

# The Origin and Diversification of Osteichthyans and Sarcopterygians: Rare Chinese Fossil Findings Advance Research on Key Issues of Evolution

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Living organisms represent only 1% of all the biota that has ever existed on earth. All organisms, living or extinct, are related to each other by sharing common ancestors at different levels, like twigs and branches connected to each other at different nodes on the great tree of life. One major task for paleontologists and evolutionary biologists is to find out how the diverse groups of organisms arose and how they are related to each other, thereby reconstructing the history of life and understanding the pattern and process of evolution.

As organisms evolve and diverge from common ancestors, they fall

into a hierarchical (or “set-within-set”) pattern of groupings on the family tree, with members of each new group united by a common ancestor and characterized by novel biological features. For instance, within vertebrates, gnathostomes (or jawed vertebrates) arose as a new group when they acquired jaws as novel features, which set them apart from jawless agnathans (lampreys, hagfishes and their relatives). Within gnathostomes, four major groups developed: the bony osteichthyans (including all bony fishes and land-dwelling tetrapods) with 53,633 living species, the cartilaginous chondrichthyans (sharks, rays and

chimaeras) with 970 living species, and the long-extinct placoderms and acanthodians. Within osteichthyans, the actinopterygian lineage (with 26,981 living species) includes sturgeons, gars, teleosts and their relatives, while the sarcopterygian lineage (with 26,742 living species) includes lungfishes, coelacanths (*Latimeria*), their extinct relatives as well as all land-dwelling tetrapods (amphibians, reptiles, birds, and mammals) (Fig.1).

The quest for their origins has fascinated the human mind since the dawn of history. For many years, scientists have puzzled over questions such as: When and how did

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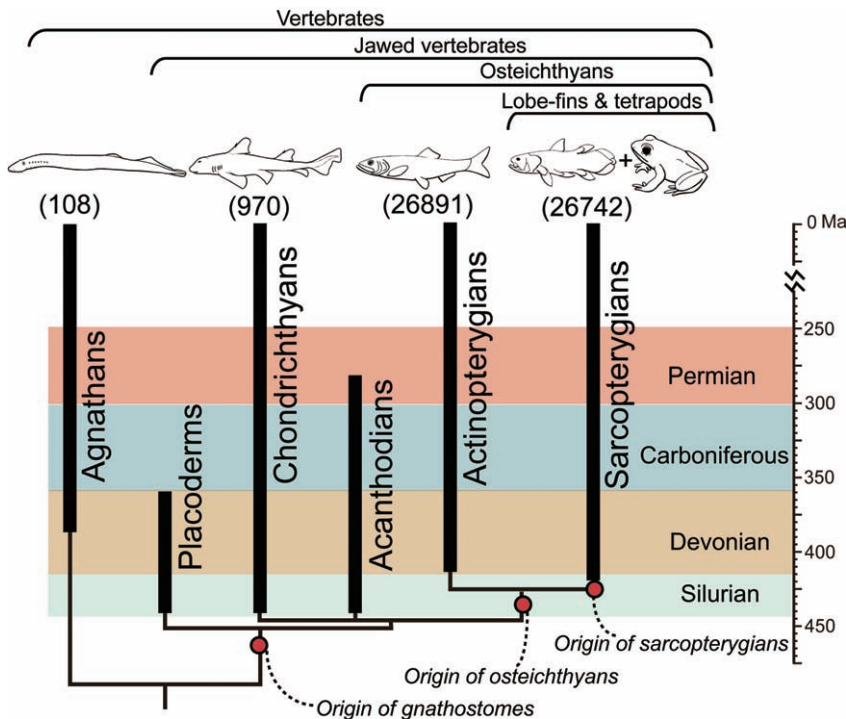


Fig. 1 The family tree and geological time range of major vertebrate groups. Numbers of living species (in brackets) indicate the relative abundance and diversity of the four living groups (Nelson, 2006).

gnathostomes arise? What would the common ancestor of all osteichthyans look like? How do osteichthyans relate to chondrichthyans, placoderms and acanthodians? How did osteichthyans diverge into the actinopterygian and sarcopterygian lineages? When and where did sarcopterygians arise and diverge? How did some sarcopterygian fishes eventually give rise to land-dwelling tetrapods, which include humans? These and related questions not only lie at the center of evolutionary research but also have broad implications for science in general. Because of recent fossil fish findings from China, the global study on these key areas of vertebrate evolution has made significant progress and is now at the threshold of an exciting breakthrough in the near future.

The most significant fossil fish finding from China is *Guiyu*, the oldest near-complete gnathostome fossil found from the 419-Myr-old muddy limestone in eastern Yunnan

(Zhu *et al.*, 2009; Fig. 2).

*Guiyu* (“ghost fish”) gets its name because of its ghostly or bazaar combination of morphological characters. Within gnathostomes, *Guiyu* sides with osteichthyans by bearing derived macromeric scales, yet it resembles non-osteichthyan chondrichthyans, placoderms and acanthodians by having a primitive pectoral girdle and median fin spine. Within osteichthyans, *Guiyu* sides with sarcopterygians by having a two part braincase with a movable joint in the middle (plus other cranial features), yet it resembles early actinopterygians by having ornamented ganoine surface covering and by the shape of its cheek and operculo-gular bones. Computerized analysis of morphological characters places *Guiyu* as an osteichthyan in the basal segment of the sarcopterygian lineage (Zhu *et al.*, 2009; Fig.3). Three other fossil fishes from Yunnan (*Meemannia*, *Psarolepis* and



Fig. 2 Reconstruction of “ghost fish” *Guiyu* as it may have lived in the Silurian waters 419 million years ago. *Guiyu* represents the earliest near-complete fossil gnathostome and fossil osteichthyan record.

Picture courtesy of Brian Choo (Victoria Museum, Australia).

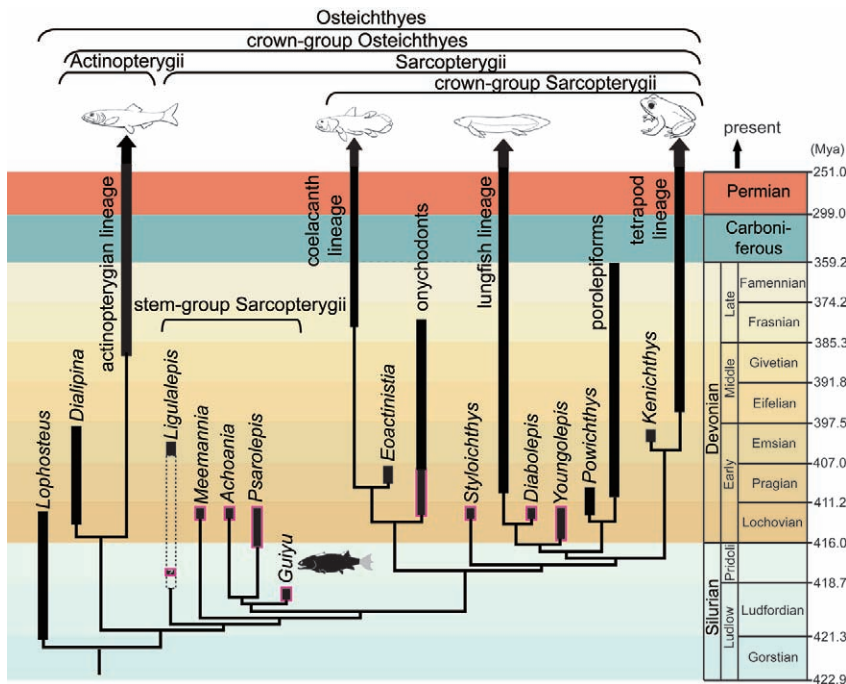


Fig. 3 The family tree and geological time range of “ghost fish” *Guiyu* and other important early osteichthyans from China. Of the nine Late Silurian or earliest Devonian (Lochkovian) sarcopterygians, eight (framed in red) come from South China, suggesting that this region was once a center of origin and diversification for early sarcopterygians.

*Achoania*) cluster with *Guiyu* as basal or stem sarcopterygians, but they come from younger ages and consist of less complete materials when compared with *Guiyu*. The earliest geologic time of appearance, a near-complete preservation of whole body structures, and a unique combination of gnathostome vs non-gnathostome characters as well as sarcopterygian vs actinopterygian characters—all these make *Guiyu* highly significant for the global study on the origin of gnathostomes, the origin and diversification of osteichthyans, and the origin and diversification of sarcopterygians.

First, *Guiyu* provides critical fossil record to calibrate the molecular clock regarding the divergence time between two major osteichthyan lineages (*i.e.*, actinopterygians and sarcopterygians). While modern biologists can determine the amount of molecular differences separating different living groups, this information can serve as a useful molecular clock only when it is

calibrated by using fossils as specific historical time markers. *Guiyu* as a basal member of sarcopterygians has an accurate dating based on the Silurian conodont zonation (419 million years old), and this indicates that the minimal estimated time for the actinopterygian–sarcopterygian split must be at least 419 million years ago (instead of the previously 416-million-year-old estimate based on *Psarolepis*—another important early sarcopterygian fossil from Yunnan). With this new calibration, the molecular clock is now more accurate than before in gauging the time dimension for accumulated molecular changes between different living groups.

Second, *Guiyu* (together with seven other early sarcopterygians from the Silurian and earliest Devonian strata of southern China) establishes the paleobiogeographic importance of ancient South China region as a center of origin and diversification for sarcopterygians. So far, Yunnan has yielded eight out of the nine

Late Silurian or earliest Devonian (Lochkovian) sarcopterygians, including four stem sarcopterygians (*Guiyu*, *Meemannia*, *Psarolepis* and *Achoania*) and four forms near the base of major subgroups of sarcopterygians (*Styloichthys*, *Diabolepis*, *Youngolepis* and an unnamed onychodont). During the Late Silurian–Lochkovian periods (about 411–422 million years ago), the South China region was a separate continent adjacent to eastern Gondwana, and its vertebrate fauna as a whole was highly endemic to the region, indicating little or no exchange between this region and other areas before the Middle Devonian period (397 million years ago). It was in this isolated or semi-isolated environment that major events in early sarcopterygian evolution unfolded and two subgroups developed, one giving rise to living lungfishes while the other giving rise to all tetrapods, including humans (Fig. 3).

Third, *Guiyu* provides the most complete morphological information for establishing the morphotype (or primitive morphological model) of early gnathostomes, osteichthyans and sarcopterygians. Based on the morphotype for each major group, paleontologists can generate hypotheses about the sequential order of morphological changes from the origin of a group to specific evolutionary events in history, such as the branching of lineages or the conquering of new environments by new groups.

Gnathostomes may have first appeared in the Late Ordovician (more than 444 million years ago), but non-osteichthyan groups (chondrichthyans, placoderms and acanthodians) left little or no complete fossil specimens before the Early Devonian period. Similarly, previously known osteichthyan fossils from the Late Silurian are fragmentary and their lineage assignment is uncertain. Thus, *Guiyu* represents the earliest near-

complete gnathostome and the earliest near-complete osteichthyan fossil known to science. Although other important osteichthyan fossils (*Meemannia* and *Psarolepis* from Yunnan, *Ligulalepis* from Australia, and *Dialipina* from the Canadian Arctic) have recently narrowed the morphological gap between different groups, they are mostly based on less complete materials and therefore are not as convincing as *Guiyu* in establishing the morphotype of early sarcopterygians and early osteichthyans. *Guiyu* provides a classical textbook case showing how scientific hypotheses can be tested through new discoveries. Before the discovery of *Guiyu*, the restoration of many features of *Psarolepis* (“speckled scale”) was sometimes regarded as weak inferences because of the isolated and disparate nature of fossil materials. The near-complete restoration of *Guiyu* (pending the discovery and description of complete *Psarolepis* specimen) provides the best possible authentication for most reconstructed features of *Psarolepis* (Yu, 1998; Zhu & Schultze, 1997; Zhu *et al.*, 1999). Together with *Psarolepis*, *Meemannia* and other forms, *Guiyu* makes it possible to interpret features found in early members of both lineages (actinopterygians and sarcopterygians) in the common framework of deep osteichthyan phylogeny. *Guiyu* shows that the early sarcopterygians and actinopterygians retain widespread primitive osteichthyan and gnathostome features, such as the cheek and operculo-gular bone pattern and the anterodorsal process of the scale.

Lastly, *Guiyu* provides paleontologists with a new research agenda to focus more research resources and efforts on finding pre-Devonian osteichthyan fossils. *Guiyu* (and *Psarolepis*) suggest that early osteichthyans might carry median fin spine and spine-bearing pectoral girdles previously thought

to exist only in non-osteichthyan groups. Consequently, many pre-Devonian spine-like materials can now be reexamined (and possibly reinterpreted) in the light of *Guiyu* and *Psarolepis*.

*Meemannia* (named in honor of Prof. Chang Meemann) is another fossil fish from Yunnan that has contributed significantly to the understanding of sarcopterygian evolution (Zhu *et al.*, 2006). Typical or crown sarcopterygians are characterized by a special and now extinct tissue known as cosmine. Lack of similar tissue in living vertebrates and the previous lack of rudimentary forms of this tissue presented a major obstacle for scientists to understand its mode of origin and its function. Typical cosmine is found only in certain extinct sarcopterygians and consists of a pore-canal network embedded in mineralized dentine units and enamel. Like its mosaic morphological features, *Meemannia* reveals previously unknown histological features intermediate between the typical cosmine tissue (found in later sarcopterygians) and the ganoine-like tissues (found in actinopterygians and some acanthodians). *Meemannia* suggests a stepwise mode of origin for cosmine and lends support to the biological interpretation of the pore-canal network as a vascular system supporting mineral deposition and resorption. Because of their sequential position on the early sectors of the sarcopterygian family tree, the cluster formed by *Meemannia*, *Guiyu*, *Psarolepis*, *Achoania* and *Styloichthys* (Fig. 3) provides scientists with unprecedented record of character changes that helps to explain how sarcopterygians arose and eventually developed into the two later lineages, one leading to lungfishes, and the other leading to tetrapods, including humans.

In addition, these and other significant Chinese fossil fishes from Yunnan have become the

“superstars” among paleontologists for many other reasons. For instance, *Youngolepis* (named after late Prof. Young Chungchien, pioneer of vertebrate paleontology in China) is an early occurring member (about 415 million years old) of the crown sarcopterygian group (Fig. 3), and is one of the few osteichthyan fossils whose internal brain structures have been studied using 3-D reconstructions of serial grinding materials (Chang, 1982; Chang & Yu, 1981). *Kenichthys* (named in honor of Prof. Ken Campbell of Australia) and *Diabolepis* (“devil scale”) are respectively the earliest members of the lineages leading to all tetrapods and leading to modern-day lungfishes (Chang & Yu, 1984; Chang & Zhu, 1993). Both *Kenichthys* and *Diabolepis* played a critical role in illuminating how tetrapods and lungfishes may have acquired their internal nostrils (or choana) as novel evolutionary features (Zhu & Ahlberg, 2004). Internal nostrils serve a vitally important function for all air-breathing animals (including humans), and its origin has puzzled paleontologists since the beginning of the 20<sup>th</sup> century. *Styloichthys* (“pillar fish”) shows what the common ancestor of modern-day lungfishes and tetrapods may have looked like and helps to explain the sequence in which the lungfish lineage and the tetrapod lineage acquired their respective characters (Zhu & Yu, 2002). *Achoania* (“without choana or internal nostrils”) is closely related to *Psarolepis* and suggests that early or stem sarcopterygians may have had an eyestalk as found in sharks and rays (chondrichthyans) and extinct placoderms (Zhu *et al.*, 2001). Last but not least, *Qingmenodus* represents one of the earliest known onychodonts (a subgroup of sarcopterygians distantly related to coelacanth) and helps to show how this ancient fish may have had the same feeding mechanism as the famous modern day living fossil

*Latimeria* (Lu & Zhu, 2010).

The paleobiological roles of these fossil fish findings cannot be fully understood without detailed study of the associated faunas as a whole. Two significant vertebrate faunas have been established: the Late Silurian Xiaoxiang fauna and the Early Devonian Xitun fauna. In addition to *Guiyu*, *Psarolepis* and other (mostly microscopic or incomplete) remains of osteichthyans, the Xiaoxiang Vertebrate Fauna includes galeaspid agnathans, acanthodians, and diversified primitive placoderms.

The research on the Xiaoxiang Vertebrate Fauna will significantly improve our understandings of early diversification of gnathostomes, especially when the morphological repertoire of acanthodians and the various primitive placoderms can be fully deciphered and analyzed in light of the new paradigm regarding the origin of osteichthyans from non-osteichthyan groups. The Early Devonian Xitun Vertebrate Fauna is characterized by the radiation and rich diversity of typical or crown-group placoderms and crown-

group sarcopterygians (Zhao & Zhu, 2010). Given the exquisitely preserved fossils with fine-scaled stratigraphic control, study on the Xitun Vertebrate Fauna promises to yield productive results regarding the rapid diversification events responsible for the appearance of crown-group sarcopterygians. All this will provide a necessary framework to generate new hypotheses regarding the paleoenvironmental and paleogeographic aspects of this exciting chapter in the distant history of vertebrate evolution.

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