Palaeophysiology of terrestrialisation in the Chelicerata

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ABSTRACT: The wide range of organs of respiration (book-gills, book-lungs, sieve- and tube-tracheae), reproduction, sensory perception, etc., among the chelicerates indicates that the major groups made the transition to land life independently. The fossil record is patchy for most chelicerate groups, certain intervals (e.g. Westphalian) being particularly rich in chelicerate-bearing Lagerstätten while in others (e.g. Mesozoic) they are sparse. Due, apparently, to their unusual hyaline exocuticle, scorpions are better preserved than other arthropods, and show a fairly continuous record from fully aquatic forms in the Silurian, to both aquatic and terrestrial faunas in the Carboniferous. In particular, new and well-preserved material of the earliest demonstrably terrestrial scorpions from the Lower Carboniferous of East Kirkton, West Lothian, suggests that book-lungs, at least in the scorpions, developed directly from book-gills by suturing of the covering plate (Blattfuss of the related eurypterids) to leave stigmata for diffusion of air. This evidence supports the ideas of early authors that the scorpion mesosomal 'sternites' are fused plates, *contra* Kjellesvig-Waering (1986) who envisaged the plates being lost to reveal true sternites beneath. The fossil evidence also indicates that by the Triassic at least two scorpion lineages had evolved intra-'sternite' stigmata.

The success of the chelicerates in their colonisation and exploitation of land habitats is unquestionable. They outnumber all other terrestrial animal species except for the insects (their major food source) at the present day, and have colonised some of the harshest physical environments on Earth. Lower Palaeozoic chelicerates were aquatic, and the earliest terrestrial forms are recorded from the Lower Devonian (Fig. 1). Fossil evidence for the transition from aquatic to fully terrestrial habits is known only in the Scorpionida and it is generally accepted (e.g. van der Hammen 1985a, b; Weygoldt & Paulus 1979) that other arachnids did not arise from the terrestrial scorpion line. (Palaeontological evidence of terrestrial trigonotarbid and other arachnids in the Devonian, contemporaneous with aquatic scorpions but before the earliest probable terrestrial scorpion, appears to support this notion.) Indeed, the diversity of organ systems among arachnid groups (Table 1) suggests that these arachnid lines diverged early in the history of the chelicerates, and each line probably came on to land independently. This is one of the hypotheses on which we seek palaeontological information. Other questions regarding chelicerate terrestrialisation are: what route(s) were taken by terrestrialising chelicerates—via the marine littoral, fresh water, interstitial habitats, or, in the case of parasites, with their terrestrialising hosts? How were these events organised temporally—rapid or slow, isolated events or together in time, and contemporaneous with plants, insects, or other organisms? Evidence concerning these questions comes from a number of sources, especially: comparative physiology of living organisms, palaeontology, and sedimentology. It is hoped that research in these areas will independently point to similar answers to these questions, but at the moment data are too minimal for firm conclusions. In this paper we review the palaeontological evidence of chelicerate terrestrialisation and how it relates to other lines of inquiry, placing particular emphasis on the scorpions.

Scorpions are a familiar component of present-day terrestrial faunas in warm climates, inhabiting environments ranging from deserts to the canopy of tropical rain forests (Williams 1987). The earliest fossil scorpions, which date from the Middle and Upper Silurian, appear to have been fully aquatic (Rolfe & Beckett 1984). In no other terrestrial chelicerate group are recognisable aquatic forebears known. This places the scorpions in a unique position and gives us the opportunity to trace the changes in morphology and physiology which accompanied their shift from aquatic to terrestrial environments.

1. The fossil record (Fig. 1)

The origins of the Chelicerata among the plethora of bizarre arthropods with mosaic characters in the early Palaeozoic has been elucidated somewhat with the discovery of a primitive chelicerate, sister taxon to all others: *Sanctacaris* Briggs and Collins, 1988. Lacking chelicerae, this animal nonetheless exhibits numerous features which indicate an origin for the chelicerates among the 'early armoured arthropods' of Manton (1977).

The Xiphosura are the best known aquatic chelicerates; representatives are alive today and though amphibious at times, they have never become terrestrial. The Xiphosura have, in the past, been linked with the Eurypterida in the Class Merostomata. Eurypterids were primarily aquatic, Palaeozoic animals and some were at least temporary air-breathers from Silurian times onwards (Selden 1984, 1985). Recent classification schemes have placed the Xiphosura as the sister-group of either all other chelicerates except *Sanctacaris* (e.g. Grasshoff 1978; Boudreaux 1979; Paulus 1979; Weygoldt & Paulus 1979; Weygoldt 1980) or of a group which includes the Scorpionida (e.g. Bergström 1979, 1981; Bergström *et al.* 1980; van der Hammen 1985b, 1986). Such a concept of the Merostomata is unnatural (Kraus 1976).

Arachnid is a convenient term describing living terrestrial chelicerates; however, it is less useful in the Palaeozoic, when some of the scorpions at least were aquatic, and depending on their phylogenetic position, the scorpions may or may not be included (see discussion in Platnick 1986).
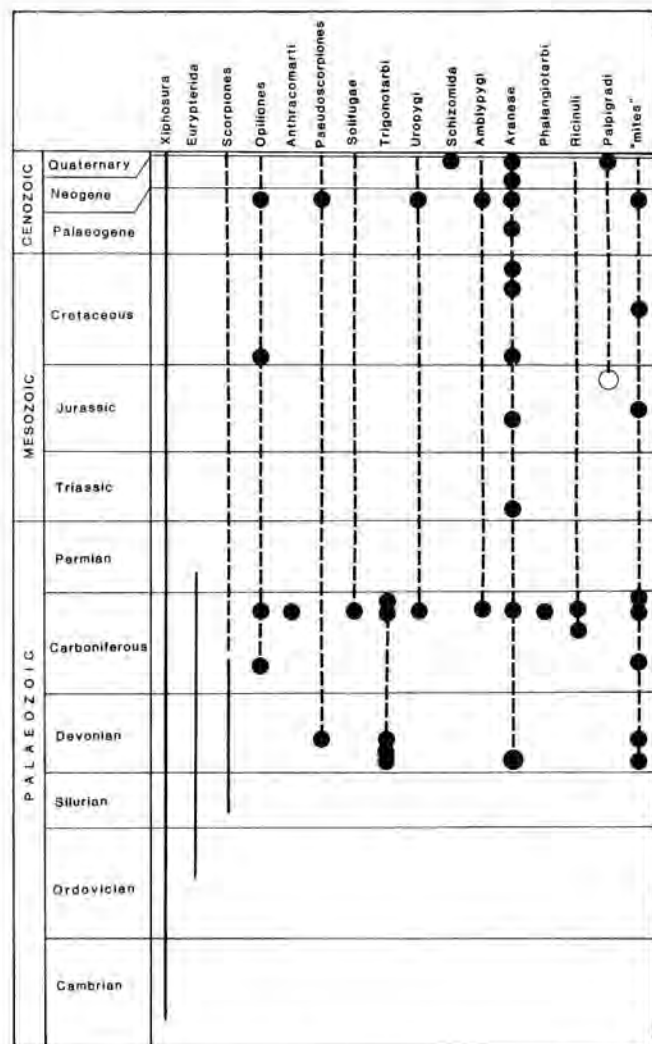

Figure 1 Fossil record of the Chelicerata, based on published and unpublished data; solid circles denote only or major occurrences; open circles are doubtful records; solid lines indicate fairly continuous records of aquatic animals; broken lines connect poor records of terrestrial forms.

The interrelationships of the remaining chelicerate groups (arachnids) are similarly debatable, discussion being beyond the scope of the present paper, but all non-scorpionid fossil arachnids described to date are terrestrial. The evidence for terrestriality in fossil chelicerates is discussed in Section 2.

The fossil record of the chelicerate groups is shown in Figure 1. The record comes principally from well-known Lagerstätten. The oldest terrestrial arachnids are found in the celebrated Rhynie Chert of Aberdeenshire, Lower Devonian (Siegenian) in age. Other important Devonian faunas with terrestrial and aquatic chelicerates are the Emsian Alken-an-der-Mosel in Germany, and the Givetian Gilboa in New York. The next major cluster of arachnid records appears in the Westphalian. Numerous Coal Measures sites in Europe and N America have yielded a relative richness of arachnid fossils. These include Mazon Creek in Illinois, Coseley in the English West Midlands, and Nyrany in Czechoslovakia. Mesozoic arachnids are extremely rare, and surprisingly virtually absent from well-known Lagerstätten such as Solnhofen, though other fine limestones (e.g. Montsech, NE Spain) are yielding a few extremely well-preserved specimens. Later occurrences are mainly of modern aspect forms in amber, and inconsequential to the present discussion.

2. The evidence

The transition from water to land involves changes in physical properties of the environment, which necessitate physiological changes in the organism to allow a terrestrial lifestyle. These are naturally reflected in morphology, and palaeophysiology is the attempt to recognise changes in physiology from the study of morphological changes in fossils. General discussion of the colonisation of land by plants and animals is provided by Selden and Edwards (in press). Palaeontological evidence for terrestriality comes from the recognition of structures which could only function in the terrestrial environment. In most cases the evidence is not clear cut, and structures which are only present in terrestrial animals today may have had a use in their aquatic ancestors (i.e. preadaptation); the plantigrade foot of scorpions is an example.

2.1. Gas exchange
Respiratory changes correlated with the transition from oxygen uptake from water to air-breathing is fundamental to

Table 1

Chelicerate group	Respiratory organs	Reproduction
Xiphosura	book-gills	external fertilisation; claspers on ♂ limb II or III
Eurypterida	?book-gills, accessory lungs	fertilisation not known; ♂ and ♀ organs; scimitar lobe on limb III, modified II in ♂ in *Baltoeurypterus*
Scorpiones	book-gills, book lungs	indirect spermatophore transfer via substrate
Opiliones	tube tracheae	direct free sperm transfer via long penis
Anthracomarti	?	?
Trigonotarbi	book-lungs	median organ only known in *Gilboarachne*
Uropygi	book-lungs	indirect spermatophore transfer via substrate
Schizomida	book-lungs	indirect spermatophore transfer via substrate
Amblypygi	book-lungs	indirect spermatophore transfer via substrate
Araneae	book-lungs, sieve- and tube-tracheae	indirect free sperm transfer via sperm-web and modified ♂ palps (limb II)
Solpugida	tube-tracheae	indirect spermatophore transfer via substrate and ♂ chelicerae
Pseudoscorpiones	sieve-tracheae	indirect spermatophore transfer via substrate
Phalangiotarbi	?	?
Ricinulei	sieve-tracheae	direct spermatophore transfer via modified ♂ leg 3 (limb V)
Palpigradi	none	?spermatophores
'mites'	tube-tracheae, or none	several methods, with or without spermatophores, direct or indirect, probably independently evolved

terrestrialisation. The potential oxygen flux across a respiratory membrane in air is $0.17 \, mol \, m^{-2} s^{-1}$, and in water is $4.2 \times 10^{-5} \, mol \, m^{-2} s^{-1}$ (Raven 1985). This great difference in oxygen availability matters little provided that the oxygen supply to the membrane is constantly replenished. It is for this reason that the gills of *Limulus*, for example, are kept well-irrigated with oxygenated water by a regular metachronal beating of the lamellae. In air, simple diffusion, or at most tidal ventilation during times of high activity, is generally sufficient.

Microscopic palpigrades and some mites take up oxygen cutaneously, but larger chelicerates have specialised organs for respiration. Since the cuticle in these larger chelicerates needs to be thicker to function as an exoskeleton, and act as a barrier to water loss in terrestrial forms, it is fairly impermeable to oxygen. Therefore respiratory membranes are localised areas of thin cuticle, greatly folded into lamellae ('books') to increase their surface area. Theoretically, the morphology of book-gills and book-lungs could be identical (Selden 1985, fig. 1), but certain features can be used to distinguish them in fossils.

Gills may be external projections from the body, as in the Devonian scorpion *Waeringoscorpio* (Størmer 1970; Brauckmann 1987), but they are usually protected by a cover plate, e.g. in *Limulus*. In contrast, book-lungs are almost completely enclosed, opening to the outside by a small pore, the stigma, in order to prevent excessive water loss from the respiratory surface. Thus to distinguish book-gills from book-lungs it is necessary to determine whether the entrance to the respiratory vestibule is restricted (i.e. stigmata are present), or not.

Kjellesvig-Waering (1986) concluded that nearly all fossil scorpions possessed five ventral abdominal appendages (abdominal plates), which it had previously been suggested by Størmer (1976) were apparently equivalent to the Blatfüsse of eurypterids. These plates were attached only at their anterior edges, with the true sternites lying above them and forming the ventral abdominal wall. In Recent scorpions, each book-lung opens to the outside via a stigma which perforates an abdominal sclerite, here termed the 'sternite'. We use inverted commas to distinguish the 'sternite' of Recent (and some fossil) scorpions from the true sternite of fossil scorpions possessing abdominal plates. This distinction is necessary because the two may not be homologous structures. It has been suggested (Wills 1946; Størmer 1963, 1976) that the stigmate 'sternites' of Recent scorpions are actually abdominal plates which have been sutured on to the ventral body wall. In the alternative hypothesis, proposed by Kjellesvig-Waering (1986), the abdominal plates were gradually reduced, and eventually lost completely, exposing the sternite. According to this hypothesis, the sternites of fossil and Recent scorpions are homologous. Central to Kjellesvig-Waering's (1986) argument is his interpretation of all scorpions possessing abdominal plates as branchiate, and therefore aquatic or at least amphibious.

In fact, the nature of the respiratory organs is known in only a few fossil scorpions, because their extremely thin cuticle has a much lower preservation potential than the rest of the exoskeleton (see Section 2.2). Størmer (1970) described gill-like structures in the Lower Devonian *Waeringoscorpio hefteri*, and his observations have been confirmed by the discovery of a second specimen (Brauckmann 1987). Insufficient detail is preserved for their precise morphology to be determined. Kjellesvig-Waering (1986) described lamellae associated with the abdominal plates of a Middle Devonian scorpion, *Tiphoscorpio*

hueberi. These appear to be gill lamellae, probably originally stacked together to form a book-gill comparable with that of *Limulus*. However, these lamellae are unusually thick-walled, with ribs and reticulate sculpture, and the very fact of their preservation in this species whilst those of other scorpions are lost, may indicate that their structure is atypical. It is clear that this species requires reinvestigation, especially since Shear (pers. comm. 1989, after a brief study of the fossil) has suggested it may not be a scorpion at all. Until now, the only acceptable record of stigmata, and therefore presumably book-lungs, in a Palaeozoic scorpion is in a small specimen from Mazon Creek (Westphalian D) of Illinois (Vogel & Durden 1966). Vachon and Heyler (1985) reported stigmata in the Stephanian scorpion *Buthiscorpius pesci*, but after a careful study of the holotype by one of us (AJJ), we are unable to confirm this record. All the other Carboniferous scorpions included in Kjellesvig-Waering's (1986) monograph had abdominal plates, and their respiratory structures are unknown. This leaves us with very little evidence of how the scorpion book-lung developed.

Recent discoveries have changed this picture substantially. The recovery of dispersed fragments of scorpion cuticle from Carboniferous sediments (Bartram et al. 1987) has resulted in the recognition of a new family of tiny scorpions, less than 4 cm in length, which have stigmate 'sternites'. These were undoubtedly terrestrial scorpions respiring through book-lungs. A second important discovery is that of well preserved lamellate structures above the true sternite of a scorpion possessing lobosternous abdominal plates (Fig. 2). These lamellate structures are impregnated with an early calcite cement, and unlike other regions of the integument of this specimen, they are preserved in three dimensions. The orientation, spacing, and size of the lamellae are similar to those of Recent scorpion book-lungs. Along the posterior margin of each lamellate structure are two rows of small lunules on the true sternite which appear to mark the boundary of a long, slit-like stigma. The underlying abdominal plates are not attached to the body wall around their lateral margins, nor is the posterior third of each attached. It is possible that the abdominal plates were either entirely free from the body wall, except along the anterior margin (as in the reconstruction in Fig 3), or that they were sutured on to the ventral body wall in the anteromedian area. In the latter case, the stigmata would lie along, or close to, the posterior suture between the dorsal wall of the abdominal plate and the true sternite. This specimen is one of many recovered recently from the Dinantian locality of East Kirkton Quarry, West Lothian (Milner 1985). At least two further specimens with traces of respiratory structures await study. A complete description of this material is currently being prepared for publication by the second author. The material demonstrates that lobosternous abdominal plates are no indication of an aquatic lifestyle as most authors have concluded (e.g. Wills 1960; Kjellesvig-Waering 1986). Moreover, it shows that, in one lineage at least, the internalisation of the book-gill to form a book-lung took place before any major change in the structure of the ventral surface of the abdominal plates occurred. Unfortunately, it does not solve the problem of whether the abdominal plate was subsequently sutured on, or lost completely. The first is strongly suggested by the morphology of the Triassic scorpions (Størmer 1976, p. 148–149) which are known from Britain (Wills 1910, 1946) and France (Gall 1971). We are aware of no convincing evidence for the second possibility.

Paired oval patches of cuticle on the ventral body wall of

the mesosoma of the Silurian eurypterid *Slimonia* were considered by Laurie (1893) and Moore (1941) to be gills. In an approximately similar position on the body, and beneath movable flaps (Blattfüsse), comparison with *Limulus* book-gills and arachnid book-lungs seemed to support this
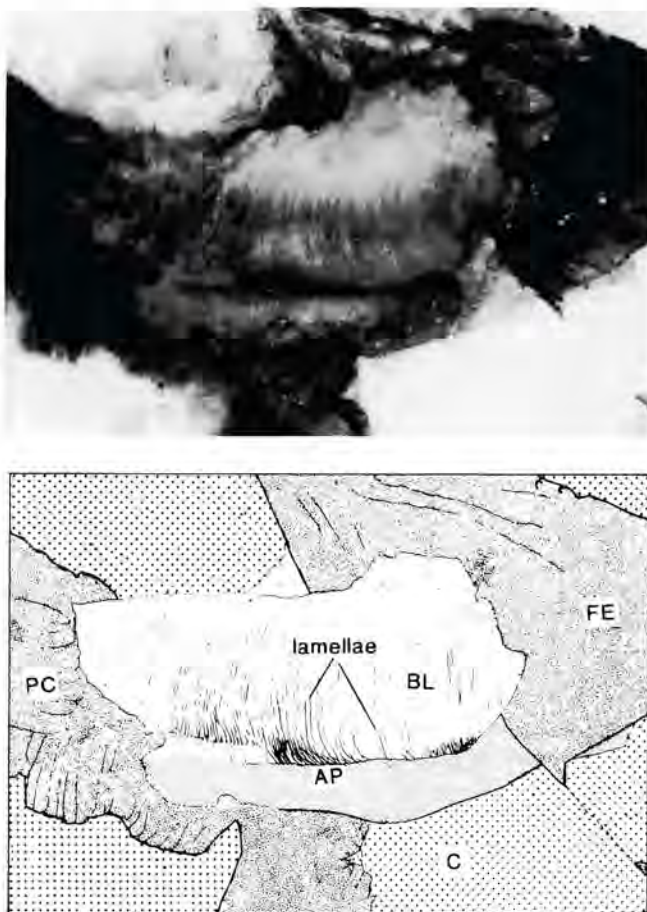
notion. However, the detailed studies of Wills (1965) on the so-called 'gill tracts' of the Silurian eurypterid *Baltoeurypterus tetragonophthalmus* revealed that their morphology was quite unlike that of a typical gill. They are not lamellate, but spongy in structure, thus resembling the pseudotracheae of isopod Crustacea (Størmer 1976). The structure and relationships of the various parts of the 'gill tract' region of the ventral body wall in the Scottish Devonian eurypterid *Tarsopterella scotica* was described in detail by Waterston (1975). In addition, fragments of characteristic spongy eurypterid 'gill tract' are present on prepared slides of Devonian mudstone from Gilboa, New York (unpublished observations by the first author). The 'gill tract' of *Tarsopterella* appears to resemble that of *Baltoeurypterus*. The question of how the eurypterid 'gill tract' could have functioned was addressed by Selden (1985), using comparative functional morphological arguments, including calculation of the 'gill tract' area to body weight ratio in eurypterids, he concluded that the structure could not have functioned as a true gill, but was most probably a secondary air-breathing device similar to the lungs developed on the branchial chamber wall in terrestrial crabs. The true gills of eurypterids, it was postulated, were not preserved and await discovery, although a specimen of an undescribed eurypterid, from the Lower Carboniferous of the Montagne Noire region of France, which shows lamellate structures in the branchial area, was mentioned by Selden (1985).

The oldest book-lungs known are in the trigonotarbid *Palaeocharinus* from the Rhynie Chert, figured by Claridge and Lyon (1961) and Størmer (1976). Two pairs are present, and the same number of stigmata has been observed in the trigonotarbid *Gilboarachne griersoni* from Gilboa (Shear *et al.* 1987, fig. 54). The lamellae can only be seen in the Rhynie specimens because of their highly unusual preservation in the chert; in the Gilboa specimens, lamellae are not observed, only the sclerotised stigmata.

Other respiratory organs of Chelicerata are tracheae, apparently independently developed in various arachnid groups (Table 1), and the plastron, a device for breathing air under water through a tracheal system, found in mites in habitats subject to periodic drowning (Hinton 1971; Pugh *et al.* 1987a, b, c).

Figure 2 Book-lung of scorpion from Dinantian of East Kirkton, West Lothian; photograph shows book-lung associated with second abdominal plate of a lobosternous scorpion, ×20; lamellae can be clearly distinguished in places; camera lucida drawing shows interpretation of photograph; AP = underlying abdominal plate, BL = book lung, C = calcite matrix, FE = femur of leg 3, LAM = lamellae of book-lung, PC = distorted pectine lamina and teeth; Royal Museum of Scotland specimen NMS Geol. 1985.4.67 cp.
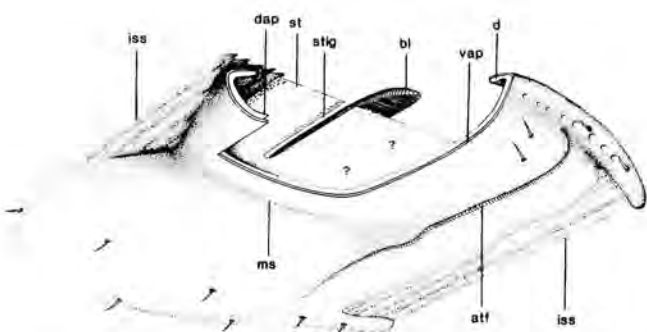

Figure 3 Possible reconstruction of the fifth abdominal plate and true sternite of a Dinantian scorpion from East Kirkton, West Lothian; caudo-ventral view with part of abdominal plate cut away to reveal the overlying true sternite and book lung; atf = anterior transverse fold, ms = median sulcus, d = doublure, vap = ventral wall of abdominal plate, dap = dorsal wall of abdominal plate, iss—intersegmental skin, st = true sternite, stig = stigma, bl = book-lung; based on Royal Museum of Scotland specimens NMS Geol. 1985.4.67 pt & cp; NMS Geol. 1985.4.66.

2.2. Water relations

Water loss is a particular problem for arthropods on land because water vapour pressure is much lower in air than in water (diffusion coefficient of water in air is $2 \cdot 42 \times 10^{-5} \, m^2 \, s^{-1}$ and in pure water is $2 \cdot 4 \times 10^{-9} \, m^2 \, s^{-1}$ (Raven 1985)). The availability of water is highly variable on land, and a number of strategies have been developed by terrestrial arthropods to cope with this. Some small chelicerates, such as mites, live aquatically in a film of water, some in continuously damp soil or leaf litter, while others perform cryptobiosis. Large animals are affected less by changes in external conditions and can maintain an internally hydrated environment (homoiohydry). Such animals need a waterproof cuticle. Waterproofing in chelicerate cuticles, as in other arthropods, is mainly provided by hydrofuge lipids in the epicuticle. This soft, exterior cuticular layer is rarely preserved in fossils. Unfortunately, the structure of fossil arthropod cuticles gives few clues about terrestrial life, even in those groups which are fairly well known. Epicuticular waxes may have been developed in aquatic forebears for osmoregulatory purposes, and conversely, some small arthropods which

obtain oxygen from air by diffusion through the cuticle use wax droplets on the cuticle surface to repel external water.

Some of the lowest rates of water loss among arthropods are recorded from desert-living scorpions: 0·032–0·091% body weight per hour at near 0% humidity (Little 1983, table 6.3). The cuticle of scorpions, and possibly those of eurypterids and xiphosurans, possess a layer immediately beneath the epicuticle termed by Kennaugh (1959) the hyaline exocuticle (see Dalingwater 1987 for a review of chelicerate cuticles). This layer may provide additional waterproofing properties, and also appears to have allowed the preservation of the fossils. Scorpion cuticle fragments are abundant in many Carboniferous coals (e.g. Westphalian of Yorkshire) and some other sediment types (e.g. Dinantian, East Kirkton, West Lothian) in the absence of cuticles of any other arthropod group. The presence of hyaline exocuticle is the only major feature setting scorpion cuticle apart from that of other arthropods, and further investigation (see Bartram et al. 1987) revealed that the thickness of the cuticle is equivalent to that of living scorpion hyaline exocuticle alone, and no ultrastructural features (e.g. broad interlaminae) characteristic of other layers in the cuticle could be seen. Presumably, therefore, some aspect of the nature of the hyaline exocuticle helps preserve this layer alone, when the rest of the scorpion cuticle and other arthropod cuticles are destroyed. Hyaline exocuticle is characterised by the structure and packing of its microfibrils (Filshie & Hadley 1979), and by its staining reactions (Kennaugh 1959), but its chemistry is not known in detail. Hyaline exocuticle is absent from intersegmental membranes (Filshie & Hadley 1979), and presumably also from respiratory membranes, which would explain why they are rarely preserved in fossils.

Some fossil scorpions (e.g. Praearcturus, Brontoscorpio) reached a metre in length (Kjellesvig-Waering 1972). Large size is an advantage on land because it aids homoiohydry (Rolfe 1980). With huge adult size comes the ability to produce large neonates, thus conferring on them the advantages of large size. However, in Recent scorpions, measures are taken to alleviate some of the physiological problems of small juvenile size on land: the young are carried on the mother's back until their first moult. It has been demonstrated that this increases the survival probability of the young (Ugolini et al. 1986), and there is some evidence that they are able to take up water from the parent (Vannini et al. 1985). It may be significant that Kennaugh (1959) was unable to find any trace of the hyaline exocuticle in the neonates he examined.

2.3. Sense organs

The different physical properties of water and air make different demands on the sense organs of animals in these media. On land, arthropods perceive, and produce, higher frequency vibrations than in water, and sound travels faster in air than in water. The different refractive indices of water (1·33) and air (1·00) ensure differences in eye structure between aquatic and terrestrial organisms. Some water beetles (Dytiscus) have eyes in which one half is air-adapted and the other water-adapted.

Among the variety of sense organs found on chelicerates the trichobothrium is the one most useful for determining terrestriality. It consists of a long, thin hair set in membrane within a characteristic cup (Reissland & Görner 1985). It is known that these receptors are used for detecting air vibrations, for anemotactic orientation, and to signal the approach of predators or prey. Among living arachnids, they occur on pseudoscorpions, scorpions, mites, and

spiders, and are useful for taxonomic purposes. Similar organs occur in insects and myriapods; morphological evidence suggests that they are independently derived in these groups, and their independent derivation in each arachnid group might also be suspected. None occur in aquatic arthropods and indeed they could not function in water because of its greater viscosity. Trichobothria have been found on fossil examples of all of the living arachnid groups which possess them and in addition occur on the Devonian trigonotarbids from Gilboa, New York (Shear et al. 1987, pp. 56–8). They are used for separating the genera of these trigonotarbids, since not all possess them. Nevertheless, they indicate that these animals were terrestrial.

The earliest definite trichobothria in scorpions occur in the Westphalian B, with a possible example from the Dinantian (Fig. 4). They are very difficult to prove in fossil
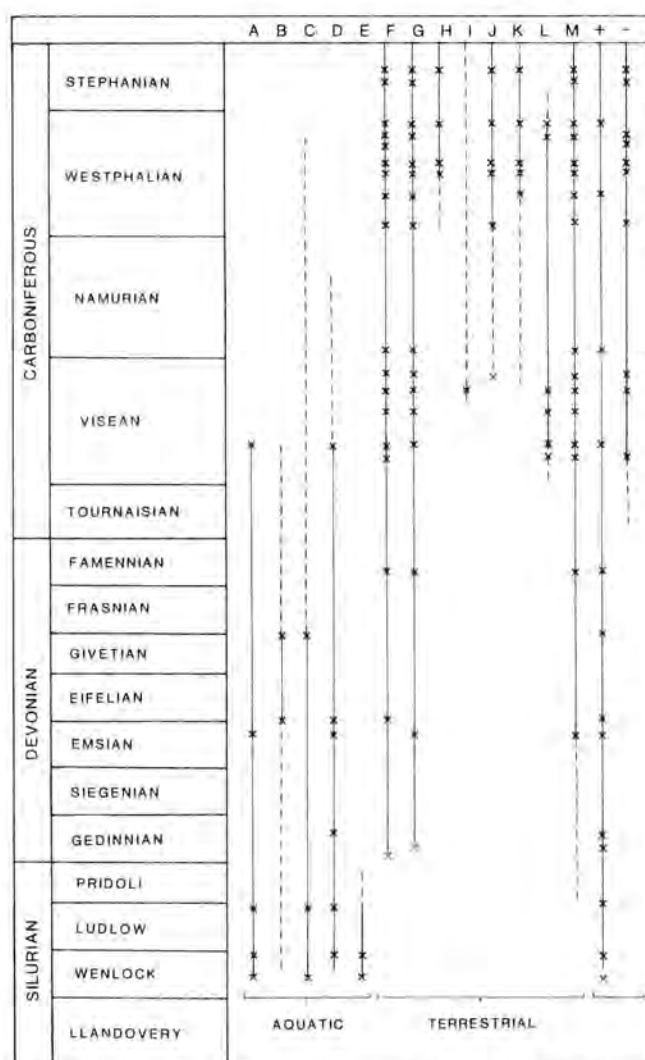

Figure 4 Distribution of morphological 'adaptations' to aquatic and terrestrial environments in Palaeozoic scorpions; crosses denote firm records of morphological characters, based on published and unpublished data; solid lines indicate a fairly continuous record, dashed lines indicate possible stratigraphic ranges based on doubtful records; 'aquatic' characteristics (A—E) are grouped on the left side of the figure, 'terrestrial' characteristics (F—M) on the right; two columns on the far right indicate presence (+) or absence (−) of eurypterids in scorpion assemblages; characters are: A = 'tubular' legs, B = gills, C = compound eyes with more than 50 ocelli, D = coxae lacking apophyses, E = digitigrade tarsila, F = hanging stance, G = coxae with apophyses, H = stigmata, I = book lungs, J = trichobothria, K = lateral eyes with less than 20 ocelli, L = pectines with more than 30 teeth per comb, M = plantigrade feet.

present time. The body fluids of marine Crustacea are iso-osmotic with sea water. Littoral crustaceans, with a few exceptions, are able to tolerate a range of internal osmotic pressures since they have to cope with wide variation in salinity in the intertidal zone. Freshwater crustaceans, on the other hand, have body fluids with low osmotic pressure, finely tuned to the narrow range of salinities encountered in their environment. Three groups of Crustacea show good transitional series to the terrestrial environment: isopods, amphipods, and decapods. The most successful terrestrial colonisers come from the marine tolerators, since they are able to withstand the vagaries of the land habitat better than the freshwater regulators. The major exceptions to this general rule, *Grapsus grapsus* and *Holthuisiana transversa* for example, are relatively large decapods, whose body fluids are less immediately affected by changes in the external conditions. All terrestrial crustaceans have high osmotic pressure: the small ones have retained this from their immediate marine littoral ancestors, some larger forms have managed to retain this in spite of an intermediate freshwater phase because of their large size.

All living terrestrial chelicerates have hyperosmotic body fluids and, with the exception of scorpions, are relatively small animals. Therefore a direct marine route is suggested (unless body size changes have occurred since their emergence). The interstitial route is more gradual since soils act as buffers to external changes in salinity. *Leptokoenenia scurra* is a palpigrade which lives among sand grains in the sea; Monniot (1966) regarded it as being primarily marine, in which case it points to a marine route for this group. Apart from scorpions, all early fossil arachnids are found either *in situ* in fully terrestrial habitats (e.g. Rhynie) or as allochthonous remains in fluvial (e.g. Gilboa) or brackish (e.g. Alken-an-der-Mosel) environments.

The high osmotic pressure of scorpion body fluids (Little 1983), coupled with large size, points to either the marine littoral or fresh water route. All Silurian scorpions occur in marine sediments, but in the Downtonian of the Welsh Borderland scorpion fragments are common in fine sandstones and siltstones containing land plant debris and eurypterids. On sedimentological grounds, the upper part of the Downtonian (of Gedinnian age) can be attributed to fluvial settings. Both *Praearcturus* and *Brontoscorpio* (see Section 2.2) occur in the Downtonian, and, although it cannot be proved that either was aquatic, it is certain that by the Lower Devonian large scorpions had entered freshwater environments or were already terrestrial. In view of the paucity of terrestrial adaptations in Lower Devonian scorpions (Fig. 4), it is most likely that they were aquatic, implying that some scorpions at least moved onto land via fresh water. It is quite possible, of course, that different scorpion lineages terrestrialised along different routes in the Palaeozoic.

4. Conclusions

Scorpion morphology can in some cases be used to infer autecology and physiology. A suite of characters which suggest adaptation for terrestrial living occur in different scorpion lineages at different times, but where several characters are combined in a single scorpion there is a strong probability that it was terrestrial. For the majority of Palaeozoic scorpions, sedimentological and taphonomic evidence remain the most convincing indicators of habitat, as has been found in some other terrestrialising groups (e.g. Campbell & Barwick 1988). It is not known whether scorpions invaded land directly from the sea, or via fresh water, but in either case the abdominal plates inherited from their presumed eurypterid-like ancestors proved crucial to this transition. The scorpion book-lung is probably homologous with the xiphosuran book-gill, and evolved by the internalisation of a book-gill above the sternite. During this transitional phase, the abdominal plate served as a moderating barrier between the respiratory structures and the environment. The book-lung may have evolved independently in a number of scorpion lineages, or it may be a synapomorphy for all terrestrial groups. The suturing on of the abdominal plates and migration of stigmata certainly did occur independently in at least two lineages, one represented by the small Westphalian B scorpions with round stigmata, and the other, by the Triassic mesophonids with long slit-like stigmata. In scorpions at least, evidence from comparative physiology, palaeontology, and sedimentology tends to concur in pointing towards a freshwater route for at least some terrestrialising scorpions.

Too little is known about other early arachnids at present to draw any firm conclusions. Certain arachnid characters such as book-lungs and trichobothria are almost certainly products of convergence, rather than a result of inheritance from a common terrestrial ancestor. Much of the evidence reviewed in this paper suggests that the main groups of arachnids moved on to land independently some time before the Middle Devonian, utilising the direct route from marine environments. The scorpions followed later, probably via freshwater habitats, employing large size and possibly their thick hyaline exocuticle to overcome the osmoregulatory problems posed by that route. Some groups may have arisen on land: spiders, for example, may have evolved from trigonotarbids, a group with which they were contemporaneous in the Devonian.

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6. References

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scorpions unless the cuticle is viewed in transmitted light. The follicles of the earliest trichobothria may be indistinguishable from those of other setae on the same animal, the characteristic form known from Recent scorpions having developed later on.

Silurian scorpions had relatively large lateral compound eyes, and a pair of small median eyes located on an eye node at the anterior margin of the carapace. This suggests that the visual sensilla were of particular importance in the location of prey. There is a general trend in fossil scorpions for a reduction in the size and number of ocelli in the lateral eye and for backward displacement of the median eyes towards the centre of the carapace (Kjellesvig-Waering 1986). Recent scorpions are active mainly at night, with the lateral eyes having a role in the maintenance of the scorpion circadian rhythm (Fleissner 1975). These changes in the scorpion visual system were probably consequential to the adoption of a nocturnal existence, since Recent scorpions detect prey by tactile sensilla (setae), and by 'remote' sensilla such as trichobothria. Work on dispersed scorpion cuticles suggests that the organisation of sensilla on the pedipalp fingers became more complex through the Carboniferous (second author, unpublished data): a further line of evidence for nocturnal activity in Carboniferous scorpions. It seems, therefore, that the shift from diurnal to nocturnal activity took place either simultaneously with the move on to land, or very shortly afterwards.

Sound-producing organs are more commonly found in terrestrial arthropods, but also occur in marine Crustacea and aquatic insects (Rolfe 1985), so the description of possible stridulatory organs in the giant Lower Devonian scorpion *Praearcturus* and the Triassic *Mesophonus* does not necessarily imply a terrestrial mode of life (Kjellesvig-Waering 1986, p. 122).

2.4. Feeding

In the aquatic eurypterids and xiphosurans, prey items are sliced up and pushed into the mouth by coxal gnathobases and endites (Manton 1964; Selden 1981). Terrestrial chelicerates are characterised by external digestion. During feeding, digestive enzymes are secreted onto the food and the resultant fluid is ingested by means of the suctorial pharynx. External digestion occurs within the preoral cavity which is floored by coxal apophyses (the coxae are effectively immobile in arachnids), walled by the pedipalp coxae, and roofed by the labrum and cheliceral parts. Størmer (1976) recognised similar structures in insects and myriapods (they are not, of course, homologous) and suggested that the preoral cavity was characteristic of terrestrial arthropods as a whole. Within the Chelicerata, preoral cavities appear to have developed independently in each group, which points to a convergent adaptation (Størmer 1976). In palpigrades, tiny, soil-dwelling forms which are considered primitive on a number of grounds, a preoral cavity is not developed (van der Hammen 1982). Størmer (1970, 1976) described how the embryonic development of the coxal apophyses in scorpions is mirrored in evolution: coxal apophyses are not present in the Lower Devonian scorpion *Waeringoscorpio*, which is presumed aquatic because of the presence of gill-like structures. Coxal apophyses do appear in scorpions as early as the Lower Devonian *Praearcturus* (Rolfe 1985) but they are still lacking in some families, for example the Archaeoctonidae and Loboarchaeoctonidae from the Lower Visean of Scotland, which on other evidence such as leg structure, size and disposition of eyes, and the arrangement of coxae, are presumed to have been aquatic (Kjellesvig-Waering 1986).

2.5. Reproduction

Marine arthropods can shed eggs and sperm into the sea for external fertilisation, a system which is obviously impractical for terrestrial forms. No chelicerate uses this simple method of fertilisation, and in *Limulus* there is an elaborate spawning behaviour in which the male is dragged to the egg-laying site by the female, attached to her by special claspers on limb II. A wide variety of sperm transfer techniques is found in the arachnids (Table 1). Cloudsley-Thompson (1976) visualised a general evolutionary trend: external fertilisation, indirect sperm transfer via spermatophores deposited on the substrate, direct transfer of spermatophores, indirect transfer of free sperm, and direct transfer of free sperm. Each of these methods could have been developed in marine ancestors (indeed some are found in living marine Crustacea), and Schaller (1979) suggested that indirect spermatophore transfer could have arisen among interstitial forms in the marine environment. Therefore, elaborate sperm transfer devices do not imply a terrestrial mode of life, but suggest it. Some eurypterids have complex devices on the anterior limbs of mature males which have in the past been described as claspers, in comparison with *Limulus,* although Selden (1984) suggested their possible function as organs for the manipulation of spermatophores, or for the direct transfer of sperm, as in arachnids.

Nothing is known of the reproductive biology of Palaeozoic scorpions. Rolfe (1980) suggested that there may have been a change in the function of the pectines since the Silurian, and Kjellesvig-Waering (1986) considered that they may have originally been more closely involved in reproduction. It is interesting to note that the pectines were at their largest and most elaborate during the Dinantian (e.g. in *Centromachus*), which is when the first records of book-lungs and trichobothria are found (Fig. 4). However, the apparent reduction in the size and number of teeth since the Dinantian may simply reflect a general drop in familial diversity since the Carboniferous.

2.6. Locomotion

The lack of buoyancy presents difficulties for arthropods in air: a hanging stance is developed, the legs require greater strength to support the body, and it is quite likely that large arthropod colonisers needed to return to the water to moult, being unable to support the body on legs with soft, new cuticle (Dalingwater 1985).

Størmer (1963) made the point that Silurian scorpions such as *Palaeophonus* had a digitigrade type of tarsal region, like that of the aquatic eurypterids, whereas Recent scorpions have plantigrade tarsi with characteristic spurs. Plantigrade tarsi, he suggested (Størmer 1970, 1976), could be indicative of a terrestrial mode of life. Additionally, terrestrial arthropods have leg joints which permit 'rocking' (Manton 1977) and this helps prevent the foot twisting and abrading on the ground. While an obvious digitigrade foot occurs in the Silurian Palaeophonidae, and good plantigrade forms occur later, there is such a variety of intermediates which may have been used on land, in water, or both, that this character is not particularly useful on its own as an indicator of terrestriality (Kjellesvig-Waering 1986).

3. Routes on to land

The best evidence for routes on to land in animals comes from comparative physiology, and was discussed by Little (1983). The general trends are exemplified by the Crustacea, a group which is in the process of emerging on to land at the

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