FOSSIL EVIDENCE, TERRESTRIALIZATION AND ARACHNID PHYLOGENY

Jason A. Dunlop: Institute für Systematische Zoologie, Museum für Naturkunde, D-10115 Berlin, Germany

Mark Webster: Department of Earth Sciences, University of California, Riverside, California 92521 USA

ABSTRACT.   Geological and morphological evidence suggests that the earliest scorpions were at least partially aquatic and that terrestrialization occurred within the scorpion clade. Scorpions and one or more other arachnid lineages are therefore likely to have come onto land independently. The phylogenetic position of scorpions remains controversial and we question Dromopoda, in which scorpions are placed derived within Arachnida, as this is not supported by scorpions' lateral eye rhabdomes, embryology and sperm morphology. We propose a synapomorphy for scorpions + eurypterids, a postabdomen of five segments as part of an opisthosoma of 13 segments. Scorpions and tetrapulmonates must have evolved their book lungs convergently while fossil evidence indicates that a stomotheca, synapomorphic for Dromopoda, is probably convergent too. 'Arachnid' characters such as Malpighian tubules, the absence of a carapace pleural margin, and an anteriorly directed mouth may also be convergent, although their status as synapomorphies can be defended using parsimony. Convergence is difficult to prove unequivocally, but when there are strong grounds for suspecting it, such characters are questionable evidence for arachnid monophyly.

Living arachnids are predominantly terrestrial, with those groups found in aquatic habitats, such as the water spider *Argyroneta* or halacaroid mites, assumed to have returned to the water secondarily. It is also reasonable to assume that the earliest chelicerates were aquatic, including the ancestors of arachnids (e.g., Kraus 1976). Terrestrialization was a key event in arachnid evolution and as there is good evidence for aquatic fossil scorpions (Jeram 1998), terrestrialization probably occurred independently within at least two arachnid lineages. The position of the scorpions within Chelicerata has proved to be controversial (e.g., Weygoldt 1998) and we do not accept that scorpions are a derived group within arachnids, nor that Arachnida is monophyletic. A number of characters which have been used to support arachnid monophyly could also be interpreted as adaptations for life on land (e.g., Kraus 1976). We consider these to include book lungs, Malpighian tubules, absence of carapace pleural margin, and an anteriorly directed mouth. Parsimony analyses (e.g., Wheeler & Hayashi 1998) suggest that these characters should be treated as homologous and apomorphic. However, if at least two arachnid lineages moved onto land independently it would be surprising to find terrestrial adaptations in the common ancestor of all arachnids, irrespective of whether or not they were monophyletic, as this was an aquatic animal. These arguments are expanded below.

THE AQUATIC NATURE OF PRIMITIVE SCORPIONS

A number of authors have suggested that some of the oldest fossil scorpions were partially or wholly aquatic (e.g., Pocock 1901; Kjellesvig-Waering 1986). This proposal has not gone unquestioned. Petrunkevitch (1953) found no evidence for scorpion gills and argued that all other arachnids have book lungs or tracheae. More recently Weygoldt & Paulus (1979) again questioned whether scorpions really were aquatic, with Weygoldt (1998) finding Kjellesvig-Waering's (1986) evidence for scorpion gills unconvincing. Størmer (1970) and Brauckmann (1987) also described scorpion gills, although these structures projecting beyond the body margin are equivocal as respiratory organs and do not resemble xiphosuran book gills. Gills in scorpions have not,

therefore, been proven, but in his recent phylogeny of Silurian and Devonian scorpions Jeram (1998) presented both sedimentological and morphological evidence that at least some of these early scorpions were aquatic. His most basal scorpion taxon comes from the Devonian Hunsrückschiefer, a fully marine sequence (Bartels *et al.* 1998), while other Silurian taxa come from marginal marine deposits. Morphological evidence for an aquatic habitat includes the presence of gnathobases in some taxa, lack of an oral tube for liquid feeding, single-clawed, digitigrade tarsi, and abdominal plates lacking book lung spiracles. Jeram (1998) further commented that two or more scorpion lineages might have come onto land independently, but that this would be difficult to detect as many of the characters he analyzed were likely to have altered state during terrestrialization.

Scorpions have obvious autapomorphies (pectines, sting, pedipalpal claws) and there is no evidence to derive any other arachnid order directly from the scorpion clade, e.g., Anderson (1973); something which would require autapomorphy reversal. It is conceivable that scorpions and other arachnids evolved on land from a common terrestrial ancestor and that some scorpions then re-entered the water and lost their terrestrial adaptations. However, as the fossil record shows an accumulation of terrestrial-related features through the Palaeozoic (e.g., Selden & Jeram 1989, fig. 4), this remains an unlikely scenario. We therefore suggest that if the oldest scorpions were aquatic (Jeram 1998), they must have diverged from the other arachnids while still in the water and moved onto land independently.

SCORPIONES + EURYPTERIDA

The phylogenetic position of scorpions remains controversial with the three principal cladistic analyses (Weygoldt & Paulus 1979; Shultz 1990; Wheeler & Hayashi 1998) including them in a monophyletic Arachnida, although differing in placement of the order. Weygoldt & Paulus (1979) and Weygoldt (1998) placed scorpions as a sister group to all other arachnids. However, the analyses of Shultz (1990) and Wheeler & Hayashi (1998) (primarily using Shultz's morphological data) placed scorpions higher in the Arachnida as a sister group to Haplocnemata (Pseudoscorpiones + Solifugae) with Opiliones as sister

group to all three, forming the taxon Dromopoda. Several authors have suggested that scorpions are most closely related to eurypterids (e.g., Versluys & Demoll 1920; Bristowe 1971; Kjellesvig-Waering 1986). These studies generally relied on overall similarities rather than discrete synapomorphies, and were justifiably criticized for this by Shultz (1990). While Shultz (1990) found scorpions to be derived arachnids, he excluded from his analysis Weygoldt & Paulus' (1979) character 21 (star-shaped lateral eye rhabdomes in scorpions and xiphosurans, quadratic in all other arachnids bearing lateral eyes). Wheeler & Hayashi (1998) did include this character. Both Wheeler & Hayashi (1998) and Shultz ignored Anderson's (1973) observation that the embryological development of scorpions and xiphosurans is similar in possession of a growth zone giving rise to both the prosoma and opisthosoma, while in all other arachnids this growth zone gives rise to the opisthosoma only. The distribution of these characters does not favor placement of scorpions as derived arachnids with Xiphosura as an outgroup. Furthermore, the analysis of Shultz (1990) found spermatozoa with a coiled flagellum axoneme to be synapomorphic in Arachnida, despite retention of a free flagellum in scorpion spermatozoa (the presumed plesiomorphic state). Weygoldt & Paulus (1979) proposed a coiled flagellum as synapomorphic only for non-scorpion arachnids. Alternatively, the eye rhabdome, growth zone character and sperm flagellum could all be reversals in the scorpion clade.

Dunlop (1998) stated that the clearest potential synapomorphy for scorpions and eurypterids is the five-segmented postabdomen, an obvious character (Fig. 1) ignored by cladistic studies. Shultz (1990) and Weygoldt (1998) argued that similarities between eurypterids and scorpions were probably symplesiomorphic, as they occurred in xiphosurans, too. Outgroup comparison with trilobites and other arachnates indicates that lack of a postabdomen is the plesiomorphic state with respect to Chelicerata, while in synziphosurines (primitive xiphosurans; Anderson & Selden 1997) and some arachnids there is a postabdomen of three segments (the pygidium of Shultz 1990). In support of the homology of the postabdomen we argue that scorpions and eurypterids have a groundplan of 13 opistho-
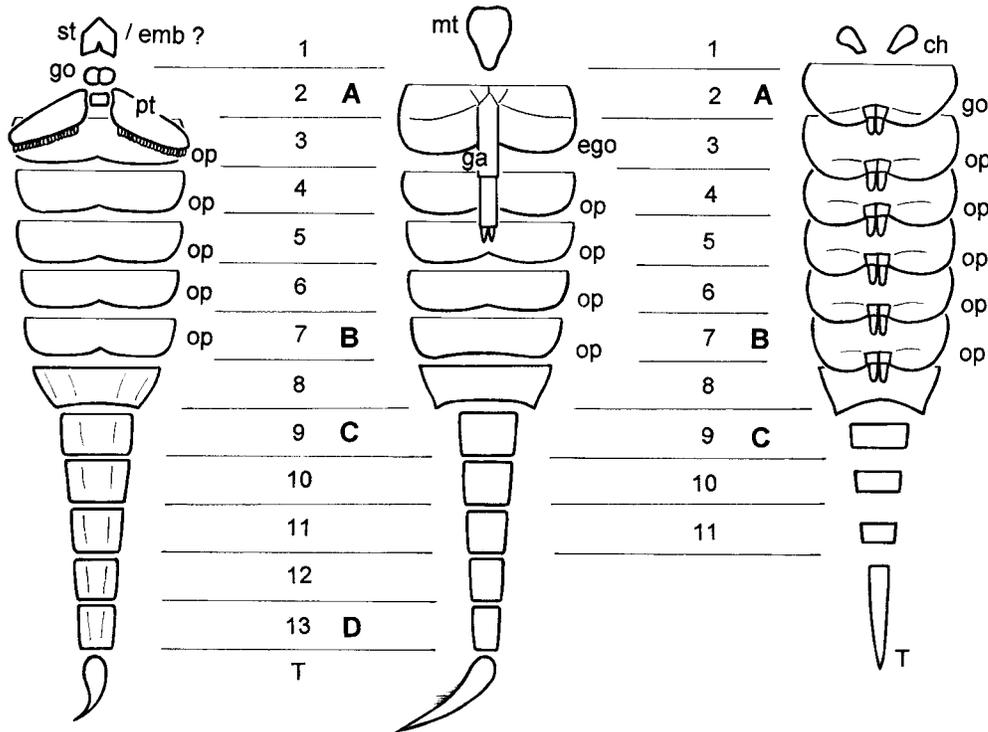
Figure 1.—Proposed homology of the ventral opisthosoma of a Paleozoic scorpion (left) a scorpion-like eurypterid (center) and a synziphosurine (right). This model differs in its placement of the pectines from Dunlop (1998, fig. 4) and it should be added that the chilaria in at least some synziphosurines may have been fully pediform (L. Anderson pers. comm.). Our model lines up four morphological reference points: the genital segment (A), the last opisthosomal appendage pair (B), the first postabdominal segment (C) and the posteriormost, 13th segment (D). Points A–C, i.e., the preabdomen, are seen in Scorpiones, Eurypterida and Xiphosura; C–D, i.e., the 5-segmented postabdomen, is synapomorphic for Scorpiones + Eurypterida. Opisthosomal segments numbered. Abbreviations: T = telson, st = sternum, emb = embryonic appendages, mt = metastoma, go = genital operculum, ego = eurypterid genital operculum formed from two fused appendage pairs, pt = pectines, ga = genital appendage, ch = chilaria, op = appendage-derived operculum, a structure usually termed Blatfuss (literally 'sheet foot') in eurypterids.

somal segments: A preabdomen (segments 1–8) and a postabdomen (segments 9–13).

THE QUESTION OF OPISTHOSOMAL SEGMENTATION

In scorpions.—The groundplan of arachnids has widely been quoted as comprising an opisthosoma of 12 segments (e.g., Kraus 1976; Shultz 1990). However, there is evidence for a transitory pair of pregenital limb buds described in scorpion embryos (Brauer 1895) representing an 'extra' segment, the nerve ganglion of which is retained (Anderson 1973). A scorpion with 13 segments, including this embryonic one, was figured by Millot (1949, figs. 52, 53). Shultz (1990) coded scorpions as lacking appendages on opisthosomal

segment 1 despite evidence for their presence embryologically in the less derived, apoikogenic scorpions (Anderson 1973). Scorpion opisthosomal segmentation has therefore been proposed as: (1) embryonic, (2) genital opercula, (3) pectines, (4–7) book-lungs, (8) last preabdominal segment and (9–13) postabdomen, plus a telson (e.g., Dunlop 1998).

In some of the earliest scorpions there is an additional abdominal plate (Jeram 1998) apparently representing an additional segment. While modern scorpions have four appendage-derived book lungs on the preabdomen, some early derivative scorpions have five appendage-derived opercula (Fig. 1) posterior to the genital operculae and the pectines. This could be interpreted as evidence that scorpi-

ons have a groundplan of 14 opisthosomal segments, e.g., (1) embryonic, (2) genital opercula (3) pectines, (4–8) book-lungs, (9) last preabdominal segment and (10–14) post-abdomen, plus a telson. However, all known fossil and Recent scorpions express only 12 tergites, the last five of which are fused with the sternites into the postabdomen (Fig. 1). It should be possible to match all tergal and sternal elements.

Weygoldt & Paulus (1979, fig. 2) accepted that there are 13 ventrally expressed structures in Recent scorpions, but cautioned that there is no musculature evidence for an additional tergal element; i.e., they interpreted scorpions as having only 12 segments. They suggested that the 'extra' segment in scorpions is the result of the division of the ventral elements of opisthosomal segment 2; for them a scorpion autapomorphy. Essentially they argued that both the genitalia and pectines belonged to opisthosomal segment 2, a proposal which we support (Fig. 1). However, these authors were not aware of the additional abdominal plate in fossil scorpions, a fully expressed structure which appears to bring us back to a body plan of 13 opisthosomal segments: (1) embryonic, (2) genital opercula + pectines, (3–7) abdominal plates, (8) last preabdominal segment, (9–13) postabdomen, plus a telson (Fig. 1).

Our model is tentative, but we believe it fits the available data and means that, like xiphosurans, the scorpion groundplan consists of eight preabdominal segments with appendages on segments 1–7 (Fig. 1). We are still 'missing' a tergite in scorpions, but the first tergite in chelicerates is often reduced and has been overlooked in eurypterids (below). This model requires loss of one abdominal plate in more derived scorpion clades. This is reflected in the cladogram of Jeram (1998, fig. 2, node F).

In eurypterids.—Eurypterids are typically reconstructed with 12 opisthosomal segments. However, Raw (1957) cited evidence found by Holm (1898, pp. 8–9, fig. 15) for an 'extra' segment in eurypterids, a proposal overlooked by recent authors. Raw (1957, pp. 160–161, fig. 8c) proposed that the membranous fold between the carapace and the opisthosoma formed a discrete but highly reduced segment in eurypterids. Raw (1957) argued that what was traditionally interpreted as the first tergite

of eurypterids does not tuck under the posterior margin of the carapace, as the tergite does in xiphosurans. Instead, the membrane behind the eurypterid carapace is reflexed forward and then doubles back on itself in a manner consistent with it being a reduced and poorly sclerotized tergite (Fig. 2). One of Holm's eurypterid preparations (British Museum Natural History specimen I. 3406 (6)) was examined and shows these reflexed membranes (Fig. 3). What has traditionally been called tergite 1 in eurypterids is in contact with the carapace at its lateral margins, but has a slightly concave anterior margin forming a narrow gap on the midline in which there is a membrane containing thin fragments of sclerotized cuticle (Fig. 3). This, we believe, is consistent with it being a highly reduced tergite; our tergite 1.

Reduced first opisthosomal tergites are common in chelicerates as shown by xiphosuran microtergites (Anderson & Selden 1997) and the pedicels of some arachnids (Shultz 1990). These eurypterid cuticle fragments could be dismissed as having simply sutured off from the carapace or adjacent tergite, and we have noted Weygoldt & Paulus' (1979) evidence against an extra tergite in scorpions above. However, eurypterid ventral anatomy can also be homologized with our scorpion model (Fig. 1). The eurypterid metastoma is interpreted as opisthosomal segment 1, though it is unclear whether it is a sternal or appendicular structure. Jeram (1998) suggested that what is traditionally called the scorpion sternum is homologous with the eurypterid metastoma, and as such both may be appendage-derived elements, homologous with xiphosuran chilaria (Fig. 1). It is conceivable that the embryonic limb buds in scorpions actually become the scorpion sternum. Both are in approximately the same position and the fate of the limb buds and origins of the sternum are equivocal. This limb bud/sternum question merits investigation. Assuming homology (segment 1), the next segment in both scorpions and eurypterids bears the gonopore (segment 2). This fits the general chelicerate pattern of a gonopore on opisthosomal segment 2, which appears to be a valuable marker for homologizing segments (e.g., Millot 1949).

The eurypterid gonopore on opisthosomal segment 2 lies at the base of the genital appendage. The appendage is part of the large
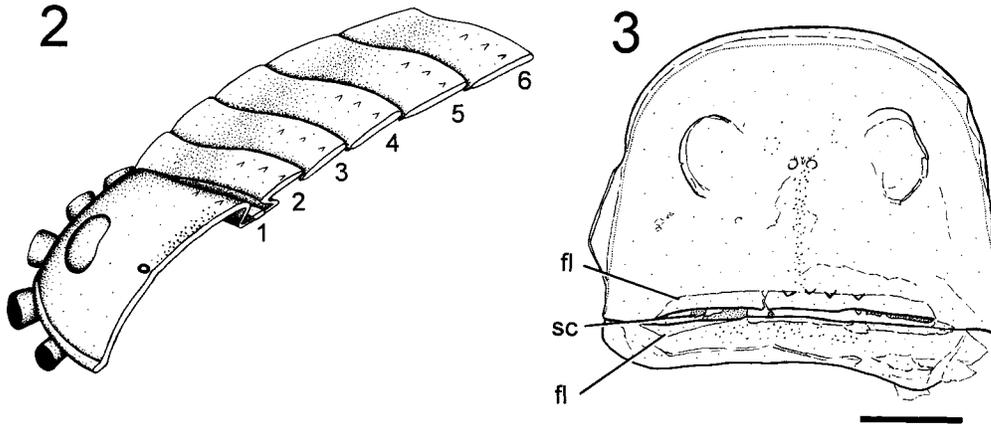
Figures 2–3.—Eurypterid dorsal segmentation. 2. Schematic adapatation of Holm's (1898) observation that the dorsal membrane between the prosoma and opisthosoma in eurypterids folds back on itself. This differs from the way that the other tergites connect to each other. Raw (1957, fig. 8C) cited this as evidence that this membrane represents a highly reduced first opisthosomal tergite giving eurypterids 13, not 12, opisthosomal segments; 3. Camera lucida drawing of BMNH I. 3406 (6) a small, translucent specimen of *Baltoeurypterus* acid-etched from the matrix. This specimen supports Raw's interpretation by showing the folding of the membranes at the prosoma-opisthosoma junction (fl) and the slight sclerotization within this membrane (sc), which we interpret as opisthosomal tergite 1. Scale = 5 mm.

genital operculum which is divided by a transverse suture, suggesting it is formed from the fused appendages of segments 2 and 3. That scorpion pectines possibly belong to the genital segment is interesting in this context. Simon Braddy (pers. comm.) suggested that the paired pectines of scorpions could be homologous with the paired furcae at the end of the eurypterid genital appendage; a structure which also appears to belong to opisthosomal segment 2 (see also Braddy & Dunlop 1997).

In eurypterids, segments 3–7 bear gill tracts (probably non-homologous with book gills [Manning & Dunlop 1995]), and the last preabdominal segment is segment 8. There is a five-segmented postabdomen (segments 9–13) plus a telson (Fig. 1). This segmentation pattern merits further investigation. Our model (Fig. 1) suggests homology of several reference points: The genital segment (A), the posteriormost opisthosomal appendages (B), the start of the postabdomen (C), and the five segments to the 13th, posteriormost segment (D). Points A, B and C also match the body plan of xiphosurans (Fig. 1). Scorpions, eurypterids, and xiphosurans share an 8-segmented preabdomen with appendages on segments 1–7, while scorpions + eurypterids show an apomorphic 5-segmented postabdo-

men. No other chelicerates show an 8-segmented preabdomen.

Thirteen opisthosomal segments could be interpreted as a synapomorphy for Scorpiones + Eurypterida, though in reality this and the postabdomen are probably best treated as expressions of the same character. We have argued that the postabdominal segments (9–13) are homologous in these taxa and that the character state is derived. No outgroup shows a 5-segmented postabdomen. The three-segmented postabdomen of some arachnids (Shultz 1990) is unlikely to be derived from this condition by loss of two segments, as this would reduce the total number of opisthosomal segments to only 11 (arachnids such as thelyphonids have 12 segments).

PROBABLE CONVERGENT CHARACTERS

We have proposed one morphological synapomorphy shared by scorpions and eurypterids. Other characters have been used to support a monophyletic Arachnida and/or a derived position for scorpions within arachnids. Some of these characters appear to be adaptations for, or associated with, life on land. If arachnids terrestrialized more than once, then terrestrial adaptations are likely to

be convergent. It would be surprising to find terrestrial characters in the aquatic common ancestor predicted by arachnid monophyly and the models of Weygoldt & Paulus (1979), Shultz (1990) and Wheeler & Hayashi (1998).

Book lungs.—Book lungs are a 'textbook' arachnid character. However, their distribution indicates that although book lungs in scorpions and other arachnids are clearly homologous with respect to the pre-existing abdominal appendages, the book lungs of scorpions are not directly homologous with those of tetrapulmonates (contra Wheeler & Hayashi 1998). Weygoldt (1998) and Dunlop (1998) independently noted that only tetrapulmonate arachnids retain a respiratory organ on the genital segment. It is absent in xiphosurans, scorpions and probably eurypterids. Weygoldt (1998) regarded loss of a respiratory organ on the genital segment as most likely being convergent. Dunlop (1998) noted that outgroups such as trilobites have a respiratory organ on all opisthosomal segments, and proposed that the most parsimonious interpretation of this character is to treat it as plesiomorphically retained in tetrapulmonates and synapomorphically lost in a xiphosuran, scorpion and eurypterid clade.

In either case, book lungs in spiders and scorpions are not directly homologous, belonging to opisthosomal segments 2–3 in tetrapulmonates and 4–7 in scorpions (Dunlop 1998; Kraus 1998). Probable independent terrestrialization of scorpions and other arachnids indicates that their book lungs evolved independently from gills in response to the demands of breathing on land. Differences in detailed lung anatomy might be predicted between scorpions and other arachnids. This represents an interesting line of research which could be applied to other morphological structures which may be terrestrial adaptations, e.g., trichobothria, and details of limb morphology and mouthpart structure.

Stomotheca.—Shultz's (1990) taxon Dromopoda is supported by a number of appendicular characters coded primarily from Recent terrestrial forms. The strongest appears to be presence of extensor muscles, but specializations of the femorpatellar and patellotibial leg articulations, and a stomotheca formed from coxal endites are included. The stomotheca creates a preoral cavity where extraintestinal digestion takes place. This feed-

ing process is less likely (although possible) in an aquatic animal. Weygoldt (1998) rejected Dromopoda, arguing that a stomotheca is clearly absent in many fossil scorpions (see also Jeram 1998, character 23), in solifuges, and in pseudoscorpions. Weygoldt (1998) concluded that either the stomotheca is convergent (supported here) or that scorpions must be paraphyletic. This example illustrates the dangers of ignoring fossil data when coding characters.

Malpighian tubules.—Malpighian tubules are endodermal extensions of the gut found in most arachnids, but not in palpigrades, opilionids and pseudoscorpions (Shultz 1990). They also occur convergently in insects. Their function is to remove excretory products such as guanine and uric acid from the body (e.g., Seitz 1987). They are not present in xiphosurans and their presence or absence is unknown in eurypterids. The tubules could be convergent terrestrial adaptations for removing dry, low-toxicity excretory products (e.g., guanine), given the importance of water conservation for animals on land (Kraus 1976).

Poorly developed carapace pleural margin.—The carapaces of xiphosurans, and to a lesser extent eurypterids, project laterally and form a cavity around the coxosternal region (Shultz 1990). This projection is not seen in arachnids. Its association primarily with taxa that masticate food using gnathobases may be significant; it is also seen in outgroups such as trilobites, although it is not apparent in fossil or Recent scorpions. Shuster (1950) noted that xiphosurans feed by burying themselves into the substrate in pursuit of worms and mollusks. The carapace pleural margin, and the associated cavity it creates, forms a semi-enclosed chamber within the substrate in which the gnathobases are free to masticate food. With a move towards terrestrialization and away from feeding in the substrate, a carapace pleural margin could become non-functional and lost. In contrast, many arachnids show a trend towards developing a preoral cavity (e.g., Selden & Jeram 1989) which surrounds the food during cheliceral mastication and extraintestinal ingestion.

Anteroventrally directed mouth.—In xiphosurans the mouth is directed posteroventrally, towards the postoral gnathobases from where they receive masticated food (Shultz 1990). Eurypterid mouths have also been re-

constructed with this orientation, and although supportive fossil evidence is weak, the interpretation is probably correct on functional grounds. Mouth orientation of fossil scorpions is unknown. Trilobites were also gnathobasic feeders and had posteroventrally directed mouths. Recent arachnid mouths are all directed anteroventrally, towards the preoral chelicerae. Terrestrialization could have caused a shift from gnathobasic mastication in water to cheliceral mastication on land. Postoral gnathobases along the length of the prosoma are of little use for mastication on land where food would drop from between the coxae. However, a similar function appears to have been retained in the palpal coxae of spiders, adjacent to the mouth, which are used to manipulate food (e.g., Bristowe 1971). Unlike xiphosurans, which trap their food in soft sediments beneath them (Shuster 1950), most arachnids live on an essentially solid substrate and generally catch their food in front of them using anteriorly directed, preoral chelicerae and/or anterior appendages. An anteriorly directed mouth can be interpreted as an adaptation for receiving prey captured preorally by a terrestrial animal.

PARSIMONY AND THE BURDEN OF PROOF

Arachnid monophyly is supported by a number of characters which may represent convergence in response to terrestrialization. These characters can be defended by parsimony and assumed to be homologous and synapomorphic until 'proved' otherwise by a parsimony analysis. Kraus (1998) discussed the limitations of parsimony analysis and argued that characters for phylogeny should be selected and weighted a priori based on structural and functional considerations. We have presented functional arguments to question some of the characters supporting arachnid monophyly. Unfortunately, unequivocal proof for convergent evolution of characters can be difficult to establish, especially when they involve characters in fossil taxa where functional morphology often has to be inferred (e.g., feeding methods in eurypterids) or where empirical data is not available. Our concern is that parsimony is being used to defend weak or inappropriate characters to which considerable objections can be raised. We support Kraus (1998) in questioning whether charac-

ters should be assumed homologous unless detailed arguments in favor of their homology are presented (e.g., our postabdomen character). We worry that in an attempt to compile ever larger databases of characters for parsimony analysis, homologies are being assumed at face value without assessment of character validity. Which is more important, the quantity or the quality of the data used?

LITERATURE CITED

Anderson, D.T. 1973. Embryology and Phylogeny in Annelids and Arthropods. Pergamon, New York.

Anderson, L.I. & P.A. Selden. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. Lethia, 30:19–31.

Bartels, C., D.E.G. Briggs & G. Brassel. 1998. The Fossils of the Hunsruck Slate. Marine Life in the Devonian. Cambridge Univ. Press, Cambridge.

Braddy, S.J. & J.A. Dunlop. 1997. The functional morphology of mating in the Silurian eurypterid, *Baltoeurypterus tetragonopthalamus* (Fischer, 1839). Zool. J. Linn. Soc., 121:435–561.

Brauckmann, C. 1987. Neue Arachniden-Funde (Scorpionida, Trigonotarbida) aus dem westdeutschen Unter-Devon. Geol. Palaeont., 21:73–85.

Brauer, A. 1895. Beiträge zur Kenntnis der Entwicklungsgeschicte des Skorpiones, II. Z. Wiss. Zool., 59:351–433.

Bristowe, W.S. 1971. The World of Spiders. 2nd ed. Collins, London.

Dunlop, J.A. 1998. The origins of tetrapulmonate book lungs and their significance for chelicerate phylogeny. Pp. 9–16. *In* Proc. 17th Europ. Coll. Arachnol., Edinburgh 1997.

Holm, G. 1898. Über die Organisation von *Eurypterus fischeri* Eichw. Acad. Imp. Sci. St. Petersburg, Mem., ser. 8, vol. 8, no. 2.

Jeram, A.J. 1998. Phylogeny and classification of Palaeozoic scorpions. Pp. 17–31. *In* Proc. 17th Europ. Coll. Arachnol., Edinburgh 1997.

Kjellesvig-Waering, E.N. 1986. A restudy of the fossil scorpions of the world. Palaeontogr. Americana, 55:1–287.

Kraus, O. 1976. Zur phylogenetischen Stellung und Evolution der Chelicerata. Entomol. Germanica, 3:1–12.

Kraus, O. 1998. Elucidating the historical processes of phylogeny: Phylogenetic systematics versus cladistic techniques. Pp. 1–7. *In* Proc. 17th Europ. Coll. Arachnol., Edinburgh 1997.

Manning, P.L. & J.A. Dunlop. 1995. The respiratory organs of eurypterids. Palaeontology, 38:287–297.

Millot, J. 1949. Classe des Arachnides. Morphologie générale et anatomie interne. Pp. 261–319. *In* Traite de Zoologié, Tome VI, (P.-P. Grassé, ed.). Masson et Cie, Paris.

Petrunkevitch, A.I. 1953. Paleozoic and Mesozoic Arachnida of Europe. Mem. Geol. Soc. America, 53:1–128.

Pocock, R.I. 1901. The Scottish Silurian scorpion. Q. J. Microscop. Sci., 44:291–311.

Raw, F. 1957. Origin of chelicerates. J. Paleont., 31:139–192.

Seitz, K.-A. 1987. Excretory organs. Pp. 239–248. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Selden, P.A. & A.J. Jeram. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. Trans. R. Soc. Edinburgh: Earth Sci., 80:303–310.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics, 6:1–38.

Shuster, C.N. 1950. Observations on the natural history of the American horseshoe crab, *Limulus polyphemus*. Woods Hole Oceanograph. Inst., 564:18–23.

Størmer, L. 1970. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 1. Arachnida. Senckenbergiana Lethaea, 51:335–369.

Versluys, J. & Demoll, R. 1920. Die Verwandtschaft der Merostomata mit den Arachnida und den anderen Abteilugen der Arthropoda. Kon. Ak. Wetenschap. Amst., 23:739–765.

Weygoldt, P. 1998. Evolution and systematics of the Chelicerata. Exp. App. Acarol., 22:63–79.

Weygoldt, P. & H.F. Paulus. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. Z. F. Zool. Syst. Evolutionsforsch., 17:85–116, 177–200.

Wheeler, W.C. & C.Y. Hayashi. 1998. The phylogeny of the extant chelicerate orders. Cladistics, 14:173–192.