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A primitive fish close to the common ancestor of tetrapods and lungfish

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The relationship of the three living groups of sarcopterygians or lobe-finned fish (tetrapods, lungfish and coelacanths) has been a matter of debate[1–5]. Although opinions still differ, most recent phylogenies suggest that tetrapods are more closely related to lungfish than to coelacanths[6–10]. However, no previously known fossil taxon exhibits a concrete character combination approximating the condition expected in the last common ancestor of tetrapods and lungfish—and it is still poorly understood how early sarcopterygians diverged into the tetrapod lineage (Tetrapodomorpha)[7] and the lungfish lineage (Dipnomorpha)[7]. Here we describe a fossil sarcopterygian fish, *Styloichthys changae* gen. et sp. nov., that possesses an eyestalk and which exhibits the character combination expected in a stem group close to the last common ancestor of tetrapods and lungfish. *Styloichthys* from the Lower Devonian of China bridges the morphological gap between stem-group sarcopterygians (*Psarolepis* and *Achoania*)[10] and basal tetrapodomorphs/basal dipnomorphs. It provides information that will help in the study of the relationship of early sarcopterygians, and which will also help to resolve the tetrapod–lungfish divergence into a documented sequence of character acquisition.

Sarcopterygii (Romer, 1955)
Styloichthys gen. nov.

Diagnosis. A sarcopterygian characterized by relatively large pores (often spoon-shaped and arranged in parallel grooves) on the cosmine surface, a jagged margin between ethmosphenoid and otoccipital shields, an otoccipital with a wide flat ventral surface carrying no vestibular fontanelle, and a lower jaw with a ventrally protruding flange formed by prearticular and meckelian bone. *Styloichthys* differs from *Psarolepis* and *Achoania* in having a lyre-shaped trajectory of the supraorbital canal, a fenestra ventralis, small internasal cavities and three coronoids in the lower jaw. *Styloichthys* differs from tetrapodomorphs and dipnomorphs in having an eyestalk, a slender postorbital pila, and a cosmine surface with relatively large pores.
Type species. *Styloichthys changae* sp. nov.
Etymology. Generic name referring to the presence of postorbital pila (Greek *stylo*, pillar; *ichthys*, fish). Specific name in honour of M.-M. Chang for her contributions to palaeoichthyology.
Holotype. V8142.1, an anterior cranial portion, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.
Age and locality. Early Devonian (late Lochkovian), Xitun Formation, Qujing, East Yunnan, China.

Remarks. The new form (Figs 1 and 2) is represented by 20 anterior cranial portions (V8142.1–20), 7 posterior cranial portions (V8142.21–27), 18 lower jaws (V8143.1–18), one maxillary (V8143.19), 4 cheek bone plates (V8143.20–23), 5 cleithra (V8143.24–28) and 4 clavicles (V8143.29–32), all showing a unique cosmine surface with relatively large pores (though smaller than those in *Psarolepis* and *Achoania*[10–12]). The assignment of these specimens to the same form is further supported by matching morphology between the anterior and posterior cranial portions (Fig. 1a–f) and between the upper-jaw and lower-jaw structures (Figs 1c, i, and 2b, d).
**Description.** The most remarkable feature of *Styloichthys* is a recessed teardrop-shaped eyestalk area immediately behind the optic canal (Fig. 1e, g, h). This unfinished area has a well-defined natural margin as indicated by the surrounding periosteal lining which dips slightly into the unfinished recess, and corresponds to the eyestalk attachment area recently reported in basal bony fishes (*Psarolepis*, *Achoania* and *Ligulalepis* formerly known as AMF101607)[10,13,14]. Ventral to this eyestalk area, a cup-shaped depression serves for eye muscle attachment. *Styloichthys* also resembles *Psarolepis* and *Achoania* in having a postorbital pila (though splinter-like and much more slender) that forms a bridge between the top of the basipterygoid process and the side of the braincase wall.

Styloichthys is quite close to *Youngolepis*[15] (a basal dipnomorph) in having an anteriorly positioned ethmoidal articulation, a fenestra ventralis and small internasal cavities, while other endocranial features seem intermediate between *Youngolepis* and *Psarolepis*/*Achoania*, such as a relatively broad suborbital ledge, a large notochordal pit, and a well-developed intracranial joint with a processus connectens giving a slightly convex profile to the posterior face of the ethmosphenoid (Fig. 1c, e, g, h). The well-ossified otoccipital (Fig. 1d, f) carries a large oval concave area for the basicranial muscle, a large keyhole-shaped bipartite facet for the hyomandibular and a large facet for the first infrapharyngealbranchial, but no vestibular fontanelle (also absent in some coelacanths and megalichthyid tetrapodomorphs such as *Cladarosymblema*[16]).

Styloichthys resembles *Youngolepis* and, to a lesser extent, *Powichthys*[17] (a basal dipnomorph) and *Kenichthys*[18] (a basal tetrapodomorph), in dermal bone features such as an inward and downward bending snout, a small independent premaxillary with high antero-medial portion and low postero-lateral portion (indicated by the outline of the premaxillary area and the sutural position of ethmoidal commissural canal), a large and long parasphenoid, a pineal foramen at the anterior margin of the parietals, a lyre-shaped trajectory of the supraorbital canal, groups of pores piercing the smooth surface between the relatively large cosmine pores, and a postparietal laterally flanked by more than two bones and posteriorly overlapped by the extrascapular. The compound cheek bone plate (corresponding to squamosal + quadratojugal + preopercular), maxillary, clavicle, and cleithrum with a tripartite scapulocoracoid (Fig. 2) are also similar to those in *Youngolepis*[19].

The lower jaw (Figs 1i, 2c, d) has three coronoids as indicated by three semilunar pockets along a shallow groove between the dentary and the prearticular, but is unique in having a very large adductor fossa (making up more than 50% of the lower jaw length), a convex ventral flange formed by prearticular and meckelian bone and protruding beyond the ventral border of infradentaries, and a prearticular carrying a shagreen of minute denticles dorsally and undulating parallel ridges ventrally.

To explore the phylogenetic position of *Styloichthys*, we modified the data matrix in ref. 10 by adding the *Styloichthys* codings and revising 21 codings for *Ligulalepis* and *Onychodus* based on newly available information[13,20]. Phylogenetic analysis[21] (see Supplementary Information) using the modified data matrix of 27 taxa and 158 characters yields 24 trees showing the same major groupings as ref. 10. *Styloichthys* is placed in a trichotomy with Dipnomorpha and
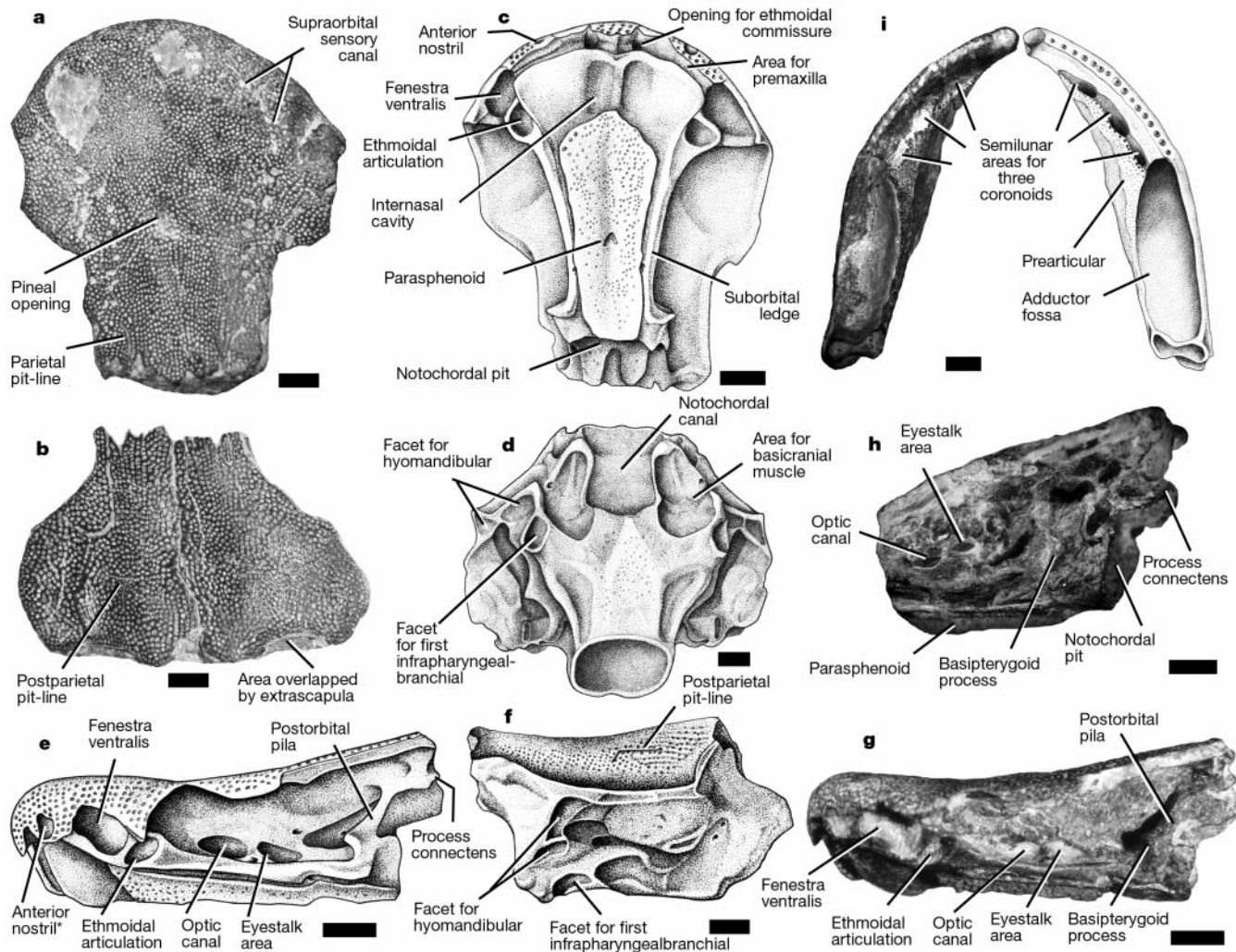
Figure 1 *Styloichthys changae* gen. et sp. nov., a primitive fossil fish close to the last common ancestor of tetrapods and lungfish. Anterior cranial portion (**a**, V8142.5; **c**, **e**, **g**, V8142.1, holotype; **h**, V8142.4), posterior cranial portion (**b**, V8142.24; **d**, **f**, V8142.21) and lower jaw (**i**, V8143.1). **a**,**b**, Dorsal view (photographs), showing the lyre-shaped trajectory of the supraorbital sensory canal, the jagged margin between the ethmosphenoid and otoccipital shields, and the relatively large pores on the cosmine surface. **c**,**d**, Ventral view (drawings), showing the large parasphenoid, large notochordal pit and canal, and the wide otoccipital with no vestibular fontanelle. **e–h**, Lateral view (drawings and photographs), showing the eyestalk area, the postorbital pila, the processus connectens and the facets for the hyomandibular and the first infrapharyngealbranchial. Left anterior nostril (marked with asterisk in **e**) is reconstructed from well-preserved right anterior nostril, partially visible in **c**. **i**, Dorsal view (photograph with mirror-image drawing) showing the semilunar areas for three coronoids and the large adductor fossa. Scale bar, 2 mm.

Tetrapodomorpha in the 50% majority rule consensus tree, but shows up more often at the base of Tetrapodomorpha + Dipnomorpha (9 trees) than at other positions (6 trees at the base of Tetrapodomorpha, 3 trees at the base of Dipnomorpha and 6 trees within Dipnomorpha). This result, together with the distribution of the eyestalk, the postorbital pila and the large-pore cosmine, suggests that *Styloichthys* is best regarded as the stem group of Tetrapodomorpha + Dipnomorpha directly below the node representing their last common ancestor (Fig. 3).

The phylogenetic position of *Styloichthys* and its unique character combination have wide implications for studying the relationship of early sarcopterygians. First, the presence of postorbital pila and large-pore cosmine in *Styloichthys* provides evidence that these are primitive features for sarcopterygians rather than autapomorphies uniting *Psarolepis* and *Achoania*, which form successive plesions, and not a monophyletic clade, in the stem-group segment of the Sarcopterygii. Together with the eyestalk, these features must have been independently lost at least twice within the Sarcopterygii (once in the coelacanths + onychodonts clade, and once in the last common ancestor of tetrapods and lungfish).

Second, *Styloichthys* allows more precise statements to be made about the sequence of character acquisition leading to the tetrapod–lungfish divergence. For instance, the straight course of the supra-orbital canal in *Psarolepis*, *Achoania* and coelacanths (for example, *Miguashaia* and *Whiteia*)[22,23], the 5 coronoids in *Psarolepis* and *Achoania* (undescribed material), and the variable pattern of 4–5 coronoids in coelacanths[22] all resemble the actinopterygian condition[24] and differ from the dipnomorph + tetrapodomorph condition. *Styloichthys* documents the first appearance of the lyre-shaped trajectory of the supraorbital canal and the three coronoid condition found in dipnomorphs + tetrapodomorphs, thereby placing the origin of these features in the internode between the coelacanths + onychodonts clade and *Styloichthys*.
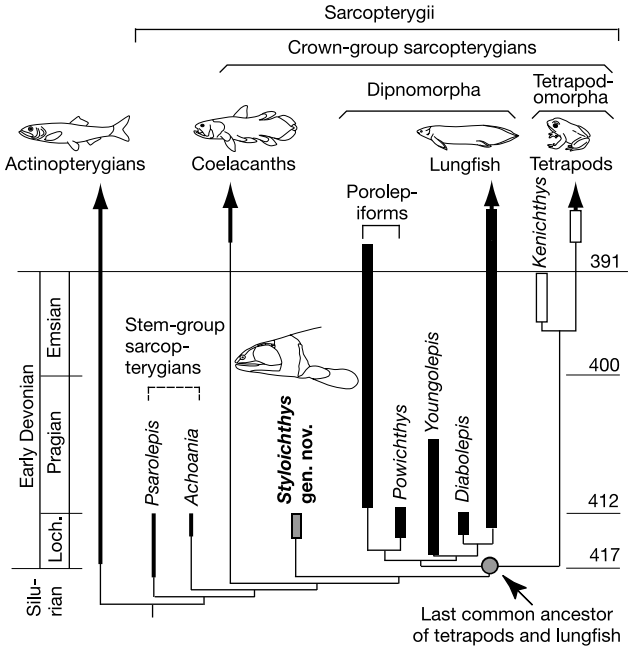
Third, *Styloichthys* provides a crucially positioned new outgroup to examine character polarity and phylogenetic relationship among dipnomorphs and tetrapodomorphs. For instance, in 6 of the 9 trees placing *Styloichthys* at the base of Tetrapodomorpha + Dipnomorpha, *Powichthys* is aligned with porolepiforms rather
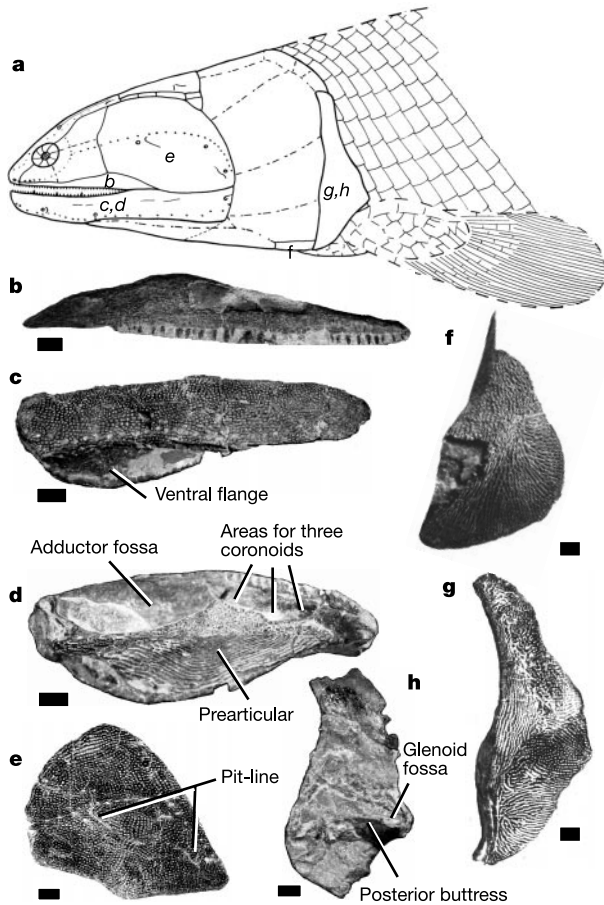
Figure 2 Skull and shoulder girdle of *Styloichthys*. **a**, Reconstructed lateral view showing positions of dermal bones. **b**, Right maxillary (V8143.19) in lateral view. **c**, Right lower jaw (V8143.3) in lateral view, showing the ventrally protruding flange. **d**, Left lower jaw (V8143.1) in medial view showing the semilunar areas for three coronoids and the large adductor fossa. **e**, Left compound cheek plate (V8143.20) corresponding to squamosal + quadratojugal + preopercular. **f**, Left clavicle (V8143.29). **g**, Left cleithrum (V8143.24). **h**, Right cleithrum (V8143.25) in medial view, showing structures of the scapulocoracoid. Scale bar, 2 mm.

Figure 3 Stratogram showing *Styloichthys* as the stem group of the clade Dipnomorpha + Tetrapodomorpha. (The position of *Styloichthys* is based on 9 out of 24 trees, the position of *Powichthys* is based on 6 trees; tree length, 328; consistency index, 0.549; homoplasy index, 0.451; retention index, 0.759; rescaled consistency index, 0.416; see Supplementary Information for details). Numbers along the right margin represent millions of years before present.

than with dipnoiforms (in the sense of ref. 8). This new tentative position of *Powichthys* (Fig. 3) may offer a more parsimonious explanation for the distribution of the intracranial joint, absent in *Youngolepis*[15], *Diabolepis*[25] and dipnoans[26] (lungfish), but present in both porolepiforms (including *Powichthys*) and tetrapodomorphs (with subsequent parallel loss in the fish–tetrapod transition)[27]. Similarly, in the context of *Styloichthys*, porolepiform-like features found in rhizodonts (such as a short snout, widely separated eyes, and extratemporals)[28,29] as well as similarities among *Youngolepis*, *Powichthys* and *Diabolepis*, porolepids and early osteolepids[30], can be more confidently explained as primitive features of dipnomorphs + tetrapodomorphs.

Last, *Styloichthys* sheds light on the possible tempo and mode of evolutionary changes surrounding the tetrapod–lungfish divergence. The Lochkovian age of *Styloichthys* and *Youngolepis* suggests that tetrapodomorphs and dipnomorphs diverged very rapidly from their common ancestor. Although the dermal bones and lower jaws in *Styloichthys* approach the tetrapodomorph–dipnomorph condition, its endocranium exhibits a mixture of features found in *Psarolepis/Achoania* and in basal tetrapodomorphs/basal dipnomorphs. This suggests that changes in dermal bones (including the lower jaw) outpaced changes in endocranial features, and probably set the stage for divergent morphological specializations leading respectively to the tetrapod lineage and the lungfish lineage. □

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Increasing dominance of large lianas in Amazonian forests

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Ecological orthodoxy suggests that old-growth forests should be close to dynamic equilibrium, but this view has been challenged by recent findings that neotropical forests are accumulating carbon[1,2] and biomass[3,4], possibly in response to the increasing atmospheric concentrations of carbon dioxide[5,6]. However, it is unclear whether the recent increase in tree biomass has been accompanied by a shift in community composition. Such changes could reduce or enhance the carbon storage potential of old-growth forests in the long term. Here we show that non-fragmented Amazon forests are experiencing a concerted increase in the density, basal area and mean size of woody climbing plants (lianas). Over the last two decades of the twentieth century the dominance of large lianas relative to trees has increased by 1.7–4.6% a year. Lianas enhance tree mortality and suppress tree growth[7], so their rapid increase implies that the tropical terrestrial carbon sink may shut down sooner than current models suggest[8–10]. Predictions of future tropical carbon fluxes will need to account for the changing composition and dynamics of supposedly undisturbed forests.

Recent field studies[1,2,3] indicate that old-growth tropical forests are absorbing 1–2 Gt C yr^{-1}, but the mechanisms and stability of the tropical carbon sink, and its implications for the ecology of tropical vegetation, are highly uncertain. Shifts in functional composition and biodiversity are expected as a result of climate changes and increased CO_2 (refs 11, 12) but so far there is no evidence of widespread compositional change in old-growth forests. This absence of evidence might imply evidence of absence—or it could simply reflect our failure to monitor adequately forest behaviour, or even to examine existing data across sufficient spatial and temporal scales. Lianas in particular are ignored in forest inventories and models alike, in spite of their key functional roles. As structural parasites, lianas exert a much greater ecological effect than their size suggests, representing less than 5% of tropical forest biomass but up to 40% of leaf productivity[13]. They also suppress tree growth and encourage tree mortality, and affect the competitive balance among trees by disproportionately infesting some taxa and suppressing the regeneration and growth of non-pioneers[7]. Climbers respond strongly to increased CO_2 concentrations[14,15] and benefit from disturbance[7,16,17], and a biome-wide trend to increased tree turnover rates has been detected in old-growth forests[18] so increases in liana densities might be anticipated[19]. Here we assemble several unique,
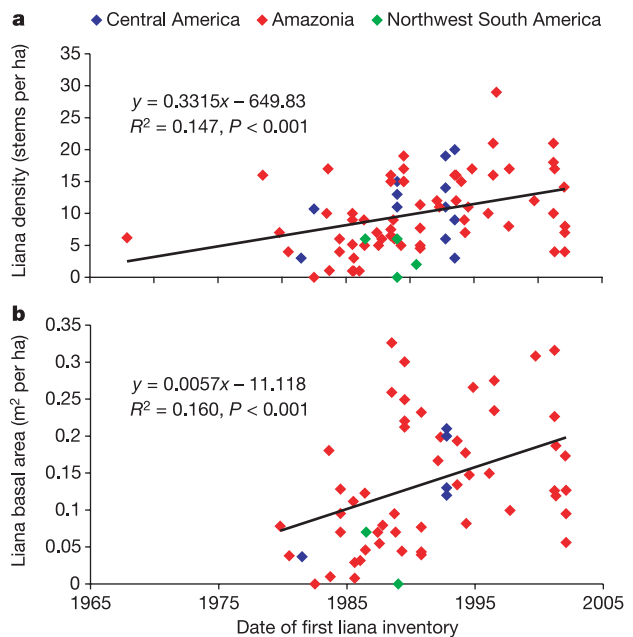
Figure 1 Structural importance of lianas over 10 cm in diameter in each neotropical site as a function of date of first inventory. **a**, Liana stem density in stems ha^{-1}; **b**, liana basal area in m^2 ha^{-1}. 'Central America' is Panama and tropical countries to the north; 'Northwest South America' is the Chocó bioregion, west of the Andes; 'Amazonia' is the Amazon river basin and contiguous forested zones of Guyana and eastern Brazil. Linear regressions are fitted to the Amazonian data.