The Rôle of the Forests in the Evolution of Terrestrial Life

by

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The first invasions of the land by invertebrate forms of life took place, as far as we can guess, in the Ordovician or Silurian periods and probably continued over a long passage of time with many failures and disasters until the Carboniferous, when life may be said to have been firmly established over immense areas of the continental surface. What these ancestral pioneers of terrestrial life were like we do not know; they may have been either molluscs or worms or arthropods, or some representatives of each of these groups, since abundant examples of all of them had been developed in the extensive shallow seas of the Cambrian period and were representative of the magnificent and widespread marine life of this time. Sooner or later however, arthropods able to move with comparative ease on dry land were bound to emerge, and this phylum is the dominant one in the first truly terrestrial period of the earth's biological history, the Carboniferous.

We can gain a vivid idea of what the invertebrate life of the 400 million years old Cambrian seas was like from the fauna of the Burgess Shales of British Columbia, which have been accurately dated as Middle Cambrian. What knowledge we have of this page torn from the remote past of our planet, we owe to a great geologist and pioneer, C. D. Walcott, Keeper of the United States National Museum and Secretary to the Smithsonian Institution, who year after year and almost single-handed described large numbers of fossil forms, all of which were unknown to science and in many cases could only with considerable reservations be included among the known divisions of coelenterates, worms and arthropods. They were borderline forms reaching down to the ancestral depths from which the invertebrate phyla branch and where the well-defined outlines of our modern classification become dim and wavy.

Year after year from 1912 onwards, Walcott's descriptions and splendid photographic illustrations in the publications of the Smithsonian Institution opened up an entirely new concept of the extent and variety of animal life in the Cambrian. In their wonderful preservation these fossils show a perfection which may be partly due to the fine grain of the sediments in which they were embedded and perhaps partly to sheer good fortune; be that as it may, in very few fossils of any age or period do we find such perfection of detail in
the preserved structures. Some of the jelly-fishes look as if they had been cast up only yesterday on some wet sandy beach; not only the scales but the sculpture of these scales are perfectly reproduced in many of the polychaet worms; even the internal structures of some arthropods, such as the ramifying diverticula of the intestine, are preserved in fine detail. All this fauna, it must be remembered, was embedded in some of the world's most ancient rocks, where for more than 400 million years it must have been subjected to almost inconceivable pressures and strains.

The Cambrian seems thus to have been the first period in the earth's history in which life was developed on a magnanimous scale and to the limits of its possibilities; though still confined to existence in a marine habitat the types or prototypes of all the main groups were already there and many of them had developed hard protective cuticles or shells; all the models were on show, presenting a wide range and variety for the forces of selection to work upon, forces which were to produce revolutionary forms capable of crossing the great divide between terrestrial and aquatic existence.

From the Ordovician onwards the plants had been slowly conquering the land, at first by means of very simple forms, but in the Devonian there was a fairly extensive and variegated covering of vegetable life in the earth's surface, culminating during the next period, the Carboniferous, in the great coal-forming forests of the palaeozoic.

The Carboniferous forests as ecological niches are perhaps as closely related to our modern tropical rain-forests as any that have ever existed. They luxuriated in a warm equable climate that prevailed over great continental areas of what is now the Northern Hemisphere, with few seasonal fluctuations of temperature or humidity. There was the same exuberant growth of the lowlier forms of plant life, the same abundance and wastefulness; there was certainly also a carpet of humus formed by the decay of other fallen trees and by the ceaseless rain of fronds and spores which floated slowly to the ground like a shower of golden snow-flakes.

In these forests life had for the first time overcome the main problems of existence upon dry land but it was by no means a complete occupation, a mastery of the entire terrestrial environment. An intelligent extra-planetary visitor from another solar system would probably have noted the two parallel lines of animal development, the vertebrate and invertebrate, but might not have been so convinced of the final superiority of the vertebrates over the invertebrates in the evolutionary race. Although the two had commenced the adventure of terrestrial existence at about the same time in geological history, the invertebrates would have appeared to have made a rather more promising start; they were represented by a numerous and diverse band consisting of generalised insects, many arachnids and myriopods, some land snails and possibly some terrestrial crustaceas and soft-bodied worms which have left no fossil traces of their existence. Petrunkevitch has noted that all the arachnid orders in existence at the present day were already established in the Carboniferous while a number of others have become extinct since that time; the same can be said of the Carboniferous myriopods though not of the
insects, most of the orders of this class having become established in more recent times.

Our celestial observer might also have placed to the credit of the invertebrates that they had produced a number of giant forms in the millipedes and early dragon-flies, larger than any that have since appeared among these groups on the earth's surface. In the Protodonata and other primitive pterygota they had also produced insects capable of flight many millions of years before the reptiles, the mesozoic champions of the vertebrates, achieved a similar success.

At the same time he would have observed that the fauna of the Carboniferous forests was singularly earth-bound; nearly all of it, both the vertebrates and invertebrates, was limited to the forest itself, while the majority of the invertebrates were confined to the soil or humus of the forest floor. The forest habitat with its colonnades of tree-trunks is not conducive to the practise of sustained flight and such flying as there would probably have been in the nature of flits and glides; there may have also been a few parachuting forms such as have appeared even among the arachnids of the present day in a few isolated instances.

Thus both the fauna itself and the conditions under which it lived were not very different in modern tropical forests and those of the Carboniferous with their uniform humidity and genial warmth, producing an atmosphere which was perpetually like that of a modern greenhouse. In both the cryptic fauna consisted in general of the same classes and orders; large Juliform millipedes like the palaeozoic Acantherpestes and small Gastropod molluscs like Strophites have been found in the fossilised trunks of the large club-moss Sigillaria, neither being essentially different from the millipedes and small molluscs which today inhabit the rotting trunks of large trees in the South African indigenous forests. If however we make a list of the most characteristic orders of invertebrates inhabiting the humus of our modern forest it will be found to include a number which have not been recorded as Carboniferous fossils. The most striking absentees are to be found among the Apterygote insects, the Crustacea, and representatives of various groups of worms, which, as entirely soft-bodied animals, have left no trace behind.

The most important of the missing orders are all animals which today have a universal distribution and are obviously of great antiquity; among the Apterygote insects the blind and antenna-less Protura, such characteristic members of the Thysanura as Japyx, Campodea and Lepisma, the Symphyla and Pauropoda among the primitive Myriopoda, and terrestrial Crustacea of the two orders Isopoda and Amphipoda.

The members of these arthropod orders, with the exception of the Crustacea, are of small or even minute size; most of them are eye-less; they practically all agree in the absence of pigment or a stout chitinous cuticle. Some are of such insignificant size that they have only attracted the attention of entomologists within fairly recent times, the Pauropoda having been discovered by Lubbock less than a hundred years ago, the Protura by Silvestri less than fifty years ago. If small but active animals can be so easily overlooked it is not difficult to understand why fossils of many orders which may
have existed in the coal-measures, 300 million years ago, have not yet been placed on record. Then again some of the Carboniferous arthropods, though of outstandingly large size, are represented in museum collections by only a handful of imperfect specimens. The Arthropleura are such a group. Some of these enormous invertebrates were almost five feet in length and superficially resembled gigantic millipedes with their large number of similar body segments each provided with a pair of biramous appendages; in their actual structure however these archaic swamp dwellers were more closely related to the Trilobites than to the Myriopoda.

There is one animal whose absence from the fossil record is difficult to explain. *Peripatus*, which is in many ways the most typical of the cryptic forest dwellers of the present day, must certainly have been in existence during the Carboniferous period. Very much older fossils, which have been recognised as near relatives of *Peripatus*, have been described from the Middle and Lower Cambrian of British Columbia and Germany, giving this animal an ancestry with the respectable antiquity of at least 400 million years. While no terrestrial types whatever are known from the Cambrian, the legs of both *Aysheia* from the Burgess Shales of British Columbia and *Xenusion* from the older Cambrian strata of Brandenburg in Germany, are in general so like those of modern *Peripatus* and so unlike swimming organs, that both may well have been amphibious or partly terrestrial animals, as are many shore-dwelling invertebrates of the present day. If such speculations are justified, these Protonychophora, as Hutchinson has called them, may have been the first animals to have achieved the great transition from the aquatic to the terrestrial environment.

In the Cambrian we have a panorama of marine life including a wide range of different arthropod types, in the Carboniferous a large number of arthropods living successfully in forests on dry land while in the intervening periods we have fossil records of only a few scorpions in the Silurian, a few Collembola and primitive mites in the Devonian. How and by what stages did these pioneers leave the sea and reach the forests? What was happening in the time intervening between the end of the Cambrian and the beginning of the Carboniferous? Or if we wish to avoid the thickets of controversy raised by the "Limulus problem" and the mono- or polyphylogenesis of the arthropods, we may simply ask how lung-books and tracheae were substituted for gills and gill-books in order to derive oxygen from the air rather than from water.

What kind of respiratory organs the various transitional stages of these arthropods used we are of course quite unable to say; it seems likely that many of the first primitive ancestors of the terrestrial arthropoda which had established a foothold in the Carboniferous forests were small thin-skinned forms, which would be one reason why no fossil evidence of their existence in these forests has yet been discovered.

At the present day a number of small primitive arthropods are able to breathe cutaneously through the general surface of the body without the aid of a specialised respiratory system or with a tracheal system which is greatly
reduced, as in the Protura, Collembola and Symphyla; in addition these forms are usually equipped with a number of simple sacs which can be filled with blood and everted by means of special muscles. We find these organs, known by various names, such as eversible sacs, coxal organs, coxal vesicles, in at least one representative of each of the three classes of arthropods which form the bulk of the humus fauna of our present-day forests as follows:

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<th>Insecta Apterygota</th>
<th>Arachnida</th>
<th>Myriopoda</th>
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<tr>
<td>The Protura</td>
<td>The Palpigradi</td>
<td>The Pauropoda</td>
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These typical representatives are in all cases the most primitive of their order or class and are further characterised by 1) small body size, and 2) a thin delicate cuticle with absence of pigment. In addition certain larger members of the cryptic fauna are provided with these eversible sacs or coxal organs. The Thysanura among the Apterygote insects, the Symphyla and some Diplopoda among the Myriopoda, while certain genera of Onychophora such as Peripatus in the New World and Opisthopatus in South Africa are also equipped with them. A pair of these organs is also found in some of the modern Arachnida, such as the African whip-scorpions Damon diadema and Titanodamon johnstoni. In none of the other arthropods are they present and they are conspicuously absent from the whole range of orders comprising the Pterygote insects, the majority of which can be regarded as of fairly recent origin.

There is no unanimity among workers as to the function of these organs and it may be that they are at the present time more in the nature of vestigial than active respiratory organs. The arthropods which possess them live continually in an atmosphere with a humidity near saturation point and are not characterised by a well developed tracheal system. The organs may thus be used by modern cryptozoa as subsidiary breathing organs or mechanisms for regulating and balancing the uptake and loss of water in the animal organism.

These structures evidently have an ancient origin for we find them well developed in the giant millipedes of the Carboniferous such as Acantherpestes, and in many of the Arachnid orders of that time, such as the Architarbi, which have since become extinct. Petrunkevitch has identified large coxal organs in Orthotarbus robustus, a member of the latter order, and they are also known in the Palaeozoic Pedipalp, Graeophonus. In the much more ancient Prot-onychophora, Xenusion and Aysheaea from lower and middle Cambrian strata respectively, Pompeckj and Hutchinson have described structures at the ventral bases of the legs which may with some probability be regarded as organs allied to the eversible sacs of the modern cryptic fauna and which may have been extremely simple and primitive organs of respiration in the early Onychophora.

Returning to the title with which this address was begun it seems that the original pioneers of terrestrial life may have been very similar in their general make-up to the more characteristic fauna of the forest soil, or what we may call the crypto-fauna. They were in all probability of insignificant size, with weak
chitinous coverings and comparatively slow in their movements. Some of them no doubt resembled the modern Protura, Palpigradi and Pauropoda, even though we have no fossil evidence that such arthropods existed in the forests of the Carboniferous. We have good evidence however, that animals which did not look very different from Peripatus were living many millions of years before this period, either as shallow water marine types or as littoral amphibious arthropodanneloids.

The typical crypto-fauna of the world’s forests have of all terrestrial invertebrates changed the least during their long history and probably do not differ greatly from the equivalent types which existed in the Carboniferous forests. They have never really been able to breathe dry air or to endure the direct impact of sunlight, and in the narrower meaning of the word are no more terrestrial in habit than are the moist-skinned amphibia among the vertebrates with their inability to withstand the effects of desiccation for any length of time. These cryptic arthropods are and probably always have been halfway animals, unable to exist for long outside of a highly humid environment; the sheltering forests were the ideal means of tempering the harsh and unequal conditions of life on land to the newcomers from a more stable marine environment. Without the forests of the Devonian and Carboniferous there might have been no life on land; at the least, terrestrial types would have taken very much longer to inure themselves to the stern disciplines required for survival on the unprotected and exposed levels of the continents.

With the forests as shelters to receive them however, the step from a marine to a terrestrial habit of life could be more easily made by a number of invertebrate orders which, by a series of migrational stages from the littoral to the hinterland, eventually became forest dwellers. Like so many other changes in the unfolding scroll of life it was another step towards a more complete population of the earth’s surface, but not the final step, for these creatures were not destined to inhabit the entire earth. Although the cryptic forest types were the first animal inhabitants of the land surface, their entire structure, especially with respect to their organs of respiration, unfitted them for the rough and tumble of life in the open lands with its daily and seasonal fluctuations of humidity and temperature.

The terrestrial kingdom thus passed at a later age under the aegis of two very different orders of creation, the small-brained flying insects and the large-brained vertebrates, both of them better fitted in every way to withstand the rigorous disciplines of life on dry land.

The cryptic invertebrates remained in the forests where they have so long existed, with little change in their structure or manner or life, participators in an act that has long since been played out. In their enclosed habitat they modify their immediate surroundings, the humus in which they live, but otherwise do not affect and are unaffected by the tides of life that sweep around them. They are thus of academic interest only, a tale that is told, a page of evolutionary history surviving from the past.