# ARTICLES

# The oldest articulated osteichthyan reveals mosaic gnathostome characters

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The evolutionary history of osteichthyans (bony fishes plus tetrapods) extends back to the Ludlow epoch of the Silurian period. However, these Silurian forms have been documented exclusively by fragmentary fossils. Here we report the discovery of an exceptionally preserved primitive fish from the Ludlow of Yunnan, China, that represents the oldest near-complete gnathostome (jawed vertebrate). The postcranial skeleton of this fish includes a primitive pectoral girdle and median fin spine as in non-osteichthyan gnathostomes, but a derived macromeric squamation as in crown osteichthyans, and substantiates the unexpected mix of postcranial features in basal sarcopterygians, previously restored from the disarticulated remains of *Psarolepis*. As the oldest articulated sarcopterygian, the new taxon offers insights into the origin and early divergence of osteichthyans, and indicates that the minimum date for the actinopterygian–sarcopterygian split was no later than 419 million years ago.

Osteichthyans, which fall into two major monophyletic groups, namely actinopterygians (bichirs, sturgeons, gars, bowfins and teleosts) and sarcopterygians (coelacanths, lungfishes and tetrapods), make up 98% of recognized living vertebrate species[1]. The rise of osteichthyans from other primitive gnathostomes is a key transition in vertebrate evolution, yet this transition is poorly documented by the fossil discoveries of the last century[2]. Major morphological gaps existed between actinopterygians and sarcopterygians, and between osteichthyans and non-osteichthyan gnathostomes (chondrichthyans, acanthodians and placoderms). The past decade has seen the gap narrowing with fossil discoveries such as *Psarolepis*[3–5], *Ligulalepis*[6,7] and *Dialipina*[8], which show fascinating combinations of osteichthyan and non-osteichthyan gnathostome characters, providing new opportunities for studying the polarity and evolution of these characters. However, the basal osteichthyan phylogeny remains uncertain[4,6,9–11] owing to the large number of unknown character states in these early forms and the provisional assignment of disarticulated remains to a single taxon. A better understanding of these fishes is therefore crucial in reconstructing the part of phylogeny close to the split between actinopterygians and sarcopterygians.

The fossil record of osteichthyans extends back to the Ludlow epoch of the Silurian period, ~422 million years (Myr) ago[2,11], yet is documented by fragmentary fossils[12–17]. *Dialipina salgueiroensis* from the Emsian of the Canadian Arctic[8] (~400 Myr ago, *serotinus* conodont zone[18]), referred to the actinopterygians[2,8,9,11,19] or stem osteichthyans[10], represents the oldest articulated and complete osteichthyan known thus far. Two articulated stem lungfishes, *Porolepis* from Spitsbergen[20] and *Uranolophus* from Wyoming[21], are older (Pragian, ~411 Myr ago) but less complete than *D. salgueiroensis*. *Psarolepis* from the latest Pridoli to the Lochkovian of China and Vietnam[3–5,17,22] is another early osteichthyan with the postcranial condition partially known, albeit based on disarticulated remains. Its tentative reconstruction[4] shows an enigmatic fish bearing mosaic gnathostome features, but the association of parts from different individuals requires testing against articulated specimens.

The new articulated fish from the Silurian of China closely resembles *Psarolepis* in cranial features, although it bears ridged ornamentation,

as present in basal actinopterygians, rather than the cosmine of early sarcopterygians[9]. This discovery extends the earliest record of near-complete articulated osteichthyans to at least 8 Myr earlier in geological history, and significantly enhances our growing knowledge of the origin of osteichthyan morphology.

## Geological framework

The new fish material was recovered from the muddy limestone of the Kuanti Formation immediately beneath the first appearance point of *Ozarkodina crispa*[23] at a locality near Xiaoxiang Reservoir, Qujing, Yunnan, China (Fig. 1). The marine Silurian strata in Qujing are subdivided into four formations in ascending order: the Yuejiashan, Kuanti, Miaokao and Yulungssu formations[24–26]. Early fishes are recorded from the sequence in association with rich invertebrates such as corals, brachiopods, cephalopods, ostracods, bryozoans and trilobites[25], and include *Psarolepis*, an indeterminable osteichthyan from the Yulungssu Formation[15,17], and two 'actinopterygians' *Naxilepis gracilis* and *Ligulalepis yunnanensis* from the Miaokao and Kuanti formations[16]. The latter three forms are only represented by scales, and the assignment of *Naxilepis* and *L. yunnanensis* to the actinopterygians is doubtful due to the meagreness of available data. The new fish is found from the bed ~140 m below the lowest occurrence of *Naxilepis*, thereby representing the earliest record of osteichthyans in China. The fish fauna (here named the Xiaoxiang fauna, characterized by the early diversification of gnathostomes) from the site also includes the agnathans, placoderms and acanthodians under study. The late Ludlow (Silurian) age of the new fish bed is mainly derived from the conodont zonation[27], although the earlier age assessment (early Ludlow or late Wenlock) of the Kuanti Formation had been proposed based on invertebrate or vertebrate assemblages[25,26,28].

Osteichthyes Huxley, 1880
Sarcopterygii (Romer, 1955)
*Guiyu oneiros* gen. et sp. nov.

**Etymology.** The generic name derives from *gui* (Chinese Pinyin), meaning ghost or secret, and *yu* (Chinese Pinyin), meaning fish.

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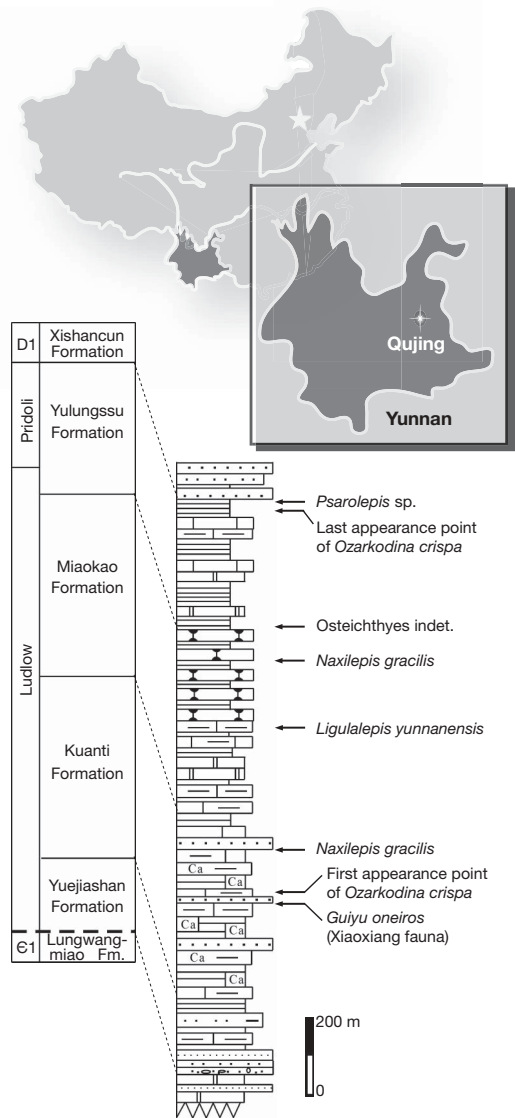
**Figure 1 | Summary Silurian sequence in Qujing (Yunnan, China), showing the stratigraphic positions of *Guiyu oneiros* gen. et sp. nov. and other bony fishes.** The stratigraphic data are taken from ref. 25.

The specific name is from the Greek *oneiros*, dream, alluding to a dream fish with mosaic gnathostome characters.

**Holotype.** IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V15541, a near-complete fish in part and counterpart.

**Referred material.** Skulls, V15542.1-6; lower jaws, V15542.7-13; scales, V15542.14-16.

**Horizon and locality.** Late Ludlow, Silurian, Kuanti Formation; Qujing, Yunnan, China.

**Diagnosis.** *Guiyu* differs from *Psarolepis*[3–5,17] and *Achoania*[29,30] in its ganoine sculpturing of dermal skeleton, anterior nostril without dermintermedial process, no teeth on median rostral, premaxillary without inturned symphyseal process, presence of prerostral bone, dentary teeth reaching anterior end of lower jaw, and lacking infradentary foramina.

## Description

The holotype in its part and counterpart represents an articulated and three-dimensionally preserved bony fish lacking only the caudal fin (Figs 2a, b and 3a, b). The dermal bones and large rhomboid scales are ornamented with ganoine sculpturing of coarse, irregular or patterned longitudinal ridges (Supplementary Information 2, section 9), characteristic of lower actinopterygians[8,19,31–34] and *Ligulalepis*[6,7,35]. The ganoine-like tissue is also present in the surface covering of acanthodians and sarcopterygians, suggesting that ganoine might be plesiomorphic for crown osteichthyans[36]. The fish has a preserved length of ~26 cm and a preserved maximum depth (although laterally compressed and distorted) of ~11 cm. The head occupies about 23% of the total body length (to the base of the caudal fin), and the body is about 2.5 times as long as it is deep, giving *Guiyu* a fusiform streamlined appearance.

The skull roof is divided into the parietal and postparietal shields by the dermal intracranial joint (Fig. 4a). The parietal shield is about as wide as it is long, and has the supraorbital sensory canal medial to the anterodorsally facing anterior nostril. The dermal bone pattern is more evidently shown in several isolated skull specimens (for example, V15542.1, Fig. 4b). Unlike *Psarolepis* and *Achoania*, the large median rostral does not form the outer dental arcade, and the premaxillary lacks the obvious inturned symphyseal process in anterior view (Fig. 4c). A separate triangular bone (preorbital, Fig. 4c) posterodorsal to the premaxillary, rather than the posterodorsal process of the premaxillary, encloses the posterior nostril; this resembles *Onychodus*[37] and possibly *Achoania*[29] but differs from *Psarolepis*[3]. The 'lacrimal' in *Onychodus*[37], which has a more anterior position than the lacrimal of rhipidistians[2], might be homologous with the preorbital of actinopterygians and *Guiyu*. Noteworthy is an unpaired tooth-bearing bone behind the premaxillaries in ventral view (Fig. 4e, f). This bone has never been found in known osteichthyans, yet topologically corresponds to the prerostral or premedian plate of placoderms[2,38]. The postparietal shield is as long as the parietal shield, as in some later sarcopterygians[38]. In *Psarolepis*, the parietal shield is about 1.5 times the postparietal shield in length. The middle and posterior pit-lines lie close to the midline of the shield, and the otic canal runs through the supratemporal and tabular, and connects the supratemporal commissural canal in the lateral extrascapular (Fig. 2b). Anterior to the extratemporal—which is a small bone lateral to the tabular and the anterior half of the lateral extrascapular—an elongate bone between the supratemporal and the opercular represents an accessory extratemporal. Three extrascapular bones are situated behind the postparietal shield; this resembles onychodonts and rhipidistians but differs from actinopterygians and most coelacanths.

Concerning the neurocranial features, *Guiyu* shows a striking resemblance to *Psarolepis*, *Achoania* and *Onychodus*. They share large pear-shaped internasal cavities, a long and narrow internasal septum in front of a small triangular parasphenoid, and the same position of ethmoid articulation on the postnasal wall (Fig. 4e, f). The neurocranium of *Guiyu* is much less ossified than that of *Psarolepis* and *Achoania*, raising difficulties in locating the anatomical structures on its lateral sides (Supplementary Information 2, section 7). However, the postorbital pillar is distinguishable as a bridge connecting the basipterygoid process and the side of the neurocranium.

The dermal bones of the cheek and operculo-gular system show a similar pattern to those of early actinopterygians[31,32], *Psarolepis* and onychodonts. Three branchiostegal rays on the left side are preserved below the big opercular and subopercular bones. The large gular bones occupy most of the space between the lower jaws as in *Onychodus*. The lower jaws of the holotype are anteriorly dislocated and broken in their upper half; however, the posterior extremity of the left lower jaw retains its natural position to the upper jaw. As supplemented by some isolated specimens (Fig. 4g, j–m), the lower jaw of *Guiyu* is nearly identical in shape to that of *Psarolepis*, and is anteriorly reflexed. The mandibular sensory canal pierces through four infradentaries, leaving a series of openings on the external surface. Posteriorly, a shallow area devoid of ornamentation represents the part of the lower jaw overlapped by the maxillary, as in early sarcopterygians[30]. In early actinopterygians, this area is usually more extensive[32]. The dentary bears a row of sharp, conical but slender teeth on the dorsal margin
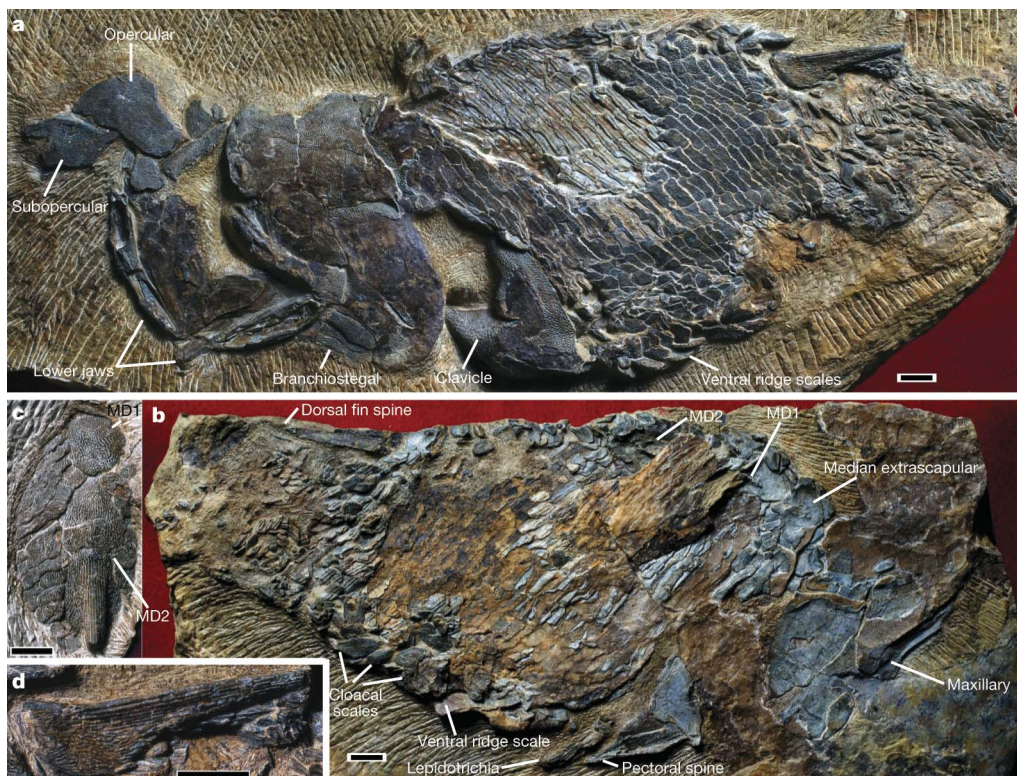
**Figure 2 | *Guiyu oneiros* gen. et sp. nov., holotype V15541. a, b,** A near-complete fish in part and counterpart. **c,** Close-up view of the anterior portion of the trunk shield in dorsal view, showing MD1 and MD2 flanked by rhomboid scales. **d,** Close-up view of the dorsal fin spine. MD1, first median dorsal plate; MD2, second median dorsal plate. Scale bar, 1 cm.

interior to a band of smaller tooth-like denticles that are present in *Lophosteus*, *Andreolepis*[11] and many crown osteichthyans. Each marginal tooth has a large pulp cavity extending close to the tip, and lacks the acrodin (Supplementary Information 2, section 9c, e). *Guiyu*

resembles *Psarolepis* in having five coronoids separating the dentary and prearticular bones, a supporting Meckelian lamina for the para-symphyseal tooth whorl (albeit less ossified and developed), and a relatively short adductor fossa. The second to fourth coronoids carry
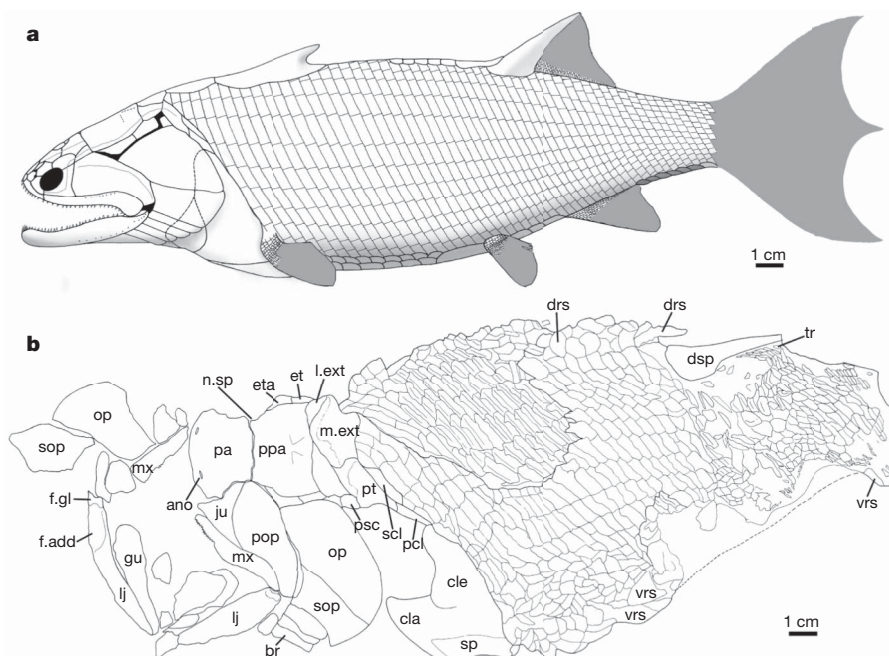


**Figure 3 | *Guiyu oneiros* gen. et sp. nov. a,** Restoration of the entire fish in lateral view. **b,** Interpretive drawing of the holotype V15541. Areas shaded in grey are unknown, and are reconstructed from other early osteichthyans[8,37]. ano, anterior nostril; br, branchiostegal ray; cla, clavicle; cle, cleithrum; drs, dorsal ridge scale; dsp, dorsal fin spine; et, extratemporal; eta, accessory extratemporal; f.add, adductor fossa; f.gl, glenoid fossa; gu, gular; ju, jugal; l.ext, lateral extrascapular; lj, lower jaw; m.ext, median extrascapular; mx, maxillary; n.sp., spiracular notch; op, opercular; pa, parietal shield; pcl, postcleithrum; pop, preopercular; ppa, postparietal shield; psc, presupracleithrum; pt, post-temporal; scl, supracleithrum; sop, subopercular; sp., pectoral spine; tr, lepidotrichia; vrs, ventral ridge scale.
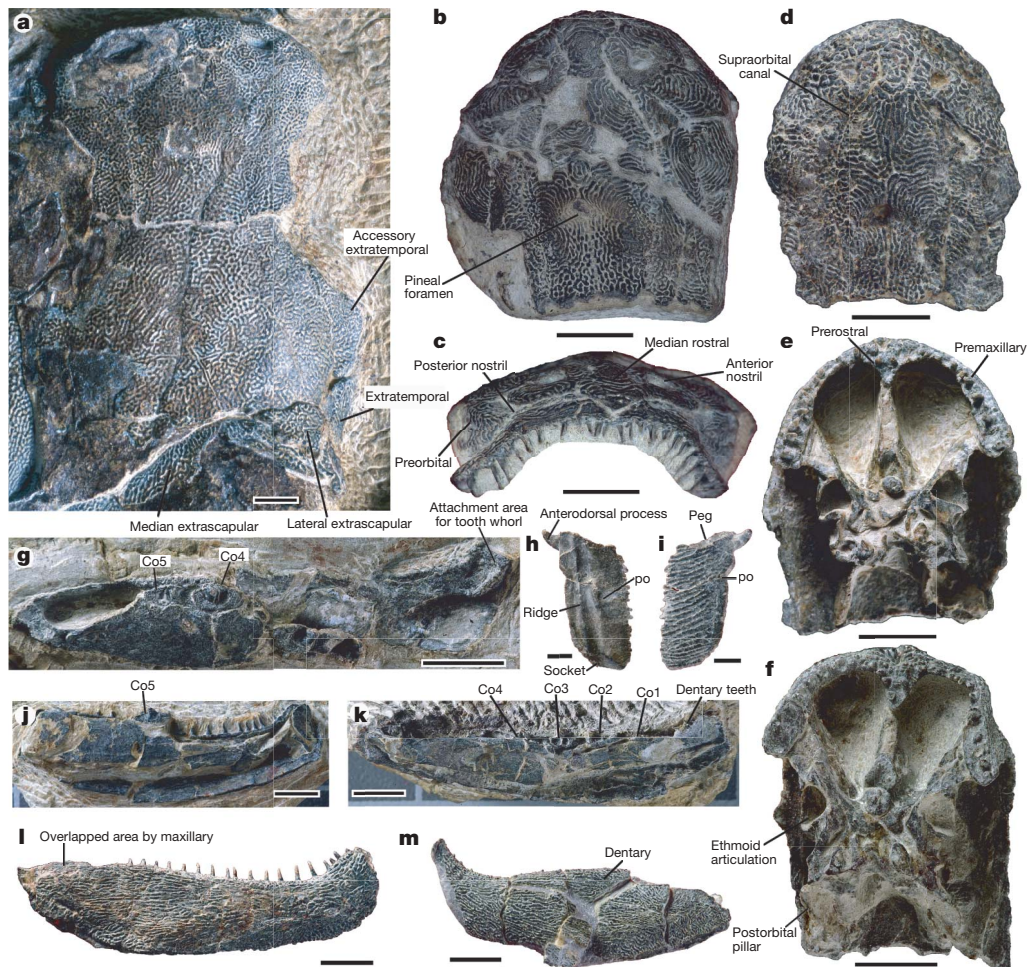
**Figure 4 | *Guiyu oneiros* gen. et sp. nov. a,** Close-up view of the head in dorsal view, holotype V15541. **b–f,** Isolated anterior cranial portions: **b, c,** dorsal and anterior views (V15542.1); **d, e,** dorsal and ventral views (V15542.2); **f,** ventral view (V15542.3). **g,** A lower jaw in internal view, V15542.7. **h, i,** An isolated scale in internal and external views, V15542.14. **j–m,** Lower jaws: **j,** internal view (V15542.8); **k,** internal view (V15542.9); **l,** external view (V15542.10); **m,** external view (V15542.11). Co1–5, first to fifth coronoid; po, pore of lateral line. Scale bar: 2 mm (**h, i**); 5 mm (**a–g, j–m**).

large tusks and a narrow lateral band with 2–4 denticle rows. The tusk has a simple histological structure and lacks any in-folding of dentine near its root, as documented by the fractured surfaces (Supplementary Information 2, section 9f, g).

The pectoral girdle of *Guiyu* is remarkable in its separate fin spine (Fig. 2b), as in *Psarolepis*[4,5], the early chondrichthyan *Doliodus*[39], placoderms and acanthodians[2]. A small bone (psc, Fig. 3b) in front of the post-temporal corresponds to the presupracleithrum of early actinopterygians[32,33]. The extensive postbranchial lamina is covered with posteriorly pointed tubercles as in *Psarolepis*, actinopterygians and placoderms. Immediately behind the median extrascapular, the postcranial skeleton is conspicuous in having two large median dorsal plates (MD1, MD2, Fig. 2a, c) that are flanked by rhomboid scales. The first median dorsal plate, as large as the median extrascapular, is about one-third of the second median dorsal plate in length. In internal view, each of these three unpaired bones bears a keel structure as in the median dorsal plate of placoderms[2,40]. In external view, the second median dorsal plate bears a posterodorsally directed spine, like the median dorsal spine of some antiarch placoderms[40]. The median dorsal plates resemble the median ridge scales or fulcral scales preceding the bases of median fins in basal actinopterygians[32,33,41]. However, they differ in that the ridge scales are much smaller and lack strong keel structure. Although the scutes of sturgeons are like the ridge scales, they are obviously derived for actinopterygians[41,42].

The dorsal fin spine is exceptional in its association with other parts of the body (Fig. 2a, b, d), and forms the leading edge of the dorsal fin. It consists of a stout base with vermiform ridges and a slender,

recurved spine ornamented with about eight longitudinal ridges. Its position in the rear half of the body indicates that the unpaired fin spine of *Psarolepis*[4,17] might be more posteriorly located than previously restored. No fin spine is found for the pelvic and anal fins. A large median ridge scale precedes the dorsal fin spine. Along the ventral surface of the body, a similar large ridge scale is found at a position anterior to the level of the pelvic fins. Between this large scale and the base of the pectoral fin, there are many oval ridge scales. The anal fin is not far from the pelvic fins, and between them are a few paired, elongate, oval cloacal scales (Fig. 2b) as present in *Moythomasia*[32]. The presence of a narrow ventral ridge scale at the posterior end of the holotype is similar to those found near the lower hypochordal lobe of basal actinopterygians and indicates the position of the missing caudal fin. The lepidotrichia are partially preserved in the holotype (Fig. 2a). The large rhomboid flank scales are arranged into at least 30 vertically oriented rows from the median extrascapular to the base of the dorsal fin spine. They bear a prominent anterodorsal process, and are ornamented with linear ridges that terminate in up to 30 posterior serrations. Internally, the scales show the peg-and-socket articulation and dual ridges as in *Ligulalepis*[35]. The isolated lateral-line scales were found in the collection (Fig. 4g–i); however, the path of the lateral line is faintly outlined in the flank of the holotype.

## Phylogenetic relationships

To determine the placement of *Guiyu* and its impact on osteichthyan relationships, we constructed a new data matrix of 153 characters and

23 taxa including three non-osteichthyan taxa (*Acanthodes*, an acanthodian, *Akmonistion*, a chondrichthyan, and *Dicksonosteus*, a placoderm), mainly revised from references [9, 10, 29, 43]. Phylogenetic analysis (Supplementary Information 1) yields a single most parsimonious tree of length 292, in which *Guiyu* is placed as the sister taxon to the clade comprising *Psarolepis* plus *Achoania*. *Meemannia* and *Ligulalepis* form successively more basal taxa among the Sarcopterygii. *Lophosteus* and *Andreolepis* represent the stem osteichthyans, and *Dialipina* forms the most basal taxon among the Actinopterygii.

### Dating the actinopterygian–sarcopterygian split

The fossil record provides a key means of molecular clock calibration[44,45]. A minimum constraint on the divergence of actinopterygians and sarcopterygians was previously based on the lowest occurrence of crown osteichthyan *Psarolepis* from the top of the Yulungssu Formation[4,17,45] (Fig. 1), dating close to the Silurian/Devonian boundary, ~416 Myr ago. The discovery of *Guiyu*, with accurate dating based on Silurian conodont zonation, provides a new minimum date for molecular-clock-based estimates of the osteichthyan crown node (Fig. 5). As the earliest known, yet not most basal, member of the crown osteichthyan lineage, *Guiyu* lived ~419 Myr ago; thus, the actinopterygian–sarcopterygian split must have occurred no later than this time.

### The mosaic of gnathostome characters in *Guiyu*

Gnathostomes have their possible earliest occurrence in the Late Ordovician[2,46]. The Silurian has yielded definite but fragmentary gnathostome remains, with the only articulated representative being a possible acanthodian from Australia[47] that merely preserves the middle part of the body and adds little novel data to early gnathostome morphology. Until now, the oldest known near-complete gnathostomes were represented by diverse acanthodians[2] and an antiarch placoderm[48] from the earliest Devonian (Lochkovian). The discovery of *Guiyu* provides not only the exceptional corroboration of weak inferences based on disarticulated remains attributed to *Psarolepis* or *Lophosteus*, but also the near-complete restoration of a

primitive fish with mosaic gnathostome characters. The trunk shield of early osteichthyans, including *Andreolepis*, *Ligulalepis* and *Meemannia*, might bear median fin spine and spine-bearing pectoral girdle as well. Isolated remains that were found in association with these early osteichthyans and referred to non-osteichthyan groups should be reviewed in the light of *Guiyu*.

The phylogenetic position of *Guiyu* and related taxa has a substantial impact on the understanding of key osteichthyan apomorphies. Our phylogenetic scenario, although it should be approached with some caution considering the lower Bremer indices at several nodes, offers new insights into the incremental acquisition of osteichthyan apomorphies, and suggests considerable parallelism between actinopterygians and sarcopterygians. For instance, the placement of *Ligulalepis* at the base of the Sarcopterygii conforms to the notion that its neurocranium reveals the primitive osteichthyan condition[6,7]. *Guiyu*, as well as *Psarolepis* and *Achoania*, is more derived with regard to its dermal and endoskeletal intracranial joints, although it shares many primitive features with non-osteichthyan gnathostomes. The resemblance of the cheek and operculo-gular bone pattern between actinopterygians and stem sarcopterygians denotes a primitive condition for osteichthyans. The anterodorsal process of the scale might be a synapomorphy of crown osteichthyans rather than the actinopterygians.

The discovery of *Guiyu* offers an exceptional example of a primitive fish close to the split of crown osteichthyans. However, our understanding of the stem section of the Osteichthyes phylogenetic tree still remains vague owing to the rarity of relevant fossils. More evidence on Silurian placoderms, acanthodians, chondrichthyans and the fragmentary osteichthyan taxa that are basal to *Guiyu* will provide tests of the present phylogeny and document further the origin of the Osteichthyes.

### METHODS SUMMARY

We adopted the traditional apomorphy-based definition of the Osteichthyes[2], considering the unresolved deep phylogeny of gnathostomes. Phylogenetic analysis was performed in PAUP4.0b10 (ref. 49) using a branch-and-bound search with default setting, with *Dicksonosteus*, *Akmonistion* and *Acanthodes* specified as the outgroup. Life reconstruction (Supplementary Information 3) was drawn by B. Choo (Victoria Museum) through communication with M.Z.
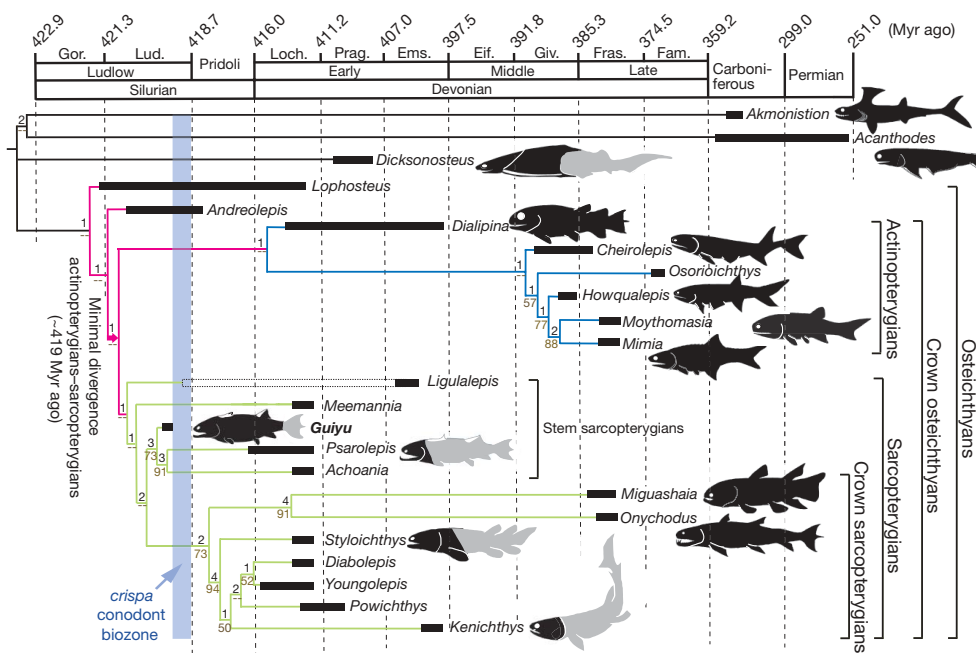


**Figure 5 | Timing of earliest evolution of the Osteichthyes.** The topology is the most parsimonious tree arising from a matrix of 23 taxa coded for 153 morphological characters (tree length = 292, consistency index = 0.572, retention index = 0.737, rescaled consistency index = 0.421). The numbers at nodes indicate bootstrap support (where the value is greater than 50%) and Bremer decay index (bottom and top numbers, respectively). The absolute age assessment is from ref. 50. Eif., Eifelian; Ems., Emsian; Fam., Famennian; Fras., Frasnian; Giv., Givetian; Gor., Gorstian; Loch., Lochkovian; Lud., Ludfordian; Prag., Pragian.

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