

Four legs to stand on...

Henry Gee

In *An Introduction to Dogs*, Ogden Nash wrote that man's best friend is distinguished by having "a tail on one end", adding that "up in front he has teeth" and, moreover, "four legs underneath". A more succinct definition of a tetrapod is hard to imagine, but its simplicity disguises the many assumptions, often unwarranted, that are used to reconstruct the history of life. The explosion of popular myths was a recurrent theme of a recent meeting*.

One assumption is that the first tetrapods had five-toed limbs. For example, the early tetrapod *Ichthyostega* from the Upper Devonian of Greenland is often reconstructed with five digits per limb, even though the bones of its feet have not been found. But the early amphibian *Tulerpeton* from the Soviet Union is now known to have had six digits per limb, and there are indications from material collected in 1987 and now under study in Cambridge that *Acanthostega* from the Upper Devonian of East Greenland (J. A. Clack and M. I. Coates, University of Cambridge) may also have had more than five. It now seems that the earliest tetrapods had a variable number of digits: pentadactyly is not a primitive feature of tetrapods, but a derived character that became established later on, after a period of evolutionary experimentation. The implication is that it cannot be used as a primitive feature against which to gauge the subsequent phylogenetic pattern of the tetrapods.

Aquatic origins

Other long-held assumptions about vertebrate life now seem to have been based more on phylogenetic inference than on actual fact. The presence of lungs in lungfish before the Permian, for example, is an assumption unsupported by anything besides the principle of parsimony (K. S. Thomson, Academy of Natural Sciences, Philadelphia). As with the primitively pentadactyl limb, it cannot be said with certainty that lungs were primitively present in lungfish, despite their name. Similarly, the common supposition of an aquatic habit in a stocky mammal-like reptile called *Lystrosaurus* is based on wishful thinking (G. M. King, South African Museum, Cape Town). That the many reconstructions of this well-known and common fossil form portray it as anything from hippo-like to a fully aquatic animal, complete with flippers, illustrates the power of popular reconstructions to pass as conventional wisdom.

Whereas it is hard to find any feature of

Lystrosaurus that unequivocally points to an aquatic lifestyle, ichthyosaurs were so completely adapted to the marine habit that judging their relationships with other tetrapods is extremely difficult. This task is made even harder by another kind of wishful thinking — the existence of fine impressions of fins on a number of ichthyosaur fossils turns out to owe more to the preparators' imaginations than fact (D. Martill, Open University, UK). Although many ichthyosaur fin impressions are undoubtedly real, those of dorsal fins are just the kind of appealing features that are carried over into reconstructions.

Vertebrate life began in the sea, but

beyond that the topic of vertebrate origins remains contentious. The problem is that any proposal to explain vertebrate origins is, inevitably, rooted in arguments about homology and structure that some will always dismiss as wishful thinking. It now seems that Garstang's ideas about vertebrate origins command respect chiefly through their perpetuation in numerous textbooks.

This explains why an obscure group of echinoderm-like fossils known as calcichordates was until recently regarded as marginal. But the presentation of no less than three papers describing new calcichordate forms (R. P. S. Jefferies, A. P. Cripps and P. Daley, Natural History Museum, London) signals a revival of interest in the general question of vertebrate origins (H. Gee, *Nature* 340, 596–597; 1989).

The status of conodonts in the debate

...for Devonian vertebrates

Per Erik Ahlberg

THE Middle Palaeozoic, comprising the Silurian and Devonian periods, was an important phase in the evolution of early vertebrates; they increased rapidly in numbers and diversity, jawed fishes began to replace the jawless forms and the first land vertebrates (tetrapods) appeared. Some of the reports at a meeting in Estonia* provided fresh evidence for re-interpretation of the environment inhabited by the earliest tetrapods and their fish ancestors.

Estonia was an appropriate venue for the conference. Fossil-rich Silurian and Devonian rocks underlie large parts of the Baltic States, and the Devonian vertebrate faunas of the region are among the finest and most diverse in the world. Because of the political thaw, some of the fossil sites are now accessible to Westerners for the first time in 50 years. On several occasions it was clear that Soviet and Western researchers had already more or less independently reached the same conclusions — none more so than with the environmental re-interpretation of the Old Red Sandstone.

Most Devonian fossil fish faunas, as well as the earliest tetrapods, occur in a widespread group of sedimentary facies collectively known as the Old Red Sandstone, or ORS. Some of these sediments are cross-bedded channel sands, others are finely laminated still-water deposits. They often contain plant fragments, lack typical marine invertebrates and have traditionally been interpreted as being freshwater in origin. Recently, many of the ORS fishes have turned up elsewhere in fully marine sediments, which has led to the sugges-

tion that the ORS itself might be partly marine.

There is far from general agreement over the 'marine hypothesis', but two of the papers given at the meeting lend it considerable support. Daniel Vézina (Parc de Miguasha, Canada) pointed out that the concentrations of calcium, magnesium and iron in the Canadian ORS of Escuminac (Scaumenac) Bay, an important Devonian fish locality, are typical of marine deposits. Visvaldis Kuršs (Latvian University, Riga) revealed that the extensive Baltic Middle and Upper ORS contains lingulid brachiopods and abundant phosphate deposits, both signs of marine influence. The Baltic ORS is most probably deltaic in origin; the precise environmental context of Escuminac Bay is less certain.

The re-interpretation of the Old Red Sandstone has important implications for our ideas about the origin of tetrapods, given the general assumption in the past that this event occurred in a freshwater environment. Both Escuminac Bay and the Baltic ORS contain fossils of panderichthyids, enigmatic lobe-finned fishes that are probably very close to the origin of tetrapods. Oleg Lebedev (Palaeontological Institute, Moscow) told the meeting that the Russian Upper Devonian tetrapod *Tulerpeton*, one of the earliest known, comes from deposits which are very probably deltaic or lagoonal. Could it be, then, that the first tetrapods emerged from the mudflats and brackish waters of Devonian deltas? □

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* 37th Symposium on Vertebrate Palaeontology and Comparative Anatomy, Leicester, UK, 18–22 September, 1989.

* The Second International Colloquium on the Middle Palaeozoic Fishes, Tallinn, Estonia, 11–15 September 1989.