schizomida (Shultz, 1989). Giribet *et al.* (2002) included this character twice.

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 femoropatellar–tibia (transpatellar) muscle: 0, muscle absent; 1, dorsoposterior surface of femur and/or posterior surface of patella; 2, distal process of femur, muscle acting as extensor of femur–patella 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 patella–tibia joint; -, inapplicable due to absence of muscle (77) [S 29, GEWB 221] (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 (Sens-enig & 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 chthoniid pseudoscorpions and all legs in 'monosphyronid' pseudoscorpions, including Feaelloidea and Cheliferoidea (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, Thelyphonida, Amblypygi, Palpigradi, Ricinulei, Solifugae (Shultz, 1989), Opilioacariformes (Van der Hammen, 1989) and *Plesiosiro* (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 Thelyphonida, 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.*, 1988).

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, Thelyphonida 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]

Chasmataspidids appear to have 13 opisthosomal somites (Dunlop *et al.*, 2004). The synziphosurans

Weinbergina (Moore *et al.*, 2005) and *Limuloides* (Anderson & Selden, 1997) appear to have ten opisthosomal somites; Moore *et al.* (2005) found no evidence of an anterior microtergite in *Weinbergina* as proposed by Anderson & Selden (1997). Xiphosurids 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), Telyphonida and Schizomida (Hansen & Sørensen, 1905) and Pseudoscorpiones (Chamberlin, 1931). Eleven somites are present in Palpigradi, Solifugae (Roewer, 1934) and Trigonotarbida (*Gilboarachne*: 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 transverse 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 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 somites. The pedicel was regarded as having two somites (VII + VIII); the following four sets of tergites and sternites were considered diplosomites (IX + X, XI + XII, XIII + XIV, XV + XVI) and the metasoma had three somites (XVII–XIX). This interpretation may have been biased by 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 premetasomal 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 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 trigonotarbids 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 Millot'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 thelyphonids, 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. *Prosoma–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 (*Cryptocellus*: 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 Trigonotarbida (Shear *et al.*, 1987). Ricinuleids also have diplotergites (101), but these appear to encompass a different combination of somites (see 95).

101. *Three diplotergites: 0, absent; present.*

State 1 is a unique synapomorphy of Ricinulei (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 chondrites: 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; Fahrénbach, 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. Størmer, 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), Trigonotarbida (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 *Pantetrapulmonata** (Platnick & Gertsch, 1976).

State 1 is present in Trigonotarbida, 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 (Acari) (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 epigastric or 'epiandrous' 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 the 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 Endeostigmata (*Alycus*: Van der Hammen, 1989) and Prostigmata (*Allothrombium*: Saboori & Kamali, 2000; *Microcaeculus*: 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 opisthosoma; -, 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* (Chasmataspidida) (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 Chasmataspidida.

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 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, Chasmataspidida, 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 primitively terrestrial and pulmonate (see also Firstman, 1973) 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 Trigonotarvida, Araneae, Amblypygi, Thelyphonida and Schizomida. Petrunkovitch (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 duobicarinatus* 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 ($\times 90$ – $\times 330$) are comparable with those illustrating the cones of *Kiemenplatten* ($\times 170$ – $\times 350$ 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 chelicerae; 5, four pairs of stigmata on dorsal surface of opisthosoma; -, inapplicable, aquatic (120)* [WP 40, ~43, 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, Opilioacariformes 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 (*Eukoenaia*: 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. *Chileogovea*) 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 *Terpsicroton*, 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 Euchelicera 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 & Horrocks, 1995/1996). They are unknown in synziphosuran Xiphosura. Median eyes are present in a variety of basal acariform mites, including Endeostigmata (but

not *Alycus*), Prostigmata (*Microcaeculus*) 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 microlenses); 2, three primary pairs (excludes microlenses); 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, Eurypterida, Chasmataspida 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 allothryrid Holothyrida and many Ixodida have a single pair of lateral lenses and the remainder apparently lack eyes (Evans, 1992). Thelyphonida 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). Trigonotarbitida 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 *Chelififer*) 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 Scorpiones. 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 uniting 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 Eurypterida (Dunlop & Braddy, 1997) appears to be based on the over-interpretation of a comparatively large notch that occurs in *Baltoeurypterus* 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 (*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 opilioacariform *Siamacarus* (Leclerc, 1989). They are also present in Araneae (Foeelix, 1996), Amblypygi (Weygoldt, 2000), Schizomida and Thelyphonida (Hansen & Sørensen, 1905). 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. *Interchelicer 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]

Klompen (2000) has noted that State 1 occurs in Opilioacariformes, 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 'horn organs', 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 carapacial 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 Holothryrida

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 spermatopositor; it functions in construction of a spermatophore (Alberti & Coons, 1999).

161. *Median organ: 0, absent; 1, present.*

State 1 occurs throughout Eurypterida (Clarke & Ruedemann, 1912) and has been observed in diploaspigid Chasmataspidida (Dunlop, 2002a; also *Loganamarpis*: 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 gonyleptid Lanitators (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, Cyphophthalmi (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 Parasitiformes (Acari) (Alberti, 1995).

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

DEVELOPMENT

169. *Yolk in early embryo: 0, concentrated (centrolecithal 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 *Tyroglyphus* (Sarcoptiformes, Astigmata) (Yoshikura, 1975) and *Archegozetes* (Sarcoptiformes, Oribatida) (Thomas & Telford, 1999) but not apparently in *Tetranychus* (Prostigmata) (Dearden, Donly & Grbić, 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 Amblypygi, Schizomida, Thelyphonida and Pseudoscorpions. 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 Pseudoscorpiones 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; Milot, 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 *Archezogetes* (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).

176. *Hexapodal larva and 1–3 nymphal stages*: 0, absent; 1, present [WP 53, S ~61, WH 27, GEWB 186]

State 1 occurs in Acari and Ricinulei (Lindquist, 1984).

177. *Hexapodal prelarva*: 0, absent; 1, present [S ~61, WH 47]

State 1 occurs in Opilioacariformes (*Neocarus*: 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 'ozopore' 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 *Chileogovea oedipus* 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 (*Neocarus*: Van der Hammen, 1989; unidentified: Walter & Proctor, 1998), Holothyrida, non-parasitic Sarcoptiformes (Evans, 1992; Walter & Proctor, 1998; Alberti & Coons, 1999) and many endostigmatids, 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 [GEWB ~38]

State 1 occurs in Scorpiones 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 (*Palaeocharinus*: Dunlop, 1994), Araneae (Firstman, 1954; Marples, 1983), Amblypygi (Millot, 1949b; Shultz, 1999), Schizomida (Millot, 1949e), Thelyphonida (Millot, 1949e; Shultz, 1993) and Phalangida (Opiliones) (Shultz, 2000; unpubl. observ.)

192. Epipharyngeal sclerite large, projecting posteriorly: 0, absent; 1, present; -, inapplicable due to absence of sclerite (191). [GEWB 32]

State 1 occurs in Amblypygi (Millot, 1949b; Shultz, 1999), Schizomida (Millot, 1949e), Thelyphonida (Millot, 1949e; Shultz, 1993), some Araneae (*Heptathela* – coded as *Liphistius* – and *Hypochilus*: Marples, 1983; not *Aphonopelma*: Firstman, 1954) and, perhaps, Trigonotarbida (*Palaeocharinus*: Dunlop, 1994).

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 (Millot, 1943), Araneae (Marples, 1983), Amblypygi, Schizomida and Thelyphonida (Millot, 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 Scorpiones 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 (Millot, 1943) and Solifugae (Roewer, 1934).

199. Postcerebral pharynx: 0, absent; 1, present. [WP ~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 (First-

man, 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.