Part I

Introduction

In this introductory section, present-day terrestrial ecosystems are first placed against a background of gradual development over more than 400 million years (Chapter 1). To give some understanding of the problems faced by aquatic animal lines moving on to land during this period, Chapter 2 compares the properties of aquatic and terrestrial environments, and points out the extent of biological influence on terrestrial climates. Chapter 3 concludes the introduction by discussing the sources of evidence available to us in tracing the origins of terrestrial animals.

1

Perspective

at successive periods of the past, the same area of land and water has been inhabited by species of animals and plants even more distinct than those which now people the antipodes, or which now co-exist in the arctic, temperate, and tropical zones.
Sir Charles Lyell (1878) *The Student's Elements of Geology*, 3rd edn. London: John Murray.

The oldest records of terrestrial animals date from the Silurian. At this time there were relatives of the present-day myriapods on land. This does not mean, of course, that there was no terrestrial fauna before the Silurian, only that we have no record of it: the fossil record provides many problems of interpretation, as will be explained in Chapter 3. Certainly, however, the diversity of animal life on land was very low. After the Silurian, in the Devonian, Carboniferous and subsequent periods, we have records of the progressively increasing diversity of terrestrial animals (Fig. 1.1). Step by step, terrestrial ecosystems evolved until by Tertiary times they became very similar to those of the present day. This invasion of the land by primitively aquatic animals, and the adaptations and diversification of animals en route to land provide the theme for this book.

One of the major characteristics of terrestrial faunas is their narrow phylogenetic base in comparison with that of aquatic faunas. While there are nearly 30 free-living macrofaunal phyla extant today, 11 of these are confined to the sea, and only 7 have truly terrestrial representatives (Table 1.1). Several more phyla, containing small forms, together with protists and bacteria, are found in the soil. No phyla are restricted to fresh water, and only one, the Onychophora, is restricted to land. This distribution has led most authorities to consider that life originated in the sea, and that freshwater and terrestrial forms evolved later (e.g. Pearse, 1936). An alternative hypothesis was developed by Hinton & Blum (1965), who suggested that life originated on land, but this has not received general

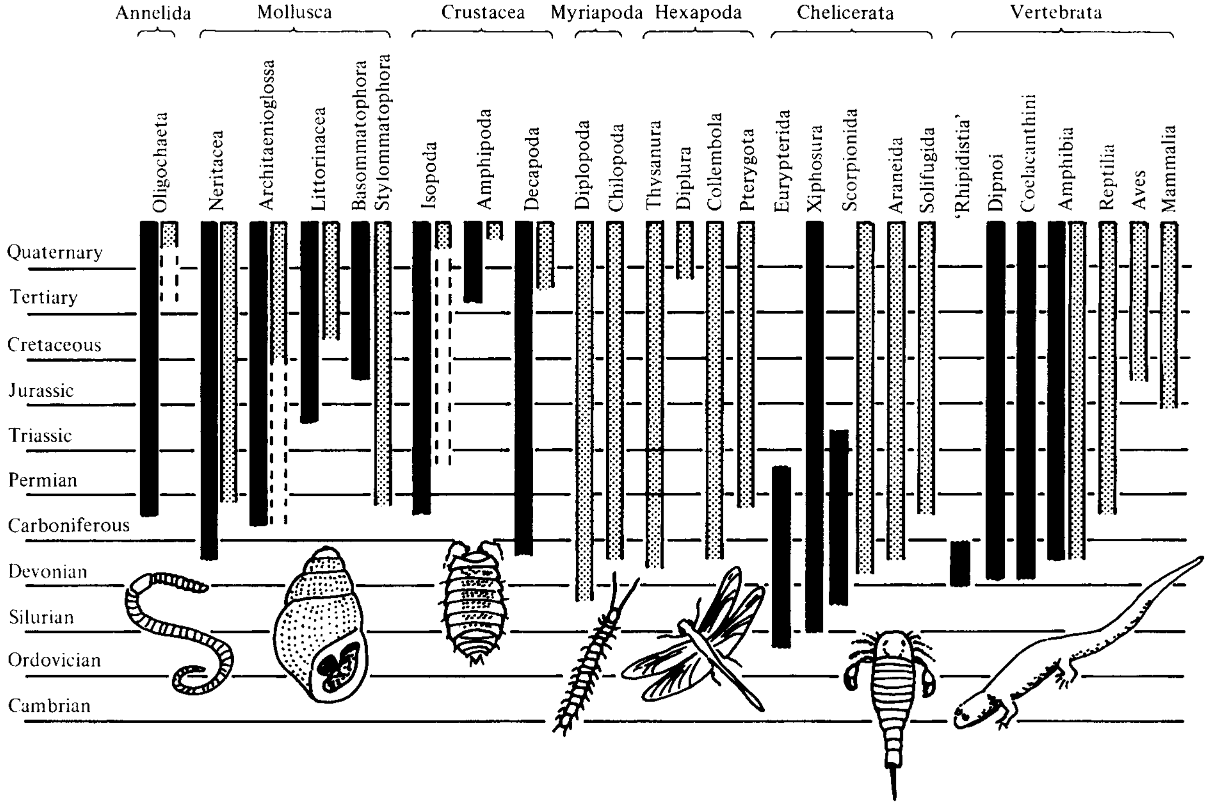

Fig. 1.1. The fossil record of some animal groups, greatly simplified. Aquatic records are shown as black bars, terrestrial records as stipple. Dotted lines show uncertain records. After Little (1983). Data taken from many authors, and modified by reference particularly to Rolfe (1985), Solem & Yochelson (1979) and D.E.G. Briggs (personal communication).

Table 1.1 *The distributions of animal phyla*

	Sea	Fresh water	Soil	Land (above soil surface)
Protista	X	X	X	—
Porifera	X	X	—	—
Cnidaria	X	X	—	—
Platyhelminthes	X	X	X	X
Ctenophora	X	—	—	—
Nemertea	X	X	—	X
Rotifera	X	X	X	—
Gastrotricha	X	X	—	—
Kinorhyncha	X	—	—	—
Nematoda	X	X	X	—
Nematomorpha	X	X	—	—
Entoprocta	X	X	—	—
Annelida	X	X	X	X
Mollusca	X	X	X	X
Phoronida	X	—	—	—
Bryozoa	X	X	—	—
Brachiopoda	X	—	—	—
Sipunculida	X	—	—	—
Echiuroida	X	—	—	—
Priapulida	X	—	—	—
Tardigrada	X	X	X	—
Onychophora	—	—	X	X
Arthropoda	X	X	X	X
Echinodermata	X	—	—	—
Chaetognatha	X	—	—	—
Pogonophora	X	—	—	—
Hemichordata	X	—	—	—
Chordata	X	X	X	X

acceptance. Wherever life evolved, most animal phyla probably developed in the sea, and only later moved on to land.

Before investigating the mechanisms involved in the transition from sea to land, and the routes taken by various animal lines, this introductory chapter attempts to give a picture of the time scale over which the invasion of the land occurred. Although much of the book then deals with the evolution of terrestrial *animals*, it is vital at this stage to consider the development of life on land as the development of a terrestrial *ecosystem*, in which green plants play an essential role. This is not the place for a comprehensive discussion of the origins of terrestrial plants, however, and good accounts of this have already been given (see Chaloner, 1970; Delevoryas, 1977; and Stewart, 1983). Fig. 1.2 shows the fossil record of

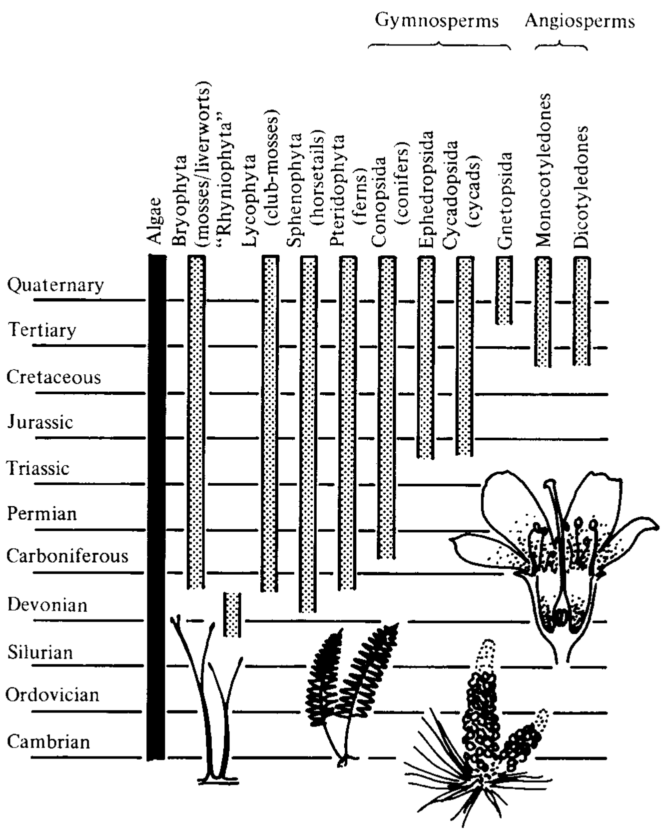

Fig. 1.2. The fossil record of some groups of plants. Aquatic records black, terrestrial records stipple. After Little (1983) from several authors.

major plant groups. The development of terrestrial ecosystems has been considered recently in more detail by Seldon & Edwards (1989) in relation to changes in the physico-chemical properties of the earth's surface. Their account gives more details of the fossil record of organisms than can be provided here, and should be consulted for further information. The physiological adaptations of plants to life on land have been detailed by Spicer (1989). The present account aims merely to provide an overall view as an introduction to later chapters.

1.1 The first life on land: Ordovician and Silurian ecosystems

Although the earliest indisputible terrestrial organisms date from the Silurian, circumstantial evidence suggests that there was some life on land earlier than this. Micro-organisms probably invaded the land during the Precambrian (Wright, 1985), and it is possible that multicellular plants evolved on land directly from unicellular terrestrial organisms, and not from multicellular aquatic plants (Stebbins & Hill, 1980). By the Ordovician, it is possible that algae and bryophytes had evolved on land, and formed a biologically active soil cover, although we have no fossil record of this invasion (Wright, 1985). It is also possible that some invertebrates had become terrestrial, although once again we have no direct fossil remains of them. In support of these suggestions, the study of fossil soils of the Ordovician (Retallack, 1985) has demonstrated the presence of burrows, possibly made by invertebrates, and other fossil structures which may represent traces of root systems or fungal mycelia. Fossil spore tetrads have also been recovered from late Ordovician deposits, so that there may have been a well-developed land flora of non-vascular plants. J. Gray (1985a,b) has argued that these plants were widespread, but like the bryophytes may have been lacking in morphological adaptations allowing them to control their water economy. Other authors (see the discussion following Gray, 1985a) have contended that the spores may not necessarily belong to land plants.

At present, any reconstruction of Ordovician land surfaces must be purely speculative, but there does seem a possibility that at least in the region of water bodies there was a fringing region of non-vascular fungi, algae and cyanobacteria. The animals that burrowed beneath these organisms, and presumably fed upon them, are unknown. Early arthropods have been suggested, but as yet no fossil remains of such have been recovered.

By late Silurian times, the situation had become quite different. The first fossils of intact vascular plants have been recorded from these rocks, most of them belonging to the 'Rhyniophyta' (recently considered to consist of several individual groups). Genera such as *Cooksonia* had erect stems with sporangia at the tips, but no leaves. All the records of these plants come from marine sediments, and they may have grown on the edge of a marine lagoon, in an analogue of the present-day saltmarsh environment, or perhaps on small islands (Edwards, 1980; Edwards & Fanning, 1985). Although most of the Silurian plants were not very tall, they had upright growth forms, and presumably cast shade and increased the humidity near the ground, as well as providing a source of detritus in the shape of fallen stems. In other words, they modified the micro-climates near the ground to a considerable degree, and, as will be described in Chapter 2, these micro-climates are critical for the survival of animals. Despite these effects, we have records of only one major group of animals from this time. These are fossils that were probably myriapods. Unfortunately, all the specimens from the Silurian are badly preserved, and somewhat ambiguous (Rolfe, 1980, 1985). Besides these, scorpions have been found in rocks of the same age, but these were aquatic, utilizing gills protected by abdominal plates (Briggs, 1987). In summary, then, we can only say that Silurian lands had very poorly developed ecosystems, with very low diversity. Plants and animals were probably limited to fringes around fresh and salt water, and as far as we know the uplands were devoid of macrofauna and macroflora.

1.2 Development of terrestrial ecosystems in the Devonian

At the start of the Devonian, several major land masses were situated near the equator, and, although they were beginning to converge, they were still separated from one another and from the southern continent of Gondwanaland which lay over and around the south pole (Fig. 1.3). By the end of the Devonian, most of these land masses had probably converged to form a large continent called Pangaea (Livermore, Smith & Briden, 1985), although it is not certain whether the gap between the northern and southern continents had been closed by then (Scotese *et al.* 1985). It is not known whether this configuration of the land masses itself provided particularly favourable conditions for the development of land plants, or whether changes in current and in climate were influential, but some speculations can be made. Because the lands that would later form North America and north-western Europe were near the equator, and were separated, water currents were able to circulate round them. There was probably little latitudinal variation in climate, and this climate was probably relatively mild. In this climatic regime, during a stage called the Frasnian, the species diversity of marine invertebrates living on the world's continental shelves reached very high levels (Valentine & Moores, 1976), possibly aided by the gradual convergence of the continents, which produced extensive low-lying and coastal areas. It seems likely that this development in the seas was connected with the rapid establishment of terrestrial fauna and flora. While the continents were coming together, but had not yet fused, extensive areas of continental shelf with divergent characteristics, and possessing faunas that had been separated for a very long time, were juxtaposed. Large shallow areas would have provided ideal opportunities for air breathing to develop, both in marine and in fresh waters. At the same time plants with aerial leaves would have experienced ideal conditions. At the end of the Frasnian stage, in the last stage of the Devonian, the Famennian, there was a mass extinction of species

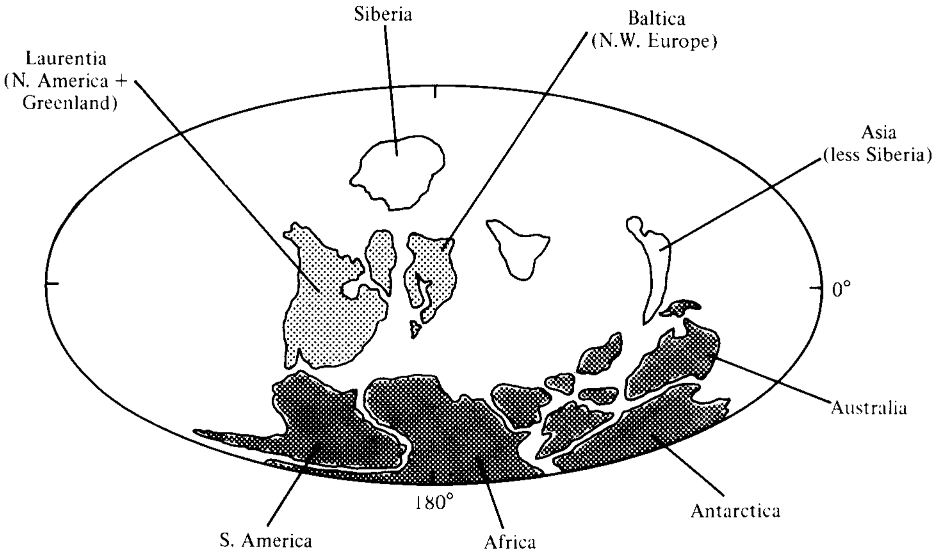

Fig. 1.3. Reconstruction of the distribution of major land masses in the early Devonian. The Old Red Continent (light stipple – Laurentia and Baltica) may or may not have been joined to Gondwanaland (dark stipple – S. America, Africa, Antarctica, Australia). After Scotese, Van der Voo & Barrett (1985) and Livermore, Smith & Briden (1985).

(McGhee, 1989). This may have been due to a global drop in temperature, and was less prominent in fresh water than in marine systems.

Whether or not the above scenario is correct, the Old Red Sandstone continent of the Devonian (essentially the present-day North America plus north-west Europe) saw the subsequent development of extensive terrestrial vegetation and of several terrestrial animal phyla. The Devonian flora was cosmopolitan (Chaloner & Lacey, 1973) and contained, as well as the 'Rhyniophyta', present in the Silurian, Bryophyta (liverworts), Lycophyta (club-mosses), Sphenophyta (horsetails) and Pteridophyta (ferns). Even the early rhyniophytes of the Devonian, such as *Zosterophyllum* and *Psilophyton*, were relatively tall compared with *Cooksonia*, and the later lycophytes and pteridophytes reached the size of small trees (Edwards, 1980). The evolution of this dramatically increased plant cover must have changed terrestrial micro-climates from those of the late Silurian to a marked degree. By providing continuous shade, lessening the effect of wind and retaining a humid atmosphere, by supplying organic detritus and a direct food supply of living material, the plants effectively created cryptozoic niches that allowed the evolution of small, desiccation-intolerant animals. Dominant among these were myriapods and early hexapods, all presumably feeding upon detritus. Centipedes and probably scorpions were present, as the first known terrestrial predators, although the first definitely terrestrial scorpions were recorded from the Carboniferous (Briggs, 1987). Into this environment the early amphibians emerged, probably as small forms dependent upon humid niches, preying upon the varied arthropod fauna. The whole Devonian ecosystem probably depended closely upon the use of cryptozoic habitats, and as far as is known there was no development of a fauna outside them.

1.3 The Carboniferous and the development of forests

It is not certain whether the ocean gap between the equatorial Old Red Sandstone continent and the southern continent of Gondwana closed in the late Devonian or in the early Carboniferous, but the closure would have disrupted ocean currents flowing round the continents, and would therefore have disrupted the accompanying moisture-laden winds. The following change of world climate to a more continental one, with latitudinal variation, built up throughout the Carboniferous, and it is possible that the southern part of Pangaea (formerly Gondwanaland) became glaciated. In spite of this latitudinal variation, the climate of the former Old Red Sandstone continent (primarily North America and north-west Europe), which was still near the equator, was tropical, and the luxuriant coal-swamp vegetation provided ideal climatic conditions for the evolution of both arthropods and vertebrates on land.

The coal-swamp forests contained many pteridophytes, but the greatest significant environmental effects were produced by the development of the conifers. These, with methods of reproduction that were somewhat independent of moist conditions, and with tall trunks and a variety of leaf form, produced environmental conditions that were much more constant than those of the Devonian. In these forest conditions the pterygote insects evolved, the land snails appeared and the reptiles evolved from amphibian stock. The ecosystems of Carboniferous time therefore had many parallels with those of today. The vertebrates and insects were the dominant forms on land, living in environments where the conditions were closely controlled by the growth of vegetation. Since vertebrates and insects were the most important herbivores, the direction of evolution of both groups was related to that of plants. The insects also produced carnivorous forms such as the dragonflies, but the role of predator was particularly taken up by the chelicerates, which produced many forms during this period. This early interaction between insects and arachnids has been retained through geological time, and is still one of the dominant characteristics of terrestrial ecosystems.

1.4 The Permian and the end of the Palaeozoic

The change of world climate towards a more continental one increased in the Permian, with the consolidation of Pangaea. The Permian period was characterized by the extensive spread of deserts, presumably with extremes of climate, and it is noticeable that during this time no new terrestrial plant or animal groups were recorded. The diversity of marine animals decreased, presumably due to the fusion of continental coastlines, and the obliteration of the large areas of shallow continental shelf.

To summarize the development of terrestrial ecosystems in the Palaeozoic, the most important phase of evolution and diversification probably occurred at a time of widespread mild or tropical climate. The two major groups of terrestrial animals, the insects and the vertebrates, emerged and underwent radiation during these conditions. The present-day distribution of both of these groups suggests that they have retained adaptations that are essentially tropical, and that their world distribution can be envisaged in terms of invasion of the temperate zones from the tropics.

1.5 The Mesozoic: Triassic to Cretaceous

The Mesozoic was characterized by the break-up of Pangaea (Dietz & Holden, 1976), and the consequent gradual return of milder conditions and decreasing latitudinal variation in climate. The Triassic saw the evolution of no new groups on land, but in the mild conditions of the Jurassic and Cretaceous the organisms that form the essential parts of present-day ecosystems appeared: the birds and mammals evolved from reptilian ancestors, the various groups of land snails underwent explosive radiations, and the angiosperms came to dominate the vegetation. It is tempting to correlate the environmental influence of the angiosperms with the massive radiations of at least some groups, particularly the land snails. Until recently, it was thought that many land snail groups appeared in the late Cretaceous, but it is now known that both the land pulmonates and one group of land prosobranchs, the Neritacea, were present in the Carboniferous (Solem, 1985). Although Solem has argued that the Carboniferous fossils indicate a very early diversification of pulmonates on land, the records of land snails do not become abundant until the Cretaceous, and it is only then that some of the prosobranch groups such as the Littorinacea