nature

NEWS & VIEWS

PALAEONTOLOGY

Beyond the Age of Fishes

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Discovery of an unusually intact and ancient fossil fish provides further evidence that the search for modern vertebrate origins requires breaking out of the Devonian and into the preceding period.

As a rule, the earliest fossils of living groups tend to be scrappy, and such fragments lend themselves to contentious interpretations. For 'bony fishes', Osteichthyes — the division of vertebrates that includes everything from humans to halibut — the record of articulated fossils peters out within the Lower Devonian[1], some 400 million years ago. Earlier stretches of osteichthyan history are littered with fossil detritus, such as isolated teeth and scales. In certain instances, bits and pieces have been reassembled into conjectural species[2–4], some of which have surprising combinations of anatomical features[2]. On page 469 of this issue, Zhu *et al.*[5] introduce a fresh — albeit long-dead — fish into this poorly resolved patch of vertebrate evolution. Crucially, this piscine offshoot of our own distant past is both unusually intact and exceptionally old.

So what kind of fish is it? A summary of vertebrate diversity helps to make sense of the answer. Of the 51,000 or more living species of vertebrates, 99.9% have jaws: these are the gnathostomes. Gnathostomes include the bony Osteichthyes and the cartilaginous Chondrichthyes. Chondrichthyes (sharks, rays and chimaeras) account for only 2% of gnathostome species, the Osteichthyes accounting for the other 98%. Around half of the Osteichthyes are Actinopterygii, or 'ray-finned fishes', and half are Sarcopterygii, or 'lobe-finned fishes'. Actinopterygians include some 28,000 species, from zebrafish to bichirs, and living sarcopterygian fishes are limited to three genera of lungfishes and one coelacanth. Land-dwelling tetrapods constitute the remaining majority of sarcopterygians.

Thus far, the origins of these major divisions of today's gnathostomes can be traced back to the Devonian, between 416 million and 359 million years ago, the Age of Fishes. Fossils that are clearly chondrichthyan are known from around 400 million to 405 million years ago[6], but we have little idea as to whether these belong within the living radiation, the 'crown group', or represent side branches of their common ancestry, the 'stem group'. As for osteichthyans, although it is agreed that fossils from the earliest Devonian[2,7] belong within the crown, osteichthyan fragments of less-certain affinity are also known from the Late Silurian[3], 423 million to 416 million years ago.

But there's more to this story, because the question of gnathostome origins also involves a pair of extinct groups of gnathostomes known to appear earlier in the geological record, the placoderms and acanthodians[1]. Importantly, recent analyses[8] have begun to reveal new relationships between early vertebrates, in which acanthodians and placoderms are scattered among the early divisions of gnathostome evolution; acanthodians, in particular, are cropping up on chondrichthyan and osteichthyan stem groups. The straightforward message is that the origin of modern gnathostomes is not a Devonian phenomenon, after all. The basal divergence between osteichthyans and chondrichthyans occurred somewhat earlier.

This, then, is the context within which to place *Guiyu oneiros*, the new species of early osteichthyan named and described by Zhu *et al.*[5]. Preserved in 418-million-year-old limestone in what is now southern China, the fossils of *Guiyu* show the skeletal anatomy of a small sarcopterygian, around 33 centimetres long. The very fact that *Guiyu* can be identified as a sarcopterygian provides further and arguably clinching evidence that a whole series of major branching events within the gnathostome crown group must have taken place well before the end of the Silurian.

Like any other fossil, *Guiyu* is a mixture of

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Figure 1 | Newcomer to the Silurian seascape. This classic view of Silurian marine life, published in the 1940s, is rich in invertebrates (corals, molluscs, arthropods, echinoderms, and more besides). But it lacks fish. Armoured jawless fishes existed throughout the Silurian (443 million to 416 million years ago), alongside early jawed fishes (placoderms and acanthodians, extinct groups whose affinities are the subject of debate[8,10]). A representative of modern fishes, ***Guiyu oneiros***[5] (inset), can now be added to the picture. ***Guiyu*** is a Silurian-aged member of the sarcopterygians (extant representatives of which include lungfishes, the coelacanth and all tetrapods). What else might be absent? Evidence of early actinopterygians (ray-finned fishes) and chondrichthyans (sharks and chimaeras) must be lurking out there, somewhere in the Silurian sediments. (Fish reconstruction by B. Choo.)

primitive and advanced features. With regard to its anatomical completeness, *Guiyu* provides exceptional corroboration for the decidedly odd reconstruction of the early osteichthyan genus, *Psarolepis*[2]. Cobbled together from a disparate set of fossils, the incongruent suite of features[9] displayed by *Psarolepis* has been viewed with caution. Now, it turns out to be thoroughly plausible. Like *Psarolepis* and other sarcopterygian fishes (including *Latimeria*, the living coelacanth), the braincase of *Guiyu* is divided into separate front and rear units. Like *Psarolepis*, the cheek bones resemble those of early actinopterygians. Like *Psarolepis* and many other early gnathostomes[1], including at least one chondrichthyan[6], the shoulder girdle bears a spine in front of the pectoral fin. Similarly, the dorsal-fin spine and anterior spine-bearing plate of *Guiyu* are probably primitive. These are all widespread features of early gnathostomes, and seeing such characteristics in *Guiyu* provides a first glimpse of the sequential order of anatomical changes that resulted in the standard set of sarcopterygian traits.

The evolutionary tree proposed by Zhu *et al.*[5] (see Fig. 5 on page 473) adds to a growing set of analyses of early osteichthyan and gnathostome interrelationships[8,10]. Uncertainties still surround the branching pattern of non-osteichthyans, but the addition of *Guiyu* to the cast of early fishes does not change the basic pattern of interrelationships among early osteichthyans. Instead, it adds support to notable consistencies in the emerging pattern of sarcopterygian evolution, including the clustering of some of the earliest-known examples to form an as-yet unnamed group.

Finally, what does the conclusion that *Guiyu* is unequivocally sarcopterygian imply? On the whole, early fossils are thought to be unreliable as minimum-date markers of evolutionary branching events[11], because they are less complete and/or lack the full anatomical signature of the group to which they are assigned. *Guiyu* might be an exception that proves the rule, for it provides a new and exceptionally reliable earliest fossil marker for a major split in vertebrate evolution. By pushing a whole series of branching points in gnathostome evolution out of the Devonian and into the Silurian, the discovery of *Guiyu* also signals that a significant part of early vertebrate evolution is unknown (Fig. 1).

The new shape of the gnathostome tree shows that early sarcopterygians, as well as actinopterygians and chondrichthyans, ought to be turning up in Silurian sediments. But where are they? Modern fish groups have Silurian roots, but these fishes are consistently absent from existing scenarios of Silurian life. The discovery of *Guiyu* should provoke a rash of new fieldwork and a fresh look at existing collections of pre-Devonian fossils. ■

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