

EVOLUTIONARY MORPHOLOGY AND PHYLOGENY OF ARACHNIDA

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Abstract This paper reports results from a cladistic analysis of the 11 Recent arachnid orders. The polarities of 64 newly discovered and traditional characters were determined through outgroup comparisons that included Eurypterida, Xiphosura, Trilobita and Crustacea. A branch-and-bound algorithm was used to discover a single tree (consistency index 0.59). The relationships suggested by this analysis differ substantially from previous interpretations of arachnid phylogeny, and a new taxonomic system is introduced to accommodate these results. This analysis suggests that Arachnida is monophyletic and composed of two principal lineages, Micrura and Dromopoda. Possible synapomorphies of Micrura include a pygidium, tritosternum, six principal lateral eyes, poorly sclerotized postgenital appendages, coxal gland orifices near leg 1, an array of microtubules associated with the spermatozoan nucleus, and absence of coxal endites on the walking legs. The micruran orders appear to have the following relationships: (Palpigradi (Araneae (Amblypygi (Thelyphonida, Schizomida)))) (Ricinulei, Acari). Possible synapomorphies of Dromopoda include transverse carapacial furrows, greatly reduced prosomal sternum, prosomal endosternite with two segmental components, stomotheca, bicondylar femoropatellar and patellotibial joints and extensor muscles. The dromopodan orders appear to have the following relationships: Opiliones (Scorpiones (Pseudoscorpiones, Solifugae)).

Introduction

This paper attempts to resolve the phylogenetic relationships of the living arachnid orders through cladistic analysis. Although arachnologists have puzzled over the ordinal relationships of arachnids for over a century, until recently the problem seemed no closer to a satisfactory resolution than when Pocock (1893) presented the first important treatment of the subject. Since then there has been a steady stream of expert opinion and taxonomic revisions, each no more convincing than the one preceding it (e.g. Versluy and Demoll, 1922; Dubinin, 1957; Savory, 1971; van der Hammen, 1977a, 1989). This situation eventually led some workers to speculate that arachnids are a polyphyletic grade of terrestrial chelicerates that evolved several times from different but unknown marine ancestors (Savory, 1971; Kraus, 1976; Manton, 1977; van der Hammen, 1977a).

Weygoldt and Paulus (1979) were the first to apply cladistic reasoning to the arachnid problem (Fig. 1). Based on information derived from an extensive review of chelicerate biology, they discovered evidence that arachnids are monophyletic. Although their results were based on only a handful of synapomorphies, and the influence of traditional interpretations was evident in many of their conclusions, Weygoldt and Paulus' explicit analysis was a welcome departure from the more subjective approach of earlier workers and provided an important foundation for further research.

Despite the progress made in arachnid systematics through application of cladistic methodology, the most prolific worker in the field, van der Hammen (1977a, 1979, 1982, 1985a, 1985b, 1986a, 1986b, 1989), has rejected cladistics as too "rigid" and "atomistic" to provide meaningful insight into the problems of arachnid evolution. He questions the use of expressed characters as a guide to phylogenetic relationships and suggests that the discovery of unexpressed "potentialities" holds the key to understanding macro-evolutionary change (van der Hammen, 1985c). Based on extensive anatomical studies

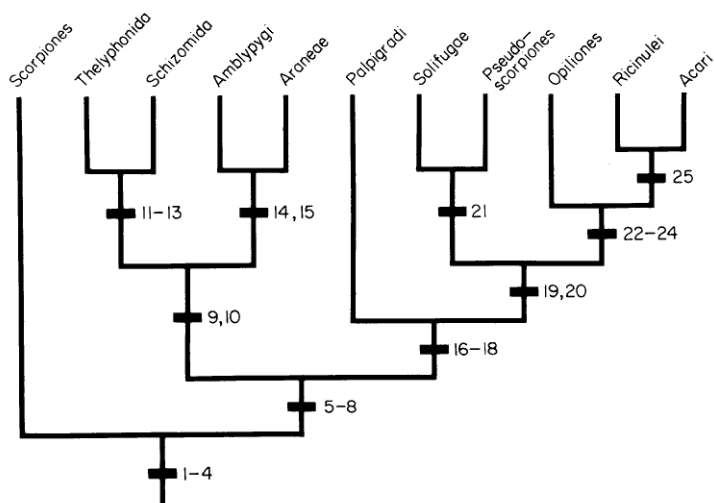


Fig. 1. Phylogenetic relationships of the arachnid orders suggested by Weygoldt and Paulus' (1979) qualitative analysis. The synapomorphies hypothesized by Weygoldt and Paulus include: 1, extraintestinal digestion; 2, endodermal Malpighian tubules; 3, five simple lateral eyes; 4, slit sensilla; 5, eyes with network of rhabdomeres; 6, spermatozoa with coiled axoneme; 7, lyriform organs; 8, leg 1 used as a tactile organ; 9, two-segmented, subhelate chelicerae; 10, 9 + 3 microtubule arrangement in spermatozoan axoneme; 11, fused pedipalpal coxae; 12, prenymp and four nymphal instars; 13, female grasps male during mating; 14, petiolus; 15, large postcerebral pharynx; 16, small body size; 17, book lungs absent; 18, two or three lateral eyes; 19, tracheae; 20, opisthosomal flagellum absent; 21, two-segmented, chelate chelicerae; 22, leg 2 used as a tactile organ; 23, aflagellate spermatozoa with specialized acrosome; 24, anterior genital opening; 25, six-legged larva and three nymphal instars. In light of the characters and interpretations of the present investigation, the topology of Weygoldt and Paulus' cladogram has a consistency index of 0.50 and a length of 159 (cf. Fig. 4).

and his concept of "unfoldment", van der Hammen concludes that Arachnida is polyphyletic and apparently envisions a pantheon of hypothetical ancestors, each endowed with the potential for producing a subset of Recent arachnids. Despite van der Hammen's apparent break with empiricism, his phylogenetic conclusions have gone largely unchallenged (although see Lindquist, 1984), and several workers have accepted his taxonomic system.

This investigation returns to the problem of arachnid phylogeny from the standpoint of phylogenetic systematics, concentrating on data and interpretations not included in Weygoldt and Paulus' seminal paper. I conclude, along with Weygoldt and Paulus, that the arachnids are probably monophyletic, but several ordinal relationships suggested by the present analysis differ substantially from earlier views.

Phylogenetic Analysis

TERMINAL TAXA

This analysis includes the 11 traditionally recognized arachnid orders: Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Ricinulei, Acari, Opiliones, Scorpiones, Pseudoscorpiones and Solifugae. Members of each order are readily distinguished, although in several instances, such as Amblypygi and Palpigradi, autapomorphic features have not been enumerated explicitly. Some workers have argued that Acari is diphyletic (van der Hammen, 1977a, 1979, 1982), but in a critical review of the problem, Lindquist (1984) concluded that Acari is monophyletic and composed of two distinct lineages.

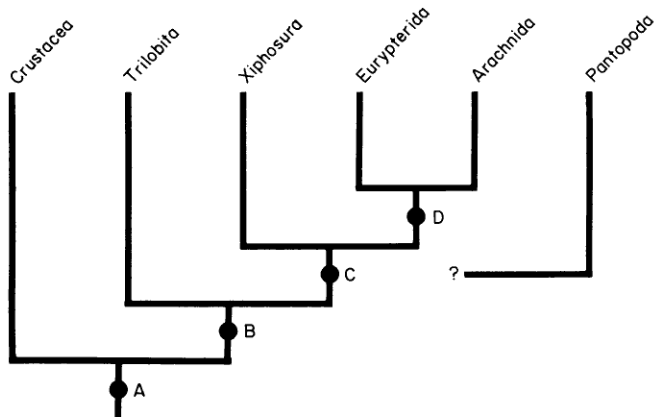


Fig. 2. Phylogenetic relationships of major arthropod groups used in polarizing characters in Arachnida. Synapomorphies: (A) sclerotized cuticle, jointed appendages, cephalon with four postoral, appendage-bearing segments, biramous appendages, nephridia limited to six postoral segments; (B) trilobation, ventral cuticle weakly sclerotized; (C) chelicerae, prosoma and opisthosoma, antennae absent, prosomal appendages specialized for locomotion, opisthosomal appendages specialized for respiration, postanal spine; (D) seventh opisthosomal segment without appendages, tarsus divided into basitarsus and telotarsus (Lauterbach, 1983; Weygoldt and Paulus, 1979; Weygoldt, 1985; present study).

In attempting to identify the ancestral character states of each order, I have given special attention to early derivative groups, lineages that are thought to have diverged early in the evolution of an order and to have retained many plesiomorphic or generalized traits. These lineages include Mesothelae and Mygalomorphae in Araneae; Opilioacarida (Parasitiformes) and Actinedida (Acariformes) in Acari; Palpatores in Opiliones; Chthonioidea and Neobisioidea in Pseudoscorpiones and Palaeozoic fossil representatives in Scorpiones. Unless stated otherwise, the characters used in this analysis are those expressed in adult instars.

CHARACTER POLARITY

Uncertainty about the phylogenetic relationships of the major arthropod lineages and the inadequacy of information provided by the fossil record have been important stumbling blocks to progress in the higher systematics of Arachnida. In the absence of a reliable historical framework to guide selection of outgroups, the polarities traditionally assigned to different characters are unconvincing. Although two nonarachnid chelicerate lineages have survived to the present, they are either so aberrant (Pantopoda) or represent such a small sample of morphologic diversity (Xiphosura) that, for a given character, there is considerable doubt as to whether the state expressed is primitive or derived. In order to minimize uncertainty in determining character polarities, I have expanded outgroup comparisons to include both living and fossil taxa, including Eurypterida, Xiphosura, Pantopoda, Trilobita and early derivative Crustacea, especially Cephalocarida. These taxa were considered within the phylogenetic framework suggested by Weygoldt and Paulus (1979), Lauterbach (1983) and Weygoldt (1985) (Fig. 2). Information on the morphology of *Limulus* (Xiphosura) was obtained from Snodgrass (1952), Manton (1964) and original dissections. I also rely heavily on Seldon's (1981) study of the prosomal exoskeleton of the eurypterid *Baltoerypteris tetragonophthalmus* and on Cisne's (1974, 1981) X-ray analysis of the trilobite *Triarthrus eatoni*. Information on the morphology of Cephalocarida was obtained from

Table 1

Characters and character states used in the phylogenetic analysis of the 11 Recent arachnid orders. Plesiomorphic states are coded with a 0. The complete data matrix is presented in Table 2.

Prosoma

1. Carapace: 0, undivided; a, transverse segmental furrows; b, divided
2. Carapacial pleural margin: 0, well developed; 1, poorly developed
3. Intercostal sternal region: 0, broad throughout; a, narrow posteriorly; b, narrow throughout
4. Prosomal sternite: 0, uniform; 1, with distinct sclerites
5. Postcerebral pharynx: 0, absent or poorly developed; 1, well developed
6. Prosomal endosternite, segmental components: 0, five; a, four; b, two; c, one; d, absent
7. Dorsal endosternal suspensor of fourth postoral segment with anterolateral carapacial insertion: 0, absent; 1, present.
8. Fenestrate endosternite: 0, absent; 1, present

Mouthparts

9. Mouth: 0, posterior; 1, anteroventral
10. Tritosternum: 0, absent; 1, present
11. Subchela chelicerae: 0, absent; 1, present
12. Scissor-like chelicerae: 0, absent; 1, present
13. Chelicero-carapacial articulation: 0, absent; 1, present
14. Stomotheca: 0, absent; 1, present
15. Rostrum: 0, absent; 1, present
16. Scorpionoid pedipalpal chelae: 0, absent; 1, present
17. Raptorial pedipalps: 0, absent; 1, present
18. Pedipalpal coxae: 0, free; 1, fused medially
19. Movable subcapitulum: 0, absent; 1, present

Walking legs

20. Leg 1: 0, unmodified, ambulatory; 1, elongate, tactile
21. Movable coxae: 0, present; 1, absent
22. *Musculi laterales*: 0, absent; 1, present
23. Coxal endites: 0, present; 1, absent
24. Coxotrochanteral joint: 0, simple; 1, complex
25. Femur, legs 3 and 4: 0, divided; 1, undivided
26. Femorpatellar joint: 0, hinge; a, bocondylar; b, monocondylar
27. Femorpatellar flexor muscle, insertion: 0, symmetrical; 1, asymmetrical
28. Posterior transpatellar muscle, origin: 0, dorsoposterior surface of femur and/or posterior surface of patella; a, distal process of femur; b, absent
29. Patellotibial extensor muscle: 0, absent; 1, present
30. Anterior transpatellar muscle, insertion on tibia: 0, anterior; a, ventral; b, absent
31. Patellotibial joint: 0, monocondylar; a, hinge; b, bicondylar
32. Anterior transpatellar muscle, insertion on tibia: 0, anterior; a, ventral; b, absent
33. Posterior patellotibial muscle: 0, present; 1, absent
34. Telotarsus with three tarsomeres: 0, absent; 1, present
35. Claw depressor muscle, tibial head: 0, absent; 1, present
36. Claw depressor muscle, patellar head: 0, absent; 1, present
37. Claw depressor muscle, origin on posterior wall of patella: 0, absent; 1, present
38. Empodium (adult): 0, absent; 1, present

Opisthosoma

39. Appendages, first opisthosomal segment: 0, present; 1, absent
40. First opisthosomal segment: 0, broad; 1, narrow
41. Genital sternite divided, incorporated into pedicel: 0, absent; 1, present
42. Genital sternite overlapping third opisthosomal sternite: 0, absent; 1, present
43. Post genital appendages: 0, opercular and/or lamellar; a, poorly sclerotized or eversible; b, absent
44. Pygidium: 0, absent; 1, present
45. Pygidial flagellum: 0, absent; 1, present
46. Pygidial defensive glands: 0, absent; 1, present

Sense organs

47. Slit sensilla: 0, absent; 1, present
48. Tibial trichobothria with 2-2-1-1 distribution: 0, absent; 1, present
49. Lateral eyes: 0, compound; a, aggregate, with six principal facets; b, aggregate, with four facets; c, vestigial; d, absent
50. Medial eyes: 0, present; 1, absent

Respiratory organs

- 51. Book lungs: 0, absent; 1, present
- 52. Tracheal system: 0, absent; 1, present
- 53. Sternal stigmata on opisthosomal segments 3 and 4: 0, absent; 1, present

Reproduction/development

- 54. Spermatozoan nucleus with microtubule array: 0, absent; 1, present
- 55. Spermatozoan axoneme: 0, free; a, coiled; b, absent
- 56. Spermatozoan axoneme, 9 + 3 microtubule arrangement: 0, absent; 1 present
- 57. Stalked spermatophore: 0, absent; 1, present
- 58. Female grasps male opisthosoma during mating: 0, absent; 1, present
- 59. Gonoporal brood sac: 0, absent; 1, present
- 60. Ovipositor: 0, absent; 1, present
- 61. Hexapodal instar: 0, absent; 1, present

Excretory organs

- 62. Malpighian tubules: 0, absent; 1, present
- 63. Coxal gland orifice, leg 3: 0, present; 1, absent
- 64. Coxal gland orifice, leg 1: 0, absent; 1, present

Table 2

Data matrix used in computer-assisted phylogenetic analysis of the arachnid orders. Plesiomorphic states were determined by explicit argumentation given in the text and are presented in the matrix by the line labeled "Ancestor". Multistate characters are coded a, b, c, etc. Missing or equivocal character states are indicated by a 9. A list of characters and character polarities is given in Table 1.

Taxon	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0
Palpigradi	b	1	0	1	0	0	1	0	1	1	0	0
Araneae	0	1	0	0	1	a	1	0	1	1	1	0
Amblypygi	0	1	0	1	1	a	1	0	1	1	1	0
Thelyphonida	0	1	a	1	0	a	1	1	1	1	1	0
Schizomida	b	1	a	1	0	a	0	1	1	1	1	0
Ricinulei	0	1	0	0	c	0	0	1	1	0	0	0
Acari	9	1	0	0	0	9	0	0	1	1	0	0
Opiliones	a	1	b	0	0	b	0	0	1	0	0	0
Scorpiones	a	1	b	0	0	b	0	0	1	0	1	0
Pseudoscorpiones	a	1	b	0	0	b	0	0	1	0	1	0
Solifugae	b	1	b	0	0	d	0	0	1	1	0	1

Taxon	Characters											
	30	31	32	33	34	35	36	37	38	39	40	41
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0
Palpigradi	0	0	0	0	0	1	0	0	0	1	1	0
Araneae	0	0	0	0	0	1	1	1	a	0	0	0
Amblypygi	0	0	0	0	1	1	0	0	1	0	a	0
Thelyphonida	0	0	0	1	1	1	1	0	1	1	1	a
Schizomida	b	0	0	1	1	1	1	0	1	a	1	1
Ricinulei	b	a	a	0	0	1	0	0	0	1	0	0
Acari	0	a	0	0	0	1	0	0	a	0	0	1
Opiliones	0	b	0	0	0	1	0	0	b	0	0	1
Scorpiones	a	b	a	1	0	1	1	0	0	1	0	0
Pseudoscorpiones	a	b	b	1	0	1	1	0	1	0	1	0
Solifugae	a	a	a	1	0	1	1	0	1	1	0	1

Hessler (1964) and Sanders (1963). The specific rationale used in assigning polarities to each character is provided below. A summary of characters and their polarities is given in Tables 1 and 2.

Carapace (1)

Two principal tagmata can be recognized in Trilobita and early derivative Crustacea, namely a cephalon and trunk. The cephalon of trilobites is generally thought to contain one or more pre-oral segments, the most posterior bearing a pair of uniramous antennae, and three or four postoral segments, each with paired biramous appendages (Weygoldt, 1985). Cisne (1974, 1981) noted only three postoral segments in *Triarthrus* and suggested that previous interpretations were based on a common preservational artifact. Bergström (1980) has countered that *Triarthrus* is a derived trilobite and may not retain a primitive cephalon, but this issue has not been resolved (Müller and Walossek, 1987). The cephalon of Cephalocarida and certain other crustaceans is similar to the problematic primitive cephalon of trilobites; it contains a pre-oral segment bearing uniramous antennae and four embryologically postoral segments bearing the second antennae, mandibles and two pairs of maxillae. Based on the anatomy of crustaceans and trilobites, the chelicerate prosoma is thought to have evolved through fusion of the cephalon composed of four postoral segments with two trunk segments (Weygoldt and Paulus, 1979).

The prosomal carapace in Xiphosura and Eurypterida shows little external evidence of its original segmentation, and this condition may be primitive for Arachnida. An unsegmented carapace is retained in Araneae, Amblypygi, Thelyphonida and Ricinulei. The transverse depressions on the carapaces of some of these taxa represent the insertion sites of large endosternal suspensor muscles and are not remnants of tergal margins (personal observations). External evidence of segmentation is present in some arachnid taxa in the form of one or two transverse furrows (1a). This feature is evident in many palpator Opiliones (Hansen and Sørensen, 1904), Pseudoscorpiones (Chamberlin, 1931) and Scorpiones. My examination of first instar *Pandinus imperator* (Scorpionidae) suggests that the large transverse carapacial furrow of adult scorpions corresponds to the anterior margin of the posterior prosomal tergite. The transverse grooves in some opilionids and pseudoscorpions are replaced by membranous regions that divide the carapace into discrete sclerites, suggesting that transverse carapacial furrows in these orders correspond to tergal margins. An ontogenetic study of palpator opilionids (Winkler, 1957) also supports this conclusion. It should be noted that transverse furrows in these taxa do not represent insertion sites of large endosternal suspensor muscles, although a pair of small suspensors may insert on or near a furrow in some taxa.

The carapace of adult Palpigradi, Schizomida and Solifugae is divided into at least three sclerites (propeltidium, mesopeltidium, metapeltidium) that appear to correspond to the primitive segmentation of the prosoma, i.e. cephalon and two posterior tergites (1b). The mesopeltidium is often divided medially by a membranous region or by the posterior part of the propeltidium. Although several early workers regarded the divided carapaces of these orders as primitive (e.g. Pocock, 1893), outgroup comparison with Eurypterida and Xiphosura suggests that this feature is derived in Arachnida (Weygoldt and Paulus, 1979). As the boundary between the prosoma and opisthosoma in Acari is uncertain, it is not yet possible to establish the state of the carapace in this order.

Carapacal pleural margin (2)

The lateral region of the cephalon and tergites (pleurotergites) in early derivative Crustacea, Trilobita and many trilobitomorph arthropods projects ventrolaterally from the primary axis of the body and forms a ventral concavity that houses the coxosternal region and feeding apparatus (Lauterbach, 1974). As a well-developed carapacal pleural margin is present in Xiphosura and Eurypterida as well, I consider the poorly developed pleural margins in all known arachnids to be apomorphic (2).

Coxosternal region (3, 4)

The medial intercoxal (sternal) region of the cephalon and trunk in Crustacea and Trilobita forms the roof of the primitive ventral food groove. The sternal region in *Triarthrus* appears to have been poorly sclerotized, except for the region just posterior to the mouth (Cisne, 1981). The intercoxal region of the prosoma in Xiphosura is formed by an unsegmented plate, the endostoma, and a similar but smaller structure is present in Eurypterida (Selden, 1981). I suggest that the coxosternal region of primitive arachnids was similar to that of xiphosurans and eurypterids (Fig. 3); there was a simple sternum bordered laterally by coxae of the prosomal appendages and posteriorly by the sternite or appendages of the first opisthosomal segment.

Among Recent Arachnida a well-defined intercoxal sternal region is present in Palpigradi, Araneae, Amblypygi and many early derivative mites, including opilioacarines and many actinedids. An intercoxal sternum is present in Ricinulei as well, but only the anterior portion is visible externally. The posterior and lateral parts are hidden by expanded margins of the coxae (Hansen and Sørensen, 1904; Pittard and Mitchell, 1972). The posterior intercoxal region is greatly reduced by medial expansion of the posterior coxae (3a) in Thelyphonida and Schizomida (Hansen and Sørensen, 1905), although a large, triangular anterior sternite and a minute posterior sternite are present.

The intercoxal region is reduced throughout (3b) in Opiliones, Scorpiones, Pseudoscorpiones and Solifugae, but a small anterior sternal sclerite is often retained and seems to be associated with the third postoral segment (Beck, 1885; Hansen and Sørensen, 1904; Chamberlin, 1931; Roewer, 1934; Winkler, 1957). The sternite or 'labium' in palpator Opiliones forms the posterior border of the pre-oral chamber but is small or absent in most laniator and cyphophthalmid opilionids. The prosomal sternite in Scorpiones is reduced to a small, ovate structure located just posterior to the mouth and serves as the insertion site for a pair of ventral endosternal suspensors (Beck, 1885). The structure is hidden from external view by the large coxal endites that form the pre-oral chamber (see Stomotheca). A small triangular sterite is retained in Solifugae between the coxae of the pedipalps and the first leg pair (Roewer, 1934; personal observation). It is not clear whether the cuticular structure located midventrally between the pedipalpal coxae is sternal in origin. Pseudoscorpions appear to lack sternites, although a posterior intercoxal sclerite is present in chthonioids (Chamberlin, 1931). The pseudosternum of sternophorid pseudoscorpions is a specialization unique to this group (Chamberlin, 1931; Harvey, 1985).

Those arachnids that retain a distinct intercoxal region may possess a single sternum or several distinct sternal sclerites. Comparison with Xiphosura and Eurypterida suggests that a single undivided sternum is primitive and that presence of distinct

sclerites is derived (4). Sternal sclerites are present in adult Palpigradi, Amblypygi, Thelyphonida and Schizomida.

Postcerebral pharynx (5)

The anterior portion of the digestive tract passes through the central nervous system in arthropods and annelids. In Chelicerata that portion of the digestive tract anterior to the CNS is termed the pharynx and is typically supplied with dilator and constrictor muscles. A postcerebral pharynx is present in some arachnids and is particularly well developed (5) in Araneae and Amblypygi. Some arachnologists regard the "sucking stomach" as synapomorphic for these two orders (e.g. Platnick and Gertsch, 1976; Weygoldt and Paulus, 1979), but others regard it as symplesiomorphic (e.g. Shear et al., 1987). A small postcerebral pharynx is present in some scorpions (Millot and Vachon, 1949a) and is vestigial in Thelyphonida (Pocock 1902a; Millot, 1949b; personal observation). A well-developed postcerebral pharynx has been reported in Palpigradi (Rucker, 1901; Börner, 1904), but this observation appears to have been mistaken (Millot, 1942).

Use of a medial carapacial depression to diagnose the presence of the postcerebral pharynx in fossil arachnids (Shear et al., 1987) is not appropriate, as these depressions represent the insertion sites of endosternal suspensor muscles in living forms (personal observation). In thelyphonids, for example, the carapace has two medial depressions associated with two pairs of dorsal endosternal suspensors, but the postcerebral pharynx is essentially absent.

Endosternite (6, 7, 8)

Comparative anatomy of early derivative Crustacea (Hessler, 1964) and X-ray reconstructions of well-preserved trilobites (Cisne, 1981) suggests that presence of an intersegmental muscular network is primitive for Chelicerata (cf. Boudreaux, 1979). In trilobites and early derivative crustaceans, two ventral longitudinal muscles traverse the length of the body and are intersected within each segment by a transverse tendon (endoskeletal bar) that is continuous with transverse suspensor muscles or tendons that arise from the pleural regions of each tergite. Paired ventral tendons (ventral suspensors) link each endoskeletal bar with the ventral exoskeleton, and a pair of dorsoventral muscles (dorsal suspensors) link the bar with the medial region of its corresponding tergite. Each endoskeletal bar is also linked with tergites of immediately adjacent segments via anterodorsal and posterodorsal suspensors. Together the paired dorsal, anterodorsal and posterodorsal suspensors resemble a box truss.

Firstman's (1973) hypothetical primitive chelicerate endosternite is similar to the intersegmental muscle system of crustaceans and trilobites, except for the absence of anterodorsal and posterodorsal suspensors. According to this interpretation, the endosternite is equipped with dorsal, ventral and transverse components within each segment. As in earlier studies, however, Firstman examined endosternal morphology without reference to other muscles. When the arrangement of carapacial muscle insertions of Recent chelicerates is taken into account, specifically those of extrinsic coxal muscles, it appears that Firstman's "transverse" suspensors are actually intersegmental and correspond to the posterodorsal suspensors of crustaceans and trilobites (Shultz, in preparation). Therefore, the endosternite in most Recent chelicerates appears to contain the same components as trilobites and crustaceans, except for the absence of

transverse and anterodorsal suspensors. True transverse suspensors may be retained in scorpions (Beck, 1885), and closer inspection may reveal their presence in other arachnids.

The endosternite in Recent chelicerates is concentrated in the prosoma, although the posterior portion is formed by elements of the first opisthosomal segment. The remaining opisthosomal components are represented by paired dorsoventral muscles within the anterior segments. It appears that the primitive prosomal endosternite in chelicerates had five components that correspond to the five postcheliceratal appendage-bearing segments, each consisting of paired posterodorsal ("transverse"), dorsal and ventral suspensor muscles (Rowland and Sissom, 1980; Shultz, in preparation; cf. Firstman, 1973). These components were integrated medially into a broad sheet of noncontractile connective tissue, the endosternite *sensu stricto*, formed by expansion and fusion of the endoskeletal bars and ventral longitudinal components of the primitive muscular network.

Among Recent Chelicerata, five segmental components appear to be retained in Xiphosura and perhaps Palpigradi (Rowland and Sissom, 1980), but the endosternite of palpigrades requires further study. Based on the number and arrangement of endosternal suspensor muscles, there appear to be four segmental components (6a) in Araneae, Amblypygi, Thelyphonida and Schizomida (Firstman, 1973; personal observation); two components (6b) in palpator and laniator Opiliones (Firstman, 1973; personal observation), Scorpiones (Beck, 1885) and Pseudoscorpiones (Vachon, 1949; Firstman, 1973); one component (6c) in Ricinulei and none (6d) in Solifugae (Firstman, 1973). There appear to be three or four segmental components in Acari (Firstman, 1973; van der Hammen, 1989), but, as there is uncertainty about the location of the prosoma-opisthosoma boundary in this order, I cannot assign a definite number of prosomal components to Acari. As noted above, one opisthosomal component is typically present in the arachnid endosternite, although two occur in palpator Opiliones.

The insertions of the dorsal endosternal suspensors have a simple metameric arrangement in Cephalocarida, Trilobita, Xiphosura and many arachnids, but those associated with the fourth postoral segment insert on the posteromedial portion of the carapace (7) in Palpigradi (Millot, 1943), mesothele and mygalomorph Araneae (Pocock, 1902c; Shultz; in preparation; cf. Firstman, 1973), Amblypygi and Thelyphonida (Firstman, 1973). These muscles are associated with the median carapacial depressions present in most of these arachnids.

The endosternite *sensu stricto* is a solid tendinous plate in Xiphosura and most arachnids, and I regard this as primitive. However, distinct fenestrae (8) are present in the endosternite of Thelyphonida and Schizomida (Firstman, 1973).

Mouth (9)

The mouths of trilobites and early derivative crustaceans are directed posteriorly and form the anterior end of a ventral food groove formed by the coxae of the segmental appendages. The coxosternal food groove is limited to the prosoma in Xiphosura and Eurpyterida, and the posteriorly directed mouth is retained. The embryos of most arthropods also have a posteriorly directed mouth, but it assumes a more anterior placement in arachnids as the anterior end of the prosoma bends dorsally during development. This bending also brings the labrum and chelicerae into a more anterior placement and is represented internally as a curvature in the neural mass (Weygoldt,

1979). Thus outgroup comparisons and ontogenetic evidence indicate that the anteroventral orientation of the mouth in Arachnida is apomorphic (9).

Tritosternum (10)

The tritosternum or labium is an anteroventral projection formed by an anterior prosomal sternite and occurs in the orders Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Ricinulei and Acari. It has no apparent counterpart in Trilobita, Xiphosura or Eurypterida and is therefore considered derived within Arachnida. In Palpigradi (van der Hammen, 1969, 1982) and Araneae (Snodgrass, 1948) the labrum and a broad tritosternum form the pre-oral chamber. The pre-oral chamber in Araneae is bordered laterally by extensions of the pedipalpal coxae, the "endites" or maxillary processes, but is otherwise similar to that found in Palpigradi. The pedipalpal coxae in Amblypygi are fused proximally and form the posterior border of the pre-oral chamber. The tritosternum persists as an elongate process with apical setae (Pocock, 1902a). The pedipalpal coxae in Thelyphonida, Schizomida and Ricinulei are fused medially, but a vestige of the tritosternum remains and gives rise to long apical setae that project anteriorly within the midventral suture of the fused pedipalpal coxae (Pittard and Mitchell, 1972; van der Hammen, 1979, 1986a). The tritosternum is distinctly paired in early derivative parasitiform Acari, including Opilioacarida, Gamasida and at least one holothyrid (van der Hammen, 1989). In some gamasids, the tritosternum takes the form of a single process similar to that found in Amblypygi. The tritosternum is absent in acariform mites (Lindquist, 1984).

Chelicerae (11, 12)

Among the known non-arachnid chelicerates, namely Pantopoda, Xiphosura and Eurypterida, the first postoral appendage, the chelicera, is typically formed by three segments, the last two forming a chela, and I regard this arrangement as primitive for Arachnida. Three-segmented, chelate chelicerae are present in Palpigradi, early derivative Acari, Opiliones and Scorpiones (Snodgrass, 1948). The chelicerae in Araneae, Amblypygi, Thelyphonida and Schizomida are composed of two segments and are subchelate; the distal segment is fanglike and articulates dorsally with a robust proximal segment (11). Ontogenetic studies of a mygalomorph spider suggest that the fanglike segment corresponds to the distal two segments of the primitive chelicera (Schimkewitsch in Dawydoff, 1949). The chelicerae of Pseudoscorpiones and Solifugae are formed by two segments as well, but they are chelate and articulate with one another at a ventral or ventrolateral joint. The chelicerae of Solifugae and early derivative Pseudoscorpiones (Chthonioidea, Neobisioidea) are massive, and the tips of the chela cross in scissor-like fashion when closed (12) (Chamberlin, 1931; Roewer, 1934).

Kjellesvig-Waering (1986) observed that the chelicerae of many fossil scorpions appear to be composed of four "segments". It should be noted, however, that the proximal cheliceral segment in certain Recent scorpions is composed of two regions that are represented by distinct sclerites (Millot and Vachon, 1949; Fig. 141). There is no evidence to support the view that these sclerites represent true segments. Similarly, Briggs et al. (1979) have questioned Raasch's (1939) frequently cited interpretation that the anterior appendages of the fossil arthropod *Aglaspis spinifer* (Aglaspida) represent four-segmented chelicerae (cf. Weygoldt and Paulus, 1979).

Chelicero-carapacial articulation (13)

The appendages of trilobites and early derivative Crustacea lack distinct articulations with the body and movement is apparently controlled by muscles, hydraulic pressure and arthro-dial membranes. The same arrangement is found in the chelicerae of Xiphosura and Eurypterida and is probably primitive for Arachnida. The primitive condition is retained in all arachnids except Solifugae and Pseudoscorpiones. Here the chelicerae join the carapace at anterolateral articulations (13) (Chamberlin, 1931; Roewer, 1934). The articular region of the carapace in Solifugae is modified as an anterolateral lobe that Pocock (1893) regarded as the third segment of the chelicera. However, presence of minute lateral eyes on this lobe (Roewer, 1934) shows that this structure is carapacial in origin. The chelicero-carapacial articulation is absent in chthonioid pseudoscorpions (Chamberlin, 1931).

Stomotheca (14)

The term stomotheca originally referred to the complex pre-oral chamber of certain Opiliones (Hansen and Sørensen, 1904), but van der Hammen (1985a) has applied the term to any pre-oral chamber formed by coxae of the walking appendages. He noted that such structures occur in Xiphosura, Opiliones and Scorpiones and placed these taxa within a group he named Myliosomata (cf. Kaestner, 1931). Outgroup comparisons indicate, however, that a feeding apparatus formed by coxae of the locomotor appendages is plesiomorphic for Chelicerata (Cisne, 1974; Weygoldt, 1985). A ventral food groove formed by the coxae of a long series of locomotor appendages is present in Trilobita (Cisne, 1974, 1981) and early derivative Crustacea (Hessler, 1964), and the prosomal components of this complex are retained in Xiphosura (Manton, 1964) and Eurypterida (Selden, 1981). Thus the stomotheca, as defined by van der Hammen, is plesiomorphic in Arachnida and cannot be used to demonstrate a special relationship between Xiphosura, Opiliones and Scorpiones.

In contrast, it is important to note that the pre-oral chambers of Opiliones and Scorpiones are similar in that they are formed largely by greatly expanded coxal endites of the first and second walking legs and pedipalps in Opiliones. The pre-oral structures of trilobites, xiphosurans and eurypterids are formed almost entirely by the coxae themselves and their gnathobases; the endites, if present, are relatively small and do not participate in forming the walls of the pre-oral chamber per se. It seems useful to redefine the stomotheca as a pre-oral chamber formed by greatly expanded coxal endites (14).

The organization of the stomotheca in certain palpator Opiliones appears to approximate a hypothetical primitive condition most closely. Here coxal endites of the pedipalps and first two pairs of walking legs are well developed and project ventrally or anteroventrally to form the walls of the pre-oral chamber. The medial surfaces of the pedipalpal endites and those of leg 1 are equipped with soft, membranous "lips". The anterior border of the stomotheca is formed by a large, beaklike labrum, the lateral borders of which are fused to the medial surfaces of the pedipalpal coxae (personal observation). The posterior border of the stomotheca in Palpatores is formed by a prosomal sternite (Winkler, 1957) supported posteriorly by the endites of leg 2. In some cases, the endites are movable and are equipped with extrinsic muscles (Hansen and Sørensen, 1904; Snodgrass, 1948; personal observation), a feature also present in Xiphosura (Manton, 1964) and perhaps Eurypterida (Selden, 1981). The posterior

components of the stomotheca, especially the labium and endites of leg 2, are reduced in laniator and cyphophthalmid Opiliones (Pocock, 1902b; Hansen and Sørensen, 1904).

The stomotheca of Scorpiones appears to be more derived. The coxal endites of the pedipalps are reduced, although the "lips" are present, and those of the first two pairs of walking legs project anteriorly to form the floor of the pre-oral chamber. In contrast to many Opiliones, where the pre-oral chamber opens ventrally or anteroventrally, the pre-oral chamber of Scorpiones opens anteriorly. Furthermore, the endites of scorpions are incapable of independent movement (Couzijn, 1976). The labrum is membranous, but its lateral borders are fused to the pedipalpal coxae as in Opiliones (personal observation).

My examination of embryos from *Centruroides vittatus* (Buthidae) shows that the endites in these ovoviviparous scorpions first develop as ventral projections that must later shift anteriorly to assume the configuration of the adult, probably through an anterodorsal rotation of the coxae themselves. Thus the endites of these scorpions pass through a stage reminiscent of those found in the adults of many palpator Opiliones. This observation is consistent with my proposal that the pre-oral chamber in certain palpator Opiliones is more primitive than that found in Scorpiones.

Rostrum (15)

The labrum is present throughout Crustacea, Trilobita and Chelicerata. It is a pre-oral structure overhanging the mouth and is typically supplied with muscles that dilate the oral cavity. Some workers believe that the labrum represents the fusion of paired pre-oral appendages (Weygoldt, 1979). The mouth is directed posteriorly in early derivative crustaceans, trilobites, xiphosurans and eurypterids and the labrum projects ventrally. Due to the anterior bending of the anterior portion of the prosoma in arachnids, the mouth and labrum assume an anteroventral orientation. The labrum in Solifugae and Pseudoscorpiones projects anteriorly between the bases of the chelicerae and forms a unique beak-like structure, the rostrum (10) (Chamberlin, 1931; Roewer, 1934; van der Hammen, 1986a).

The proximal portion of the rostrum is fused to the medial surfaces of the pedipalpal coxae, as in Opiliones and Scorpiones, and the rostrum is bordered laterally by paired processes (Chamberlin, 1931; personal observation) reminiscent of the pedipalpal endites of palpator Opiliones. It is tempting to speculate that the pre-oral chamber formed by the rostrum and pedipalpal processes in Pseudoscorpiones and Solifugae corresponds to the anterior portion of a greatly reduced stomotheca similar to that found in Opiliones.

Pedipalps (16, 17)

The second postoral appendages are modified as mandibles in Crustacea but are similar to walking legs in Trilobita. These appendages, known as pedipalps in Chelicerata, are also leg-like in most Eurypterida but have well-developed chelae in Xiphosura, as do all prosomal appendages in Recent members of this group. Comparative studies of pedipalpal morphology suggest to me that leg-like pedipalps are primitive in Arachnida (Fig. 3).

At present, the only reasonable alternative to this view is to assume that xiphosurans reflect the morphology of the primitive arachnid pedipalp and to conclude that this appendage is primitively chelate. Pedipalpal chelae are found in several arachnid

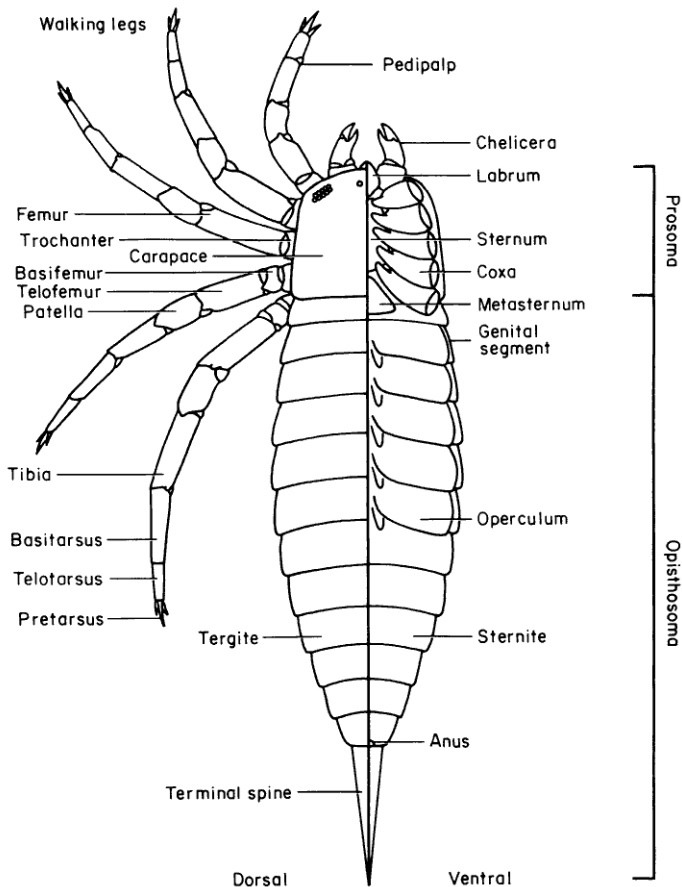


Fig. 3. Hypothetical arachnid illustrating plesiomorphic states of major external characters used in the present analysis.

groups, namely Ricinulei, Thelyphonida, Scorpiones and Pseudoscorpiones, but the chelae in most of these taxa do not appear to be homologous with those found in Xiphosura. The chelae in Xiphosura are operated by antagonistic opener and closer muscles, suggesting that the movable finger corresponds to the pretarsus of other chelicerates. The pretarsus is the only distal segment of the chelicerate appendage equipped with antagonistic muscles. This arrangement is found elsewhere only in the minute chelae of the highly specialized pedipalps in ricinuleids (van der Hammen, 1979). The chelae in Thelyphonida are usually poorly developed, but they are well developed in some species. The chelal articulation corresponds to the tibiotarsal joint and is operated by a closer muscle only. The mobile digit has two segments, pretarsus and tarsus, and contains remnants of the antagonistic pretarsal muscles (Barrows, 1925). The powerful pedipalpal chelae of Scorpiones and Pseudoscorpiones are very similar to one another but differ from those found in Xiphosura and Thelyphonida. The chelal articulation appears to correspond to the tibiotarsal joint, but there is no evidence of segmentation in the movable digit. The chela is operated by a closer only with heads arising in the chelal hand (tibia) and patella (16) (Alexander, 1967; Chamberlin, 1931; Dubale and Vyas, 1968). In summary, I consider the pedipalpal chelae of Xiphosura,

Ricinulei and Thelyphonida to be unique specializations within each of these groups, and those of Scorpiones and Pseudoscorpiones as potentially synapomorphic. The pedipalps are distinctly raptorial (17) in Amblypygi, Thelyphonida and Schizomida (Shear et al., 1987).

Pedipalpal coxae (18, 19)

The coxae of the pedipalps are independently movable in Xiphosura (Manton, 1964; Wyse and Dwyer, 1973) and probably Eurpyterida (Selden, 1981), and this is considered primitive for Arachnida. The pedipalpal coxae in Thelyphonida, Schizomida, Ricinulei and Acari are fused along their medial margins and form the floor of the pre-oral chamber (18) (Börner, 1903; Snodgrass, 1948). The fused pedipalpal coxae in Ricinulei and Acari are separated from the rest of the prosoma by a distinct articulation that permits movement of the coxae, labrum and pharyngeal apparatus as a unit (19), and I consider this feature, the subcapitulum, to be derived (cf. Lindquist, 1984; van der Hammen, 1986b).

Sensory appendages (20)

Weygoldt and Paulus (1979) noted a tendency for arachnids to use leg 1 as a sensory organ and hypothesized that this feature is synapomorphic for nonscorpion arachnids (Fig. 1). A kinematic study of walking scorpions suggests, however, that leg 1 is used, in part, as a tactile organ (Bowerman, 1975), and it appears that this behavior is widespread among pedestrian arthropods, both terrestrial and benthic. Thus I regard this feature as a poor phylogenetic character. In contrast, certain arachnids show distinct morphologic specializations associated with increased use of walking legs as tactile organs. Modifications of leg 1 in Palpigradi, Amblypygi, Thelyphonida, Schizomida and Solifugae are especially noteworthy. Here the legs are often elongate, antenniform structures that do not play a role in propulsion (20).

Weygoldt and Paulus also suggest that a tendency to use leg 2 as a tactile organ is synapomorphic for Opiliones, Ricinulei and Acari, but I consider this feature autapomorphic for Opiliones. Early derivative Acari do not appear to use leg 2 in this manner (Lindquist, 1984), and our understanding of ricinuleid behavior and sensory physiology is too rudimentary to draw any firm conclusion with regard to this character.

Coxal movability (21)

Arachnologists disagree about the evolutionary history of the coxa in the chelicerate walking leg. According to one view, coxae are primitively absent or incompletely developed in ancestral arachnids but were derived later as modifications of the sternal region of the prosoma, the epimera. This hypothesis was advanced to account for the absence of distinct coxae in acariform mites (van der Hammen, 1977a, 1985b; Lindquist, 1984). An alternative view maintains that distinct, movable coxae were present in the arachnid ancestor and that absence of movable coxae is derived (Manton, 1977). The latter position is supported by the existence of apparent movable coxae in trilobites (Cisne, 1981), xiphosurans (Manton, 1964) and eurypterids (Selden, 1981) and by comparative studies of extrinsic coxal musculature in Recent chelicerates (Shultz, in preparation).

Movable coxae are retained in Palpigradi (van der Hammen, 1982), Araneae,

Amblypygi, Thelyphonida, Schizomida (personal observation), opilioacarine Acari (Lindquist, 1984) and many palpator Opiliones (Hansen and Sørensen, 1904). Coxal movement is essentially absent (21) in Ricinulei, Scorpiones, Pseudoscorpiones and Solifugae. Limited coxal movement is present in leg 4 of Ricinulei and functions in the locking and unlocking of a unique coupling mechanism between the prosoma and opisthosoma (Hansen and Sørensen, 1904; Pittard and Mitchell, 1972). Slight movements of the coxae of leg 1 in Scorpiones are associated with feeding (Couzijn, 1976).

Musculi laterales (22)

Reconstruction of musculature in the trilobite *Triarthrus* has revealed five basic groups of extrinsic leg muscles, two endosternocoxal muscles arising from the endoskeletal bars (endosternite) and three tergocoxal muscles from the dorsal exoskeleton (Cisne, 1981). One tergocoxal muscle inserts on the anterior margin of the coxa, one of the posterior margin and one near the lateral (pleural) margin. This basic arrangement of tergocoxal muscles is present in *Limulus* and many arachnids, including Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Opiliones and Scorpiones (Shultz, in preparation), and probably represents the primitive condition for Arachnida. The lateral tergocoxal muscle in Araneae and Thelyphonida inserts on the pleural membrane adjacent to the coxa rather than on the coxa itself (22). Spider anatomists term this derived form of the lateral tergocoxal muscle the *musculi laterales* (Wilson, 1970; Palmgren, 1978), and some have speculated that these muscles produce hydraulic pressures used in propulsive leg extension (Wilson, 1970; Anderson and Prestwich, 1975; cf. Palmgren, 1981).

Coxal endites (23)

The medial surface of each coxa is equipped with a process, the endite, in Xiphosura and Eurypterida (Selden, 1981), and this is probably primitive for Arachnida (Fig. 3). Endites are retained on the coxae of legs 1 and 2 in Scorpiones and many opilionids (see Stomotheca) and on legs 3 and 4 in certain ischyropsalidoid opilionids (Shear, 1986). Coxal endites are absent on the walking legs of all other Recent arachnid orders (23), although a coxal process of some kind is typically present on the pedipalps. Endites appear to form on the coxae of the walking legs in certain mygalomorph Araneae during embryonic development, but eventually disappear (Schimkewitsch in Beklemishev, 1969), an observation consistent with the hypothesis that coxal endites are a primitive feature in Arachnida and that their absence is derived.

Coxotrochanteral joint (24)

The coxa joins the trochanter at a simple biocondylar articulation in the walking legs of Xiphosura, Eurypterida (Selden, 1981) and many arachnids (van der Hammen, 1977b; personal observation), and this feature is probably primitive for the arachnid orders. The posterior articulation of the coxotrochanteral joint of Araneae, Amblypygi, Thelyphonida and Schizomida is formed by two intercalary sclerites embedded in the arthrodistal membrane, a proximal (coxal) sclerite and a distal (trochanteral) sclerite (24). Each sclerite articulates with its respective leg segment through a loose joint that permits promotion-remotion movements. The sclerites meet one another at a complex articulation that can undergo levation-depression as well as promotion-remotion, a

greater range of movements than the primitive bicondylar joint permits. The trochanteral sclerite is small or absent in Araneae, but the coxal sclerite is well developed (Clarke, 1986). Both sclerites are well developed in Amblypygi, Thelyphonida and Schizomida (personal observation; cf. van der Hammen, 1986a). A somewhat analogous arrangement is present at the coxotrochanteral joint of the posterior legs in some scorpions (personal observation).

Divided femur (25)

There has been considerable disagreement about how segments within the legs of different arachnid orders should be homologized (Weygoldt and Paulus, 1979; van der Hammen, 1985b; Shultz, 1989), a situation that appears to stem from the variety of 'key' criteria different arachnologists have employed (Couzijn, 1976). For example, conclusions derived from Gaubert's (1892) postural criterion has led to the widely accepted view that the patella is absent in Pseudoscorpiones and Solifugae, a conclusion that inspired one worker (van der Hammen, 1977b, 1986a, 1989) to place these orders in a new class, Apatellata. A recent survey of appendicular morphology (Shultz, 1989) shows that the patella is present in all arachnids and that most of the diversity found in walking appendages can be accommodated by a simple system that recognizes seven segments: coxa, trochanter, femur, patella, tibia, divided tarsus and pretarsus (Fig. 3). However, the third and fourth walking legs in Ricinulei, early derivative Acari and Solifugae have eight segments rather than seven, and this feature is also found in the anterior leg pairs of many acariform mites. Walking legs of certain trigonotarbid, extinct relatives of spiders, appear to have an extra segment, the annulus, between the trochanter and femur (Shear et al., 1987).

Comparative analysis of appendicular musculature (Shultz, 1989) and studies of postembryonic development (Grandjean, 1954; Coineau and van der Hammen, 1979) suggest that these extra segments result from a division of the femur. It is important to note, however, that the muscles associated with the extra joint are also present within the undivided femora of many Recent arachnids and *Limulus* (Shultz, 1989). The presence of these unusual muscles and the fact that eurypterids and pycnogonids (Pantopoda) also appear to have divided femora on legs 3 and 4 suggest that presence of two femoral segments (basifemur, telofemur) in these appendages is primitive for Arachnida (Fig. 3). I conclude that presence of a basifemur and telofemur in each walking leg is primitive for Chelicerata and that the basifemur-telofemur joints of legs 1 and 2 fused or failed to develop in the common ancestors of Eurypterida, Arachnida and perhaps Xiphosura (Fig. 2). I consider presence of undivided femora on legs 3 and 4 (25) to be a derived feature within Arachnida and Xiphosura.

Femoropatellar joint (26)

The femoropatellar joint is formed by a transverse dorsal hinge articulation in Xiphosura, Eurypterida (Selden, 1981) and perhaps Trilobita (Cisne, 1981), and it is reasonable to conclude that this feature is primitive for Arachnida. This arrangement is retained in Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Ricinulei and Acari (Shultz, 1989). The femoropatellar joint is formed by a transverse bicondylar articulation (26a) in palpator and laniator Opiliones, Scorpiones and early derivative Pseudoscorpiones and by an anterodorsal monocondylar joint (26b) in Solifugae (Shultz, 1989).

Femoropatellar flexor muscles (27)

The flexor muscle complex of the femoropatellar joint in *Limulus* consists of anterior, median and posterior components that insert symmetrically on the ventral margin of the patella, and this appears to be primitive for Arachnida (Shultz, 1989). Symmetrical femoropatellar flexors are present in all arachnid groups except Amblypygi, Thelyphonida and Schizomida. The anterior and median components of these three orders insert together on a sclerite that attaches to the anterior margin of the patella via ligaments, and the posterior components inserts broadly on the ventral margin of the patella itself (27).

Transpatellar muscles (28, 29, 30)

The patella in *Limulus* is transversed by a symmetrical pair of muscles that arise from the distodorsal surface of the femur and walls of the patella and insert on the anteroventral and posteroventral margins of the tibia, respectively. This arrangement appears to be primitive for arachnids and occurs in Palpigradi, Acari, and, with some modifications, Araneae, Amblypygi and Thelyphonida (Shultz, 1989).

The posterior transpatellar muscle in palpator and laniator Opiliones, Scorpiones and early derivative Pseudoscorpiones arises from a distodorsal process of the femur and lacks a direct connection to the patella (28a). These modifications suggest that the posterior transpatellar muscle functions as a femoropatellar extensor in these groups. In its primitive condition, the posterior transpatellar muscle inserts on the posterior margin of the tibia, but it inserts dorsally in Scorpiones and Pseudoscorpiones and appears to act as a patellotibial extensor (29). The posterior transpatellar muscle is absent (28b) in Ricinulei, Schizomida and Solifugae (Shultz, 1989).

The primitive anterior transpatellar muscle inserts on the anterior or anteroventral margin of the tibia, but it inserts ventrally or posteroventrally (30a) in Scorpiones, Pseudoscorpiones and Solifugae. This muscle is absent (30b) in Ricinulei and Schizomida.

Patellotibial articulation (31)

The patellotibial joint of the walking leg has a dorsal monocondylar articulation in Xiphosura (Shultz, 1989) and Eurypterida (Selden, 1981), and I regard this as primitive for Arachnida. This feature is retained in Palpigradi, Araneae, Amblypygi, Thelyphonida and Schizomida (Shultz, 1989). Van der Hammen (1979 and Shear et al. (1987) hypothesized that a monocondylar patellotibial joint is synapomorphic for Araneae, Amblypygi, Thelyphonida and Schizomida, but this view should be rejected in light of results from outgroup comparisons. The patellotibial joint is formed by a hinge articulation (31a) in Ricinulei, Acari and Solifugae. It takes the form of a simple bicondylar articulation (31b) in Opiliones, Scorpiones and early derivative Pseudoscorpiones, a condition that appears to have evolved through the addition of a ventral condyle to the primitive dorsal one (Shultz, 1989).

Patellotibial muscles (32, 33)

Six pairs of muscles insert on the proximal rim of the tibia in the walking legs of Xiphosura, including the transpatellar muscles discussed above and paired dorsal muscles that have no counterpart in Arachnida (Shultz, 1989). The last pair of

muscles, the patellotibial muscles, are simple in structure. The anterior patellotibial muscle arises on the anterior wall of the patella and inserts on the anterior margin of the tibia; the posterior muscle arises on the posterior wall of the patella and inserts on the posterior rim of the tibia. This arrangement is also present in Araneae, Amblypygi, Thelyphonida and Opiliones, and I consider it primitive for Arachnida. The patellotibial muscles may also occur in Palpigradi and Acari, but their fibers cannot be distinguished from the patellar heads of the transpatellar muscles. The anterior patellotibial muscle has a ventral rather than anterior insertion on the tibia (32a) in Ricinulei, Scorpiones and Solifugae, and it is absent (32b) in Pseudoscorpiones (Shultz, 1989). The posterior patellotibial muscle is absent (33) in Schizomida, Scorpiones, Pseudoscorpiones and Solifugae.

Tarsus (34)

The penultimate segment of the arachnid walking appendage, the tarsus, is usually divided into at least two tarsomeres, a proximal basitarsus (=metatarsus) and distal telotarsus (=“tarsus”) (Fig. 3). This condition is present in most arachnids but is absent in certain derived lineages, such as monosphyronid pseudoscorpions (Chamberlin, 1931) and acariform mites (Lindquist, 1984). Using Recent Xiphosura as an outgroup, Shultz (1989) suggested that the divided tarsus is synapomorphic for the arachnid orders. However, an analysis of appendicular joint structure of eurypterids (Selden, 1981) suggests that these chelicerates possess a divided tarsus as well (podomeres 7 and 8 in Selden’s system), and it is likely that this feature is synapomorphic for Eurypterida and Arachnida (Fig. 2).

Subdivision of the telotarsus occurs in many arachnid orders, including Palpigradi, Ricinulei, Amblypygi, Thelyphonida, Schizomida, Opiliones and Solifugae, but the number of tarsomeres varies between taxa and often within a taxon. The only apparent interordinal pattern occurs in Amblypygi, Thelyphonida and Schizomida, where the telotarsi of walkings legs 2–4 are composed of three distinct tarsomeres (34) (Shultz, 1989). This similarity was overlooked by most earlier workers due to a persistent misinterpretation of the distal podomeres within the amblypygid walking leg. Amblypygids differ from most other chelicerates in that the tibiae are divided by one or more adesmatic joints. Many workers interpreted the distal part of the divided tibia as a basitarsus and concluded that amblypygids have a four-segmented telotarsus (e.g. van der Hammen, 1986a). Comparisons of leg muscles reveal that amblypygids possess a single short basitarsus and a telotarsus with three tarsomeres. In some amblypygids, one of the tarsomeres bears a ring of reduced sclerotization that superficially resembles a joint, but the division is not complete and condyles are lacking (Hansen, 1893; personal observation). Outgroup comparisons with Xiphosura and Eurypterida indicate that the undivided telotarsus is plesiomorphic for Arachnida.

Pretarsus (35, 36, 37, 38)

The terminal segment of the chelicerate walking appendage, the pretarsus, is operated by a pair of muscles, a levator and depressor. The depressor originates within the tarsus in Xiphosura and Pantopoda, but it arises from the tibia (35) in all arachnids studied thus far and extends into the patella (36) in early derivative Araneae, Thelyphonida, Schizomida, Opiliones, Scorpiones, Pseudoscorpiones and Solifugae (Shultz, 1989). The heads of the pretarsal depressor usually arise from the dorsal surface of the leg in

Pantopoda and most arachnids, and this situation is probably primitive. The patellar head of the pretarsal depressor in Thelyphonida and Schizomida arises broadly from the posterior surface of the patella, a feature that I consider derived (37).

The pretarsus is sclerotized in Xiphosura, Eurypterida and most arachnids, where it takes the form of a median or empodial claw. The pretarsus in adult Pseudoscorpiones and Solifugae is present as an eversible organ, the empodium (38). This structure is also present in the early instars of certain other arachnids, such as Amblypygi, Uropygi and Scorpiones. Ontogenetic evidence (Roewer, 1934) supports the view that the empodium is homologous with the pretarsus.

Chilaria (39)

The appendages of the first opisthosomal segment in Xiphosura, the chilaria, are located between the coxae of leg 4 and form a part of the feeding apparatus (Manton, 1964). Homologous appendages may occur in Eurypterida but are fused into a plate-like structure, the metastoma, that overlaps the medial portions of the coxae of leg 4 (Størmer, 1944). Although all known arachnids lack appendages on the first opisthosomal segment (39), the sternite (metasternum) is retained and appears to have been incorporated as a functional part of the prosoma in many groups. This feature is especially evident in early derivative Araneae, Thelyphonida, Schizomida, Amblypygi (Hansen, 1893) and Scorpiones and has fueled disputes over the number of segments in the arachnid opisthosoma.

Pedichel (40, 41, 42)

Outgroup comparisons with Xiphosura and Eurypterida indicate that a broad connection between the prosoma and opisthosoma is primitive for Arachnida. This feature is retained in Acari, Opiliones, Scorpiones and Pseudoscorpiones. Any modification of the anterior opisthosoma that forms an apparent waist is termed a pedicel. Pocock (1893) recognized a pedicel in Palpigradi, Araneae, Amblypygi, Thelyphonida and Schizomida and placed these orders together within Caulogastra. Börner (1902) tentatively placed Ricinulei ("Cryptostemmata") in Caulogastra due to the presence of a constriction of the anterior opisthosomal segments that is usually hidden by a unique coupling device between the prosoma and opisthosoma. Recent authors have tended to be more restrictive in their application of the term. Weygoldt and Paulus (1979) hypothesized that the pedicel ("petiolus") is synapomorphic for Araneae and Amblypygi (Fig. 1), but Shear et al. (1987) have argued that this resemblance reflects similar functional demands, not homology.

A closer inspection of the pedicel in different arachnid groups shows greater diversity within this feature than is generally supposed. A constriction of the first opisthosomal segment (40) is present in several arachnid lineages, but it also includes a part of the second opisthosomal segment in Araneae, Amblypygi, Thelyphonida and Schizomida. The second opisthosomal segment in these arachnids is divided into a small anterior sternal sclerite and a large posterior genital plate or operculum. The anterior sternal sclerite is embedded within a flexible membrane that forms the ventral surface of the pedicel (41), and the dorsal surface is formed by the reduced tergite of the first opisthosomal segment. The genital plate projects rearward and overlaps the sternite of the third opisthosomal segment (42). The genital opening lies between the genital plate and the third opisthosomal sternite. This arrangement of the genital aperture is also

present in Palpigradi, but the pedicel does not appear to include elements of the genital segment.

The anterior sternal sclerite of the second opisthosomal segment is traditionally considered the first opisthosomal sternite (Börner, 1902), but this appears to be incorrect. Dissections of amblypygids, thelyphonids and schizomids reveal that several anterior opisthosomal segments contain paired dorsoventral muscles running from tergite to sternite. The dorsoventral muscles arising from the second opisthosomal tergite insert on the sternal sclerite not on the genital plate, which is traditionally and erroneously regarded as the sole component of the second opisthosomal sternite. The dorsoventral muscles of the first opisthosomal tergite attach to the "prosomal" endosternite. It appears that the first opisthosomal sternite is that "prosomal" sclerite generally known as the metasternum and is situated between the coxae of the fourth leg pair. Muscles arise from the metasternum and insert on the ventral surface of the endosternite and probably represent the ventral component of the dorsoventral muscles of the first opisthosomal segment. The external features of mesothele spiders conform to my description of Amblypygi, Thelyphonida and Schizomida (see also Börner, 1902: Fig. 2D). The metasternum is represented by an intercoxal sclerite, and a small, weakly developed sclerite is embedded within the ventral membrane of the pedicel. I have not examined the muscles of a mesothele spider. The ventral region of the pedicel in other spiders is variable (personal observation).

Postgenital appendages (43)

Primitive chelicerates probably had a series of sclerotized postgenital appendages associated with respiratory lamellae, portions of which are retained as internal book lungs in some lineages. Except for the opercula of Xiphosura, Eurypterida and fossil Scorpiones, external postgenital appendages were eliminated in most arachnids (43b). Postgenital appendages or appendage-like structures are retained in Palpigradi, Acari, Araneae and Amblypygi, but unlike the primitive condition, these organs are poorly sclerotized and are not associated with respiratory lamellae (43a). In some palpigrades these structures take the form of paired eversible vesicles on opisthosomal segments 4–6 (van der Hammen, 1982). Similar structures are present on opisthosomal segment 4 in many amblypygids (Weygoldt and Paulus, 1979). Postgenital appendages also occur in spiders on opisthosomal segments 4–5 and function as spinnerets. Three pairs of genital papillae occur in early derivative Acari (van der Hammen, 1979, 1982).

It is interesting to note that postgenital appendages or appendage-like structures in Recent arachnids occur on opisthosomal segments 4–6, and, if fewer than three pairs occur, they are absent from the posterior segments. Ontogenetic studies of Palpigradi and acariform mites show that the appendages develop in an anterior to posterior sequence, one pair per molt (van der Hammen, 1982). Yoshikura (1975) noted that in the mesothele spider *Heptathela*, the anterior medial spinnerets develop before the posterior medial spinnerets, but the lateral spinnerets do not show this pattern (cf. Marples, 1967). It is tempting to speculate that reduction of postgenital "appendages" has occurred through neotenic suppression.

Pygidium (44, 45, 46)

Hansen and Sørensen (1904, 1905) erected the superordinal taxon *Arachnida micrura* to accommodate those orders that bear a tail-like structure, the pygidium, formed by

reduction of the last three opisthosomal segments (44). A pygidium is present in Palpigradi, Amblypygi, Thelyphonida, Schizomida, Ricinulei and in the extinct orders Trigonotarbida and Kustarachnida (Petrunkevitch, 1955; Beall, 1986; Shear et al., 1987). The pygidium terminates in a multijointed flagellum (45) in Palpigradi, Thelyphonida and female Schizomida. Pygidial defensive glands (46) are found in Thelyphonida and Schizomida (Hansen and Sørensen, 1905). The pygidium in Ricinulei is retractable (Pittard and Mitchell, 1972), and van der Hammen (1982) speculated that the retractable anal segment of opiliocarine Acari could be homologous with the terminal segment of the ricinuleid pygidium. In the absence of more convincing evidence, however, I consider the pygidium absent in Acari. Hansen and Sørensen (1904) recognized the affinities of Araneae to certain "micruran" orders and suggested that the anal tubercle of spiders represents a reduced pygidium. Inspection of the opisthosomal tergites in *Liphistius* (Mesothelae) shows that the anal tubercle represents only one segment and that the pygidium is absent in this order (Millot, 1949a; personal observation). It should be noted, however, that a distinct metasoma ("postabdomen") composed of several posterior opisthosomal segments appears during embryonic development in certain spiders (Dawydoff, 1949).

Beall (1986) re-examined the poorly preserved fossils that are the sole occupants of the order Kustarachnida and concluded that these "micrurans" belong within the order Opiliones. Beall based his interpretation on the presence of three features, namely triangular coxae, long, slender legs and two eyes on a median tubercle, and suggested that the pygidium is plesiomorphic for Opiliones. As none of the features Beall cited is reliably diagnostic for Opiliones, his interpretation is not conclusive, and I therefore consider the pygidium absent in Opiliones.

Slit sensilla (47)

Slit sensilla are unique to Archnida and function in the detection of compressional forces acting on the exoskeleton. They appear as small clefts or slits in the cuticle, especially near joints or other areas where compressional forces regularly occur. Several slit sensilla may be arranged in parallel and are collectively termed a lyriform organ (Barth and Stagl, 1976). Weygoldt and Paulus (1979) noted that slit sensilla are found in all arachnid orders except Palpigradi and Ricinulei, although the presence of slit sensilla in Ricinulei has been known for some time (Pittard and Mitchell, 1972). Weygoldt and Paulus also hypothesized that lyriform organs are synapomorphic for nonscorpion arachnids (Fig. 1), even though Hansen (1893) observed and illustrated well-developed lyriform organs in scorpions. Still, as the difference between groups of slit sensilla and lyriform organs appears to be subjective, I question the phylogenetic relevance of this distinction.

Trichobothria (48)

Trichobothria are elongate setae that function in the detection of airborne vibrations and currents. Although the distribution of trichobothria on the bodies of arachnids is often used by systematists, few interordinal patterns are apparent. However, a unique pattern of trichobothria occurs on the walking legs of Thelyphonida and Schizomida. The distodorsal surface of the tibia of legs 1 and 2 has two well-developed trichobothria and that of legs 3 and 4 has one (48) (Hansen and Sørensen, 1905). Similar trichobothria are present in certain Trigonotarbida (Shear et al., 1987).

Eyes (49, 50)

Outgroup comparisons with Xiphosura and Eurypterida suggest that arachnids originally had two kinds of eyes, a pair of simple medial eyes and a pair of compound lateral eyes (Paulus, 1979; Weygoldt and Paulus, 1979) (Fig. 3). The lateral eyes of Recent arachnids, when present, possess simple lenses that probably represent the subdivision of compound eyes. Although Weygoldt and Paulus regarded the presence of simple lateral eyes as synapomorphic for Arachnida (Fig. 1), there is evidence that simplification or loss of lateral eyes occurred more than once. Kjellesvig-Waering (1986) demonstrated that many fossil scorpions have well-developed compound eyes, indicating that scorpions acquired simple lateral eyes after diverging from other chelicerates. In addition, the lateral eyes of certain trigonotarbids consist of six large facets and many smaller lenses (Shear et al., 1987), and each of the six eyes of phalangiotarbids may be composed of up to 17 facets (Kjellesvig-Waering, 1978). The conditions present in these extinct arachnid lineages may represent intermediate stages in the transition from compound to simple eyes.

Among Recent arachnids, six principal lateral eyes (49a) are found in Araneae, Amblypygi and Thelyphonida. The presence of six lateral eyes may be primitive for Acari as well, as this feature occurs in at least one genus of early derivative Acari, *Paracarus* (Opilioacarida) (van der Hammen, 1979, 1989). Six lateral eyes are also characteristic of the fossil order Phalangiotarbida (Petrunkevitch, 1955; Kjellesvig-Waering, 1969, 1978), a group of arachnids that may be closely related to Acari (van der Hammen, 1979; Beall, personal communication). Two pairs of simple lateral eyes (49b) are present in many pseudoscorpions, some solifuges and many mites. Vestigial lateral eyes (49c) are found in certain ricinuleids (van der Hammen, 1979) and some schizomids (Hansen and Sørensen, 1905). Lateral eyes are absent in Palpigradi and Opiliones (49d). Medial eyes are absent (50) in Palpigradi, Schizomida, Ricinulei and Pseudoscorpiones.

Respiratory lamellae (51)

Postoral segmental appendages in trilobites are biramous; that is, the basal podomere (coxa?) gives rise to two branches, a ventrolateral endopodite and a dorsolateral exopodite. The endopodite apparently served in locomotion, and the exopodite, a long, multi-jointed rod equipped with a series of long, thin lamellae, probably functioned in respiration (Bergström, 1979). There are similarities between the opisthosomal appendages of Recent xiphosurans and the trunk appendages of trilobites (Størmer, 1933; Bergström, 1979). The appendages are biramous in each group, but the endopodite and exopodite on opisthosomal segments 2–7 in Recent xiphosurans are partially fused and flattened to form a series of overlapping opercula. Each exopodite is greatly expanded compared to that of trilobites, and those of opisthosomal segments 3–7 carry broad, flat respiratory lamellae, the book gills, on their proximodorsal surfaces. In contrast to xiphosurans, neither arachnids nor eurypterids appear to have appendages or their remnants on opisthosomal segment 7, and this loss may be synapomorphic for these groups (Figs 2, 3).

Comparative morphologic and ontogenetic studies indicate that internal respiratory lamellae, or book lungs, are homologous with the book gills of Xiphosura (Simmons, 1894; Kaestner, 1929). Paired book lungs (51) are present on the second and third opisthosomal segments of mesothele, mygalomorph and paleocribellate Araneae;

Amblypygi; Thelyphonida and certain extinct groups, including Trigonotarbida (Claridge and Lyon, 1961; Shear et al., 1987). The posterior pair of book lungs is modified as tracheae in most neocribellate spiders (Levi, 1967) and is absent in Schizomida (Hansen and Sørensen, 1905). Some authors have suggested that the tracheae of opisthosomal segments 3 and 4 in Pseudoscorpiones and Solifugae are derived from book lungs, because they develop at the base of appendicular rudiments.

Book lungs are also present in Recent Scorpiones, but these appear to have evolved well after scorpions diverged from other chelicerates. The ventral surface of the opisthosoma in most Palaeozoic scorpions has distinct opercula that apparently served to protect respiratory lamellae in some groups (Kjellesvig-Waering, 1986). The respiratory system found in all Recent scorpions, book lungs opening through sternal stigmata on opisthosomal segments 3–6, is known from the Carboniferous (Vogel and Durden, 1966; Kjellesvig-Waering, 1986). Thus I contend that external respiratory lamellae are a primitive feature of Arachnida and that book lungs evolved more than once, at least once within Scorpiones and one or more times in other arachnids.

Tracheal system (52, 53)

Although the respiratory system of primitive arachnids probably consisted of respiratory lamellae, many Recent arachnid groups transport respiratory gases through a system of cuticular tubes, the tracheae, that communicate with the external environment through openings, the stigmata (52). Pocock (1893), Börner (1902), Firstman (1973) and Weygoldt and Paulus (1979) (Fig. 1) have suggested that the tracheal systems of the different arachnid orders are homologous and placed these groups together within the superordinal taxon Holotracheata.

In contrast, diversity in placement of tracheal stigmata suggests that tracheal systems evolved independently several times. Paired stigmata in Pseudoscorpiones and Solifugae open on the ventral surfaces of opisthosomal segments 3 and 4 (53), with additional stigmata occurring on the ventral surface of the prosoma and opisthosomal segment 5 in Solifugae (Roewer, 1934). The tracheal system in Opiliones opens through a pair of stigmata on the second opisthosomal segment (Hansen and Sørensen, 1904). The paired stigmata of Ricinulei are located in the pleural region of the prosoma adjacent to the coxae of legs 3 and 4 (Millot, 1945). Stigmata in opilioacarine Acari are found on the tergites of several anterior opisthosomal segments, and some of these are probably homologous with the stigmata of certain other parasitiform mites (Lindquist, 1984). It appears that tracheal systems are primitively absent in acariform mites, although tracheae have evolved in certain derived groups (Lindquist, 1984).

Spermatozoa (54, 55, 56)

Among Recent Chelicerata, *Limulus* (Xiphosura) retains the most generalized or primitive spermatozoa. The mature free-swimming spermatozoan consists of an acrosomal complex, a large nucleus and a well-developed axoneme with the typical 9 + 2 microtubule arrangement. The base of the axoneme is surrounded by a collar, the middle piece, containing mitochondria (Baccetti, 1979). An acrosomal complex of some sort is present in all arachnids examined thus far, except Palpigradi (Alberti, 1979a). The nucleus is associated with an array ("manchette") of microtubules (54) in Araneae, Amblypygi, Thelyphonida, Schizomida and Ricinulei, and this structure may be derived as it is absent in Xiphosura (Alberti and Palacios-Vargas, 1987).

The axoneme is absent (55b) in Palpigradi (Alberti, 1979a), Acari (Alberti, 1980a, 1980b) and Solifugae (Alberti, 1980c), a condition that is undoubtedly derived. The axoneme is greatly reduced in most Opiliones as well, but a functionless flagellum with a $9 + 0$ microtubule arrangement is retained in at least one cyphophthalmid (Juberthie et al., 1976), and $9 + 0$ centrioles and mitochondria occur in palpator and laniator Opiliones (Juberthie and Manier, 1978). A well-developed axoneme with a $9 + 2$ microtubule arrangement is present in some Scorpiones (Alberti, 1983), Pseudoscorpiones (Legg, 1973) and Ricinulei (Alberti and Palacios-Vargas, 1984). A $9 + 3$ arrangement (56) is present in Araneae (Osaki, 1969; Baccetti et al., 1970), Amblypygi, Thelyphonida (Jespersen, 1978; Tripepi and Saita, 1985) and Schizomida (Alberti and Palacios-Vargas, 1987). Thelyphonida and Schizomida are alone among those arachnids that retain a well-developed axoneme in lacking a middle piece (Alberti and Palacios-Vargas, 1987).

Scorpions are the only Recent arachnids in which the spermatozoa appear to maintain a free flagellum throughout their development. In all other arachnids studied thus far, the flagellum is either absent or passes through a phase where it is coiled about the nucleus (55a). As a result, Weygoldt and Paulus (1979) hypothesized that a coiled flagellum is synapomorphic for nonscorpion arachnids (Fig. 1). This scenario seems reasonable, but several complications should be noted. First, the spermatozoan flagellum in *Limulus* coils upon penetration of the ovum (Shogar and Brown in Alberti and Palacios-Vargas, 1984). Second, the coiled flagella of Pseudoscorpiones and some spiders uncoil and become motile within the female genital tract. Third, details of the coiling process appear to vary in different lineages. Thus there are reasons for arguing that the coiling process is plesiomorphic for Arachnida, expressing itself at various times during maturation, if at all, or, on the other hand, that the process is convergent in different lineages.

Sperm transfer (57, 58)

An external method of fertilization is present in Xiphosura, and this may be primitive for Arachnida. Both sexes in Eurypterida are equipped with apparent gonopods (Clarke and Ruedemann, 1912), but the precise function of these structures is unknown. Although some method of internal fertilization is the rule in Recent arachnids, this process is achieved through a variety of mechanisms. The most common method is through the transfer of a sperm packet or spermatophore (Weygoldt, 1975). The male constructs a stalked spermatophore (57) in Amblypygi, Thelyphonida, Schizomida, early derivative acariform Acari, Scorpiones and Pseudoscorpiones. This procedure is often one step in an elaborate courtship. The female in Thelyphonida and Schizomida grasps the opisthosoma of the male prior to spermatophore formation. The male walks forward, pulling the female to the spermatophore (58). In scorpions and many pseudoscorpions, the male grasps the pedipalps of the female with his own and initiates an elaborate "dance". The male deposits the spermatophore and, in many cases, pulls the female over it (Alexander, 1956; Mathew, 1957; Weygoldt, 1969; Polis and Farley, 1979). As many early derivative pseudoscorpions do not show elaborate courtship, it is not clear whether this behaviour is primitive for the order.

Brood care (59, 60)

Oviparity occurs in Xiphosura and is considered primitive for Arachnida. The eggs in Amblypygi, Thelyphonida and Schizomida are protected within a brood sac attached to

the ventral surface of the female's opisthosoma (59) (cf. Shultz, 1987). Female pseudoscorpions construct a similar structure, but it houses embryos that feed on maternally produced secretions rather than on yolk (Weygoldt, 1969). An ovipositor (60) is present in Opiliones and many early derivative Acari.

Hexapodal instar (61)

All instars have four pairs of walking legs in Xiphosura and most Arachnida, but there is a hexapodal larval instar in Ricinulei and Acari (61) (Weygoldt and Paulus, 1979). An additional hexapodal instar (prelarva) is present in certain early derivative Acari (Lindquist, 1984).

Malpighian tubules (62)

Endodermal Malpighian tubules (62) are unique to Arachnida and represent extensions of the midgut. The insect analog of these excretory organs represents extensions of the ectodermal hindgut. Malpighian tubules may be synapomorphic for arachnids (Fig. 1) but are absent in Palpigradi, Opiliones and Pseudoscorpiones (Weygoldt and Paulus, 1979). Kraus (1976) suggested that Malpighian tubules arose independently in different lineages in response to the demands of a terrestrial lifestyle, and Clarke (1979) notes that this process could have occurred through elaboration of primitive midgut caeca. This hypothesis has yet to be explored (cf. Caldwell and Henderson, 1988).

Coxal gland orifices (63, 64)

Onychophorans and some arthropods bear a series of paired excretory organs, the coxal glands, that open onto the body surface near the bases of segmental appendages. These organs may be homologous with the nephridia of annelids (Buxton, 1913; Alberti, 1979b) and appear to function in ion excretion and water balance (Edney, 1977). The coxal fluid in Xiphosura is produced by a series of interconnected coxal glands that exit the body through paired orifices at the base of the third pair of walking legs, and a similar arrangement may have occurred in Eurypterida (Selden, 1981). Thus I suggest that presence of coxal gland orifices associated with leg 3 is primitive for Arachnida, a feature retained in many mygalomorph Araneae, charontid Amblypygi (Buxton, 1917), some schizomids (Yoshikura, 1975), Opiliones (Moritz, 1959), Scorpiones (Buxton, 1913) and Pseudoscorpiones (Weygoldt, 1969). These orifices are absent (63) in Acari, Ricinulei, Palpigradi, Thelyphonida, many Amblypygi and most araneomorph Araneae. A second pair of coxal gland orifices is associated with leg 1 (64) in Acari (Lindquist, 1984), Ricinulei (Millot, 1945), Palpigradi (Millot, 1942), Araneae (Buxton, 1913), Amblypygi, Thelyphonida and Schizomida (van der Hammen, 1986a). Coxal gland orifices in Solifugae occur near the pedipalps (Alberti, 1979b), a feature that appears to be autapomorphic.

COMPUTER ANALYSIS

The computer program PAUP (Phylogenetic Analysis Using Parsimony, version 2.4, Swofford, 1985) was used to find the most parsimonious distribution of the 64 characters listed in Table 1. No assumptions were made concerning the direction or probability of transformations in multistate characters. The data matrix (Table 2) was analyzed using

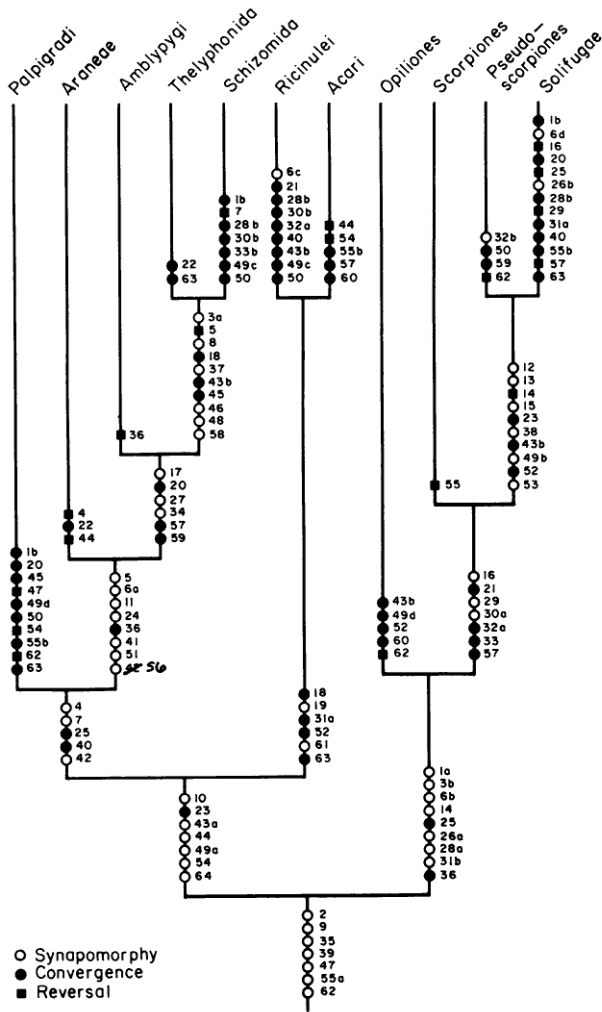


Fig. 4. Cladogram showing possible relationships of the Recent arachnid orders. This minimal length topology was discovered through branch-and-bound analysis of 64 characters. The most parsimonious distribution of characters has a consistency index of 0.59 and a length of 134 steps. Reinterpretation of a single character (54) increased the length of the tree by one step but does not affect the branching pattern discovered by parsimony analysis. See text for details.

the branch-and-bound option, and the cladogram was rooted with an "ancestor" that consisted of the plesiomorphic states of all characters. The program found a single minimal-length cladogram (Fig. 4) with a consistency index of 0.59 and a length of 134 steps. A reinterpretation of one character (54) increases the length of the tree by one step but does not alter the branching pattern derived from parsimony analysis. The reasons for this amendment are discussed in the next section.

The computer program MacClade (version 2.1, Maddison and Maddison, 1987) was used to aid in the discovery of equally parsimonious character distributions within the minimal-length topology discovered by PAUP. In several cases, ontogeny, fossils or complexity of the character itself provided reasons for selecting one distribution from a set of equally parsimonious alternatives. In those instances where no such information

Table 3

A new taxonomic system for Arachnida based on the results of the present study.

Arachnida Lamarck, 1801
Micrura Hansen and Sørensen, 1904
Megoperculata Börner, 1902
Palpigradi Thorell, 1888
Tetrapulmonata (new taxon)
Araneae auct.
Pedipalpi Latreille, 1810
Amblypygi Thorell, 1883
Uropygi Thorell, 1882
Thelyphonida Cambridge, 1872
Schizomida Petrunkevitch, 1945
Acaromorpha Dubinin, 1957
Ricinulei Thorell, 1887
Acari Sundevall, 1833
Dromopoda (new taxon)
Opiliones Sundevall, 1833
Novogenuata (new taxon)
Scorpiones Hemprich and Ehrenburg, 1810
Haplcnemata Börner, 1904
Pseudoscorpiones Pavesi, 1880
Solifugae Sundevall, 1833

was available, I chose distributions that minimized convergences in derived features and favored convergent losses over convergent gains.

Arachnid Taxonomy

ARACHNIDA LAMARCK, 1801

Arachnida consists of 11 orders of chelicerate arthropods (Table 3) that appear to be united by seven apomorphies: reduced carapacial pleural margin (2), anteroventrally directed mouth (9), pretarsal depressor muscle with tibial heads (35), first opisthosomal segment without appendages (39), slit sensilla (47) (absent in Palpigradi), spermatozoa with coiled axoneme (55a) and, perhaps, endodermal Malpighian tubules (62).

Although I suggest that Malpighian tubules are synapomorphic for Arachnida and secondarily absent in Palpigradi, Opiliones and Pseudoscorpiones, there are two additional distributions of this character that also consist of four evolutionary steps. It is possible that this character arose independently in Tetrapulmonata, Acaromorpha, Scorpiones and Solifugae, or that it arose in Tetrapulmonata, Acaromorpha and Novogenuata and was lost in Pseudoscorpiones. The existence of aquatic scorpions in the Palaeozoic indicates that arachnids may have acquired a terrestrial lifestyle several times, and, given that guanine production by Malpighian tubules is generally considered a terrestrial adaptation, it may seem unreasonable to suggest that these organs are synapomorphic for arachnids. It should be noted, however, that guanine is produced in the midgut caeca of *Limulus*, a primitively marine chelicerate, and so specializations associated with production of this waste product may not be exclusive to terrestrial animals. In any event, there is little evidence to support any one of the three equally parsimonious distributions, and my hypothesis should be regarded as tentative.

Weygoldt and Paulus (1979) also recognized pre-oral or "extraintestinal" digestion and simple lateral eyes as potential synapomorphies (Fig. 1). However, the presence of

internal digestion in Xiphosura, Acari and Opiliones and the variety of feeding mechanisms in other orders greatly weakens the view that pre-oral digestion is synapomorphic for Arachnida. The presence of compound eyes in fossil scorpions also refutes the hypothesis that simple lateral eyes are synapomorphic for the arachnid orders.

Several workers have suggested that Arachnida is polyphyletic, but most rely on subjective criteria to reach this conclusion (e.g. van der Hammen, 1977a, 1985a, 1986b; Savory, 1971). The view that scorpions are more closely related to eurypterids than to other arachnids is a recurring theme in discussions of the higher systematics of Chelicerata (e.g. Beklemishev, 1969; Bergström, 1979; Rolfe, 1985; Kjellesvig-Waering, 1986). Despite the popularity of this view, none of its proponents has offered an explicit justification other than overall resemblance. Kjellesvig-Waering (1986), for example, states that scorpions differ from eurypterids in only three traits, pedipalpal chelae, pectines and opisthosomal venom glands. "The overall conclusion of these comparisons is that eurypterids and scorpions are closely related and deserve a high classification that bespeaks this" (Kjellesvig-Waering, 1986: 27). In fact, the similarities between scorpions and eurypterids, including compound eyes, opisthosomal opercula, mesosoma-metasoma, are probably symplesiomorphic, as these features also occur in Xiphosura or Synziphosura (Bergström, 1975). In contrast, I have identified at least 12 readily fossilizable derived characters that distinguish Scorpiones from Eurypterida (see below). Eleven of these characters, and 12 more that are not usually preserved in fossils, may be synapomorphic for Scorpiones and other arachnid groups (Fig. 4). Given current evidence, the hypothesis that Scorpiones is more closely related to Eurypterida than to other arachnids is untenable.

MICRURA HANSEN AND SØRENSEN, 1904

Hansen and Sørensen erected *Arachnida micrura* to accommodate those arachnid orders with a pygidium (44) and their obvious relatives (Araneae); they did not include Acari as an original member. Other possible synapomorphies of *Micrura* include presence of a tritosternum (10), the absence of coxal endites on the walking legs (23) (convergent with Haplocnemata), poorly sclerotized postgenital "appendages" on opisthosomal segments 4, 5 or 6 (43a) (absent in Uropygi and Ricinulei), six principal lateral eye facets (49a) (reduced in Ricinulei, Palpigradi and Schizomida) and coxal gland orifices near leg 1 (64). I also suggest that presence of microtubules associated with the spermatozoan nucleus (54) be regarded as synapomorphic for *Micrura* and that the absence of this feature in the highly derived spermatozoa of Palpigradi and Acari be regarded as independent losses. This interpretation conflicts with parsimony analysis, which indicates that the feature arose independently in Tetrapulmonata and Ricinulei. However, given the complexity of this character and the paucity of derived features uniting Ricinulei with other arachnid lineages, I have chosen to highlight this one similarity by suggesting that it represents homology. It is likely that certain fossil groups, particularly Trigonotarvida, Kustarachnida and Phalangiotarvida, are members of *Micrura*.

MEGOPERCOLATA BÖRNER, 1902

Megopercolata is named for the presence of a large genital plate ("operculum") (42) that overlaps the sternum of the third opisthosomal segment. Members of this taxon are

also characterized by a dorsal endosternal suspensor muscle that sweeps rearward to insert posteromedially on the carapace (7) (reversed in Schizomida), undivided femora on legs 3 and 4 (25) (convergent with Dromopoda), and a constriction of the first opisthosomal segment (40) (convergent with Ricinulei and Solifugae). All members except Araneae also possess a prosomal sternum with three or four distinct components in addition to the tritosternum (4). Yet there is evidence of sternal segmentation in most adult mygalomorph Araneae in the form of insertion sites of eight ventral endosternal suspensors. In addition, segmented prosomal sterna have been noted in early instars of several spider species (Giltay, 1926).

PALPIGRADI THORELL, 1888

Palpigrades are characterized by a large number of distinct features, including a divided carapace (1b) (convergent with Schizomida and Solifugae), elongate anterior walking leg (20) (convergent with Pedipalpi and Solifugae), multijointed pygidial flagellum (45) (convergent with Uropygi), absence of slit sensilla (47), absence of eyes (49d, 50), absence of the microtubular manchette (54) (reversal, convergent with Acari) and axoneme (55b) (convergent with Acari and Solifugae) in the spermatozoa, absence of Malpighian tubules (62) (convergent with Opiliones and Pseudoscorpiones), and absence of the coxal gland orifice associated with leg 3 (63) (convergent with Thelyphonida, Acaromorpha and Solifugae). Autapomorphic features include a paired anteromedial sensory organ (Roewer, 1934) and trochanterofemoral joint in the walking legs formed by a dorsal hinge articulation (Shultz, 1989).

TETRAPULMONATA (NEW TAXON)

Tetrapulmonata receives its name from the presence of paired book lungs (51) occupying the second and third opisthosomal segments, although the posterior pair is absent in Schizomida. Previous synonyms of this lineage are rejected; *Caulogastra* (Pocock, 1893) refers to the pedicel (40), which is symplesiomorphic for the lineage and convergent with Solifugae, and *Arachnidea* (van der Hammen, 1977a) is easily confused with *Arachnida*. Other synapomorphies of Tetrapulmonata include a large postcerebral pharynx (5) (reduced in Uropygi), prosomal endosternite with four segmental components (6a), subchelate chelicerae (11), a complex coxotrochanteral joint in the walking legs (24), a pretarsal depressor muscle arising in the patella (36) (convergent with Dromopoda, lost in Amblypygi), a pedicel formed, in part, by ventral elements of the second opisthosomal segment (41) and a spermatozoan axoneme with a 9+3 microtubule arrangement (56).

ARANEAE AUCT.

Araneae is characterized by an undivided prosomal sternum (4) (reversal), *musculi laterales* (22) (convergent with Thelyphonida) and absence of a pygidium (44) (reversal, convergent with Acari). Autapomorphic features include a copulatory organ on the male pedipalp, cheliceral venom glands, opisthosomal silk glands and absence of the primitive trochanterofemoral depressor muscle in the walking legs (Shultz, 1989).

PEDIPALPI LATREILLE, 1810

This taxon originally included Amblypygi and Uropygi, although Börner (1902) expanded the taxon to include Palpigradi. In recent years, there has been a widespread

consensus that Amblypygi is more closely related to Araneae than to Uropygi (Platnick and Gertsch, 1976; Wygoldt and Paulus, 1979). Thus Pedipalpi was considered diphyletic. There is now abundant evidence that Amblypygi and Uropygi should be reunited as sister taxa. Apomorphic features of Pedipalpi include raptorial pedipalps (17), elongate anterior walking legs (20) (convergent with Palpigradi and Solifugae), a femorpatellar flexor muscle with an asymmetrical patellar insertion (27), telotarsus with three tarsomeres (34), stalked spermatophores (57) (convergent with Acari and Novogenuata) and brood sac (59) (convergent with Pseudoscorpiones).

AMBLYPYGI THORELL, 1883

It would be difficult to confuse amblypygids with another arachnid order, but few autapomorphic features of this group have been explicitly identified. According to my analysis, amblypygids are characterized by a pretarsal depressor without a patellar head (36) (an apparent reversal), a vestigial labrum, large anterior coxal apodemes on all walking legs (Shultz, in preparation), divided tibiae and immovable patellotibial joints (Shultz, 1989). Shear et al. (1987) mistook the elongate patella of the first walking leg in Uropygi for a fused patellotibia and suggested that this trait is synapomorphic for Pedipalpi. My inspection of the joints and muscles of these segments clearly shows that a fused patellotibial joint is autapomorphic for Amblypygi.

UROPYGI THORELL, 1882

The taxonomic conventions associated with this group are confusing. Some authors consider Uropygi to be an order equivalent to the taxon here designated Thelyphonida, and Schizomida is separated into an order of its own. Others consider Thelyphonida and Schizomida suborders of the order Uropygi. Although the latter has priority (Weygoldt and Paulus, 1979), I am more concerned here with establishing phylogenetic relationships than arguing for or against specific taxonomic ranks.

Thelyphonida and Schizomida share several features, including an intercoxal region narrowed posteriorly (3a), reduction or absence of a postcerebral pharynx (5) (reversal), fenestrate endosternite (8), fused pedipalpal coxae (18) (convergent with Acaromorpha), a pretarsal depressor muscle originating from the posterior wall of the patella (37), the absence of postgenital appendages (43b) (convergent with Ricinulei, Opiliones and Haplocnemata), a multi-jointed pygidial flagellum (45) (convergent with Palpigradi), pygidial defensive glands (46), an unusual pattern of tibial trichobothria (48), unique mating behavior (58) and absence of a distinct middle piece associated with the spermatozoan axoneme.

THELYPHONIDA CAMBRIDGE, 1872

Thelyphonida is characterized by *musculi laterales* (22) (convergent with Araneae), absence of coxal gland orifices associated with leg 3 (63) (convergent with Acaromorpha and Palpigradi), pygidial ommatoids (Hansen, 1893), two pairs of small accessory lateral eyes (Hansen and Sørensen, 1905) and pedipalpal chelae in which the movable finger is supplied with internal musculature (Barrows, 1925).

SCHIZOMIDA PETRUNKEVITCH, 1945

The apomorphic features of schizomids include a divided carapace (1b) (convergent with Palpigradi and Solifugae), absence of a posteriorly directed dorsal

endosternal suspensor (7) (reversal), absence of both transpatellar muscles (28b, 30b) (convergent with Ricinulei), absence of the posterior patellotibial muscle (33) (convergent with Novogenuata), vestigial lateral eyes (49c) (convergent with Ricinulei), absence of medial eyes (50) (convergent with Palpigradi, Ricinulei and Pseudoscorpiones), specialized pygidial flagellum in the male, and enlarged femur on leg 4 (Hansen and Sørensen, 1905).

ACAROMORPHA DUBININ, 1957

Acaromorpha includes two orders, Ricinulei and Acari, united by presence of pedipalpal coxae that are broadly fused medially (18) (convergent with Uropygi), a movable subcapitulum (19), patellotibial joints equipped with hinge articulations (31a) (convergent with Solifugae), tracheae (52) (convergent with Opiliones and Haplcnemata), a hexapod larval instar (61) and absence of coxal gland orifices associated with leg 3 (63) (convergent with Palpigradi, Thelyphonida and Solifugae). Lindquist (1984) suggested a scaly or denticulate labrum and two "trochanters" on legs 3 and 4 as possible synapomorphies of Ricinulei and Acari. However, the first character is speculative, as Lingquist himself acknowledges, and the second is regarded here as symplesiomorphic.

RICINULEI THORELL, 1887

Ricinuleids are characterized by a large number of features (Fig. 4). The most notable autapomorphic features of this order include an endosternite with one segmental component (6c), a movable cucullus, prosoma-opisthosoma coupling mechanism and a male copulatory organ on leg 3 (Weygoldt and Paulus, 1979).

ACARI SUNDEVALL, 1833

In a series of papers, van der Hammen (1977–1986) argued that parasitiform mites ("Anactinotrichida") share a more recent ancestry with Ricinulei than with acariform mites ("Actinotrichida") and that acariform mites are, in turn, allied with Palpigradi. The conclusion that Acari is diphyletic was reached within the framework of a peculiar method of systematics that emphasizes recognition of "potentialities" (van der Hammen, 1985c). In a recent cladistic analysis of the problem, Lindquist (1984) provides evidence that Acari is monophyletic and that Ricinulei is its sister group. In addition, some of the morphologic interpretations upon which van der Hammen's argument depends have been questioned (Weygoldt and Paulus, 1979; Lindquist, 1984; Shultz, 1989).

Acari is characterized by absence of a pygidium (44) (reversal, convergent with Araneae), aflagellate spermatozoa (55b) (convergent with Palpigradi and Solifugae), stalked spermatophore (convergent with Pedipalpi and Novogenuata), an ovipositor (60) (convergent with Opiliones), hexapodal prelarva and rutella (see Lindquist, 1984 for a discussion of these and other characters).

DROMOPODA (NEW TAXON)

Dromopoda includes the orders Opiliones, Scorpiones, Pseudoscorpiones and Solifugae, arachnids that possess extensor muscles and specialized articulations at the femoropatellar and patellotibial joints (26a, 28a, 31b). This clade is also united by distinct transverse furrows on the prosomal carapace corresponding to margins of

segmental tergites (1a) (replaced by distinct sclerites in Solifugae), a greatly reduced intercoxal sternal region (3b), a prosomal endosternite composed of two segmental components (6b) (absent in Solifugae), undivided femora on legs 3 and 4 (25) (convergent with Megoperculata, reversed in Solifugae) and a pretarsal depressor muscle with a patellar head (36) (convergent with Tetrapulmonata). I also suggest that presence of a stomotheca, a pre-oral chamber formed by endites of the pedipalps and anterior walking legs, is synapomorphic for Dromopoda (14) and that this feature was lost in Haplocnemata. One could propose the equally parsimonious alternative that the stomotheca arose independently in Opiliones and Scorpiones, but, given the complex nature of this character and evidence for a reduced stomotheca in Haplocnemata, this view seems less convincing than the one adopted here.

OPILIONES SUNDEVALL, 1833

Members of Opiliones are characterized by the presence of tracheae (52) (convergent with Acaromorpha and Haplocnemata) and an ovipositor (60) (convergent with Acari) and by the absence of postgenital appendages (43b) (convergent with Ricinulei, Uropygi and Haplocnemata), lateral eyes (49d) (convergent with Palpigradi) and Malpighian tubules (62) (convergent with Palpigradi and Pseudoscorpiones). Autapomorphic features of this order include elongation of the second pair of walking legs for use as tactile organs, a trochanterofemoral joint with a vertical bicondylar articulation (Shultz, 1989), paired tracheal stigmata on the genital segment, penis and prosomal defensive glands.

NOVOGENUATA (NEW TAXON)

The novogenuate arachnids are united by modifications of the patellotibial joint (29, 30a, 32a) that permit flexion-extension rather than the promotion-remotion typical of most other arachnids, Xiphosura and probably Eurypterida. This "new knee" apparently evolved through a 90° rotation of a joint similar to that found in Opiliones (Shultz, 1989). This clade is also characterized by pedipalpal chelae (16) (lost in Solifugae), immovable coxae (21) (convergent with Ricinulei), the absence of a posterior patellotibial muscle (33) (convergent with Schizomida) and a stalked spermatophore (57) (convergent with Pedipalpi and Acari, lost in Solifugae).

Although one could interpret the presence of pedipalpal chelae and a stalked spermatophore as convergent in Pseudoscorpiones and Scorpiones without increasing the length of the cladogram, unique similarities within each character suggest that they arose in a common ancestor. As noted above, the pedipalpal chelae differ substantially from those of other arachnids and possess similar muscles. The spermatophores of certain scorpions and pseudoscorpions are also similar (Franke, 1979), as are certain aspects of courtship behavior. The evidence available suggests that these features are homologous in Scorpiones and Pseudoscorpiones, but a more rigorous treatment of the matter must await advances in the higher systematics within each order.

SCORPIONES HEMPRICH AND EHRENBURG, 1810

Although the phylogenetic position of Scorpiones is in dispute, the limits of the order itself are clear. There has been some speculation that fossil scorpions are more closely related to Eurypterida than to Recent scorpions (Weygoldt and Paulus, 1979), but a

recent review of fossil scorpions shows that this is inappropriate (Kjellesvig-Waering, 1986). Most fossil scorpions appear to have pectines and eurypterids do not. Likewise, many fossil scorpions have a stomotheca, at least one transverse carapacial furrow and bicondylar femoropatellar joints that show them to be members of Dromopoda, and they have chelate pedipalps and derived patellotibial joints that are characteristic of Novogenuata. Recent scorpions differ from other arachnids in having spermatozoa with free flagella throughout their development (55) (a possible reversal), opisthosomal venom glands, a pretarsal levator muscle originating in the tibia (Shultz, 1989) and enlarged apodemes on the 1989 coxae of legs 1 and 2 (Beck, 1885; Couzijn, 1976; personal observation). The state of these characters in fossil scorpions is unknown.

HAPLOCNEMATA BÖRNER, 1904

The close phylogenetic relationship between Pseudoscorpiones and Solifugae was recognized by Weygoldt and Paulus (1979) based on a single synapomorphy, namely two-segmented, chelate chelicerae (12). Van der Hammen (1986a) added a second, the presence of a specialized feeding complex, the rostrum or "rostrosoma" (15). I have added several more in the course of this study, including an anterolateral chelicero-carapacial articulation (13), the absence or reduction of stomotheca (14) and coxal endites (23) (a reversal or reduction of the primitive dromopodan condition and a convergence with *Micrura*), an empodium retained in the adult (38), absence of postgenital appendages (43b) (convergent with Opiliones, Uropygi, Ricinulei), two pairs of lateral eyes (49b), tracheal system (52) (convergent with Acaromorpha and Opiliones) with stigmata on the third and fourth opisthosomal segments (53).

PSEUDOSCORPIONES PAVESI, 1880

Pseudoscorpions are united by the absence of an anterior patellotibial muscle in the walking legs (32b), the absence of medial eyes (50) (convergent with Palpigradi, Schizomida and Ricinulei), a gonoporal brood sac (59) (convergent with Pedipalpi), the absence of Malpighian tubules (62) (convergent with Opiliones and Palpigradi), complex brood care and cheliceral silk glands.

SOLIFUGAE SUNDEVALL, 1833

Several unusual features of Solifugae, including two notable reversals, divided carapace (1b) and divided femora on legs 3 and 4 (25), have tempted some systematists to remove this order from Arachnida (e.g. Grasshoff, 1978), but the present study shows that this view is unwarranted. The order is also characterized by absence of an endosternite (6d), absence of pedipalpal chelae (16) (reversal), leg 1 modified as a tactile organ (20) (convergent with Palpigradi and Pedipalpi), a femoropatellar joint formed by a monocondylar articulation (26a), the absence of the posterior transpatellar muscle (28b) (convergent with Schizomida and Ricinulei), absence of a patellotibial extensor muscle (29) (reversal), a patellotibial joint with a hinge articulation (31a) (convergent with Acaromorpha), constriction of the first opisthosomal segment (40) (convergent with Megopericulata and Ricinulei), flagellate spermatozoa (55b) (convergent with Palpigradi and Acari), absence of a stalked spermatophore (57) (reversal), absence of coxal gland orifices associated with legs 3 (63) (convergent with Acaromorpha, Palpigradi and Thelyphonida), malleoli and sternal prosomal stigmata (Roewer, 1934).

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