PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Introduction

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Introduction

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The late Silurian–early Devonian time period, around 400 million years ago, has always attracted particular interest because of the environmental and evolutionary events that were taking place at that time. A wide ocean, called the Iapetus Ocean, which had stretched across the North Atlantic region for more than 200 million years was approaching its final closure, which resulted in the building of high mountain ranges and an extensive area of land. The borders of this new North Atlantic continent were characterized by river systems flowing from the mountain ranges into the sea. Lagoonal, brackish-water, estuarine and fluviatile conditions were widespread, and terrestial deposits also common. The semi-arid climate resulted in the oxidation of many of the deposits, giving the typical colour of the Old Red Sandstone rocks of late Silurian to Devonian age.

Over the last 25 years, international debate on the positioning of the Silurian–Devonian boundary and the initiation of the I.G.C.P. project 'Ecostratigraphy' (covering Wenlock to Gedinnian strata) have intensified studies on rocks and fossils of this age. These studies have resulted in great improvements in correlation, classification and knowledge of palaeoecology, most particularly involving the invertebrate animals. In addition, because of the importance of this period in evolutionary history, a tremendous amount of detailed work has been done on the plants and the vertebrates which appear to have migrated onto the land areas around this time.

The speakers at this Discussion Meeting were asked to keep in mind a series of important questions and to attempt to answer them. The major question, however, that dominated the whole meeting was 'what environmental and evolutionary changes were taking place at this time, and were they related?'

The first question to be asked when discussing evolution and environment during a limited period of geological time is 'How can we establish that certain events, widely separated in space, actually occurred at the same time?' After describing the stratigraphical framework of the interval under discussion, Professor Holland considers the various methods of time correlation. He concludes that, at present, fossils still provide the most valuable means of determining the approximate age equivalence of strata, much more precisely than radiometric dating. In the marine facies, graptolites provide the greatest precision, although with increasing competition from microfossils and contributory evidence from other invertebrate groups. In the non-marine facies, however, the early fish and the land plants and their spores become more important for correlation. Spores of land plants, dispersed into a wide range of sedimentary environments are increasingly offering a means of effecting correlation, particularly where access is limited to borehole sections. The zonal schemes for the two major facies (marine and continental) can be approximately tied together where marine and non-marine strata interdigitate. During the subsequent discussion the view was expressed that the time might come when reversals in the earth's magnetism could provide precise correlation, even in rocks of this age.

In the second session of the meeting, the three speakers (R. A. Livermore, C. R. Scotese and A. J. Boucot) were asked to provide a picture of the geography of the world in late Silurian to early Devonian times. This is obviously a very difficult assignment and it is not surprising to find considerable differences between the various versions of the world maps. Palaeomagnetism is usually accepted as the main tool but suffers from a presumably permanent limitation in its lack of ability to determine palaeolongitudes. It is in this respect that fossils of terrestrial and marine organisms may contribute in giving evidence of continuity of migration routes indicating land or sea connections in the longitudinal positioning of land bodies.

A temporary limitation in the application of palaeomagnetism lies in the lack of sufficient data for some major regions, such as Gondwanaland. The palaeomagnetic evidence has, therefore, to be supplemented by evidence from studies of the palaeobiogeography and palaeoclimatology. The evidence from these sources often appears to conflict but the differences between the reconstructions are gradually diminishing. An earlier closure of the large gap between Gondwanaland and Laurussia is commonly postulated and the mid-Palaeozoic development of Pangaea is now generally agreed.

Of some considerable relevance to the theme of the meeting is the question of whether there was now more land than hitherto. The process of colonization would clearly have occurred without reference to the total 'land area available'; but the widespread occurrence of transient fresh-water bodies and adjoining moist environments on land, representing intermediate habitats, may well have influenced the selection of land-adapted organisms. The palaeomagnetists operate with continental blocks, however, so that it needs sedimentary and fossil evidence to assess the extent of shelf seas over these continents.

Boucot maintains that there was a lot (one third to a half, perhaps) more land during the early Devonian than in either the late Silurian or middle Devonian. All the evidence certainly points to a greatly increased aggregation of the lithospheric blocks, particularly in the north Atlantic region. However, Boucot points out that there were truly extensive land areas before late Silurian times, for example, much of Africa and the Brazilian Shield. Whether these land areas presented suitable environments for colonization by plants and animals is difficult to decide. Suitability would certainly involve climatic factors, and perhaps the presence of large river systems and extensive marginal seas. The environment most favourable to the establishment of a flora of land macrophytes might possibly differ from that which would most favour the adaptation of animals to terrestrial conditions. The organisms themselves would also have needed to develop the ability to adapt to the new environments, perhaps in the form of various preadaptations.

In the third session the geological evidence for a change from marine to non-marine conditions was presented. The Welsh Borderland area has been intensively studied from this point of view and J. R. L. Allen's paper uses it as a case history. From a study of Recent sediments in shallow seas, on beaches and in various types of river systems it is now possible to interpret the environment of ancient sediments. By this means, Allen reconstructs the palaeogeography of the Welsh Borderland area in late Silurian to early Devonian times and demonstrates the vertical transition from marine to fresh water deposits. His study is corroborated by fossil records, for example, the occurrence of depleted marine faunas or the presence of animals such as the brachiopod, *Lingula*, which can tolerate brackish water

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conditions at the present day, in the absence of a full marine fauna or the occurrence of fish and plant remains in river-deposited sediments, where they are unlikely to have been washed up from the sea.

Allen demonstrates the marine to non-marine transition from the exhaustively studied Welsh Borderland area but a similar transition occurs at around this stratigraphical level over most of the North Atlantic region around the margins of the so-called 'Old Red Sandstone Continent' which resulted from the closure of the Iapetus Ocean and the final development of the Caledonian mountains. In Gondwanaland, however, a transition to continental red beds is well known only from Australia.

The question also arises of whether this transition took place at the same time over the whole North Atlantic region or whether it was markedly diachronous. As M. G. Bassett points out in the discussion, the evidence from Scandinavia demonstrates that the Old Red Sandstone facies developed there early in Silurian times. In the marginal areas of the British Silurian (for example, the Midland Valley of Scotland and Pembrokeshire) red beds appear in mid-Silurian times. Such diachronism is not surprising. In the closure of an ocean the marginal areas are liable to be the first to develop a non-marine facies. Also, if the closure were oblique and scissor-like, the Old Red Sandstone facies would develop first in the area of early closure (Scandinavia) and be delayed at the open part of the ocean (North America). The interesting question then poses itself to the palaeobiologist: did land plants and fresh water fish appear earlier in the regions of early closure: and if not, why not? The present evidence does not suggest an earlier invasion related to the diachronism: the postulated Ordovician land-plants of Boucot and Gray are too early to relate to this environmental change.

G. Retallack considers the evidence offered by fossil soils for the timing and nature of the colonization of the terrestrial environment. Slightly different views are expressed in discussion by V. P. Wright and J. Catt. There is little doubt that microbial (bacterial, fungal and algal) populations must have existed on moist terrestrial surfaces, at least back into Precambrian time. These must have had a significant role in the weathering (and in a broad sense, soil forming) process. Retallack presents evidence from a late Ordovician palaeosol profile and concludes that certain invertebrate burrows represent animal colonizers of a relatively dry, terrestrial soil habitat. This highlights the problem of distinguishing between biogenic traces (burrows, leaf impressions) incorporated in the original subaqueous deposition of the bedrock and those features incorporated in the soil-forming subaerial environment.

The role of vascular plants in controlling erosion of modern land surfaces is well documented, but the effect of their advent on previously 'untenanted' land surfaces is less obvious. The role of algal–fungal or bacterial mats is known to be important in stabilizing mud surfaces in the (modern) intertidal zone, and comparable biota may have been important in controlling land surface stability in early (pre-Silurian) terrestrial communities. However, at present we lack direct evidence of this.

D. Edwards and J. Gray review the evidence from macrofossils and microfossils, respectively, for the timing and nature of the land colonization by plants. Their conclusions are considered in discussion by H. P. Banks and J. B. Richardson. Edwards documents the middle and late Silurian appearance of macroscopic 'rhyniopsid' plants with simple morphology, spore-bearing structures and in some cases *in situ* water-conducting tissue. Gray documents the occurrence of spore tetrads, triradiate spores, cuticle fragments and tubes with annular thickenings. There is a paradox in the relative abundance and widespread occurrence of Ordovician and early

Silurian microfossils in these categories, and the paucity of our understanding of the structure and habitat of the plants from which they must be assumed to derive. However, it is clear that both resistant spores formed in tetrads and cuticular covering of a cellular surface appear earlier in the fossil record than secure record of xylem (as we now see it in the vascular tissue of living plants) and stomata. We have no evidence of xylem before the mid-Silurian or of stomata before the early Devonian. Xylem-like tubes with annular thickenings appear earlier (Silurian), but their relationship to spore-bearing and cuticle-covered plants remains conjectural.

W. D. I. Rolfe and H. P. Banks (in discussion of D. Edwards) touch on direct evidence of plant–animal interactions in early terrestrial ecosystems. The role of land plants in creating a moist, sheltered environment with availability of primary productivity for early herbivores is self-evident, but essentially derived by extrapolation from modern ecosystems. Devonian plant fossils give only indirect evidence of the occurrence of spore-eating, and of stem lesions and wound-reactions in the tissue of early vascular plants.

Several authors note the possibility that microscopic green algae, adapted to a limited habitat range of moist (?soil) terrestrial environments may have been the ultimate source of subsequent vascular land plants. If this was the course of events, then the development of a vascular plant flora was one of structural and physiological modification within the terrestrial environment, rather than a land-colonizing migration. This presents a very different picture from the conventional concept of sizeable, multicellular, green algae effecting land migration, rather on the scale on which fish gave rise to tetrapods.

The fifth session dealt with the rise of non-marine invertebrates. P. A. Selden's paper considers the eurypterids, an important arthropod group which adapted to a wide range of environments: marine, brackish water, fresh water and perhaps even terrestrial. Changes in the means of respiration were obviously of key importance. W. D. I. Rolfe discusses the earliest land animals with a particular emphasis on the arthropods, of which the myriapods are dealt with in more detail by J. E. Almond. Rolfe emphasizes that most terrestrial organisms appear in the fossil record in a highly organized form and the fossil record is too poor to establish links with marine ancestors: he does, however, discuss some possibilities. It is likely that some of the adaptations for marine existence may have been easy to modify for a non-marine habitat. Rolfe admits the possibility, even the probability, that there could have been several independent, parallel land migrations but emphasizes the lack of any direct evidence for this.

Some of the non-marine invertebrates other than arthropods are mentioned by N. Morris in discussion, particularly the fresh water molluscs. On the land, there is evidence of worms and even (in Retallack's account) of burrowing metazoans which may not have been worms. It is possible that the gastropods may have emerged onto the land by this time.

The sixth session covered the rise of non-marine vertebrates. L. B. Halstead's paper describes how the early vertebrates appear to have adapted successively to the transitions in habitat from marine through brackish into the fresh waters of rivers and lakes. There was a dramatic radiation of fish groups in the Devonian and P. Janvier describes the diversification of the Osteostraci. He discusses particularly the question of habitat as there is evidence for both marine (almost certainly near-shore) and fresh water environments.

In the following session, A. A. Bray deals more fully with the physiological problems that had to be overcome in the vertebrate migration from the sea into fresh water and then on to land. Urea formation and retention, and the effecting of gaseous exchange were functions of major significance. J. A. Raven considers the fascinating but elusive question of the comparative physiology of early land plants and land arthropods. There are evident parallels in the shared problems of gas exchange and water retention, but these are accompanied by some basic physiological differences. It would be satisfying if we could build up a picture of the more direct, ecological relationships between all the plants and animals that inhabited the early Devonian land areas, but the inadequacy of fossil evidence makes this a speculative exercise.

In the final session Boucot considers events in the marine realm which took place at the same time as the important developments on the continental areas. He is able to recognize some speeding up of the rate of phyletic evolution owing to an increased provincialism, related to the palaeogeographical changes. However, the evidence considered from numerous groups of marine invertebrates shows conclusively that there was neither a marked extinction event towards the end of the Silurian nor a consequent major marine adaptive radiation in the early Devonian. The great events on land are not mirrored in the marine realm.

Despite the progress in our understanding of events in the period here considered, many issues of underlying process and causality remain obscure.

The fossil evidence points very clearly to a number of separate, independent terrestrial migrations (or adaptations) by different animal phyla surviving to the present day. This was evidently the case for the arthropods (undoubtedly the earliest true terrestrial colonizers, probably effecting several independent land migrations), the vertebrates, the gastropods (land snails, slugs) and the annelids. Plants, in contrast, seem to have made a single primary adaptation–migration in the form of the archegoniates (bryophytes plus tracheophytes), which must have been derived from a green algal ancestry. Perhaps the different pathways of plant and animal evolution reflect the fact that green photosynthetic plants exploited the available land habitats from the outset, so presenting a spectrum of plant-controlled niches which were then occupied by competing animal colonizers. There is a very real possibility that other plant (algal) groups did play a role in the early phases of land colonization, but were subsequently extinguished in competition with the archegoniates. We may be seeing this in the range of enigmatic Palaeozoic plants such as *Prototaxites*, *Parka* and *Nematothallus*, but the fossil record is equivocal on their origin and affinity.

Was there some aspect of the Silurian–Devonian interval which presented a particular environmental stimulus to land colonization? Had environments suitable for land migration presented themselves from Precambrian time onwards, (and indeed been occupied by successive groups of microorganisms, and subsequently by higher plants and animals)? The 'case history' represented by the period considered here seems to be an ideal one in which to explore the influence of intrinsic and external factors in the major evolutionary changes involving plant and animal life. The papers presented here certainly contribute to our seeing these questions in a common perspective but offer answers which remain, for the moment, controversial.

Recent general references

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