Invasion of the metaphors

The Terrestrialization Process: Modelling Complex Interactions at the Biosphere–Geosphere Interface

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GEOLOGICAL SOCIETY OF LONDON: 2011. 187PP. £75.00

The term 'terrestrialization' has traditionally been used to describe the ecological changes that accompany the filling of lakes and bogs by sediments. In this entertaining summary of the evolution of life on land, terrestrialization refers to the invasion of the land by plants and animals from the sea, lakes and rivers. This collection of papers focuses on major evolutionary events on land from the Cambrian to the Devonian periods of geological time, around 520–354 million years ago. The transformation of land vegetation from microbial crusts to forests is a prominent theme, as is the evolutionary transition between fish and amphibians.

The boldest assertion in this collection of essays is that early tetrapods — four-limbed animals such as *Ichthyostega* — invaded the land from the sea (as opposed to from fluvial systems) during the Devonian period. This new idea is based largely on sedimentary and biogeographic evidence, superimposed on a reconstructed evolutionary tree detailing relationships between early tetrapod fossils. This same evolutionary tree is also coded to reflect the traditional view that early tetrapods evolved in rivers and floodplains, so that the differences between the marine and fluvial ideas can be assessed in the context of the great variety of transitional fossils between fish and tetrapods.

In defence of the traditional idea that tetrapods evolved in fluvial systems, it is difficult to date tetrapod fossils accurately, as revealed in a later chapter. The difficulty stems mainly from a paucity of marine fossils and geochemical indicators in the vicinity of the tetrapod remains studied so far. As subsequent chapters reveal, Devonian tetrapods come from fluvial sedimentary settings in Pennsylvania and East Greenland. The account of sedimentary structures and fossilized plants associated with the famous Greenland tetrapods *Acanthostega* and *Ichthyostega* was a delight to this armchair geologist, who has longed to see these remote regions. This new evidence counters the suggestion that tetrapods originated in the oceans, as does my own recent fieldwork in the US, Australia and Poland.

When the book turns to land plants, the metaphors of terrestrialization and the invasion of the land break down. This is particularly apparent in a chapter entitled 'Effects of terrestrialization on marine ecosystems', which argues that the drawdown of atmospheric carbon dioxide due to the evolution of land plants significantly reduced marine phytoplankton diversity. According to this chapter, the earliest non-vascular land plants appeared during the late Early Cambrian around 520 million years ago, locally displacing more ancient cyanobacterially dominated microbial crusts. Over ensuing geological periods, successive phases of vegetation included low-growing herbaceous early land plants and Devonian forests. Although the proposed Cambrian origin of non-vascular land plants is called into question in a later chapter, the evidence for such an ancient origin looks reasonable. As Stebbins and Hill proposed 32 years ago, multicellular land plants may have evolved from terrestrial unicellular creatures, rather than from successive waves of multicellular invaders from lakes and seas.

Similarly, the evolutionary innovations that led to the development of Devonian trees and seeds are considered as "cornerstones in the terrestrialization of land plants", but there is no evidence of a marine or lacustrine basis for these events. Two distinct kinds of Early Devonian tree are delineated. The anatomy of the Devonian *Callixylon-Archaeopteris* was shown by Charles Beck in the 1960s to be the template for most modern trees. But there is evidence for another kind of Devonian tree: the extinct group of plants known as the cladoxylaleans possessed a novel mode of growth, comprising vascular bundles of secondary wood. This book makes a strong case for the independent evolution of trees in at least six evolutionary lineages of early land plants. In contrast, early seed plants are regarded as a single clade, and the surprising evolutionary diversity of Devonian fossil seeds is considered evidence for adaptive radiation from a single lineage.

The Terrestrialization Process is a slim volume summarizing much data about Palaeozoic life on land, and I am glad to have it on a nearby shelf for reference. Like a good French feast, it provides both meaty and tasty courses alternating with shorter palate cleansers. It is a thought-provoking foray into an understaffed area of palaeontology that is still full of surprises.

However, the book deepens my uneasiness with the military metaphors of invasion and the conquest of terrestrial environments. My own research is showing that ancient soils were not as barren or hostile to life as is commonly assumed. An alternative analogy is that plants and animals coevolved with soils in evolutionary processes more akin to human invention than arms wars or invasions. As this book demonstrates, it is easy to be seduced by a metaphor. ❐

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