PALAEOBIOLOGY II

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To the memory of J.J. Sepkoski Jr

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1.3.6 Terrestrialization of Animals

P.A. SELDEN

Introduction

The diversity of animals on land greatly exceeds that in the sea; this is almost entirely accounted for by the insects, which make up 70% of all animal species alive today. However, of over 30 animal phyla, only the arthropods, molluscs, annelids, and vertebrates have significant numbers of macroscopic terrestrial representatives. A larger set of phyla includes those with very few terrestrial species, cryptobiotic representatives, and internal parasites on terrestrial organisms. The body plans of some highly successful marine groups seem to have 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 clade has become extinct, as far as is known. Outstanding questions on terrestrialization are: (1) what physiological mechanisms enabled animals to emerge on to land, and did each taxonomic group use similar mechanisms; (2) what routes on to land did animals use and did they terrestrialize simultaneously, suddenly, or gradually; and (3) how were the earliest terrestrial ecosystems organized? Some evidence comes from comparative physiology, but palaeontology can test hypotheses based on neontology, give evidence for plant–animal interactions, and uniquely can provide the dimension of time.

Animals moving on to land from the sea experience profound changes in all aspects of life (Little 1983). On land, water supply is variable, and commonly seasonal. Oxygen is more available in air than in water because the diffusion coefficient (partial pressure per unit length) of oxygen in air is 11.0, but in water is 0.000 034, so supply of oxygen to tissues by diffusion is an option in terrestrial animals with small cross-sections. Support is more of a concern in the less viscous aerial medium than in water, but once this problem is overcome, locomotion becomes 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 animals. On land, internal fertilization is the norm, and greater protection (e.g. from drought) is necessary for the developing embryos. Changes in nutrition, ion balance regulation, and excretion are also necessary for terrestrialization.

Four groups of land animals can be defined on their management of water availability. (1) Aquatic animals avoid the problem by living in interstitial water in soils; these include microscopic protozoans, ostracods, and nematodes. (2) Cryptic forms differ from those in group 1 by being macroscopic, but similarly inhabit environments of constantly high humidity, such as soil and tropical forest litter; included in this group are earthworms, leeches, flatworms, isopods, slugs, insect larvae, and some amphibians and myriapods. (3) Poikilohydric (desiccation-tolerant) organisms require high humidity to function but can tolerate desiccation by rehydrating when conditions become favourable again; cryptobiotic rotifers and mites belong to this group, as do some animals with desiccation-tolerant dormant stages, such as the eggs of fairy shrimps and tardigrade tuns (cysts). (4) Homoiohydric organisms have achieved the true conquest of the land by the use of waterproof cuticles, transport systems, and osmoregulation; in this group are tetrapods, insects, arachnids, and some isopods and molluscs.

Many terrestrial animals took the littoral route on to land; living in the highly variable environment of the seashore gave them preadaptations for life on land. Others took different routes, via fresh water for example, and there is evidence that some Late Silurian terrestrial biotas occupied a saltmarsh habitat.

Fossil evidence of terrestrialization

There are two main types of fossil evidence for terrestrial life: body fossils and trace fossils—direct and indirect evidence, respectively. Trace fossils include burrows and trackways in subaerial sediments, coprolites, and plant damage; other evidence for terrestrial life, such as chemical fossils, could be included here. Trace fossils can provide evidence that animals were present on land, possibly what they were doing, but not necessarily what kind of animal left the traces. Body fossils give direct indications of the type of animal present, but it may be unclear whether or not it lived in a terrestrial environment. Commonly, the nature of the sediment provides the clue to terrestriality. However, there are some good morphological indicators: gills and lungs have different morphologies, with the latter normally being enclosed in the body and connected to the outside by stigmata; trichobothria are fine hairs sensitive to airborne vibrations which could not function in water; a hanging stance, plantigrade foot, and leg-rocking joints occur in land arthropods; and copulatory systems are generally necessary in terrestrial animals but not aquatic ones.

Body fossils

A study of the fossil record (Fig. 1.3.6.1) reveals that modern land animal groups did not terrestrialize simultaneously. There is no fossil record of free-living terrestrial flatworms, nemerteans, or nematodes, although fossil examples of parasitic and aquatic nematodes are known, mostly from ambers. Oligochaete annelids are known from the Carboniferous, though they may not have been terrestrial at that time. Two groups of land snails, helicinid prosobranchs and stylommatophoran pulmonates, are recorded from the Upper Carboniferous. The earliest basommatophoran pulmonate is Late Jurassic in age, although basommatophorans are thought, on comparative morphological grounds, to be ancestral to other pulmonates. The development of ground shade and deciduous leaf litter (probably in the Early Carboniferous) may have been necessary before land snails could be assured of the damp conditions required for colonization. The record of Onychophora begins with marine lobopodians from the Cambrian, but no fossil terrestrial forms are known. A possible marine tardigrade larva has been described from Cambrian Orsten of Siberia. Tardigrades withstand periods of desiccation by forming cysts known as tuns. Aerial dispersal of tuns may have enabled these tiny creatures to have inhabited moist environments alongside the earliest terrestrial plants.

'Myriapods', once thought to be a monophyletic clade allied to insects, have been shown to be paraphyletic. There is insufficient evidence to confirm that supposed myriapods in Cambrian marine sediments are, in fact, arthropods, but good milliped and centiped fossils occur in Late Silurian and Devonian strata, including scutigeromorph centipeds among the earliest land animals (Jeram *et al.* 1990). By Devonian times, myriapods had reached greater ordinal diversity than today, and some reached giant proportions (2 m) in the Carboniferous forests. All extant hexapods are terrestrial or secondarily aquatic. Evidence for a closer hexapod–crustacean than hexapod–myriapod relationship is emerging, though precisely at what point(s) in the phylogeny of hexapod ancestors terrestrialization occurred is unclear. There seems to have been independent evolution of respiratory organs numerous times amongst tracheates, possibly corresponding to separate terrestrialization events. The earliest apterygotes are found in Devonian rocks, but the first pterygotes are Carboniferous in age.

Amongst chelicerates, 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 and subaerial trackways. They illustrate a failed attempt at terrestrialization. Scorpions, close relatives of eurypterids, succeeded in terrestrialization by converting gills into lungs. Whilst all Silurian scorpions appear to have been aquatic, book lungs appear first in Lower Devonian scorpions, and aquatic, terrestrial, and amphibious forms probably coexisted through the Devonian. All other arachnids are primarily terrestrial today. The oldest are the trigonotarbids, extinct relatives of spiders, with unequivocal terrestrial features such as book lungs. Trigonotarbids are among the oldest land animals, from the Silurian of Shropshire (Jeram *et al.* 1990), and are common in all early terrestrial ecosystems. Mites, pseudoscorpions, and spiders are also found in Devonian strata, and by Carboniferous times there were more arachnid orders than today; the spiders radiated more dramatically in later periods.

The fossil records of many crustacean groups are generally good because of their mineralized exoskeletons. 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 mid-to-late Mesozoic, or earlier. The terrestrial talitrids, with no fossil record, are considered by some to have emerged on to 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 Oniscidea are known only from the Eocene onwards. Similarly, whilst crabs and crayfish first appeared in the Jurassic, the important crab radiations did not occur until the Cretaceous and Palaeogene, with true terrestrial forms appearing in Neogene times.

No fewer than 10 genera of tetrapods are known from Late Devonian deltaic and lacustrine palaeoenvironments worldwide. Morphological and sedimentological evidence suggests that these animals were aquatic carnivores at that time. A 20 myr gap in the tetrapod record during the Early Carboniferous makes it difficult to relate these early examples to later, terrestrial forms. Tetrapod origins and evolution are discussed in Section 1.3.7

Trace fossils

Although the first body fossils of terrestrial animals appear in the Late Silurian (Jeram *et al.* 1990), trace fossils attributed to their activities are known from the Ordovician. Trackways in subaerial deposits in the Caradocian Borrowdale Volcanic Group of north-west England may have been produced by animals making limited

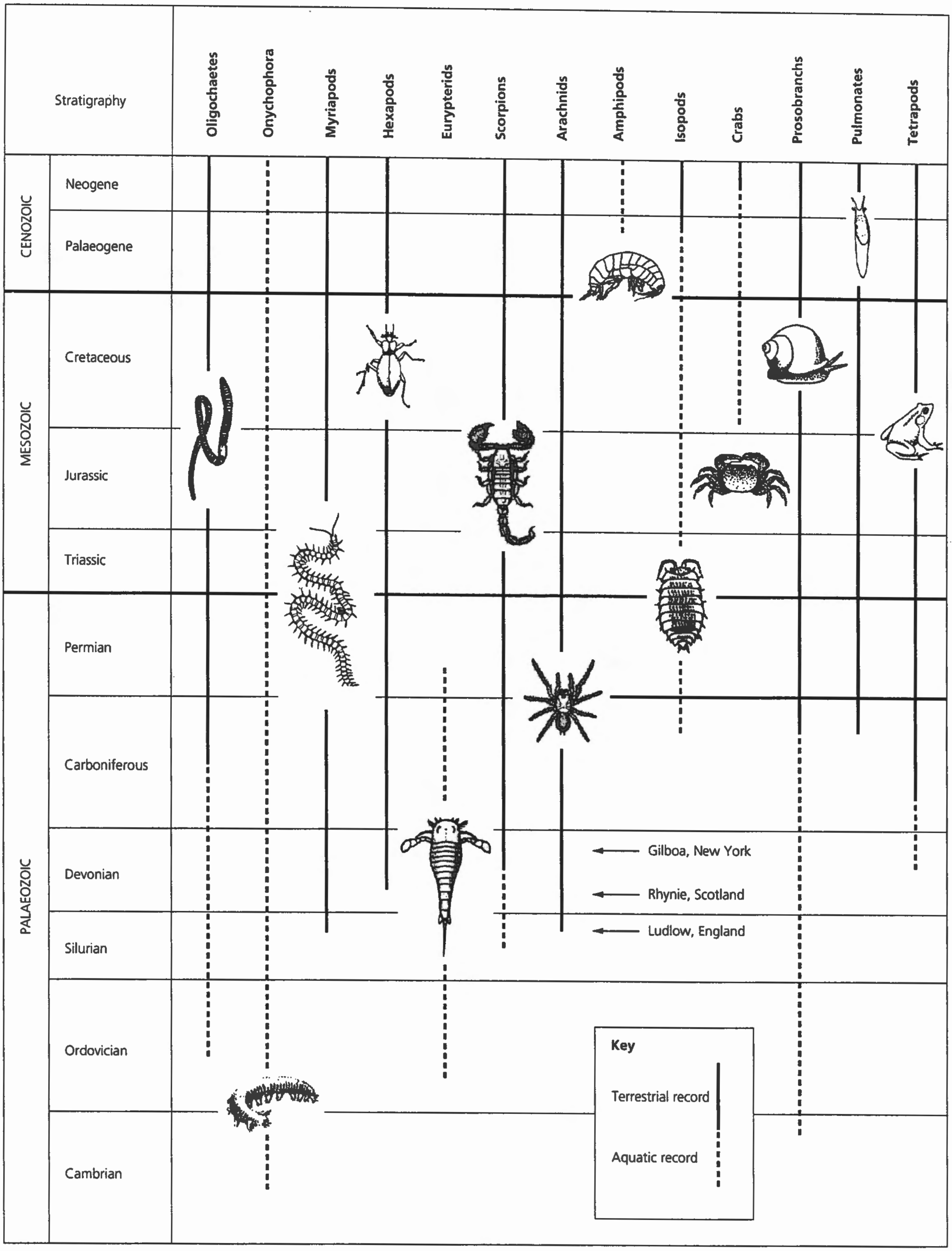

Fig. 1.3.6.1 Fossil record of terrestrial animals and their forebears, and stratigraphic positions of three major early terrestrial Lagerstätten.

excursions on to land or, indeed, they could have been terrestrial. Meandering, subvertical, back-filled burrows in an upper Ordovician palaeosol in Pennsylvania bear some resemblance to modern milliped burrows, but it is impossible to say what produced them. Late Silurian trackways, attributable to terrestrial or semiterrestrial arthropods, are relatively abundant. For example, a rich diversity of trackways and burrows in the Upper Silurian Tumblagooda Sandstone of Western Australia is considered the work of myriapods, eurypterids, scorpions, and euthycarcinoids. Whilst some were made under water, a large number represent animals walking on sediments exposed to the air, and possibly on dry, windblown sand. Annelid traces, including burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards; they may have emerged on to land with the first humic soil. Evidence for terrestrial locomotion by Devonian tetrapods is ambiguous.

Another line of trace fossil evidence comes from coprolites. Coprolites bearing plant remains provide direct evidence of plant–animal interaction in early terrestrial ecosystems. Upper Silurian and Lower Devonian coprolites attributable to small arthropods have been described. For example, coprolites packed with different spore types are known from Silurian and Devonian sites in the Welsh Borderland (Edwards *et al.* 1995). The coprolites were initially thought to be sporangia, but their regular shape, lack of a sporangial wall, presence of up to nine spore types in some specimens, and other debris, ruled out this possibility. The coprolites were probably produced by terrestrial detritivores (litter-feeders) which were ingesting spores and spore masses but not digesting them, in a similar way to modern millipeds. Plant damage, probably caused by arthropods, is common in some early terrestrial ecosystems, such as the Rhynie chert (see Section 3.4.5). Damaged specimens of *Psilophyton* from the Lower Devonian of Gaspé, Québec, include several types of wounding and wound reaction, suggesting attack by animals with sucking mouthparts and subsequent response by the plants. Possible coprolites were also found both within and outside these plant stems. It is likely that the main interactions between plants and animals in the earliest terrestrial ecosystems were directly through sap-feeders and indirectly through litter decomposers.

Ecosystems

The best-known early terrestrial Lagerstätte is still the Rhynie chert (396 Ma) of Scotland, first described in detail in the 1920s (see Section 3.4.5). Over the last 30 years, however, a number of other early terrestrial ecosystems have become almost as well studied (Fig. 1.3.6.1), including the Gilboa, New York, and Ludlow, England, Lagerstätten (see reviews: Shear 1991, Edwards and Selden 1993; Shear and Selden, in press). This work has revealed that the familiar plant–herbivore–carnivore food chain of today's world had not evolved by the Devonian period. The animals present in Siluro-Devonian Lagerstätten were either carnivores (e.g. arachnids, centipeds) or occupied the decomposer niche (e.g. Collembola, millipeds). Tetrapod herbivory is not known before the Late Carboniferous. In fact, many modern food chains, such as the soil ecosystem, are decomposer-based, and herbivores commonly rely on gut microorganisms to break down green plant matter before it can be ingested. The evolution of herbivory may have been a result of gradual short-circuiting of the decomposer food chain by animals harbouring decomposing microorganisms in their guts, thus enabling the aerial parts of green plants to be eaten. The development of the tree habit may have provided a stimulus in this direction.

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1.3.7 Origin of Tetrapods

M.I. COATES

Introduction

The origin of tetrapods, i.e. amniotes (mammals, birds, reptiles) and amphibians (frogs/toads, salamanders, apodans), has been linked traditionally to vertebrate terrestrialization. Scenarios of this key event usually include sparsely vegetated, seasonally arid Devonian