Phylogeny, classification and evolution of Silurian and Devonian scorpions

Andrew J. Jeram

Department of Geology, Ulster Museum, Botanic Gardens, Belfast, BT9 5AB, UK

Summary

A cladistic analysis of all Silurian and Devonian scorpion genera is presented. *A posteriori* weighting of characters is employed to resolve polytomies and character conflicts, because a high proportion of character states in the analysis are indeterminate. Criteria are established to determine the relative strength of characters. The resulting cladogram provides the basis for a revision of fossil scorpion systematics. The early evolution of scorpions is discussed. Most gross morphological change in scorpions can be attributed to the transition from aquatic to terrestrial habitats during the Palaeozoic, particularly modification of the coxosternal region and legs to meet changing locomotory and feeding requirements.

Introduction

The phylogenetic position of scorpions within the Chelicerata has been the subject of much debate in recent years (e.g. Weygoldt & Paulus, 1979; Bergström, 1980; Van der Hammen, 1989; Shultz, 1990; Starobogatov, 1990), but it revolves around one primary question: are scorpions part of a monophyletic Arachnida, or are they "merostomes" which exhibit a terrestrial grade of existence? Inclusion of data from the scorpion fossil record within phylogenetic analyses of the chelicerates tends to support the latter contention.

It is apparent from an examination of the fossil record that several of the supposedly derived characters which have been used to support a monophyletic concept of the Arachnida including scorpions, such as the possession of book lungs, simple ocelli rather than compound eyes, and trichobothria, are absent in some Palaeozoic scorpions. However, the significance of character distributions within the Palaeozoic scorpions is open to question in the absence of a convincing account of scorpion phylogeny. After all, it is possible that the characters in question (and indeed others) have undergone reversal in some Palaeozoic scorpion clades. A cladistic analysis of early scorpion phylogeny, the subject of this paper, is an essential step towards settling the question.

There has never been a generally agreed stable classification of the Palaeozoic scorpions. Each worker approaching the problem has performed a fundamental revision of previous schemes. This is partly because of a poor database (both in terms of numbers of specimens and knowledge of their morphology), and partly because early scorpions exhibit a mosaic of morphological characters which defy any obvious "natural" grouping of taxa. There are few characters which can be determined in the majority of early scorpion body fossils, and fewer still which show a range of morphological variation useful in classification and the construction of a phylogeny. Earlier workers (e.g. Petrunkevitch, 1955; Kjellesvig-Waering, 1986; Starobogatov, 1990) have emphasized the significance of particular characters, such as the shape of the abdominal plates, the shape of the sternum, and the structure of the coxosternal region. Their classification schemes depended on topological resemblance of taxa, and their schemes naturally varied according to what the particular author considered to be the "most important" characters. The resulting alternative accounts of scorpion phylogeny are equally discordant. Only Stockwell (1989) has attempted to identify apomorphies which characterize monophyletic clades among Silurian and Devonian scorpions.

Scope of this study

Scorpion fossils from the Silurian and Devonian are very rare. Sixteen species belonging to fifteen genera have been described, the majority from a single specimen. In this study, all previously described genera of Silurian and Devonian scorpions, two new undescribed Silurian species from Ontario (Waddington & Jeram, in prep.), and also a few apparently primitive Carboniferous scorpions, are included. Archaeoctonus. Pseudarchaeoctonus and Loboarchaeoctonus, all from the Viséan Glencartholm fauna of Scotland (Kjellesvig-Waering, 1986), may be cogeneric (Stockwell, 1989), so only the genus Archaeoctonus appears in the analysis. A representative Carboniferous mesoscorpion (Pulmonoscorpius) and neoscorpion (Palaeopisthacanthus) were also included, so that the results of previously published fossil scorpion cladograms (Jeram, 1994a [mesoscorpions], 1994b [Orthosterni]) could be more easily integrated with this study. This makes a total of twenty included genera. All are monospecific, except Palaeopisthacanthus (two species), and possibly Archaeoctonus (see above, two or three species).

Kjellesvig-Waering (1954) described a second species of *Palaeophonus* from the late Silurian of England, although the material on which it is based consists of an isolated pedipalp chela and its generic identity is far from certain. *Palaeophonus* can therefore be regarded as essentially monospecific. The same author (Kjellesvig-Waering, 1972) also described a Lower Devonian scorpion, *Brontoscorpius anglicus*, from only an isolated pedipalp, so this species has also been omitted.

The author has examined material of all the included taxa, except *Palaeophonus*, *Archaeophonus*, *Stoermeroscorpio*, *Waeringoscorpio*, and *Labriscorpio*. In these, all available published descriptions and figures have been used in the determination of character states.

Selection of characters

Fossil taxa are never as completely known as modern taxa, and a lack of knowledge of character states can make cladistic analysis of fossils problematic. Scorpions lack a mineralized integument, and their almost invariably flattened remains are difficult to interpret (e.g. Jeram, 1994a). Commonly, just the dorsal or ventral surface of a fossil scorpion species is known, and many specimens are incomplete. Owing to the vagaries of preservation and taphonomy, the quality and quantity of morphological data which can be obtained from fossil scorpions are highly variable. Thus, useful characters are generally those gross morphological features whose states can be determined with a reasonable degree of certainty in the majority of taxa included in the study.

From the outset, it was inevitable that the data set would include a high proportion of indeterminate character states. One consequence is that any cladogram generated from it will contain numerous polytomies (Smith, 1994), and the effects of homoplasy may be amplified. Some taxonomically useful characters, such as pedipalp and cheliceral dentition, have had to be omitted because they could not be determined sufficiently reliably in most of the included taxa. In other cases, for example, abdominal plate shape or sternum shape, previous studies have indicated that their inclusion would certainly introduce homoplasy, and so they too were excluded. If the quality of the data was better, it would be preferable to be as inclusive as possible. Where possible, linked characters have been aggregated to reduce bias in the analysis. For example, the presence of curved tarsal claws (ungues) is always accompanied by the presence of lateral lobes on the telotarsus and a reduction in size of the apotele, so only a single character state is warranted. Twenty-six binary characters were employed in the final analysis.

Several important character transition series are present (see below), and some of the characters could be coded as multistate. However, to simplify the data and obtain a clearer phylogenetic signal, variable features such as the coxosternal region (see Kjellesvig-Waering, 1986, text-figs. 110-114) are reduced to a few key binary characters. In such cases, the plesiomorphic and derived states may be end members of a transition series, and they will usually have a clear functional distinction.

Discussion of characters

The characters are individually discussed below. The plesiomorphic state is given first, followed by the derived state and a brief discussion of the character. Character states were polarized by reference to eurypterids and xiphosurans, where applicable, but neither outgroup was included in the analysis so the cladogram is unrooted.

1. Cuticle. Surface non-reticulate : surface reticulate. Dorsal cuticle of many late Palaeozoic scorpions, and some modern ones, has a distinctive reticulate surface micro-ornament (e.g. Wills, 1960). This has not been observed in any Silurian or Lower Devonian scorpion.

2. Setae. Macrosetae absent : macrosetae present. Silurian and Lower Devonian scorpions, in which sensory setae are known, have tiny conical microsetae sparsely distributed over the cuticle surface, rather than long straight macrosetae typical of more recent scorpions.

3. Carapace. Anterior margin rounded or cultrate : anterior margin with median emargination. A few Silurian genera have a distinctive median emargination in the anterior margin of the carapace. This state is not seen in eurypterids, nor in other fossil scorpions, so it is regarded as derived. A similar emargination is present in some Recent scorpions, particularly among the Scorpionidae, presumably by convergence.

4. Median eyes. Anterior : posteriorly displaced. In eurypterids and other "merostome" chelicerates, the median eyes are located near the middle of the prosomal shield, and this is also their situation in palaeostern and orthostern scorpions (Jeram, 1994b). In most Palaeozoic scorpions, median eyes are near the anterior margin of the carapace (Kjellesvig-Waering, 1986) and, although clearly derived relative to the "merostomes", this is considered to be the plesiomorphic state for the taxa under consideration because no scorpions are known prior to the Upper Carboniferous with posteriorly displaced eyes. Posterior displacement in the neoscorpions (Orthosterni + Palaeosterni) is a character reversal, and thus a derived state in this context.

5. Abdominal plates (a). Five : four. Eurypterids have five plate-like appendages bearing respiratory organs on the ventral surface of the mesosoma, the anterior plate being fused with the external genitalia to form the genital operculum (Wills, 1965). The number of abdominal plates present in many fossil scorpions is not reliably determinable, but some definitely have five. Kjellesvig-Waering (1986) assumed that all Palaeozoic scorpions (except *Palaeopisthacanthus*) had five abdominal plates, and labelled his figures accordingly, but all Carboniferous scorpions with a well preserved ventral mesosoma have just four (Jeram, 1994a).

6. Abdominal plates (b). No ornament : posterior ornament. The abdominal plates of most Palaeozoic scorpions lack any form of marginal ornament, but a posterior row of tubercles is present in Gen. Nov. A, and may be regarded as an autapomorpy of that taxon. The development of a posterior ornament on mesosomal sclerites, e.g. tergites, is widespread among arthropods and seems to be a labile character which is subject to frequent reversal. It is very common among eurypterids, and reoccurs among later scorpions, e.g. Triassic mesophonids (Wills, 1947).

7. Abdominal plates (c). Stigmata absent : stigmata present. Stigmata perforate the "sternites" (= sutured-on abdominal plates) of all Recent scorpions, the Carboniferous orthosterns (Jeram, 1994b), some undescribed Upper Devonian scorpions with orthostern affinities (pers. obs.), and mesophonids. Reports of marginal stigmata in some Upper Carboniferous mesoscorpions (Kjellesvig-Waering, 1986) have not been confirmed by the author's examination of relevant specimens. They are absent from Silurian and Devonian scorpions.

8. *Postabdominal segments (a)*. Preanal segment approximately equal in length to preceding segment : preanal segment distinctly shorter than preceding segment.

9. Postabdominal segments (b). Preanal segment approximately equal to or shorter than preceding segment : preanal segment longer than preceding segment.

10. Chelicerae. Large : small. There is a general trend among fossil scorpions towards a reduction in the size of the chelicerae through the Upper Palaeozoic. This is probably due to changes in feeding behaviour, as scorpions adopted liquid feeding as opposed to ingestion of solid food particles (Kjellesvig-Waering, 1986; Selden & Jeram, 1989). This character is included with some misgivings, because it is subject to continuous change and difficult to determine objectively. It may also be subject to frequent reversal, for example, the Recent genus *Opisthophthalmus* has enlarged chelicerae which it uses for burrowing.

11. Pedipalps (a). Patella shorter than, or equal in length to manus : patella longer than manus. All Silurian scorpions and some Devonian species have a distinctly shorter manus than later species.

12. Pedipalps (b). Carinae on pedipalp femur and patella lack a prominent row of tubercles : tubercle rows present.

13. Pedipalps (c). Rami of pedipalp chelae short : rami long. The pedipalp fingers of many early scorpions are relatively short, not exceeding the length of the manus, whereas those of late Palaeozoic scorpions are generally longer. The length of the fingers in proportion to the manus is used because it is easily measurable, and because it allows comparison between taxa with different degrees of overall pedipalp elongation. This character is subject to reversal, as demonstrated by the distribution of long and short fingers within modern scorpion families.

14. Legs (a). Femur and patella cylindrical : femur and patella laterally compressed. Podomeres of eurypterid legs are typically circular in cross-section (e.g. Selden, 1981), as are those of some Silurian scorpions. All other scorpions show some degree of lateral compression, most noticeably of the femur and patella. Lateral compression serves to increase the strength of the leg (Dalingwater, 1985), and reaches its maximum development in Recent orthostern scorpions.

15. Legs (b). Eurypterid-like stance : orthostern-like stance. This character is used to summarize the overall leg structure of scorpions. In eurypterids there is relatively little differentiation in the relative lengths of podomeres: successive podomeres along a typical unspecialized walking leg generally decrease in length from the femur to the tarsus. Most scorpions show marked differentiation in the length of podomeres, and an increased degree of flexure noticeably on some joints, most the femur-patella and patella-tibia joints. Determining the state of this character in fossil taxa may be subjective, particularly in "intermediate" species or where preservation is poor.

However, for the majority of fossil scorpions it is not difficult.

16. Legs (c). Posterior walking leg does not reach posterior margin of tergite 7 : posterior leg reaches posterior margin of tergite 7. This character is a measure of overall leg elongation. It crudely distinguishes long-legged scorpions from those with short legs. By comparison with eurypterids the short-legged condition is presumed to be the plesiomorphic state. To determine this character in fossil scorpions the length of the posterior leg, when straightened, is compared with the distance from the origin of the leg (coxa) to the posterior margin of tergite 7 (end of mesosoma), allowing for mesosomal distention and post-mortem distortion.

17. Legs (d). Telotarsus shorter than, or equal in length to, basitarsus : telotarsus longer than basitarsus.

18. Legs (e). Basitarsus and telotarsus lack ventral thorns : ventral thorns present. Most late Palaeozoic and Recent scorpions have prominent rows of fixed cuticular thorns or stout movable setae on the inferior surface of the basitarsus and telotarsus. Two or, less frequently, four rows may be present on the basitarsus, with usually a single row on the telotarsus. This character is difficult to determine in fossils unless cuticle preservation of the tarsila is good.

19. Legs (f). Telotarsal spurs present : tarsal claws present. The walking legs of eurypterids terminate with a prominent spur-like post-tarsus, which is frequently flanked at its proximal end by a pair of smaller tarsal spurs. This condition is seen in some early fossil scorpions, but most fossil scorpions, and all modern ones, have a greatly reduced post-tarsus, and the tarsal spurs converted to a pair of curved claws.

20. Coxae (a). Opposing bases of all pairs of walking-leg coxae meet in front of sternum : bases of posterior pair of coxae (at least) separated by sternum. In eurypterids and xipho-surans leg coxae are gnathobasic and the medial ends of opposing pairs meet at the midline. Some primitive scorpions also had gnathobasic coxae, but in terrestrial scorpions the coxae are immobile, with the posterior two pairs separated by the sternum.

21. Coxae (b). Second pair of leg coxae do not abut sternum : second pair of leg coxae abut sternum.

Jeram: Phylogeny of scorpions

22. Coxae (c). Anterior pair of leg coxae do not abut sternum : anterior pair of leg coxae abut sternum. Characters 20 and 21 are successive phases in the immobilization of leg coxae by the relative anterior movement of the sternum between the coxae. Coxal immobilization can contribute to more efficient walking (Manton, 1977). In scorpions, it correlates broadly with elongation of the posterior legs and of the coxosternal region, both of which also increase stability during walking.

23. Coxae (d). Coxal apophyses absent : apophyses present on coxae of first two pairs of walking legs. This character codes for the presence or absence of a well-developed oral tube, a structure associated with liquid-feeding in scorpions. Poor preservation of many early scorpions prohibits tracking the development of the coxal apophyses. Kjellesvig-Waering (1986) reported small lobes on the anterior pair of coxae in Praearcturus and Stoermeroscorpio. These are present in Praearcturus, but the situation in Stoermeroscorpio is ambiguous. Because of this, the presence or absence of apophyses on both pairs of anterior leg coxae is coded for, as this can be determined with some certainty in the majority of scorpion fossils.

24. Pectines (a). Lamina broad, without discrete lamellae : lamina narrow, with discrete lamellae. The detailed pectinal morphology of most Silurian and Devonian scorpions cannot be determined because of poor preservation, but in general these scorpions have relatively broad plate-like laminae with a small number of short rounded teeth. The lamina is not observed to be divided into discrete lamellae like those of late Devonian and Carboniferous mesoscorpions, and Recent orthostern scorpions.

25. Pectines (b). Fewer than 20 teeth per comb : more than 20 teeth per comb. Early scorpions tend to have relatively few teeth on each pectine comb compared with later Palaeozoic scorpions. For the purposes of this study the derived state has arbitrarily been defined as more than 20 teeth, although the taxa coded as derived actually have 30–160 teeth per comb. Orthostern scorpions, including Upper Carboniferous examples, frequently have fewer than 20 teeth.

26. *Genital operculum*. Operculum composed of two discrete plates : operculum a single plate. This character has been included because some

Devonian, and most Lower Carboniferous, scorpions have a genital operculum consisting of a single broad plate, which has no clear median suture. By contrast, all other scorpions have a pair of plates which may be separate, or fused along the mid-line although retaining a clear median suture. However, because the genital operculum is seldom well preserved, it can be difficult to ascertain whether the primitive or derived state is present. It is also unclear whether a single plate is apomorphic for a discrete clade of Devonian and Lower Carboniferous scorpions, or whether reversals have subsequently taken place in some mesoscorpions and orthosterns.

Method

The character state matrix (Table 1) was analysed using the program PAUP (Phylogenetic Analysis Using Parsimony: Swofford, 1993). Some of the equally parsimonious trees and Consensus trees were plotted by MacClade (Maddison & Maddison, 1992).

An Adams consensus tree and a Majority Rule (MR) tree were also generated. The Majority Rule tree was annotated with the positions of character state changes (Fig. 1). Lack of resolution was largely due to indeterminate character states rather than conflicting characters. The optimization criterion used by PAUP delays character state changes to the latest possible node when character states are unknown. When many characters are missing this results in "bunching" on nodes where a character changes state which is determinate in the relevant taxa. All changes, including convergences and reversals forced by the tree topology, were indicated (Fig. 1).

Smith (1994) recommends *a posteriori* weighting of characters as the most parsimonious means of selecting a tree from among equally parsimonious alternatives. Given the high number of equally parsimonious trees in this case, it was not considered feasible to work through each tree node by node resolving the polytomies. Instead, the Majority Rule tree, which contains the groupings with the greatest support from among the equally parsimonious trees, was used as a framework for construction of a cladogram more fully resolved by *a posteriori* weighting.

Species	7	14	12	6	18	8	20	4	5	3	10	2	1	11	13	9	16	15	19	17
Character																				
3	0	1	1	1	?	0	0	0	0	0	0	?	0	?	?	0	0	0	0	0
6	0	?	0	0	?	?	0	?	0	0	?	?	1	?	0	?	?	0	0	0
17	0	?	0	0	0	0	0	1	1	1	?	0	0	?	1	0	1	0	0	0
22	0	?	?	0	1	?	1	?	1	1	1	0	0	0	0	?	0	0	0	0
4	0	0	0	0	?	?	0	0	0	0	0	?	0	?	?	0	?	?	0	1
7	0	?	0	0	?	0	0	0	0	0	0	?	0	?	0	0	?	0	0	1
9	?	?	0	0	?	0	?	0	0	0	0	?	?	?	?	?	0	0	0	1
5	?	?	?	?	?	?	0	?	?	0	?	0	0	?	?	?	?	?	1	1
8	?	?	0	0	?	0	?	0	0	0	0	?	?	?	?	?	0	0	1	0
1	?	?	?	?	?	0	0	0	?	?	?	0	0	0	0	0	?	1	1	0
18	?	?	0	0	?	0	?	0	?	0	?	0	0	?	?	?	?	1	1	1
24	?	?	?	0	?	?	0	?	0	0	?	0	0	?	0	0	?	1	1	1
12	?	?	0	0	0	0	?	?	0	0	?	0	0	?	0	?	?	1	1	1
2	?	?	?	?	?	0	?	?	?	?	?	0	0	?	0	?	?	1	1	1
25	?	?	?	0	?	?	0	?	0	0	?	0	0	?	0	1	?	1	1	0
26	0	?	?	?	?	?	?	?	0	0	0	?	?	?	?	1	1	?	1	0
11	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	?	1	1	1
23	0	?	?	0	0	?	0	?	0	0	0	0	0	0	1	?	1	1	1	1
16	0	?	0	0	0	?	0	0	0	0	0	1	1	?	1	1	1	1	1	1
10	?	0	0	0	?	0	0	0	0	0	1	?	1	?	?	0	?	1	1	1
19	0	?	0	0	?	1	1	1	1	1	?	0	1	?	?	1	1	1	1	1
13	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	?	?	1	1	1
14	0	?	0	0	1	?	1	?	?	1	1	1	1	?	1	1	1	1	1	1
15	0	?	0	0	?	?	1	1	1	1	1	1	1	?	1	1	1	1	1	1
21	0	?	?	0	1	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1
20	0	?	?	1	1	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1

Table 1: Character state matrix. Plesiomorphic state indicated by "0", derived state by "1" and indeterminatecharacter state by "?". Characters numbered down vertical axis are described in text. Taxa numbered along hor-izontal axis as follows: 1 Gen. Nov. A; 2 Gen. Nov. B; 3 Proscorpius; 4 Archaeophonus; 5 Stoermeroscorpio;6 Allopalaeophonus; 7 Palaeoscorpius; 8 Hydroscorpius; 9 Acanthoscorpio; 10 Waeringoscorpio;11 Praearcturus; 12 Palaeophonus; 13 Branchioscorpio; 14 Dolichophonus; 15 Petaloscorpio;16 Hubeiscorpio; 17 Palaeopisthacanthus; 18 Labriscorpio; 19 Pulmonoscorpius; 20 Archaeoctonus.

The procedure for resolving polytomies was as follows: Characters in conflict at a node are identified from the annotated MR tree (Fig. 1). Homoplasy involving these characters elsewhere in the tree was noted. Using the character state matrix, alternative positions for branches allowed by missing data were identified (usually in a downward direction-see above). The most parsimonious topology was chosen by weighting conflicting characters according to their relative strength. Solutions which favoured the loss of a structure (reversal) were selected in preference to those which required parallel evolution (de Pinna, 1991). Furthermore, Smith (1994) considered that

complex structural features are less likely to be evolved in parallel than simple ones. If a solution was not forthcoming after these criteria were applied, the following additional criteria, given in their order of application, were employed:

1. Characters known to exhibit homoplasy in a closely related group which is not included in the analysis (in this case, Recent scorpions) are regarded as weaker than those which do not.

2. Convergence or reversal of a character are more likely to have occurred in stratigraphically later members of a clade than earlier ones.

3. Where one or more of the characters in conflict are part of a recognized character transition

22



Fig. 1: Majority Rule tree. Annotated to indicate characters supporting each branch (apomorphy), and to show character convergences and reversals forced by this topology. Percentage support for groupings most frequent among equally parsimonious trees is indicated.

series, the continuity of the series should be maintained as far as possible. Note that "missing" taxa may be a cause of discontinuity.

4. A character which can be very reliably determined is regarded as stronger than one which may require subjective judgment in its definition or determination.

5. A character which can be determined in most of the taxa under consideration is stronger than one which can be determined only in a few.

Additional information which was not strictly part of the character state definition, but which was useful in deciding the relative strength of characters, is given in the discussion of characters above.

Results

PAUP analysis retained approximately 1200 equally parsimonious trees, characterized by multiple polytomies. This was expected, given the large number of indeterminate character states in the matrix. The strict consensus tree indicated 100% support for only one clade, consisting of the genera *Proscorpius*, *Stoermeroscorpio* and *Archaeophonus*, the rest of the included taxa collapsing to an unresolved bush from the basal node.

The primary cladogram produced after application of character weighting is given in Figure 2, annotated to show all remaining cases of character conflict. The node at which some character states (i.e. 5, 10, 18) change is uncertain because of indeterminate character states. Characters 10 and 18 could be moved down one node, whilst 5 could move up one node. Moving characters 5 or 18 would make no difference to the tree topology because the nodes they are positioned at are supported by other characters. However, it should be noted that character 5 is moved down to its lowest possible position (node E), nodes D and E would collapse together forming a polytomy.



Fig. 2: Cladogram. Annotated to indicate characters supporting each branch (apomorphy), and to show convergences and reversals required by this topology. See text for explanation.

Nodes A and B are resolved from the basal polytomy of the Majority Rule tree. Node A is unsupported, but would have been supported by the scorpion apomorphies, the pectines, poison sting, and chelate pedipalps, if a "merostome" outgroup had been included to root the tree. Palaeoscorpius is clearly the most plesiomorphic taxon in the analysis, and emerges as the sister taxon to all other scorpions. It does not exhibit any uniquely derived characters. Three taxa, Allopalaeophonus, Palaeophonus, and Dolichophonus, are united by character 3 (node O). Relationships among these genera are not resolvable on the basis of this analysis. However, Allopalaeophonus and Palaeophonus are indicated as sister taxa because of their similar morphological appearance and close stratigraphic occurrence. If it were not for the differing abdominal plate shapes of these taxa, they might be regarded as cogeneric, as indeed they were prior to Kjellesvig-Waering's (1986) revision. Dolichophonus becomes the sister taxon to this grouping by default, and perhaps also by virtue of its elongated pedipalp patella (character 11). Dolichophonus originated from the basal polytomy in the Adams consensus tree, but was bumped up a node in the MR tree by virtue of its convergent character (11, convergent autapomorphy), and because 21 out of the 26 characters are indeterminate in this genus.

Node C is supported by five derived characters. The equivalent grouping in the MR tree is also highly supported (although note comments on Dolichophonus above). One major departure from the MR tree topology was the use of character 22 to define the grouping at node L. The MR tree requires that this character state arose independently in four different plesions, but given that this is a complex character which is strongly tied to a particular mode of feeding, multiple convergence seems extremely unlikely. The grouping of Proscorpius, Archaeophonus and Stoermeroscorpio is supported in the strict consensus tree: indeed it is the only grouping with 100% support from the equally parsimonious trees. However, it is not possible to resolve either the relationships between these genera or solve the trichotomy at node L without additional analysis involving more characters. The topology used in the cladogram is unstable because of indeterminate characters and minor homoplasy. Waeringoscorpio constitutes one Order SCORPIONES Hemprich & Ehrenberg Plesion (Genus) *Palaeoscorpius* Lehmann

Plesion (Family) Palaeophonidae Thorell &

Lindström

Genus *Palaeophonus* Thorell & Lindström Genus *Allopalaeophonus* Kjellesvig-Waering Genus *Dolichophonus* Petrunkevitch

Plesion (Family) Proscorpiidae Scudder Genus *Proscorpius* Whitfield

Genus Archaeophonus Kjellesvig-Waering

Genus Stoermeroscorpio Kjellesvig-Waering

Genus Waeringoscorpio Størmer

Genus Archaeoctonus Pocock

Genus *Pseudarchaeoctonus* Kjellesvig-Waering Genus *Loboarachaeoctonus* Kjellesvig-Waering

Genus Labriscorpio Leary

Genus Hydroscorpius Kjellesvig-Waering

Plesion (Family) Praearcturidae Kjellesvig-Waering Genus *Praearcturus* Woodward

Genus Gen. Nov. B

- Plesion (Genus) Gen. Nov. A
- Plesion (Genus) Branchioscorpio Kjellesvig-Waering

Plesion (Suborder) Mesoscorpionina Stockwell Secondary plesion (Genus) Acanthoscorpius

Kjellesvig-Waering

Infraorder (un-named Group A)

- Infraorder (un-named Group B)
- Plesion (rank undetermined) "palaeostern" scorpions
- Plesion (Genus) Corniops Jeram
- Plesion (Genus) Compsoscorpius Petrunkevitch
- Plesion (Genus) Cryptoscorpius Jeram
- Plesion (Genus) Palaeopisthacanthus Petrunkevitch
- CROWN GROUP (Rank undetermined)

Table 2: Classification of the Palaeozoic scorpions. See text for explanation.

plesion by virtue of the apparently derived condition of its chelicerae (character 10, convergent autapomorphy), whilst the third plesion consists of another unresolved trichotomy at node M, containing the genera *Archaeoctonus*, *Labriscorpio* and *Hydroscorpius*. These last two might be considered sister taxa by virtue of the reversal of character 13 present in both genera, but this is a weak character, and both genera are otherwise poorly known, so for the time being the polytomy is considered unresolved.

Praearcturus is very poorly known (19 of 26 characters indeterminate). In the MR tree it originates from the same node as Gen. Nov. A, Gen. Nov. B, and a well supported clade containing the six remaining genera. It shares several unique characters with Gen. Nov. B (cuticle ornament, sternum shape, coxal shapes), but these were among the characters excluded from the analysis because of uncertainty in coding or determination in other taxa (see above). In view of this additional evidence, they are regarded as sister taxa (node K), a relationship which is permitted, but not specifically supported, by the current analysis. The position of this clade is also rather ambiguous. As indicated in Figure 2, its accepted position at node D requires reversal of character 19, the plantigrade foot complex, in Gen. Nov. B. This is a "strong" character, and insertion of the clade below node C would eliminate the requirement for it to undergo reversal. However, that solution would require that the relatively "weaker" character 16 (leg length) was reversed at node L. Although arguably the latter is more likely from an evolutionary point of view, it is strictly less parsimonious, because reversal of character 16 at node L decreases the consistency index. Thus the higher position supported by the MR tree is adhered to. As noted above, movement of character 10 to its alternative permitted position (node D) would result in a polytomy. As this would have no significant effect on the interpretation of the cladogram, the topology given is preferred.

The grouping supported at node F is also well supported in the MR tree, but its resolution in that tree is poor due to conflicting characters (Fig. 1). Application of the weighting criteria (above) substantially improved resolution. In particular, note that Branchioscorpio and Hubeiscorpio, united as sister taxa in the MR tree on the basis of a shared "weak" character (17), have been separated, leading to a considerable reduction in postulated homoplasy. Although unsupported by any character employed in this analysis, the sister taxa relationship between Hubeiscorpio and Pulmonoscorpius is supported by previous work on the mesoscorpions (Jeram, 1994a).

Classification of the scorpion stem group

That scorpions comprise a monophyletic clade is accepted by most recent studies (e.g. Shultz, 1990; Wheeler et al., 1993; Dunlop, 1997) but the position of the clade within the Chelicerata is contentious. One consequence of this is that the group has been placed at various taxonomic ranks according to its perceived relationships Kjellesvig-Waering, (e.g. 1986 [order]: Stockwell, 1989 [class]; Starobogatov, 1990 [superorder]). At present, the scorpions (including fossil forms) are generally ranked at the ordinal level (e.g. Sissom, 1980). Thirteen extant scorpion families are currently recognized (Fet et al., in press), constituting a monophyletic crown group, with a post-Carboniferous latest common ancestor (Jeram, 1994b). All Palaeozoic scorpions belong to the stem group of this clade. Relationships within the crown group have not yet been fully resolved, although cladistic studies, such as those of Lamoral (1980) and Stockwell (1989), suggest that suprafamilial ranks may ultimately be accepted.

Whatever rank the crown group is ultimately given, by traditional systematic practice its sister group (i.e. the highest stem group clade, *Palaeopisthacanthus*) should be recognized at the same rank. Whilst the rank of the crown group is uncertain there is no point of reference with which to establish traditional hierarchical ranks for the stem group clades. For this reason, stem group clades are here recognized as plesions (Patterson & Rosen, 1977), and the total group retains its currently accepted rank of order (Table 2).

The Palaeophonidae are united by the emargination in the anterior of the carapace. Stockwell (1989) included these three genera, plus *Palaeoscorpius*, in his order Protoscorpiones, which was supported by the same character, but here *Palaeoscorpius* is assigned to its own plesion because it appears to lack the emargination and has a plesiomorphic coxosternal arrangement.

The Proscorpiidae plesion is roughly equivalent to the order Palaeoscorpiones of Stockwell (1989), but is expanded to include *Hydroscorpius*. Only one well supported monophyletic grouping within the plesion is revealed by this study (see above) and, because of this lack of resolution, the plesion is provisionally ranked at the familial level. Additional analysis of the constituent genera may clarify relationships within the plesion, requiring additional ranks.

The Suborder Mesoscorpiones was created by Stockwell (1989) to accommodate a diverse clade dominated by Carboniferous scorpions. In this analysis it is represented by *Petaloscorpio*. Hubeiscorpio, and Pulmonoscorpius. The clade supported by node H corresponds very closely to the emended concept of the Mesoscorpiones proposed by Jeram (1994a), and thus the name and rank are retained for the plesion here. The mesoscorpions have not yet been subjected to a cladistic study, so relationships within the group are poorly understood. Jeram (1994a) identified two groups within the Mesoscorpiones, and revised the classification of one of them, Group A. These groups are here provisionally recognized at the rank of infraorder, although it is appreciated that they may not stand up to cladistic scrutiny. Jeram (1994a) assigned all three of the mesoscorpion genera included in this analysis to Group A, which contains two families. The Gigantoscorpionidae has two genera, including Petaloscorpio, whilst the Centromachidae contains five genera, including Pulmonoscorpius. Four genera, including Hubeiscorpio, could not be placed because of poor preservation, and were considered Mesoscorpiones (Group A) incertae sedis.

The Upper Carboniferous mesoscorpions, most of which can apparently be assigned to Group B, require complete reassessment. *Acanthoscorpius* lies on the mesoscorpion stem, and is therefore included in this scheme as a secondary plesion within the Mesoscorpionida.

The position of *Palaeopisthacanthus* as the most crownward stem group plesion was established by Jeram (1994b). In that study, Jeram included the genera *Palaeopisthacanthus*, *Compsoscorpius* and *Cryptoscorpius* in the family Palaeopisthacanthidae, rendering it paraphyletic. In the classification above, these three genera are each included as separate plesions, which is consistent with Jeram's (1994b) analysis, although the trichotomy [*Compsoscorpius* + *Cryptoscorpius* + (*Palaeopisthacanthus* + crown group)] implicit in that analysis remains unresolved (see discussion in Jeram, 1994b).

Early scorpion evolution

The mid-Devonian Palaeoscorpius emerges as the most plesiomorphic scorpion in this analysis, rather than any of the Silurian genera (Fig. 3). Although this may appear counterintuitive, order of stratigraphic occurrence does not necessarily correlate with the order of cladogenesis (Norell & Novacek, 1992), particularly when the fossil record of a group is very sparse. It is also worth noting that the Hunsrückshiefer, in which Palaeoscorpius occurs, represents a fully marine facies, whilst all the Silurian taxa come from marginal marine to brackish or hypersaline lagoonal facies. Palaeoscorpius is, by any standard, poorly preserved; nevertheless, the coxosternal arrangement can be determined. The grouping of coxae anterior to the sternum is very similar to the coxal arrangement of eurypterids (see Selden, 1981). In view of this plesiomorphic state, and the relative anterior displacement of the sternum discussed below, there is a strong case for regarding the scorpion sternum as homologous to the eurypterid metastoma, a metasternite derived from the first opisthosomal segment. By analogy with eurypterids and xiphosurans, it is very likely that the coxae of Palaeoscorpius were both movable and gnathobasic, although this cannot be demonstrated from the only known specimen. Neither the shape of the sternum, nor details of the coxae, can be determined with any degree of confidence in Palaeoscorpius.

The sister group to *Palaeoscorpius*, i.e. all other scorpions, is characterized by relative anterior movement of the sternum (= metastoma) and presumably the mouth, which lies above the anterior margin of the metastoma in eurypterids. The posterior pair of leg coxae are separated by the sternum, lose their gnathobasic function, and become fixed. This is the condition present in *Palaeophonus*.

In the sister group to the Palaeophonidae this trend is continued, with at least the posterior two pairs of coxae completely separated by the sternum. These scorpions share derived characters, such as the possession of laterally compressed podomeres, relatively long legs, development of the stance typical of Recent scorpions, reduction of the post-tarsus and development of curved tarsal claws—which indicate that a wholesale modification of the scorpion locomotory mechanism was taking place. Immobilization of the coxae is linked to this change, as it increases locomotory stability. It should be stressed that this change in scorpion locomotion did not occur all at once, as the cladogram might be taken to imply, but was a rather prolonged process accompanying the shift from aquatic to terrestrial environments (Selden & Jeram, 1989; Jeram, in press). However, some of the major modifications to the scorpion locomotory system necessary to permit efficient locomotion on land were certainly in place by the late Silurian. The morphology of the coxosternal region in Xiphosura, eurypterids, and early scorpions balances the dual roles of this sclerite complex in locomotion and a particular mode of feeding. The two functions are intimately linked in this way. Thus changes to the coxosternal structure in scorpions which increased locomotory efficiency necessarily had an impact on the feeding mechanism.

In the proscorpiids, promotion of the sternum continued, so that this family is characterized by having only the first pair of leg coxae meeting in front of the sternum. One particularly well preserved specimen of Proscorpius proves the gnathobasic function of the anterior pair of coxae (Kjellesvig-Waering, 1986) Gnathobasic scorpion coxae have also been found in late Silurian dispersed cuticle assemblages (pers. obs.). The structure of the sternum and coxae are quite variable in the proscorpiids, and the presence of a labrum anterior to the sternum has been reported in three genera. The best preserved example of the supposed labrum is in the specimen of Proscorpius mentioned above (Kjellesvig-Waering 1986, text-fig. 12A). The anterior of the sternum in Proscorpius is slightly concave, giving it a very similar appearance to the characteristic eurypterid metastoma. The proscorpiids inherited some of the initial leg and coxosternal modifications associated with a shift towards terrestrial locomotion, but show nothing like the degree of terrestrial adaptation evident in their sister group. Evidence from the functional morphology of the proscorpiids, and their preservational environments, suggests that they were fully aquatic (Selden & Jeram, 1989).

The coxae of the second pair of legs were not separated in the sister group to the proscorpiids. They have coxae which are tightly fitted against each other and the sternum, marked elongation of the posterior two pairs of leg coxae, longer legs, and greater differentiation of podomere lengths. These adaptations add further to the strength and stability of the legs. All members of this group possess enlarged coxal endites (apophyses) on the anterior two pairs of leg coxae, forming an oral tube anterior to the mouth. The only possible exceptions are the two undescribed genera from the Silurian of Ontario, specimens of which are poorly preserved anterior to the sternum. The combination of characters possessed by these scorpions suggests that they were all terrestrial (Selden & Jeram, 1989; Stockwell, 1989), again with the possible exception of the two Silurian genera. The recent discovery of book lungs in a Lower Devonian scorpion (Shear et al., 1996) supports this interpretation.

The scorpion fossil record in the Upper Devonian and Carboniferous is dominated by members of the diverse mesoscorpion plesion. Mesoscorpions frequently attained large size (300–700 mm length) and must have occupied an important niche as predators in the Upper Palaeozoic. However, mesoscorpions exhibited relatively little gross morphological innovation during their tenure. Much of the change which did occur involved progressive fine tuning of the locomotory and sensory systems to the terrestrial environment, which continued right through the Carboniferous (pers. obs.).

The sister group to the mesoscorpions originated in the early to mid-Devonian. The palaeosterns are only recorded from the Upper Carboniferous, but appear to have diverged early in the history of this clade, having only a few derived characters such as posteriorly displaced median eyes and reduced lateral eye groups (Stockwell, 1989). The more crownward plesions, e.g. Palaeopisthacanthus and Compsoscorpius, also occur in the Upper Carboniferous. Trichobothria and intra-sternite stigmata first appear in these taxa. Together with other aspects of their morphology, they suggest that the cryptozoic and nocturnal habits typical of modern scorpions were adopted at this time (Jeram, 1994b, in press).

Discussion

The cladogram is inherently unstable because, with so many indeterminate character states, almost any change to the included taxa,



Fig. 3: Evolutionary tree for the Palaeozoic scorpions. The included genera are all known from single horizons, so bars are not intended to indicate stratigraphic ranges. Dashed lines indicate the unresolved relationships among genera. The ranges of major clades are indicated by shading. Note that the Mesoscorpionina and "palaeosterns" include 35 Carboniferous genera which were not included in this analysis.

characters, or coding of characters, would have significant effects on the tree topology. Nevertheless, the cladistic approach employed in this study has yielded a phylogenetic hypothesis which is more consistent with the available data than the competing hypotheses of Petrunkevitch (1955), Kjellesvig-Waering (1986), or Starobogatov (1990). A valid test will be to see how robust the preferred topology is as new taxa are discovered and included. The systematic positions of some taxa will always be in doubt because of lack of data.

The results of this study are consistent with those of Stockwell (1989), but add considerably more detail because of greater inclusivity of fossil taxa and characters.

The use of weighting criteria, such as those outlined above, to select between equally parsimonious solutions in cases of character conflict or to reduce polytomy resulting from missing data, was found to be essential to this study, but they must be applied as objectively as possible. A single most parsimonious (by all criteria) solution is offered here (Fig. 2), but because application of the weighting criteria might be considered to be somewhat subjective, as full an explanation as possible of the topology is given in the text. The determination of character state polarity is also a source of subjectivity. Interpretations of original morphology from often indifferently preserved fossils can vary widely between authors. For this reason, there are a few instances in the character state matrix where the indicated polarity of a character directly contradicts a previously published interpretation. More frequently, characters were coded as indeterminate when there were grounds for considering that a previous interpretation was questionable.

One aspect of the analysis which should not be overlooked is that the majority of the available characters were involved in the terrestrialization process (Størmer, 1976; Selden & Jeram, 1989). If two or more lineages of scorpions colonized terrestrial habitats independently, morphological convergence might be anticipated because of identical selection pressures. The paucity of independent characters in this study means that it is highly unlikely that lineages terrestrializing in parallel would be detected.

The lack of resolution within the proscorpiid and mesoscorpion plesions is also due to the limited range of characters employed. As noted above, these characters tend to be gross morphological characters which can be determined in the majority of the included taxa, and they reveal the major phylogenetic relationships. If all available characters were determinable in all taxa, then obviously a single fully inclusive analysis is warranted, and additional characters could be included which might solve relationships within these groups. However, when there is a high level of indeterminate character states in an analysis, it may be preferable to analyse relationships within these multi-taxon plesions separately, so that the best suite of characters (see discussion of character selection above) can be employed for each plesion, without introducing a higher level of indeterminate character states to other taxa in the primary analysis.

Acknowledgements

The author wishes to thank Jason Dunlop for his considerable help in performing the computer analyses, and also Janet Waddington, who assisted in compiling the character state matrix. The organizers of the 17th European Colloquium of Arachnology, particularly Paul Selden, are thanked for inviting this contribution. Without their encouragement, I might never have completed this work.

References

- BERGSTRÖM, J. 1980: Morphology and systematics of early arthropods. *Abh. Verh. naturw. Ver. Hamburg N.F.* 23: 7–42.
- DALINGWATER, J. E. 1985: Biomechanical approaches to eurypterid cuticles and chelicerate exoskeletons. *Trans. R. Soc. Edinb., Earth Sci.* 76: 359–364.

- DUNLOP, J. A. 1997: Palaeozoic arachnids and their significance for arachnid phylogeny. In M. Żabka (ed.). Proceedings of the 16th European Colloquium of Arachnology. Siedlce: WSRP: 65–82.
- FET, V., SISSOM, W. D., LOWE, G. & BRAUNWALDER, M. E. In press: *The catalog of scorpions (Arachnida, Scorpiones) of the World.* New York: New York Entomological Society.
- HAMMEN, L. VAN DER 1989: An introduction to comparative arachnology. The Hague: SPB Academic Publishing.
- JERAM, A. J. 1994a: Scorpions from the Viséan of East Kirkton, West Lothian, Scotland, with a revision of the infraorder Mesoscorpionina. *Trans. R. Soc. Edinb., Earth Sci.* 84: 283–299.
- JERAM, A. J. 1994b: Carboniferous Orthosterni and their relationship to living scorpions. *Palaeontology* 37: 513–550.
- JERAM, A. J. In press: Chapter 16. Paleontology. In P. Brownell & G. A. Polis (eds.). Scorpion biology and research. Oxford: Oxford University Press.
- KJELLESVIG-WAERING, E. N. 1954: Note on a new Silurian (Downtonian) scorpion from Shropshire, England. J. Paleont. 28: 485–486.
- KJELLESVIG-WAERING, E. N. 1972: Brontoscorpio anglicus; a gigantic Lower Paleozoic scorpion from central England. J. Paleont. 40: 359–375.
- KJELLESVIG-WAERING, E. N. 1986: A restudy of the fossil Scorpionida of the world. *Palaeontogr. am.* 55: 1–287.
- LAMORAL, B. H. 1980: A reappraisal of suprageneric classification of Recent scorpions and of their zoogeography. *In J. Gruber (ed.)*.
 8. *Internationaler Arachnologen-Kongreβ Wien* 1980 Verhandlungen. Vienna: H. Egermann: 439–444.
- MADDISON, W. P. & MADDISON, D. R. 1992: *MacClade: Analysis of phylogeny and character evolution.* Version 3.0. Sunderland, MA: Sinauer Associates. [Computer program].
- MANTON, S. M. 1977: *The Arthropoda: habits, functional morphology, and evolution.* Oxford: Oxford University Press.
- NORELL, M. A. & NOVACEK, M. J. 1992: The fossil record and evolution: comparing cladistic and paleontologic evidence for vertebrate history. *Science*, *N.Y.* **255**: 1690–1693.
- PATTERSON, C. & ROSEN, D. E. 1977: Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull. Am. Mus. nat. Hist.* **158**: 81–172.

Jeram: Phylogeny of scorpions

- PETRUNKEVITCH, A. I. 1955: Arachnida. In R. C. Moore (ed.). Treatise on invertebrate paleontology. Part P. Arthropoda 2. Boulder, CO: Geological Society of America and Lawrence, KA: University of Kansas Press: P42–P162.
- PINNA, M. C. C. de 1991: Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7: 367–394.
- SELDEN, P. A. 1981: Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Trans. R. Soc. Edinb., Earth Sci.* 72: 9–48.
- SELDEN, P. A. & JERAM, A. J. 1989: Palaeophysiology of terrestrialisation in the Chelicerata. *Trans. R. Soc. Edinb., Earth Sci.* 80: 303–310.
- SHEAR, W. A., BONAMO, P. M. & JERAM, A. J. 1996: Fossils of large terrestrial arthropods from the Lower Devonian of Canada. *Nature, Lond.* 384: 555–557.
- SHULTZ, J. W. 1990: Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6: 1–38.
- SISSOM, W. D. 1990: Systematics, biology and paleontology. In G. A. Polis (ed.). The biology of scorpions. Stanford, CA: Stanford University Press: 64–160.
- SMITH, A. B. 1994: Systematics and the fossil record. Oxford: Blackwell Scientific Publications.
- STAROBOGATOV, Ya. I. 1990: The systematics and phylogeny of the lower chelicerates (a morphological analysis of the Paleozoic groups). *Paleont. Jour.* 1: 2–16. [Translated from *Paleont. Zhur.* 1: 4–17].

- STOCKWELL, S. A. 1989: *Revision of the phylogeny* and higher classification of scorpions (*Chelicerata*). Ph.D. thesis, University of California, Berkeley. Published by University Microfilms International, Ann Arbor, Michigan. [Available in printed form].
- STØRMER, L. 1976: Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of the land by arthropods. Senckenberg. leth. 57: 87–183.
- SWOFFORD, D. L. 1993: PAUP, Phylogenetic Analysis Using Parsimony, version 3.1. [Computer program, Apple Macintosh compatible].
- WEYGOLDT, P. & PAULUS, H. F. 1979: Unterzuchungen zur Morphologie, Taxonomie und Phylogeny der Chelicerata. Z. zool. Syst. EvolForsch. 17: 85–116, 177–200.
- WHEELER, W., CARTWRIGHT, P. & HAYASHI, C. Y. 1993: Arthropod phylogeny: a combined approach. *Cladistics* 9: 1–39.
- WILLS, L. J. 1947: A monograph of the British Triassic scorpions. *Palaeontogr. Soc.* (*Monogr.*) 100 & 101: 1–137.
- WILLS, L. J. 1960: The external anatomy of some Carboniferous "scorpions", part 2. *Palaeontology* 3: 276–332.
- WILLS, L. J. 1965: A supplement to Gerhard Holm's "Über die Organisation des *Eurypterus Fischeri* Eichw.", with special reference to the organs of sight, respiration and reproduction. *Ark. Zool.* 18: 93–145.