

6 | Early Invertebrate Terrestrial Faunas

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Abstract: The few faunas known indicate that their dominant members, the arthropods, were amphibious (Xiphosura, Eurypterida) or fully terrestrial (Arachnida, Myriapoda) by the early Devonian, and thus were available to tetrapod predators. Carnivorous arachnids in these faunas imply the availability of unfossilizable small metazoan and protozoan prey.

Primary producers (plants) probably preceded primary consumers (myriapods) onto land in the Silurian (the Ludlow *Necrogammarus* may be a giant myriapod). Arthropod aeolian feeders and cryptobiotic, aerially dispersed microarthropods could even have preceded some plant pioneers, and aided colonization by "leap-frogging". Secondary and higher trophic level consumers probably succeeded each other in time (trophic level succession or web) as terrestrial invaders, inducing increased variety and biomass at lower levels of the trophic pyramid. Many early arthropods were important decomposers, building up early humus levels and soil structures via coprolites. Some of these arthropods were large, a possible adaptation for reducing water loss.

Trace fossils, important in being autochthonous, hint at the presence of a diversity of Devonian terrestrial arthropods. Experimental neoichnology with millipedes produces different traces under different conditions. Until variables are explored it will remain difficult to identify arthropod groups responsible for Devonian ichnocoenoses.

By the Upper Carboniferous, terrestrial arthropods had evolved explosively. Insectivorous reptiles probably played a larger part in the co-evolution of insects than of arachnids. The latter have shown little evolution since the Carboniferous, and many groups today are similarly confined to humid niches.

Nematode oligochaete and nemertean worms are known from the Carboniferous, but they are all aquatic. Several genera of small land snails are known from the Carboniferous; these probably inhabited tree-trunk base and forest-floor litter.

Systematics Association Special Volume No. 15, "The Terrestrial Environment and the Origin of Land Vertebrates", edited by A. L. Panchen, 1980, pp. 117-157, Academic Press, London and New York.

INTRODUCTION

There are few early invertebrate terrestrial faunas in the sense of complete fossil assemblages from the time of the origin of tetrapods – presumably Upper Devonian (Panchen, 1977, p.729). Such Devonian faunas as do exist will be reviewed here, together with observations on single fossils that may be relevant to the terrestrialization of invertebrate groups. More abundant faunas occur in the Upper Carboniferous, but to review these adequately would be beyond the required remit. Instead, observations on certain Carboniferous faunas are presented, with generalizations about the major groups present. Unlike plants and vertebrates, very little modern work has been done on fossils of fully terrestrial members of the most relevant invertebrate group – the arthropods.

TERRESTRIALIZATION OF ARTHROPODS

1. Origin

Terrestrial arthropods were probably derived independently from several aquatic stocks, although opinion differs on the extent of sclerotization of those stocks prior to their emergence (Størmer, 1976, p.134; cf. Manton, 1977, pp. 25–26). Such sclerotization may well have occurred “more than once during the evolution of arthropods, taking place independently on the sea and on the land” (Manton, 1970, p.29; 1977, p.31). *Aysheaia*, a lobopod from the Middle Cambrian, is the best example of one of these ancestral stocks (Whittington, 1978). It scarcely differs from living onychophorans – terrestrial animals highly adapted to squeeze through the narrowest of crevices (Manton, 1977, p.284) – in having a terminal mouth but lacking jaws and a projecting posterior. From such a lobopod group probably descended both the living Onychophora and the Tardigrada (Whittington, 1978, p.195; Manton, 1977, pp. 288, 498).

2. Terrestrialization

Tardigrades are unknown as fossils before the Cretaceous, probably on account of their small size – they do not exceed 1.2 mm long (Kaestner, 1968, p.16). Their significance lies in their ability to undergo

cryptobiosis – the ability to survive almost total dehydration and remain in suspended animation for years, until revitalized by rehydration (Crowe and Cooper, 1971; Hinton, 1971b, 1977). Such an ability would obviously prove of great significance in distributing early microarthropods, since the desiccated tuns can be dispersed aerially like plant spores, their small size permitting them to fall without injury (Hinton, 1977, p.71). Tardigrades are mainly herbivores, sucking out the content of algal and other plant cells (Kaestner, 1968, p.24). Such microarthropods could therefore have accompanied the “greening of the landscape” that occurred with the spread of algae over land surfaces during the early Palaeozoic (Edwards, Chapter 4 of this volume), once ultraviolet levels had fallen sufficiently. Before that time, such ancestral forms may have scavenged on the shoreline, at night, when the ultraviolet radiation was cut out (Smart, 1971, p.305).

Arthropods could probably only evolve from this miniaturized phase (although small size is an important attribute of land arthropods – Edney, 1977, pp. 2-3) when sufficient plant debris had accumulated to provide protective litter and soil layers. Although this may have occurred with seaweeds rotting on beaches to form soil (Lawrence, 1953, p.367), no great spread can have occurred until the first land plants evolved and colonized the land during the Ludlovian (Edwards, Chapter 4 of this volume). As in present-day tropical and subtropical forests, leafmould probably merged with algal debris of the supralittoral (Bliss and Mantel, 1968, p.674), permitting the ready exploitation by arthropods of the new environment. Such early arthropods probably played a part in assisting the distribution of early plants (Kevan *et al.*, 1975).

Some living terrestrial arthropods can survive above the height at which plants can grow, and feed off wind-blown plant detritus in what has been termed the aeolian zone (Hutchinson, 1965, p.5). Similar habits occur in arthropods of extreme regions such as the Namib Desert. There are no autotrophs in these situations, which may provide an analogy with Palaeozoic continental interiors. Such ecological pioneers could assist the spread of early plants, by pelletizing spores in coprolite substrates, after passage through the gut (Kevan *et al.*, 1975, p. 406; Chaloner, 1976, pp. 4-5).

Most workers accept a marine origin for terrestrial arthropods, but Hinton (1977, pp. 72-73) has proposed that the cryptobiotic

common ancestor of arthropods lived in a saturated terrestrial environment or just beneath the soil surface. Cryptobiosis might have existed in other lobopod stocks (as it does today in brine shrimp eggs and, secondarily, in midge larvae) to give rise to various groups of arthropods. Other lines, e.g. the myriapods, could be more conventionally derived, but again from a lobopod ancestor. In this sense, the Arthropoda are monophyletic (Patterson, 1978; cf. Manton, 1977).

3. Routes Ashore

Arthropods probably terrestrialized by different routes, as is reflected in their divergent habits and associated functional morphology to cope with the new habitats (Manton, 1973, pp. 316-317; 1977, pp. 25-36). Some may have ventured "across sandy beaches or the rocky intertidal zone, through mangrove swamps, or by way of freshwater lakes and streams" (Bliss and Mantel, 1968, p. 674). As Rapoport and Tschapek (1967, pp. 6-7) point out, access via the littoral zone is more difficult than via estuaries or swamps, since all the problems of terrestrialization exist at the same time — especially those of terrestrial locomotion, aerial respiration and temperature fluctuation. One of the few groups that may have followed this route is the isopod crustaceans, whose evaporative water cooling reflects the large, rapid temperature fluctuations of the littoral zone where water is nevertheless abundant (Edney, 1977, p. 95).

Manton (1973, p. 316) and Størmer (1976, p. 134) therefore favour "emergence from quiet estuaries, where terrestrial vegetation and cover exist right to the water's edge . . . The early inhabitants of the land probably gained shelter wherever it could be found, under larger bits of the substratum or plant matter, and by shallow penetration into soft soil without pushing and unaided by any morphological facilitations". Subsequent rapid differentiation of habits, following uniramian arrival on land (Manton, 1977, p. 489), led to the separation of Onychophora and the four myriapod and five hexapod classes, as explained by Manton (1974, p. 164).

There has been much "experimentation", but little consequent radiation within the Merostomata (Eldredge, 1974, p. 38). Although many "eurypteroids" probably attempted to come ashore,

only two lines met with success – the scorpions and the arachnids. Many of the latter owe their survival to the adoption of a cryptozoic habit (Savory, 1977b, p. 312).

THE EARLIEST TERRESTRIAL FOSSILS

Many separate records indicate that the myriapods are the oldest terrestrial fossils. Little is known about this material, although current research under Professor H. B. Whittington's supervision at Cambridge should improve this position. The oldest record is that of *Archidesmus loganensis* from the Llandovery/Wenlock of Lesmahagow (Peach, 1899, pp. 123–125). This specimen (Fig. 4B; I.G.S. Edinburgh 5974) is very poorly preserved, and there is nothing to prove that it is a myriapod. The specimen may have deteriorated since its collection (see also Størmer, 1976, p. 151), but it now resembles some of the plant debris which occurs in the same *Jamoytius* horizon, as first pointed out by Ritchie (1963, p. 125). Ritchie collected a new specimen (Royal Scottish Museum 1970.2) from a higher horizon, the Fish Bed Formation fish bed (Walton, 1965, p. 196) of Wenlock/Ludlow age (Westoll, 1977, p. 72). This (Fig. 4A) resembles a juliform diplopod in having *c.* 20 similar somites with an ornament of terrace-lines, but it is impossible to be certain of this fossil's true affinity.

Necrogammarus salweyi Woodward, from the channel-fill Ludlow of Leintwardine (Whitaker, 1962) is even more problematical (Fig. 1). Originally compared with amphipod crustaceans by Huxley and Salter (1859), this unique specimen (B.M. (N.H.) In 43786) was later referred to the Diplopoda by Peach (1899, p. 126). The two body somites show a lateral sulcus such as is present on Old Red diplopods, and this suggests diplosomites are present. Two limbs are appended to one diplosomite, and one to the other, which is also a diplopodan character. Presupposing 11 somites were originally present, a body length of at least 275 mm is indicated. There are no characters to suggest that this large arthropod must have been terrestrial and the beast may have been an aquatic precursor of terrestrial forms (see Bergström, 1978, pp. 19–25). It *could* have been washed down-channel from a terrestrial situation, and the uniqueness of the specimen may be seen as evidence of such an origin, although

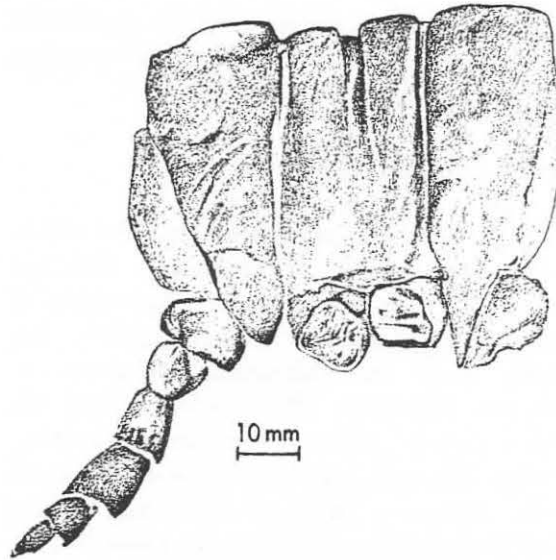


Fig. 1. *Necrogammarus salweyi* Woodward, a large millipede? from the Ludlow of Leintwardine, Herefordshire (after Huxley and Salter, 1859).

the shoreline was many miles distant. Local shallowing did occur and islands may have formed (J. D. Lawson, personal communication), which could give a more immediate origin for such a fossil – if it were terrestrial.

1. Old Red Sandstone Myriapods

More material is available here, but revision is also required. *Archidesmus* and *Kampecaris* (but not *Anthracodesmus* and *Pattonia* – cf. Hoffman, 1969, p.R. 578) are known from much of the Lower Old Red Sandstone of Scotland, probably of Gedinnian age (Westoll, 1977, pp. 72,76), as is also *Kampecaris* from England (Clarke, 1951; Allen, 1977, p. 45). Specimens as old as “Infra-Gedinnian” occur at Stonehaven and as young as Siegenian in Ayrshire (Westoll, 1977, pp. 72, 73). Many of the specimens are decalcified (e.g. *Kampecaris obanensis*, Fig. 4D), and it is not clear whether this is due to pre-moult autolysis, or to diagenesis. Only exceptionally is the heavily calcified exoskeleton preserved as in *Archidesmus macnicoli* (R.S.M. 1891-92-72), and this reveals it to have large paratergal lobes. “Such ‘flat-backed’ millipedes are adepts at widening crevices which tend to split

open along one plane, such as under bark or in layered decaying leaves" (Manton, 1977, p. 357). Others may be rounder-bodied juliform types, e.g. *Kampecaris forfarensis* (R.S.M. 1969.16 – Fig. 4E). Such millipedes burrow into soil and decaying wood by head-on pushing (Manton, 1977, pp. 352–356), rather than by wedging. Both millipedes imply the presence of decaying vegetation and perhaps soils well inland by the early Devonian. Specimens are often found on slabs accompanied by much plant debris.

Their comparative abundance as fossils may be due to the habit of some millipedes of forming subterranean moulting chambers: "hollows in the soil, of material which has passed through the gut, smoothed internally by rocking movements performed by the animal". Others construct subterranean tents of mineral-rich soil, stuck together to form continuous sheets (Heath *et al.*, 1974, pp. 455, 462). The moulting process may take up to three weeks (Kaestner, 1968, p.409), and the chamber serves both as a protection from cannibalistic members of its own species (Evans, 1910, pp. 289–290) and to prevent desiccation. Tropical forms may remain throughout the dry season in such moulting chambers (O'Neill, 1969; Lewis, 1974). Against this habit favouring preservation must be set the fact that most millipedes eat their moults (Cloudsley-Thompson, 1968, p. 45), as well as their own dead (Cloudsley-Thompson, 1949, p. 137).

2. The Rhynie Chert Fauna

This fauna, of Siegenian age (Westoll, 1977, p. 76), has been reviewed by Kevan *et al.* (1975, pp. 392–396), and will only be summarized here. A unique fauna, largely of microarthropods, is known, due to the exceptional preservation of this silicified peat bog. The terrestrial fauna comprises the collembolan *Rhyniella*, a mite *Protacarus*, a spider *Palaeocteniza*, and the trigonotarbid arachnids *Palaeocharinus* and *Palaeocharinoides* (fig. 2). An additional arthropod, *Heterocrania rhyniensis* has been described but is too fragmentary to be interpreted as a chelicerate. Kevan *et al.* (1975, p. 394) note that collembolans are generally herbivorous or saprophagous, and suggest *Rhyniella* fed on soil micro-organisms and spores. Like *Protacarus*, *Rhyniella* might have obtained plant juices through the puncture wounds which disfigure so many *Rhynia* axes. The other arthropods are carnivorous, although Kevan *et al.* (1975, p. 395) were misled by the literature into

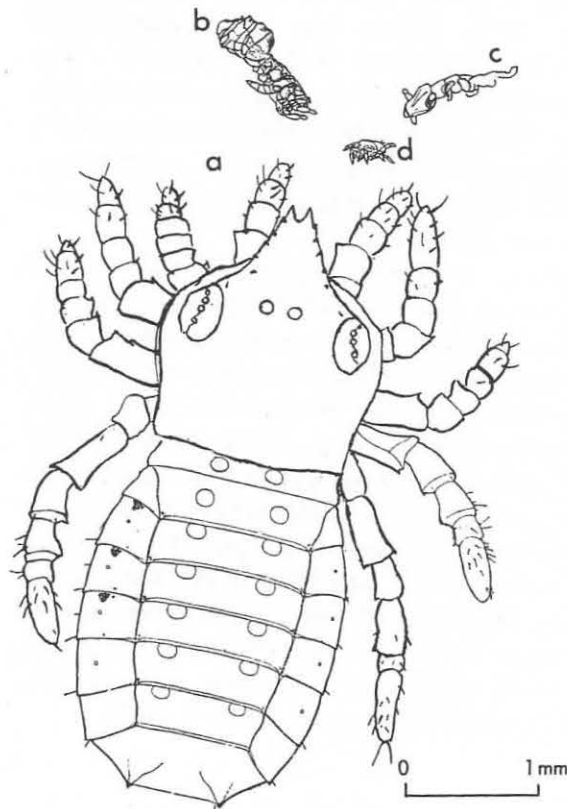


Fig. 2. Representative terrestrial arthropods of the Rhynie Chert to show relative sizes of predator and prey. All to the same scale ($\times 17$ — after Hirst, 1922). (a) A small individual trigonotarbid arachnid *Palaeocharinus* sp. (new reconstruction based on several specimens, with limbs of *Palaeocharinoides* type, eye detail from Hirst and Maulik (1926)). The largest individual known would be twice the size of this page, to the same scale. (b) Possible liphistiid spider *Palaeoecteniza crassipes* Hirst. (c) Collembolan *Rhyniella praecursor* Hirst & Maulik. (d) Pachygnathid mite *Protacarus crani* Hirst.

thinking that they were all small — less than 3 mm long. They suggested that these small predators fed on an unfossilized element of the food web — soft-bodied protozoans and small metazoans. The Hunterian Museum Kidston collection of thin sections shows several vertical sections (Kid. 2405, 2406) across palaeocharinid opisthosomata 6.5 mm broad, implying a total body length of at least 14 mm.

A similar cross-section was illustrated by Størmer (1976, Pl. 9, Fig. 1 – inverted), showing the median ventral projection of the anterior opisthosomal sternite. Such sections also reveal the book-lungs, the earliest unequivocal evidence of a truly terrestrial arthropod. That arachnids of this size existed in the Rhynie Chert is confirmed by a series of almost horizontal sections preserved in the Entomology Department of the British Museum (Natural History), one of which (In 24691) shows practically an entire body measuring 14 mm long. It seems most unlikely that such a large arachnid was even a facultative herbivore (cf. Kevan *et al.*, 1975, pp. 395–396) and it must have preyed upon the Rhynie microarthropods. A normal-sized palaeocharinid is shown to scale in Fig. 2a.

Kevan *et al.*, (1975, p. 396) and Chaloner (1976) suggested that the palaeocharinids found within hollow stems and sporangia (Rolfe, in Kevan *et al.*, p. 396, Pl. 56) were spore-feeders, and associated such feeding with the predatory habit and evolution therefrom. It is possible that the small arthropods were inhabiting these damp, rotted hollows in order to conserve their body moisture – always a problem with terrestrial arthropods – much as do many living land arthropods. They could readily prey upon other microarthropods seeking refuge in such a humid niche, and also evade their larger predatory relatives outside. It is tempting to imagine such small arachnids actually lurking in dehiscid sporangia while the latter were borne upright upon the parent plant (although cf. Kevan *et al.*, 1975, p. 406). Rather than snipping spores, they might have preferred to await the arrival of food in the form of early insect, or other arthropod, visitors to the sporangium for spore-feeding and dispersal (Kevan *et al.*, 1975, pp. 402–406). The large numbers of dismembered fragments seen in such hollows (one such hollow is 14 mm long – B.M. (N.H.) In 24704) may represent the sucked-dry husks of former victims of the dominant preying arachnids. Edwards (1973 and personal communication) has examined *c.* 15 dehiscid sporangia interpreted as being in growth position, both from the alignment of the parent stems (roughly perpendicular to the soil layer) and from the presence of spores in the basal portion only of the sporangium. None of these contains arthropod fragments, which argues against the above interpretation. The relationship between the palaeocharinid spirit level infill and the axis of the *Rhynia* shown by Rolfe (in Kevan *et al.*, 1975, Pl. 56, Fig. 1) indicates that the stem was far from vertical.

Together with the disrupted nature of such Rhynie "straws", this suggests the stems only became occupied by arthropod fragments after they had fallen. That some are also *post mortem* assemblages is shown by B.M. In 38236, a fungus-covered arthropod with its body cavity filled with arthropod fragments, as well as a large fungal resting phase. Finally, the small arachnids so regularly found within stems may only be "spiderlings". Complete individuals occasionally closely accompany one another inside stems (e.g. B.M. In 27756 – Hirst and Maulik, 1926, Fig. 1), and were presumably instantly killed by silification in this biocoenosis. It suggests that they were juveniles since "only during their first instar do the spiderlings of most species stay together". Their behaviour is fundamentally different then, since they are absorbing embryonic yolk filling the mid-gut. By their first moult, they "are able to eat other food and would kill each other, as they do in captivity, but for the new and powerful inner urge to disperse" (Petrunkevitch, 1952, p. 109).

Although difficult to interpret, and known only from the holotype, *Palaeocteniza* appears to be a mygalomorph spider, a group known also from the Carboniferous. This group includes the trap-door spiders today, and the living *Liphistius*, thought to be a "living fossil". *Liphistius* burrows have about eight long, straight threads radiating downwards from the rim of the burrow, which serve as trip-wires indicating the passage of crawling invertebrates (Bristowe, 1975, p. 115). Pit-fall studies indicate how abundant such prey is (F. R. Wanless, personal communication), and the spider has only to rush out and overpower the victim. Predation by such primitive hunting spiders (and also early amphibians and insects? – Smart 1967, p. 116) upon early wingless insects may have been one of the main factors leading to the evolution of insect wings. "When their prey took to the air to escape, spiders evolved aerial webs as a means of trapping it in flight" (Cloudsley-Thompson, 1968, p. 186; 1975, p. 192). This escape by flight may well have taken place under the impetus given by the advent of late Devonian trees, which not only provided a launching pad, but also a new, tree-top ecosystem (Kevan *et al.*, 1975; Scott, Chapter 5 of this volume). It is worth recalling that the high canopy of modern tropical rain-forests contains a little-known but large biomass not only of insects, but also of large mygalomorph and web spiders, as well as millipedes (Elton, 1973, p. 91). It seems likely that many arachnid predators pursued their insectan

prey up trees as they evolved, and that a high-canopy ecosystem evolved during the Upper Devonian–Carboniferous. This may have been simpler and less sophisticated than the present tropical forest ecosystem, which is the fragile end-product of evolutionary interaction between predator and prey (Elton, 1973).

Crowson (1970 and personal communication) believes that both the mite and collembolan of the Rhynie Chert are so indistinguishable from living forms, that they must be Tertiary or later contaminants. According to Zakhvatkin (1952, p. 24) the Rhynie mite *Protacarus* can be placed in one of the modern families Alycidae, Alicorhagiidae or Nanorchestidae. Other workers have commented on this remarkably modern aspect of the collembolan, although the mite is often said to be “primitive” (Kevan *et al.*, p. 394). Crowson believes that this view of the mite is based on circular reasoning since the “primitiveness” of the families of pachygnathid mites, with which the Rhynie fossil is compared, are regarded as such by acarologists since they are known to occur in the Rhynie Chert! A primitive mite should resemble the segmented *Opilioacarus* instead of the unsegmented Rhynie form. It is worth recording that Crowson came to this view as a result of a section of Rhynie Chert referred to him by the late John Walton. It contained a thysanopteran insect nymph which Crowson was able to identify with a living form, that must have crawled into a crevice in the chert. He believes it is significant that the collembolan and mite are small habitual crevice seekers. Rapid examination of relevant material at the British Museum (Natural History) shows little optical discontinuity between the silica containing the mite and its matrix. It is conceivable that mobilization of silica could lead to such contaminants being preserved, although one would expect to be able to see evidence of such diagenesis in the rock. Some acarologists do consider this group of mites to be “primitive” on other grounds, however. Thus Hirst (1922, p. 458) noted the group was regarded as primitive in his original description of the Rhynie form, and D. Macfarlane (personal communication) points out that the setation and other characters are truly “primitive”. The ancient origin of the group and its extremely conservative nature is also borne out by the discovery of a Jurassic mite attributable to the *living* genus *Hydrozetes* (Sivhed and Wallwork, 1978). Furthermore “nothing like *Protacarus* exists at present” according to Vitzthum (Petrunkevitch, 1953, p. 57).

Dubinín (1962, pp. 462–464) has created an additional two genera to accommodate the variety of form shown by the Rhynie mites. All the families to which these mites are referred characteristically inhabit environments subject to alternate wetting and drying (J. B. Kethley, personal communication). Such mites today are fungivores or algal feeders, as far as is known, but Kethley points out that the mouthparts may not be diagnostic of feeding habit.

3. The Alken Fauna

This fauna, from Alken an der Mosel in Germany, is of Lower Emsian age (Størmer, 1970–1976). In addition to a marine fauna, the locality yields brackish, amphibious and terrestrial forms. An extensive Hunsrück Island, fringed by tidal flats with occasional lagoons, existed in the Lower Devonian of the Mosel–Rhine area. Alken represents one of these elongate, land-locked lagoons, communicating by channels with the sea at high tide. The lagoon was surrounded by psilophytes and other land plants, although the suggestion that some of them were partially submerged to create a “mangrove” ecosystem (Størmer, 1976, pp. 127–133) is no longer accepted by palaeobotanists (Edwards, Chapter 4 of this volume). Such a situation was suitable for the preservation of terrestrial and amphibious faunal elements, and these may be summarized as follows.

There are at least three terrestrial forms at Alken – the arthropleurid myriapod *Eoarthropleura*, and the trigonotarbid arachnids *Alkenia* (Fig. 3b) and *Archaeomartus*. An additional arthropod fragment was doubtfully referred to the Carboniferous spider *Archaeometa* (Størmer, 1976, pp. 115–116).

Eoarthropleura is the earliest arthropleurid known (the Siegenian *Bundenbachiellus* is now thought to be based on distorted specimens of *Cheloniellon* – Stürmer and Bergström, 1978). It probably lived among and fed off decaying and damp plant litter in the psilophyte groves. With its relatively longer limbs and greater trunk flexibility coupled with smaller size, *Eoarthropleura* was probably more agile than the Carboniferous *Arthropleura*. It may have been able to twist its way through the dense psilophyte stands, rather than forcing a passage like *Arthropleura* (Briggs *et al.*, 1979, p. 288). *Alkenia* and the little known *Archaeomartus* approach the size of the largest palaeo-

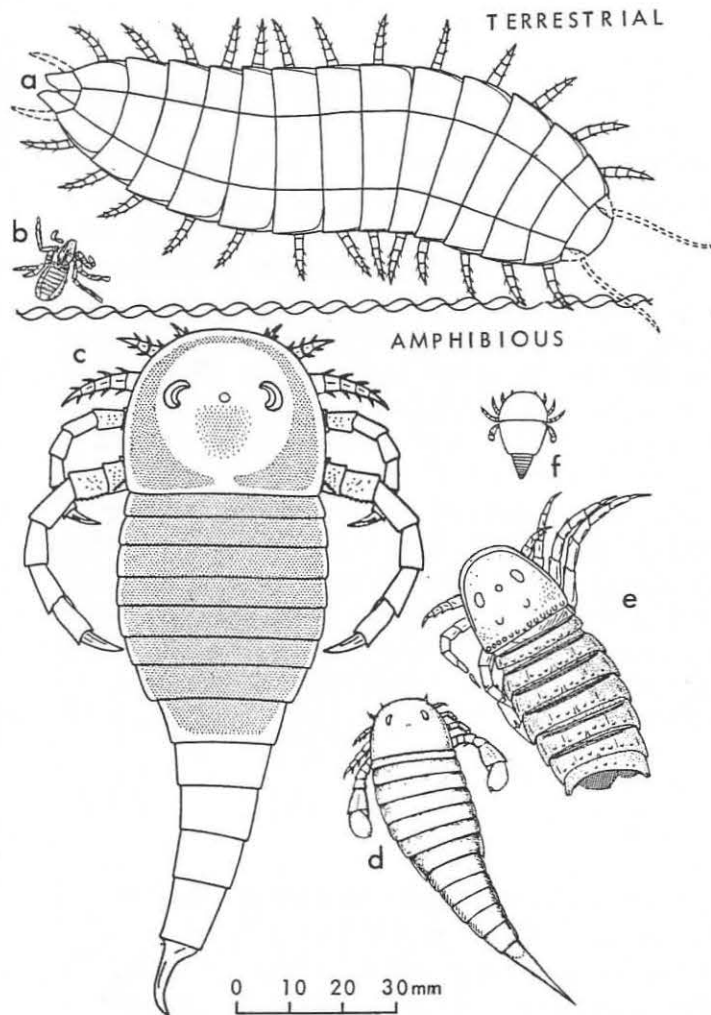


Fig. 3. Representative elements of the Alken amphibious and terrestrial arthropod fauna.

(a) Arthropleurid myriapod *Eoarthropleura devonica* Størmer (limb phasing not corrected – v. Briggs *et al.*, 1979).

(b) Trigonotarbid arachnid *Alkenia mirabilis* Størmer.

(c-e) Eurypterids. (c) Drepanopteroid *Moselopterus ancylotelson* Størmer

(d) Hughmillerioid *Parahughmilleria hefteri* Størmer. (e) Rhenopteroid *Rhenopterus macrotuberculatus* Størmer (body of *R. diensti* restored to suggest appearance).

(f) Chasmataspidid xiphosuran *Diploaspis casteri* Størmer.

Natural size, after Størmer (1936, 1969, 1970, 1972, 1973, 1974, 1976), with permission of the author and the *Senckenbergische Naturforschende Gesellschaft*.

charinids mentioned above from the Rhynie Chert. They probably led a similar, predatory mode of life.

Many other arthropods from Alken have been suggested by Størmer to be more or less amphibious (Fig. 3c-f), since they are now known to be pseudotracheate. Many of the eurypterids may have been able to leave the water and move into the Alken swampy hinterland. Even those such as *Parahughmilleria* that were well adapted for swimming may have used their paddles for crawling along, as the existence of a Silurian eurypterid trail suggests (Hanken and Størmer, 1975). Forms without paddles, such as *Drepanopterus*, *Alkenopterus*, *Moselopterus*, *Willwerathia* and *Rhenopterus* would be better adapted for such excursions. They were probably more terrestrial than the living *Limulus*, which can spend a considerable time on shore or on the river banks (Størmer, 1976, pp. 137, 143). The small chasmataspidid xiphosurans *Diploaspis* and *Heteroaspis* (Fig. 3f) had a ventral shield protecting the gills from desiccation. They too may have crawled about in the psilophyte thickets bordering the lagoon. The Alken scorpion *Waeringoscorpio* possessed gills and is considered to have been completely aquatic (Størmer, 1976, pp. 129, 151).

4. Other Devonian Faunas

Faunas probably exist elsewhere in the geological record, but have yet to yield sufficient material for description. The early Upper Devonian Escuminac Formation, for example, contains "a fragment tentatively identified as *Arthropleura*", in addition to many fish and plants, conchostracans and a scorpion (Schultze, in Carroll *et al.*, 1972, p.94). Work with early fossil plants has shown how successful the study of such fragmentary fossils can be, and it is therefore important that all such scraps be retained in collections for future investigation. A third Devonian terrestrial arthropod fauna has recently been discovered in the Givetian of New York State by P. Bonamo and D. Grierson.

5. Trophic Level Succession.

With the emergence of plants in the Silurian, the first trophic level, producers, was established on land. The second trophic level, primary

consumers (herbivores) probably emerged immediately thereafter, as shown by Gedinnian myriapods. It is possible that third and fourth trophic level consumers (carnivores and predators) succeeded each other in time, producing a trophic level succession with time – and this had probably happened by the Siegenian, as the Rhynie fauna indicates. This model is probably too simple to be very fruitful, although it can indicate the absence of members of particular food-chains from fossil assemblages. It has already been suggested above, for example, that the first primary consumers accompanied or even locally preceded the producers inland.

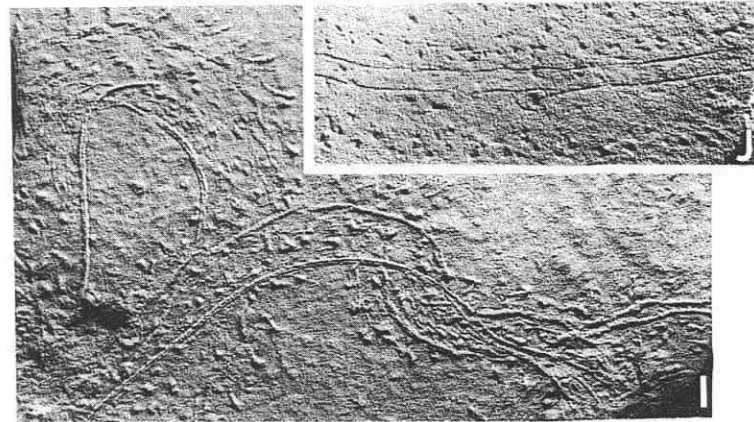
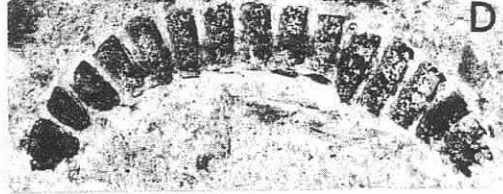
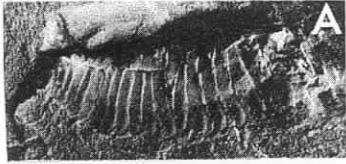
TRACE FOSSILS

Trace fossils yield potentially important evidence of early terrestrial life, since they are known to be autochthonous, unlike many body fossils. They also give direct evidence of habit and behaviour of early terrestrial organisms, and indirect evidence of their morphology. Thus, the Devonian trail *Paleohelcura* (= *Beaconichnus*) *antarcticum* (Gevers) may provide evidence for the amphibious nature of early large scorpions (Briggs *et al.*, 1979, p. 279) such as *Brontoscorpio* (Kjellesvig-Waering, 1972) or *Praearcturus* (Rolfe, 1969). This also exemplifies the ambiguity of trace fossil evidence, since *Paleohelcura*-type trackways are also left by jumping thysanuran insects (Manton, 1977, p. 332, Fig. 7.13h).

1. Ichnocoenoses

Müller (1975) has reviewed aspects of the ichnology of terrestrial arthropods. Several Palaeozoic assemblages are known, e.g. the Orcadian Middle Devonian (N. H. Trewin, personal communication) and Rotliegenden (Boy, 1976), but little interpretation is possible in the absence of relevant neoichnology. One promising assemblage comprising many hundreds of specimens has been collected from the Lower Old Red Sandstone of Dunure, Ayrshire (Smith, 1909), and is being re-studied by Dr J. Pollard and myself.

The siltstone and mudstone of this deposit occur as baked, laminated and occasionally penecontemporaneously upended sediments, which require investigation: they are either aeolian or from lava-surface wash. Most of the trace fossils of this deposit are of arthropod origin,



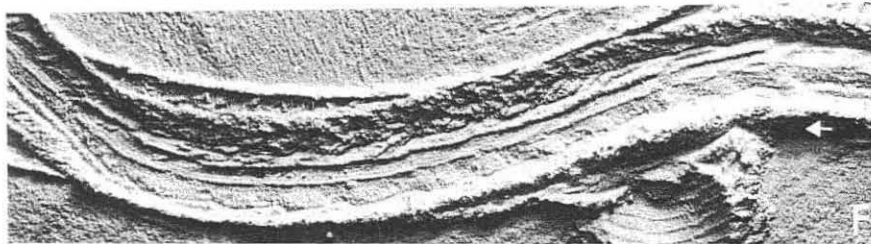
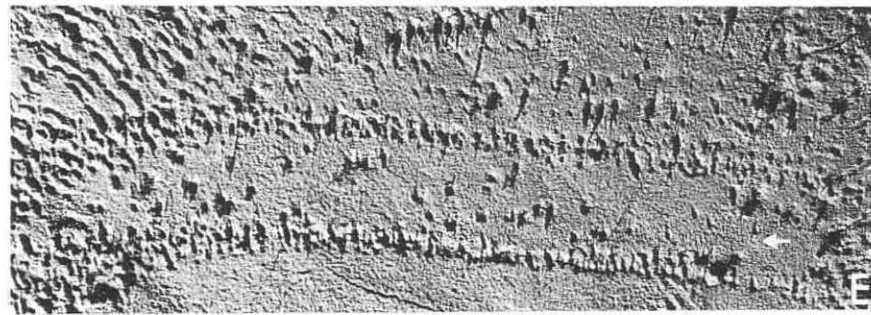
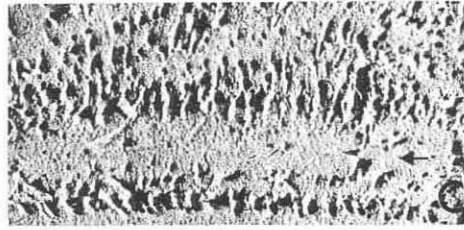
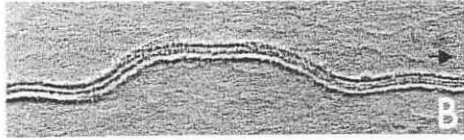
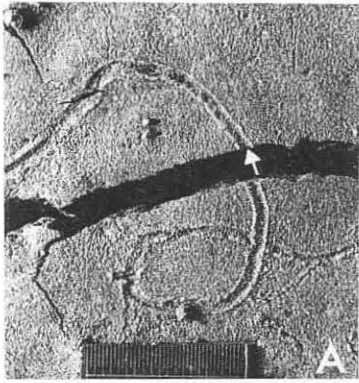
and millipede traces do appear to be present (Fig. 4). The unique specimen of the body fossil *Kampecaris tuberculata* Brade-Birks (1923) comes from this deposit, formed in the Old Red temporarily desert environment (Bluck, 1978).

2. Experimental Neoichnology

Manton (1977) has done much work on locomotion of arthropods, but her arthropods left traces on smoked plates, and these records are not readily comparable with traces left in soft substrates. A few references are available (Chamberlain, 1975, p. 436; Demoor, 1890, 1891; Fiori *et al.*, 1966; McKee, 1947) but emphasis on indigenous non-marine aquatic traces meant that few terrestrial arthropods were dealt

Fig. 4. Siluro-Devonian millipedes and trackways. (A) Possible millipede from Fish Bed Formation, Wenlock/Ludlow, Hagshaw Hills, Lanarkshire. R.S.M. 1970.2. $\times 2.0$. (B) Holotype of *Archidesmus loganensis* Peach, *Jamoytius* horizon, Llandovery/Wenlock, Lesmahagow. I.G.S. (E) 5974. $\times 2.0$. (C) Calcareous, flat-backed millipede, *Anthracodesmus macconochiei* Peach, Lower Carboniferous, Lennel Braes, Coldstream (resembles the Lower Old Red Sandstone *Archidesmus macnicoli* Peach). I.G.S.(E) 2176. $\times 6.5$. (D) Decalcified millipede, *Kampecaris obanensis* Peach, L.O.R.S., Kerrera, Oban, Argyll. I.G.S.(E) 10385. $\times 4.0$. (E) Round-bodied? millipede, *Kampecaris forfarensis?* Peach, Cairnconnan Series, L.O.R.S., Mirestone Quarry, Angus. R.S.M. 1969.16. $\times 3.0$.

(F-K) Lower Old Red Sandstone millipede? trackways from Dunure, Ayrshire, all $\times 1.0$. (F) *Stiaria simplex* Smith, a typical, simple millipede trackway. I.G.S.(E) 13480. (G) Holotype of *Narunia lunanova* Smith, showing median structures possibly left by sternites and eversible vesicles. I.G.S.(E) 13478. (H) Holotype of *Keircalia multipedia* Smith, showing multiple grooves caused by "miring" of posterior limbs, which are then dragged behind body. I.G.S.(E) 13463. (I) *Stiallia/Danstairia* trackway with grooves possibly made by terminal locomotor? filaments, postulated to exist in both early myriapods and hexapods (Müller, 1975, p. 81; Sharov, 1966). H.M. 1082A. (J) *Danstairia vagusa?* Smith, trackway with posterior limbs only occasionally touching substrate. Such behaviour recalls the "posterior antennal" role of the last pair of legs, which are trailed backwards on the ground, in the blind geophilid centipedes. Such animals living in cramped surroundings are able to move backwards as well as forwards, without turning the body as a whole (Lawrence, 1953, pp. 87, 89). I.G.S.(E) 13479. (K) *Danstairia kennediea* Smith, trackway with central groove, perhaps made by head (cf. Fig. 5F,G). I.G.S.(E) 13481.



with in the recent volume by Frey (1975), and millipedes scarcely warrant a mention. Since the millipedes are the earliest known terrestrial animal fossils, their trace fossils are likely to be widespread.

Despite much recent work, relatively little is known about the kinds of traces left by many living arthropods, particularly the nature, limits and origin of their variability. A few experiments recently conducted by Miss Elaine Walker and myself at Glasgow University only serve to reveal the extent of the problem. As expected (Müller, 1975, p. 82) any one arthropod's trace will vary with many factors: type and size of organism, habit and gait, substrate grain-size, inclination and moisture content, and temperature (Müller, 1975, p. 81).

3. Traces of Modern Millipedes

On a wet mud depth of unconsolidated substrate the small millipede *Julus* leaves a broad simple groove (Fig. 5A) caused by body drag, which would yield a trace fossil resembling *Gordius* (cf. Boy, 1976, Fig. 41b). On a dry muddy silt substrate, a trail of two or three distinctly incised grooves is left (Fig. 5B; cf. McKee, 1947, p.27), comparable with *Aulichnus* or *Beaconichnus darwinum* (Gevers). The large (25 cm long) burrowing millipede *Scaphiostreptus* – morphologically very like *Julus* – does not leave a simple trail in wet mud, like the small *Julus*, but a complex trackway (Fig. 5C,E). These may be compared with the many myriapod ichnogenera listed by Briggs *et al.* (1979, p. 288) and with *Beaconichnus gouldi* (Gevers). On a dry substrate the head of *Scaphiostreptus* bulldozes a deep median groove (Fig. 5F) in advance of its trackway – which differs from that left in the wet sediment. It is not known whether this groove is made deliberately, to create a tunnel to ensure the limbs and spiracles are not clogged by sediment. It may only be inadvertent since the

Fig. 5. Trackways of living myriapods (see text for detail). All natural size, juliform millipedes, except (D) which is a centipede. Arrows indicate direction of travel. (A,B) *Julus sp.* c. 25 mm long; (A) wet mud substrate, (B) dry powder substrate. (C, E-G) *Scaphiostreptus seychellarum*, c. 250 mm long; (C, E) wet mud substrate, (F,G) dry powder substrate, (F) thick substrate, (G) thin substrate, but head groove present; individual tracks discernible on right of trackway, but obliterated on left side by trailing limbs (cf. Fig. 4K). (D) *Geophilus sp.*, dry powder substrate.

darkling beetle *Blaps* also makes a groove, but with the tip of its abdomen, in dry sediment (Müller, 1975, Taf. 3, Fig. 1), which it does not do under other conditions (Graber, in Chamberlain, 1975, p. 436, Fig. 19.1). When the unconsolidated substrate is kept thin, so that *Scaphiostreptus* can support the head and body well above the substrate during locomotion, no median groove results (Fig. 5G).

4. *Beaconites*

Müller (1975, pp. 82–83, Pl. 1, Fig. 3) has described Recent surface trails superficially resembling the smaller Devonian trails attributed to *Beaconites*. These were made by beetles climbing up steep, blown sand banks. Gravitational slumping of individual transverse tracks produces a structure resembling the supposed stuffed-burrow menisci of *Beaconites*. It is worth speculating whether longer *Beaconites* originate from desert-inhabiting arthropods which construct a burrow system, rather than from early amphibians (Pollard, 1976). Menisci might then be formed by passive slumping, at intervals determined by the arthropod's footfalls. Such slumping should only occur in steeply inclined regions of the burrow system, and existing evidence from *Beaconites* (Pollard, 1976) may be sufficient to rule out this hypothesis. It is a tempting notion, however, since arthropods (like many other animals) are known to burrow in the desert seeking increased relative humidity and avoiding extremes of temperature, only emerging at optimal temperatures (Cloudsley-Thompson, 1975a, p. 80; Müller, 1975, p. 81). Proof could come from the tracing of the burrow structure into a surface trace, a situation observed in the Recent desert cockroach *Arenivaga* (Edney, 1977, pp. 198–200, Fig. 91).

CARBONIFEROUS FAUNAS

By the Upper Carboniferous, terrestrial faunas, at least of arthropods, had evolved explosively. It would be beyond the requirements of this volume to review these in detail, and very little modern work is available to permit such a review. Coal Measures invertebrate faunas were reviewed by Calver (1968), although the emphasis there is on aquatic forms. The evidence will be briefly reviewed on a systematic

basis, omitting some major arthropod groups which are dealt with subsequently. Only the most terrestrial *in situ* fauna, that of Joggins, will be examined closely.

1. Insects

The earliest insects are known from two specimens in the Namurian of Poland and Pennsylvania (Orders Protorthoptera and Miomoptera – although one of these records may rather be Palaeoptera – Carpenter, 1977, pp. 65–66). Very many orders are known from the Upper Carboniferous, although part of the previous picture of this radiation was a monographic burst. Carpenter (1977, p. 63) has stated that of the 52 extinct, mainly Palaeozoic, orders named, only nine are acceptable in yielding the minimal criteria of fore and hind wings, heads and mouthparts: the remainder must remain order unknown. Nevertheless such insects show highly specialized adaptations by that time (Carpenter, 1971): more orders than in the existing fauna had mouthparts for piercing and sucking up liquid food (see also Kukalova-Peck, 1980); many had ovipositors for depositing eggs in particular substrates, and even cockroaches must have laid eggs singly at a considerable depth in soil, decaying vegetation or soft plant tissue (Carpenter, 1971, p. 1244). Of particular interest is the discovery of eye-spots on the Upper Carboniferous insect *Protodiamphipnoa* (Carpenter, 1971, p. 1250, Figs 13–15). This is probably a warning response, since the insect has raptorial front legs and “when one is poisonous, noxious tasting or otherwise disagreeable or dangerous, it pays to advertise . . . It seems clear that [such] aposematic coloration evolved in response to vertebrate predators” (Matthews and Matthews, 1978, pp. 322–323). Insectivorous reptiles, as well as arachnids (see the section on the Rhynie Chert), probably played a large part in the coevolution of insects (Olson, 1976, pp. 6–9).

2. Arachnids

The arachnids show a similar explosion in the Carboniferous. Most of the existing arachnid orders are known from this period, and their fundamental evolution was completed by the Carboniferous – there has been little since (Petrunkevitch, 1953, p. 115). Of 16 orders

known from the Carboniferous, 11 survive to the present day (Petrunkevitch, 1955; Savory, 1977a, p. 97).

"Arachnids today comprise the dominant invertebrate carnivores on land" (Manton, 1977, p. 15), and the same probably applied in the Carboniferous as well. The most familiar group of arachnids is the spiders, which are preyed upon today not only by each other, but also by "... toads and frogs, birds, shrews, wasps and centipedes. Invertebrate enemies are very much more numerous, and probably destroy larger numbers of spiders than do vertebrates" (Cloudsley-Thompson, 1968, p. 210). Carboniferous spiders are broadly divisible into the older groups of liphistiomorph and mygalomorph spiders, and the more modern arachnomorphs. The habits of the first group have already been referred to in the discussion of the Rhynie Chert spider. It is probable that the Coal Measure forms wove simple silk traps between aerial fronds of plants, as well as trapping early wingless insects and nymphs on the ground. Details of the spinnerets of the Carboniferous arachnomorph spiders are unknown (Petrunkevitch, 1953, p. 100), and spiders with the ability to spin the more efficient orb-webs for trapping insects are not known until the Tertiary. This may partially account for the instant success of the insects in their new milieu — they attain their greatest diversity in the Permian (Carpenter, 1977), and aerial vertebrate predators do not appear before the Mesozoic, as gliding lizards in the Triassic.

Turning to other groups of arachnids, the modern vinegaroon, practically unchanged from the Carboniferous *Prothelyphonus*, eats insects, centipedes, woodlice, worms and slugs (Cloudsley-Thompson, 1968, p. 146). Living solpugid arachnids kill and eat insects, spiders, scorpions and lizards using "the most formidable jaws in the animal world" (Savory, 1977a, p. 236). In turn they are preyed upon by lizards and other reptiles, as well as by birds and mammals (Cloudsley-Thompson, 1968, p. 116). They are the most active of living arachnids, and the most independent of atmospheric moisture (Lawrence, 1953, p. 139). One fossil solpugid is known, *Protosolpuga* from the Westphalian of Mazon Creek.

Almost nothing is known of the enemies of "living fossil" arachnids such as the Ricinulei. Doubtless they are preyed upon today by frogs, toads, lizards, small mammals, spiders, centipedes and various insects, as are most living arachnids, including the Opiliones (Cloudsley-Thompson, 1968, p. 176) which also occur in the Carboniferous.

Amphibians and reptiles figure prominently among arachnid predators, as they probably did in Carboniferous times. Such prey is often inconspicuous and retiring, and hence may not have occupied more than a small proportion of tetrapods' diet.

Plump ricinuleid arachnids live today much as their Carboniferous ancestors must have done, skulking motionless under rotten logs, behind leaf fronds on wet mud and in wet leaf-axils (lamine leaf-bases are known since the Devonian *Archaeopteris*), emerging only to catch and eat living spider and insect prey (Cooke 1967; Pollock, 1966, 1967). They illustrate very well how such terrestrial arthropods take advantage of plants to control their environment for them. By remaining in the shade of large leaves – the laminate leaf evolved in the Carboniferous – such arachnids manage to keep their temperature down in tropical climates. Plants act as wind-breaks, with locally humid niches, so arachnids are able to conserve their moisture which otherwise would be lost by transpiration across their cuticles – they lack the wax layer typical of many terrestrial arthropods.

3. Mazon Creek

Much work remains to be done on the palaeoecology of the arthropod fauna at this Westphalian D locality. Of 170 invertebrate genera listed from Mazon Creek by Horowitz and Richardson's 1978 computer print-out, no less than 137 are terrestrial arthropods (21 of them non-scorpionid arachnids, 99 insects). At species level, too, 85% of the Braidwood Mazon Creek fauna has been found to be terrestrial (Johnson and Richardson, 1966; Richardson and Johnson, 1971). All four arachnid orders found at the contemporaneous locality of Nýřany, Czechoslovakia, also occur at Mazon Creek, along with seven other orders. Two of the eight Nýřany genera also occur at Mazon Creek. This is only weak evidence supporting the theory of commonality of terrestrial faunas of this time, derived from study of the tetrapods (Milner and Panchen, 1973; Panchen, 1977). The absence of *Arthropleura* from Nýřany, although it is widespread elsewhere in the Euramerian flora belt, suggests that Nýřany is insufficiently rich in terrestrial arthropods to permit adequate comparison of Europe with North America. A comparison of Mazon Creek with the more arachnid-rich British Midlands localities might be more profitable. At lower taxonomic levels, Petrunkevitch (1913, pp. 23-

26) believed the North American fauna was distinct from that of Europe, and developed on different lines.

A variety of myriapod taxa is present at Mazon Creek.

4. Joggins

This celebrated Westphalian B locality is important in preserving a terrestrial fauna *in situ* within *Calamites* and *Sigillaria* stumps. It has been authoritatively reviewed by Carroll *et al.* (1972, pp. 64–80) and the arthropods have been discussed by Briggs *et al.* (1979, pp. 286–287). The hollow stumps were buried, creating pit-falls which are thought to have sampled the truly terrestrial fauna. “With the exception of one or two coelacanth scales (which may have been someone’s dinner) no fish are known from the stumps, nor are there any strictly aquatic amphibians” (Carroll *et al.*, 1972, p. 67). Besides the land snail *Dendropupa* (see Section 5 “Snails”), the remaining invertebrates are all arthropods. Eight millipede species have been recorded as abundant in the trunks, and millipedes may well have sought out tree stumps both as a damp refuge, and as food substrate. In turn, they were preyed upon to some extent (their abundance suggests not greatly – R. L. Carroll, personal communication) by the tetrapods, since millipede somites (and other cuticles) are recorded from their coprolites (Dawson, in Scudder, 1895). Two arachnids are known, the anthracomartid *Coryphomartus triangularis* (Petrunkevitch) and the whip-spider *Graeophonus carbonarius* Scudder (Petrunkevitch, 1913, pp. 69, 101; 1953, pp. 60, 99). These doubtless came from tree-trunks (R. L. Carroll, personal communication). Many fragments of eurypterid cuticle occur, and these can be compared with *Dunsopterus*, *Hibbertopterus* and *Vernonopterus* (C. D. Waterston, personal communication). Dr J. Dalingwater has confirmed the eurypterid nature of the cuticle by SEM, and compares the cuticular microstructure with that of *Mycterops*? (Dalingwater, 1975). How did these eurypterid fragments enter the hollow stumps? Were they carried there by predatory tetrapods, like the coelacanth scales? Or did eurypterids fall into, or seek out, the pits whilst crawling about the new land surface? All the eurypterids mentioned are morphologically unusual forms which characteristically occur

incomplete elsewhere, and are practically confined to non-marine localities. Or, finally, were they washed in by flooding of this "bayou" country, giving mixed aquatic and terrestrial biotae, in death if not in life, as K. E. Caster suggests (personal communication)? In favour of this explanation is Woodward's (1918, p. 464) point, that the stumps are occasionally found with *Spirorbis* ("more characteristic of swamp facies"—Calver, 1968, p. 163) attached both to outside and inside of the "bark". Without the most detailed palaeoecological study of a stump, it is impossible to decide this point, but the overwhelmingly terrestrial ecology of the rest of the fauna, stressed by Carroll *et al.* (1972), leads one to favour the second explanation here.

5. Snails

The earliest land snails are known from the Carboniferous, although this had been denied (Knight *et al.*, 1960). They have been reviewed by Solem and Yochelson (1979): *Dendropupa* from Joggins and Poland, *Anthracopupa* from the Little Captina Limestone of the Dunkard Basin (Yochelson, 1975) and the British Stephanian (Calver, 1968, p. 155), and *Dawsonella* from Illinois. Other genera are known (e.g. *Maturipupa*), but there is less agreement about their pulmonate nature and this also applies to earlier records. Solem and Yochelson suggest that *Dendropupa* lived in the tree-trunk base debris of the Joggins forest. In modern forests similar snails inhabit the buttress and tangled root litter accumulations of large trees. The elongate form of the shells is consistent with their being climbers on such vertical surfaces, rather than creepers along horizontal substrates (Cain, 1977). Such snails would doubtless have formed part of the diet of the contemporary arachnids and other carnivorous arthropods.

6. Worms

No truly terrestrial worms are known from the Palaeozoic (Clark, 1969). Aquatic oligochaetes probably preceded terrestrial ones (S. Conway Morris, personal communication) and the earliest record is the Carboniferous *Pronaidites*. A possible terrestrial oligochaete from the Carboniferous has been illustrated by Zangerl and Richard-

son (1963, p. 128, Pl. 21). Fossil nematodes infest the body of the Lower Carboniferous *Gigantoscrapio* (Størmer, 1963) but these are probably aquatic.

WATER BALANCE AND SIZE

“The arthropod level of organisation is highly successful for land life, and a large part of this success may be put down to the arthropods’ effective water balance mechanisms which permit rigorous conservation while allowing for rapid elimination of excess water when this is necessary” (Edney, 1977, p. 244). There is no simple correlation between arthropod group and cuticular permeability to water: the correlation is rather with ecology — desert scorpions show the lowest permeability of any arthropod.

Size is another important factor, and animals such as desert scorpions that combine low permeability with large size are well adapted to withstand desiccating conditions for long periods (Edney, 1977, pp. 57–60). It is tempting to suggest that the several parallel and iterative trends toward gigantism in fossil arthropods — in scorpions, eurypterids, millipedes, arthropleurids and insects — are manifestations of this relationship. Some of them may reflect successive attempts at terrestrialization by various arthropod stocks. Some of these arthropods may have had thicker cuticles than the fossil record suggests and this may have been one way of reducing cuticular permeability. Thus, a Westphalian arthropod cuticle found in a borehole core by Dr M. Calver superficially resembles bone, is 1.3 mm thick, but locally reaches as much as c. 8 mm thick.

A similar relationship between size and cuticular permeability has been noted by Carroll (1977, p. 419) in Palaeozoic amphibians, which are large and covered with overlapping scales. Modern amphibians which depend on cutaneous gas exchange are of small size, and restricted to damp environments. The latter also applies to many terrestrial arthropods. As Hinton (1977, p. 73) has pointed out, since the oxygen molecule is larger than the water molecule, any membrane for oxygen transfer will leak water. Respiratory membranes are wet because water leaks through them, not because a water film assists respiration. On the contrary, such a film greatly inhibits the rate of oxygen diffusion. Insects and some arachnids are the only arthropods to deal successfully with the incompatible

demands of dry environments. They do this by oxygen- and water-proofing their cuticles with a continuous fatty-acid layer, and at the same time invaginate an enormous surface area as tracheae for respiration.

EURYPTERIDS

Recent work on the respiratory structures of eurypterids by Størmer (1976), Waterston (1975) and Wills (1965) has culminated in the view that the "eurypterid gill tract might have acted both as gill and pseudotrachea" (Størmer, 1976, p. 143). This discovery was made on one of the most aquatically adapted eurypterids, *Baltoeurypterus*, although similar structures have also been found in the larger more amphibious-looking *Tarsopterella*. It implies that "several eurypterids at least might have been able to leave the water and stay on land for shorter or longer periods. They may have been able to remain above the supra-littoral zone, and thus be more terrestrial in their habits than the Recent *Limulus*" (Størmer, 1976, p. 143). Such amphibious eurypterids probably lived on sandy and muddy beaches, and in the early plant thickets on the land beyond. Like modern *Limulus* they probably burrowed, only shallowly, for worms and molluscan prey (Manton, 1964, p. 35) and, like Recent land hermit crabs, fed on seaweed and other plant debris, such carrion as was available and sick members of their own species (Kaestner, 1970, pp. 329-330).

1. Gill-tracts

Størmer (1976, p. 142) noted the similarity of the microstructures of the *Baltoeurypterus* gill-tract to similar structures in some insects and land isopods. He suggested that they might serve to trap air or prevent clogging of the fine respiratory passages in insects, isopods and thus eurypterids. The remarkable similarity of these structures to those of the plastron – a gaseous gill of insects and mites, formed by the trapping of a thin layer of air over areas of the cuticle (Edney, 1977, p. 215) – has been pointed out elsewhere (Rolfe, 1980). Such a plastron could conceivably have formed the normal eurypterid respiratory structure, although in modern aquatic arthropods it is only used as such by small forms. It is commoner in living terrestrial arthropods, to overcome the risk of drowning: "To be submerged in

water for several hours or even days is not a rare or isolated event, but a normal hazard of the environment" (Hinton, 1971a, p. 1185; 1977, p. 72). This would imply that the eurypterids were habitual air breathers. In other forms, however, the plastron is hydrophilic to combat desiccation, and this may have been its purpose in eurypterids.

2. Mesosomal Enlargement

In the light of this new, amphibious view of eurypterids, the enlargement of the first two mesosomites in *Woodwardopterus*, and of at least the first (genital) mesosomite in *Mycterops*, may be significant. It may represent an adaptation to accommodate larger book-lungs or pseudotracheae, to enable better respiration on land (Rolfe, 1980).

3. Limbs and Size

There seems to have been a trend in the Old Red Sandstone for various eurypterids to increase their size (e.g. *Tarsopterella*, *Ctenopterus*, *Pterygotus anglicus*). Such a size increase would serve to reduce desiccation loss, by increasing the surface to volume ratio (see the section "Water Balance and Size"), and would have been selectively advantageous to those eurypterids that were to survive the periodic droughts of that environment. As with crossopterygians (Romer, 1966, p. 86; Størmer, 1976, p. 143), individuals that survived may have evolved adaptations such as the stylonuroid walking limbs in order to migrate to the nearest available waterhole, rather than for terrestrial ambitions. With the advent of the less rigorous conditions of the Carboniferous, the need for such an adaptation would have waned, but large stocks may then have proved pre-adapted to move onto land. Such forms are only known from fragments at present – as their palaeoecology would demand – and include e.g. *Vernonopterus*, *Dunsopterus*, *Hibbertopterus* and *Woodwardopterus*, and probably *Mycterops* (see Waterston, 1957, 1968). These forms all have relatively thick cuticles (e.g. Dalingwater, 1975), an adaptation which would confer great strength to the limbs.

Several of the presumed amphibious eurypterids had long, stylonuroid-like legs. Størmer (1974, p. 399) has suggested that the longer posterior legs of *Moselopterus* may indicate that the opisthosoma was held up at quite a high angle, as in scorpions, so that the

telson could be used as a weapon to kill prey held by the anterior prosomal appendages. Such long legs would also enable their owner to "stilt", like some modern scorpions. In this behaviour pattern the legs are straightened to lift the body clear of the ground. Increased circulation of air around the stiling animal enables it to maintain a constant body temperature, whilst the environmental temperature rises rapidly (Alexander and Ewer, 1958). Above a certain temperature range, stiling no longer protects the animal, and the animal would need to seek cover: in the case of Joggins, perhaps a hollow tree stump refuge? It may be objected that, as in the giant Japanese crab *Macrocheira*, such legs would be insufficient to support the body weight in air. This is doubtless true of an extreme form such as *Ctenopterus*, although functional morphological investigation is required. *Hibbertopterus*, however, has short, stubby limb segments and is noticeably hexapodous: it would seem well adapted for movement on land despite its bulky opisthosoma. Its anterior limbs are modified as sensory appendages (Waterston, 1957). The limb form of most other Carboniferous genera is unknown in detail. *Woodwardopterus* has remarkable *Limulus*-like pushing spines (Manton, 1964; 1977, p. 48) on its limbs, useful for crawling across, or burrowing shallowly in, a moist substrate. Such locomotion as there was might well have involved an ungainly, crawling gait. Certainly, however, the apparent massiveness of *Pterygotus anglicus* might have prevented its locomotion on land (Waterston and Størmer, in Størmer, 1976, p. 143). This bulk may be deceptive, however, as it is in the burrowing-adapted *Limulus* (Manton, 1964), and it is doubtful if the whole body cavity was packed with weighty muscle. With the (co-evolutionary?) rise of predatory tetrapods, such feeble attempts to terrestrialize would be doomed to failure, and might explain the demise of these large eurypterids with the Carboniferous, as of the large pterygotids earlier in the Devonian (Waterston, 1967).

4. Claspers

The presence of a particular kind of clasper in some eurypterids may be additional evidence of their at least partially terrestrial habit. Many groups of terrestrial arthropods develop clasping structures on the limbs to hold the female during courtship and especially to

manoeuvre her over a previously deposited spermatophore (Lawrence, 1953, pp. 223-239; Kaestner, 1968). Subaquatic arthropods also develop claspers, however, for copulation or spermatophore transfer (Kaestner, 1970, p. 37 *et seq.*) and it is not therefore a simple matter of equating claspers with terrestriality. But there may be claspers and claspers. Størmer and Kjellesvig-Waering (1969, p. 209, Fig. 2a) have found it difficult to understand from the morphology of the scimitar lobes of *Eurypterus* (Wills, 1965, Ppl. 1, Figs 2-6) how these could have served as body claspers, and have suggested they were used for scooping an egg-laying hollow. It seems more likely that those structures are an immobilizing type of clasper, used to immobilize fangs (as in living spiders - Lawrence, 1953, Fig. 92A) during courtship and to prevent biting by the hostile mate, or to contain the stinging response (as in the scorpion - Lawrence, 1953, Fig. 104; Kaestner, 1968, pp. 105-106). Cloudsley-Thompson (1968, p. 219) has suggested that the function of such "courtship is to provide releaser stimuli for the mating instinct which at the same time block hunger drives". That such cannibalism existed in the early Palaeozoic eurypterids is suggested by the long coprolite of *Megalograptus*, containing undigested *Megalograptus* cuticle fragments (Caster and Kjellesvig-Waering, 1964, p. 337, Pl. 51, Fig. 4). This type of clasper (present also in *Mixopterus?*), presumably implying a terrestrially deposited spermatophore, might then prove to be an index of terrestrial forms.

SCORPIONS

The early Siluro-Devonian scorpions are now regarded as aquatic, and the earliest unequivocal terrestrial scorpion, with stigmata, is *Palaeopisthacanthus*, from the Westphalian D of Mazon Creek. Aquatic scorpions continued throughout the Carboniferous, however, and possibly even into the Triassic. Conversely, some of the earliest Palaeozoic forms may have been amphibious.

Confirmation of the long-suspected aquatic nature of at least some of the early forms comes from the Emsian *Waeringoscorpio* from Alken, which has filamentous gills (Størmer, 1970; 1976, p. 151). Other criteria used to assess the degree of terrestriality of scorpions are: the walking legs - whether digitigrade or plantigrade; the nature of sensory setae; the degree of resemblance to eurypterids;

and the nature of the faunal assemblage (Størmer, 1970, pp. 350–351). Several of these lines of evidence can prove equivocal, however.

Three large fossil scorpions are known, between half a metre and one metre long. Two of them are Gedinnian — *Brontoscorpio* (Kjellesvig-Waering, 1972) and *Praearcturus* (Rolfe, 1969, p. R622). The latter is only here recognized as a scorpion, independently by L. Størmer (personal communication, c. 1974) and by E. N. Kjellesvig-Waering (personal communication, 1978) from published figures (Rolfe, 1969, Fig. 395 — cephalothorax inverted!). The narrowness of the sternite and forward swing of the coxae in *Praearcturus* suggests a preoral chamber was formed, to permit the external digestion of prey. In Recent scorpions, food is chewed in this chamber by the pedipalpal coxae, while digestive juice from the mouth is poured over the food and alternately sucked back. Chewing may be executed for as much as three hours (Manton, 1964, p. 29), and such external digestion is the rule in arachnids (Petrunkevitch, 1955, p. P53). It “is not a suitable mode of feeding in the water where dissipation of digestive juices must take place” (Manton, 1977, p. 265). Størmer has pointed out the analogy with the evolution of a digestive oral cavity in terrestrial vertebrates. It is not impossible, however, that early scorpions developed the habit of eating their prey whilst holding it above water, as do some Recent insect larvae (R. A. Crowson, personal communication). This would then be another pre-adaptation for life on land. Respiratory structures are unknown from these Gedinnian genera, but, if the trace fossil evidence discussed above is acceptable, it suggests such scorpions may have been at least partly terrestrial. *Gigantoscorpio*, from the Tournaisian of Scotland, is another large scorpion, c. 500 mm long (Størmer, 1976, p. 153). It has been suggested to be amphibious from its plantigrade feet, the presence of setae rather than trichobothria and the nature of the ventral plates concealing gills (Størmer, 1963).

All these scorpions might provide suitable prey for early tetrapods, and vice versa. Recent scorpion enemies include centipedes, arachnids, lizards, snakes and birds; baboons tear off the tails of scorpions before devouring the rest of the body (Cloudsley-Thompson, 1968, p. 93). Romer (1958, p. 367) has objected that scorpions “do not appear to be too nourishing a base on which to found a flourishing terrestrial vertebrate fauna”, and it is likely that they only formed a supplementary item of diet.

The characteristic pectines of Recent scorpions are probably a sense organ for testing the dryness or humidity of the air, for determining a suitable substrate for spermatophore deposition, and for detecting vibrations of the ground, giving warning of the approach of enemies or prey (Kaestner, 1968, p. 103; Savory, 1977, p. 119). There would appear to be little use for such organs in aquatic scorpions, and it may be significant that none have yet been confirmed in Silurian scorpions (Størmer, 1963, p. 94). Størmer has suggested the function of the organs might have changed from their aquatic ancestors. Huge pectine-like structures are found on the enigmatic chelicerate *Cyrtoctenus*, which has been interpreted as an aquatic animal simply from its large size (Størmer and Waterston, 1968). It serves to emphasize that there are many Palaeozoic arthropods, some of them amphibious or terrestrial, yet to be recognized.

The scorpions are unusual among arachnids in having experienced much extinction: on one classification, of nine Palaeozoic superfamilies only one survives today (Savory, 1977, p. 97). Characters used in classification reflect the nature of the respiratory organs and the preoral chamber, i.e. the degree of terrestrialization. Such extinctions may therefore indicate a sequence of unsuccessful attempts to terrestrialize.

MYRIAPODS, INCLUDING ARTHROPLEURIDS

1. Habits

The variety of morphology shown by living millipedes is largely governed by their habits of burrowing or splitting their way through the decomposing plant substrates off which they feed (Manton, 1977, pp. 352-368). Carboniferous millipedes show a similar variety of morphology, implying similar habits (Burke, 1973, 1979; Kraus, 1974; Rolfe, 1980). Other forms, such as *Euphoberia*, *Myriacanthepestes ferox* and *Acantherpestes major* differ from most living millipedes in having an armament of long spines. Such spines were clearly defensive, since they are occasionally crushed or broken off, presumably the result of exchanges with would-be predators (Rolfe, 1980). This spinosity may be combined with large size, as in *A. major* which reached up to c. 300mm long (Scudder, 1882, p. 151), and with

the presence of large compound eyes. As Kraus (1974) has pointed out, these forms must have been surface dwellers, which climbed over plants as shown in Scudder's (1882, Pl. 10) evocative reconstruction. They are no longer thought to be amphibious, however, as that reconstruction suggests (Burke, 1973, pp. 20-22; Kraus, 1974, pp. 21, 22).

2. Predators

Repugnatorial gland openings have been reported on some Carboniferous forms, although Hoffman (1969, p. R582) has been unable to confirm this. The caustic repugnatorial fluids of recent millipedes will deter, or even blind, predators. Lizards will turn away an inch or so from *Tachypodoiulus*, and one which persisted eventually rejected the prey and rubbed its mouth in sand (Cloudsley-Thompson, 1949, p. 139). Amphibians and birds are their most effective predators today. They are a constant article of diet of the American toad — 77 having been found in one's stomach, and 10% by bulk of the food of this species is composed of millipedes. Nevertheless, enemies do not play a large part in the ecology of myriapods: their numbers are chiefly governed by the physical conditions of the environment (Cloudsley-Thompson, 1949).

3. *Arthropleurids*

Whether or not the giant 1.8m long Carboniferous *Arthropleura* is a myriapod (Rolfe, 1969) or represents a separate group within the Uniramia (Manton, 1977, p. 27) is uncertain, but its habits must have resembled those of living polydesmoid millipedes. Such "flat-backed" forms split their way through litter which, in the case of *Arthropleura* was probably of branches and logs, rather than leaves, which would be sparse on such a tropical forest floor. The gut contents of tracheids (Rolfe and Ingham, 1967) suggest *Arthropleura* fed off the woody central stele of lycopods (A. C. Scott, personal communication), and such large animals may have found food, shelter and a natural moulting chamber within the rotted pith cavity of *Lepidodendron* trunks. That *Arthropleura* could leave these humid confines is shown by trace fossils from the Namurian of Scotland and the Westphalian of Joggins (Briggs *et al.*,

1979). These trackways suggest that *Arthropleura* traversed sand-plugged distributory channels on delta surfaces.

In such an open environment, *Arthropleura* would doubtless be more vulnerable to a wider range of predators than in the forest. The leathery cuticle and sheer size of a fully grown *Arthropleura* would protect it from much predation, although younger instars would doubtless succumb, along with other myriapods. Some Coal Measure tetrapods probably behaved like the modern coati, which "spends the greater part of its effort searching among ground litter and debris for invertebrates, as well as digging them out of the soil, using its sense of smell to locate them. Coatis also tear apart rotting logs to get at sheltering invertebrates . . . they will systematically dissect such logs for frogs, snails, centipedes and the like (mostly sheltering nocturnal species)" (Elton, 1973, p. 94).

4. Decomposition

Terrestrial ecosystems contrast with marine ecosystems in that the greatest proportion of primary production passes through the decomposer chain. Myriapods and *Arthropleura* played a vital role as decomposers in Coal Measure and earlier forests, a topic which is enlarged upon elsewhere (Rolfe, 1980). Mite droppings are known from tunnelled plant fragments in coal-balls, and mites comminuted further the plant debris left by millipedes, to contribute to soil formation. This is further evidence of the close interdependence that had developed between plants and arthropods by Carboniferous times.

5. Centipedes

Despite the doubt cast upon the existence of Palaeozoic centipedes and onychophorans by Hoffman (1969, p. R598), recent work has shown that both a scutigermorph and a cryptopid are present in the Westphalian D of Mazon Creek, and suggests that a Palaeozoic geophilomorph is known from Canada (Mundel, 1979). This restores an important group of invertebrate carnivores to the Palaeozoic record. Knowledge of this publication, as of that recording onychophorans from the same deposit (Jones and Thompson, 1980), was received too late to permit fuller discussion here.

CONCLUSIONS

The early terrestrial invertebrate fossil record is made up of two sparse faunas, with only one arachnid order in common, supplemented by many records of myriapods. Trace fossil assemblages hint at the presence of a diversity of terrestrial arthropods during the Devonian, but neoichnology is required before progress will be possible in evaluating them. Later Carboniferous faunas could yield much palaeoecological and palaeobiogeographical information, but these are all after the event of tetrapod origin. They represent well-established communities, of which the arachnids survive today with little change. Devonian and particularly Carboniferous communities were doubtless governed, like their living counterparts, by water requirements, and are only known from humid regions of the palaeotropics. Other groups such as eurypterids and scorpions were amphibious during the Devonian and were available to tetrapod predators. Decomposer organisms played a significant part in building up early humus levels and soil structures, and fossils of these animals or their products have recently been recognized. The present record is clearly grossly incomplete and yields only a distorted picture of the situation that must have existed.

ACKNOWLEDGEMENTS

I am indebted to the following for much help and guidance during the preparation of this paper: P. Bonamo, P. Brand, D. E. G. Briggs, R. L. Carroll, W. G. Chaloner, S. Conway Morris, R. Crowson, J. Dalingwater, D. S. Edwards, Dianne Edwards, D. Grierson, J. B. Kethley, E. N. Kjellesvig-Waering, D. Macfarlane, D. Maclean, S. Morris, J. Pollard, Julia Rolfe, A. Scott, L. Størmer, E. Walker, F. Wanless, C. D. Waterston and R. B. Wilson.

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