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Other non-marine invertebrates

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N. J. MORRIS (*British Museum (Natural History), Cromwell Road, London SW7 5BD*). Two classes of Mollusca have successfully emerged from the sea: the Bivalvia to fresh waters but the Gastropoda, in addition to invading the fresh water habitat, have also become fully air-breathing and live on the land. There is today a complete range from those taxa that are in every respect fully marine to those that are completely independent of the sea.

The possible pathways from the sea to these environments are by surviving reduced or varying salinities, which it might be assumed occur in intertidal or estuarine conditions, or by surviving periodic and increasing exposure in air, again a condition of the intertidal environment. The prerequisite for emergence from the sea must have been the presence of food. In the initial emergence this could have been provided by detritus derived from the sea and deposited along a feature such as a storm beach. Such an environment is probably important for some Ellobiidae today. To spread onto the land and into the fresh water Mollusca, as other essentially grazing or suspension feeding animals, were presumably preceded by Bacteria or plants, or both. The initial modifications to metabolic and reproductive processes, outlined by Little (1983), may have taken place high in the littoral zone, supported by detritus and, as in the Ellobiidae, remaining dependent on the sea during larval life. The expansion and radiation of the Mollusca that has followed may have been related to the increase in habitats made available by the plants.

It is interpreted from living Mollusca that the two classes have each emerged from the sea on several occasions; prosobranch gastropods as well as true pulmonates live both on the land and in fresh water. Several superfamilies of bivalves are represented in the fresh water environment while having marine relatives and, it is assumed, separate marine ancestors. Although Mollusca are preserved in increasing diversity from the base of the Cambrian, as yet, no non-marine Mollusca have been recognised before the Devonian. This might however, reflect the very great increase in the real extent of non-marine sediments of Devonian age over those of Lower Palaeozoic age.

The earliest non-marine gastropods are found in the fish beds of the Gaspé Sandstone Series, of late Lower to early Middle Devonian age in argillaceous and brecciated limestones on the South Bank of the Ristigouche River about 1 km above Campbelltown, New Brunswick, Canada. They occur with 'fish' of the family Phyllytaeniidae which are predominantly, but not exclusively, a fresh water group (Fowler 1947), together with spirorbids and plant remains. They have been described and separated as two species of '*Cyclora*' (Holopeidae) by Whiteaves (1881), *C. valvatiformis* and *C. imbricata*. An examination of additional material in the British Museum (Natural History) shows them to be very small, featureless, naticiform gastropods of unknown affinity. There is no evidence as to whether or not they are closely related to the better known and next certain non-marine gastropods from the Upper Carboniferous, recently reviewed by Solem & Yochelson (1979) of which some are confidently placed in primitive living pulmonate families.

The earliest non-marine bivalves so far discovered are from the Raglan Marl Group on the West Bank of the River Severn, Lydney, Gloucestershire, considered to be of Lower Gedinnian age: they were discovered by Professor J. R. L. Allen. Although not well preserved they seem to belong to the genus *Actinodonta* which occurs with a diverse inshore marine fauna in Wenlock times in Pembrokeshire. Higher up the Silurian succession, it normally occurs in monospecific, but still apparently marine, shell accumulations. It is, however, found in the Gedinnian as bivalved individuals in a small aggregation of just the one species, in a red silty mud that is very unlikely to have been formed in normal marine salinity.

The next occurrence of non-marine bivalves is that of *Archanodon jukesi* in the well-known Kiltorcan Plant Beds of Ireland, and their equivalents in the Catskill Hills of Eastern North America, both these are considered to be of Famennian age. Diagnostic features that might determine the taxonomic position of *Archanodon* are not well preserved. However, the overall shell shape of this large bivalve suggest that it might be related to the mytiloid genus *Modiomorpha*. It is unlikely that *Archanodon* is closely related to either *Actinodonta* mentioned above or to the non-marine bivalves of the Carboniferous which are now thought to have two quite separate origins, one in the Ambonychiacea and the other in a small species ascribed to *Sanguinolites* that may be a primitive member of the subclass Anomalodesmata (Eagar 1978).

The three Devonian examples of non-marine Mollusca mentioned above may be interpreted from their sedimentary environment to be an invasion from the sea through water of varying and sometimes lower salinity. This is in contrast to the generally accepted interpretation of the early history of the pulmonate snails, the most important of the terrestrial Molluscan groups. From the biology and habitat distribution of the primitive superfamily Ellobiacea, it is suggested that their invasion of the terrestrial environment has taken place via some intertidal environment comparable to a salt marsh or mangal, directly to the land. There is no evidence of this having taken place before the Carboniferous, although perhaps the relevant environments are just those that are seldom preserved.

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