Section 1.8.1). From the middle Ordovician onwards microfossils morphologically convergent with those from later tracheophytes suggest a novel vegetation, possibly with thalloid organisms covered by cuticle and spore producers with liverwort life-style; aerial dispersal indicates the attainment of some stature. The appearance of *Ambitisporites* in the Llandovery heralded a new phase — the advent of pteridophyte-like plants with axial organization, possibly forming a 'turf' just a few centimetres high. The larger size permitted by homoiohydry, the concomitant maintenance of turgor and hence a hydrostatic skeleton, conferred potential superiority over poikilohydric forms in terms of wind dispersal of propagules and in shading, thus limiting the productivity of smaller forms. Throughout the late Silurian there is an increase in axis diameter and length of fragments: sprawling *Baragwanathia* probably formed thickets. Lower Devonian assemblages suggest that many of the tracheophytes grew in monotypic stands, extensive cover resulting from prolonged rhizomatous activity. Such plants would have provided mutual support — some of the Emsian trimerophytes attained a height of over 1 m. As to habitats, the best direct evidence comes from the Rhynie Chert, but as all these early pteridophytes were homosporous (i.e. with spores of one size), the free-living gametophyte would have required moist conditions both for vegetative growth and reproduction. With regard to route of terrestrialization for higher plants, physiological considerations support transmigration from fresh water on to land.

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1.8.3 Invertebrates

P. A. SELDEN

Introduction

The diversity of invertebrate species on land greatly exceeds that in the sea; this is almost entirely due to the terrestrial insects which form 70% of all animal species alive today. However, of over 30 invertebrate phyla, only the arthropods, the molluscs, and the annelids have significant numbers of macroscopic terrestrial representatives. A greater number of phyla include very few terrestrial species, cryptobiotic representatives, or internal parasites on terrestrial organisms. The body plans of some highly successful marine phyla have apparently precluded their terrestrialization; these include the sipunculid, echiuroid, and priapulid worms, cnidarians, lophophorates, chaetognaths, pogonophores, hemichordates, and echinoderms. No phylum originated on land, and no major terrestrial taxon has become extinct, as far as is known.

Outstanding questions on terrestrialization are: what physiological mechanisms enabled invertebrates to emerge onto land; did each taxonomic group use similar mechanisms; were their routes onto land the same; did they all come onto land simultaneously, suddenly or gradually, or in different invasions? The hardest evidence comes from comparative physiology, but palaeontology has the power to test theories based on living material, and uniquely adds the dimension of time.

Invertebrates moving from seawater to land experience profound changes in all aspects of life (Little 1983). On land, water supply is at least variable, and commonly seasonal. To invertebrates, whose air breathing mechanisms utilize diffusion to a far greater extent than ventilation, oxygen is more available in air than in water because the diffusion coefficient (partial pressure per unit length, in ml/[min x cm^2 x cm × atm]) of oxygen in water is 0.000034, but in air is 11.0. Support is more problematical in the less viscous aerial medium than in water, but once overcome, locomotion is easier and faster. The difference in refractive index between air and water poses a problem for visual sense organs in transition, but high frequency vibrations can be perceived more easily in air, resulting in a greater use of sound by terrestrial invertebrates. On land, internal fertilization is the norm, and greater protection (e.g. from drought) is afforded to the developing embryos. Changes in nutrition, ion balance regulation, and excretion are also necessary for terrestrialization.

Some land animals avoid the difficulties of water supply by living in soil interstitial water; strictly, such animals (e.g. protozoans, ostracodes, and nematodes) should not be regarded as terrestrial. Poikilohydry is used only by small terrestrial animals, such as protozoans, tardigrades, nematodes, and rotifers, whose habitat is subject to seasonal drought periods. Many soil, litter, and crevice dwellers are able to take advantage of the high humidity in such habitats, and though they are often able to foray in drier situations (e.g. woodlice across the kitchen floor), retreat to the humid home base is essential to prevent desiccation. In addition to woodlice, the centipedes, millipedes, flatworms, leeches, and earthworms are included in this group. Some animals, such as many land snails, can withstand desiccation during dry periods by aestivation, but require water or high humidity for activity at other times. Finally, the true invertebrate conquerors of the terrestrial habitat, not requiring a humid environment in which to flourish, but active in dry, and even desert, conditions, are the majority of insects, many arachnids, and a few crustaceans. All terrestrial arthropods have waterproofing in the cuticle, but the form this takes differs in each arthropod group and is not always well studied. The differences may be important for palaeontology, however, since the preservation potential for different cuticles is not the same.

The fossil record

The fossil record of terrestrial invertebrates is shown in Fig. 1 (Rolfe 1980; Chaloner & Lawson 1985). There is no fossil record of terrestrial flatworms, nemerteans, or nematodes, although fossil examples of parasitic and aquatic nematodes are known (Conway Morris 1981). Oligochaete annelids are known from the Carboniferous. Their traces, including burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards. They may have emerged onto land with the first humic soil (Section 1.8.1).

Land snails, both helicinid prosobranchs and stylommatophoran pulmonates, are recorded from the Upper Carboniferous, indicating that they had already become significant members of the land fauna by that time. The earliest basommatophoran pulmonate is Late Jurassic in age; this contradicts evidence from comparative morphology, which suggests that basommatophorans were ancestral to the other pulmonates. Possibly the development of ground shade and deciduous leaf litter (probably Lower Carboniferous) was necessary before land snails could be assured of the damp conditions necessary for colonization (Solem 1985).

All extant insects are terrestrial or secondarily aquatic, and there were no terrestrial trilobites, as far as we know. The record of Onychophora, which includes the Recent *Peripatus*, appears to begin with *Aysheaia* from the marine, Middle Cambrian Burgess Shale. Terrestrial uniramians (myriapods and insects) were thought to have evolved from land-living onychophorans, but there is new evidence that the earliest myriapods were marine. This comes from myriapod-like fossils in marine sediments from the Silurian of Wisconsin and the Middle Cambrian of Utah. By the Devonian, millipedes, centipedes, and arthropleurids had appeared in terrestrial faunas, and some reached giant proportions in the Carboniferous forests. The earliest apterygote insects occurred in the Devonian, but the first pterygotes were Carboniferous in age.

Eurypterids ranged from Ordovician to Permian and were predominantly aquatic animals, but from the Silurian onwards some were amphibious, as evidenced by their accessory lungs. They illustrate a failed attempt at terrestrialization using a method now being tried by the Crustacea. Their close relatives, the scorpions, succeeded however, by changing their gills into lungs. All other arachnids are primarily terrestrial today, and the evidence from comparative morphology suggests that each arachnid group emerged onto land independently. The oldest are the trigonotarbids: extinct, close relatives of spiders, with good terrestrial features, from the Lower Devonian of Rhynie, Aberdeen. In the Devonian are also found mites, pseudoscorpions, and possibly spiders, and by the Carboniferous there were more arachnid orders than today; only the spiders have radiated more dramatically in later periods.

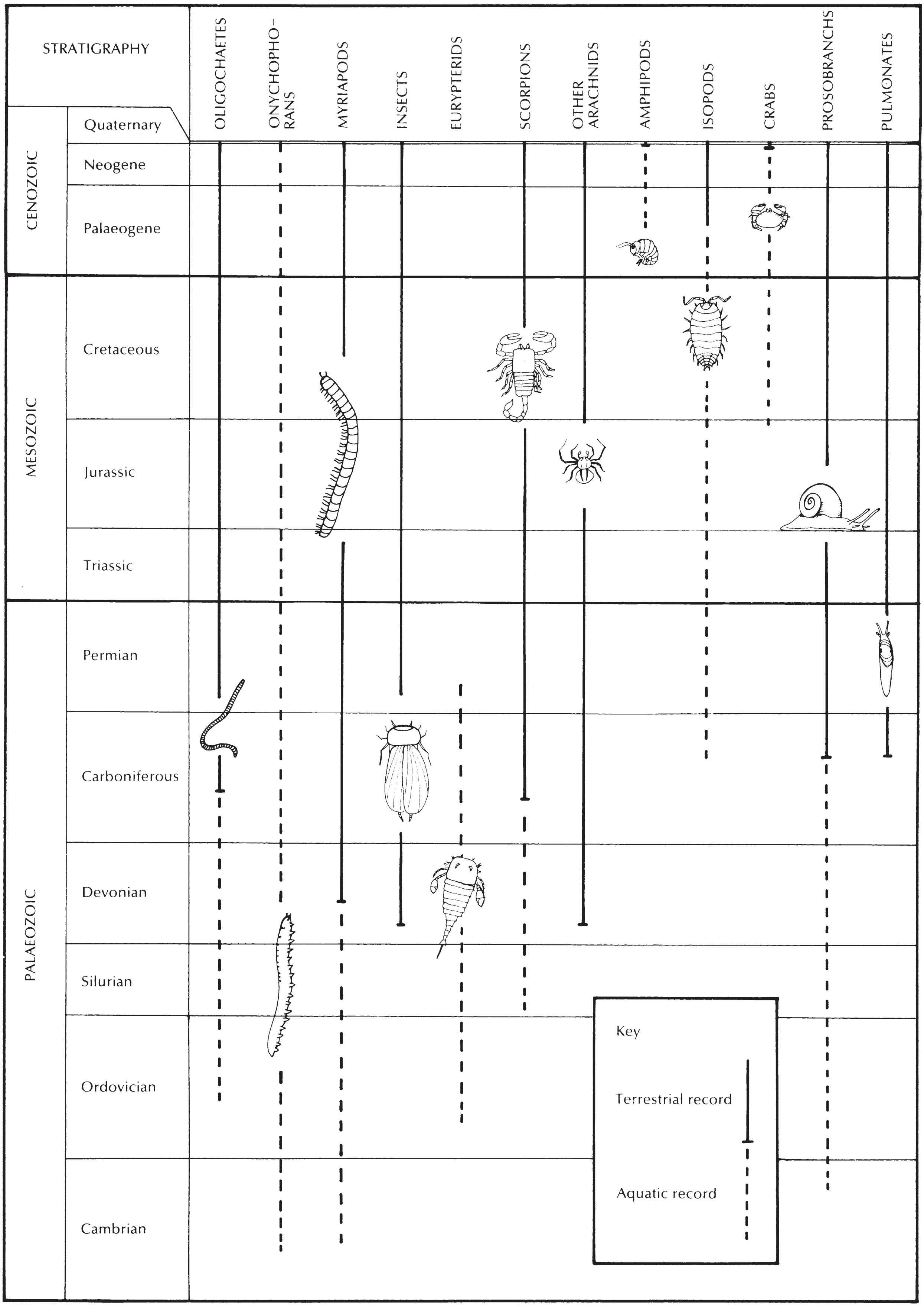

Fig. 1 The fossil record of terrestrial invertebrates and their forebears.

The fossil record of crustaceans is generally good because, like the trilobites, they have a mineralized exoskeleton. However, the terrestrial groups show very short fossil ranges. The first amphipods are Upper Eocene, although it has been suggested, on biogeographical grounds, that their origins lie in the Middle to Late Mesozoic at least. The terrestrial talitrids, with no fossil record, are considered by some to have emerged onto land when the first angiosperm forests became established in coastal regions. The isopods have a long fossil record, from the Upper Carboniferous, with their supposed origins in the Devonian, but the terrestrial Oniscoidea are known only since the Eocene. Although crabs and crayfish first appeared in the Jurassic, the important crab radiations did not occur until the Cretaceous and the Eocene; families with terrestrial representatives first appeared in the Palaeogene, but true terrestrial forms not until the Late Neogene.

Morphological adaptations for life on land

A major problem for terrestrializing animals is that both oxygen and carbon dioxide molecules are larger than the water molecule, so that any membrane across which the respiratory gases are diffusing will leak water. This may not be too disastrous in moist environments like the soil, in which animals such as earthworms can use cutaneous respiration, but inhabitants of dry habitats need a waterproof skin and have developed special respiratory organs to reduce water loss. Respiratory organs can be broadly classified into gills, (evaginations) used primarily in water and lungs (invaginations used primarily in air). A great many animals utilize cutaneous gas exchange in conjunction with gills or lungs. Aquatic animals which venture onto land for short periods of time may use their gills for air breathing, but if much time is spent on land, accessory lungs are usually developed. Many examples of animals with both lung and gill can be found among the gastropods and the Crustacea. In some instances, the lung developed not for land life, but to withstand poorly oxygenated water or drought periods (cf. lungfish).

True lungs among the invertebrates are found only in gastropod molluscs and arthropods. Among gastropods the pulmonates (land snails and slugs), and a few prosobranchs (e.g. helicinids), are the only truly terrestrial forms. The gastropod lung is formed from a highly vascularized part of the mantle cavity, which in pulmonates opens by a small pore (the pneumostome) to the outside. In the arthropods, book-lungs, tracheae, and pseudotracheae are all types of lung which have evolved independently in a number of groups. The book-lungs of arachnids are homologous with the gills of the aquatic chelicerates, and appear to have been derived from them simply by sealing the edges of the gill covers and leaving a hole (the stigma) to connect to the outside. The early scorpions (Silurian to Carboniferous) were aquatic and gills are known in the Devonian *Waeringoscorpio* from Germany; but by the Lower Carboniferous, pulmonate scorpions had appeared alongside the aquatic forms. In the related, extinct eurypterids, the so-called gills actually resemble some crustacean air-breathing organs, which suggests that this was their real function, and that true gills, being thin membranes, have not been preserved or recognized in fossils. As in the pulmonate gastropod lung, dendritic structures resembling insect tracheae have developed within the book-lungs of some arachnids; additionally, some arachnid groups have developed tracheal systems. Among the chelicerates, therefore, respiratory organs developed independently in each group by modification of various pre-existing organs according to need.

The insect tracheal system is a dendritic pattern of tubes arising from apertures (spiracles) in the body wall, and penetrating to every tissue in the body to supply oxygen directly to the cells. Since the insects appear to have evolved from terrestrial myriapods, the problems of terrestrialization have never troubled them, which may explain their success. A variety of tracheal systems occurs among the myriapod groups. Several independent terrestrial lines are found in the Crustacea (Powers & Bliss 1983), principally the talitrid amphipods, the isopods, and the land crabs. In the land crabs, secondary lungs are developed that work alongside the gills (which are never lost). The isopods are more terrestrialized than the crabs, and their pleopods (gills) bear invaginations (termed pseudotracheae, from their resemblance to insect tracheae) for air breathing.

For small animals, hydrostatic skeletons work as well on land as in water; witness the success of the slug form. Arthropods moving onto land evolved the hanging stance for stability, and additionally use some form of leg 'rocking' or jointing mechanism to prevent the plantigrade foot from twisting on the ground (with consequent abrasion and loss of grip) during walking; such features can be seen in fossils. Arthropods become vulnerable during moulting, and it is possible that pioneer terrestrial forms returned to the water for ecdysis. Sense organs on fossils can give clues to terrestriality: trichobothria (fine hairs which respond to air vibrations) found on Devonian arachnids prove their terrestrial mode of life, and stridulatory organs on the same animals at least suggest it. Complex copulatory organs preserved in fossils suggest a terrestrial habitat and their absence is evidence for an aquatic life.

Routes onto land

The physiological barrier between sea and land can be crossed by a number of routes. Invertebrates which moved onto land across the marine littoral environment include the talitrids, the isopods, and most crabs, within the Crustacea, and possibly the chelicerates and the uniramians. There is evidence that some terrestrial forms emerged via brackish water (some crabs) or salt marshes (some pulmonate snails). The freshwater route was used by the oligochaetes, leeches, prosobranch gastropods, and the burrowing potamonid crabs and crayfish. Interstitial forms have utilized both fresh- and salt water routes, and it is possible that the very earliest land animals followed this route. Indeed, a late Ordovician palaeosol from Pennsylvania is full of coprolite-bearing burrows which have been attributed to the activities of microarthropods, possibly myriapods (Section 1.8.1).

From the fragmentary record, it would appear that most terrestrial invertebrates arrived on land with, or shortly after, the Silurian plant invasion (Section 1.8.2). The first records are of fully adapted land animals (the Rhynie Chert of Aberdeen, the Alken fauna of Germany, and the Gilboa fauna of New York), which points to a pre-Devonian terrestrialization period for most groups. The major exception is the Crustacea, which are attempting terrestrialization now. The pressures, or advantages, which cause terrestrialization are undoubtedly various (e.g. escape from predators, more abundant food supply) and invite speculation. What is clear, however, is that animals came onto land together with their biotic interactions, and hypotheses should seek to explain the invasion of the land by biotas rather than individual taxa.

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1.8.4 Vertebrates

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Introduction

The earliest terrestrial radiation is presumed to have been of fish-like tetrapods (four-legged land vertebrates — amphibians, reptiles, birds, and mammals) capable of moving on land and breathing air. Modification of structure, function, and physiology in subsequent radiations led to a monophyletic group of truly terrestrial vertebrates, the amniotes. The amniotes comprise two sister groups: theropsids, which include mammals; and sauropsids, which include reptiles and birds. Amniotes evolved a totally terrestrial life cycle, eliminating an independent aquatic larval phase by means of a relatively waterproof extraembryonic membrane (amnion) which encloses the developing embryo in fluid, and a shelled egg. This reproductive strategy enabled colonization of the terrestrial environment, and early amniotes diversified into lineages leading ultimately to mammals and birds.

The earliest tetrapod record

Tetrapod remains first appear in the fossil record in the Frasnian stage of the Upper Devonian. The only abundant skeletal remains are those of the ichthyostegalians, discovered in the nineteen-thirties in the Famennian red beds of East Greenland (Jarvik 1980). Three genera have been recognized, *Ichthyostegopsis*