

A primitive fish provides key characters bearing on deep osteichthyan phylogeny

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Osteichthyans, or bony vertebrates, include actinopterygians (teleosts and their relatives) and sarcopterygians (coelacanth, lungfishes and tetrapods). Despite features found in basal actinopterygians (for example, *Dialipina* and *Ligulalepis*)^{1–3} and basal sarcopterygians (for example, *Psarolepis* and *Achoania*)^{4,5}, the morphological gap between the two lineages remains wide and how sarcopterygians developed a dermal surface covering known as cosmine (composed of a pore–canal network and a single layer of odontodes and enamel) is still poorly known^{6–10}. Here we describe a primitive fossil fish, *Meemannia eos* gen. et sp. nov., that possesses an actinopterygian-like skull roof and a cosmine-like dermal surface combining a pore–canal network (found in various fossil sarcopterygians) with superimposed layers of odontodes and enamel (previously known in actinopterygians and some acanthodians^{11–13}). This 405-million-year-old fish from the Lower Devonian of Yunnan (China) demonstrates that cosmine in many fossil sarcopterygians arose step by step through the acquisition of a pore–canal network followed by the subsequently developed ability to resorb previous generations of odontodes and enamel. *Meemannia* provides key characters for studying deep osteichthyan phylogeny and indicates a possible morphotype for the common ancestor of actinopterygians and sarcopterygians.

Sarcopterygii (Romer, 1955)
Meemannia eos gen. et sp. nov.

Diagnosis. A basal osteichthyan fish with a cosmine-like dermal surface composed of a pore–canal network and up to four superimposed layers of odontodes and enamel. Parietals anteriorly separated by an anteriorly broad, triangular postrostral. Parietal almost twice as long as postparietal. Postparietal longer than wide, flanked by large supratemporal with extensive postero-lateral flange. Supraorbital canal passing through the anterior portion of parietal with no connection to the otic canal. Middle and posterior pit-line close to median line. Oto-occipital with an extensive supraotic cavity connected to a large crescent-shaped posterior dorsal fontanelle.
Type species. *Meemannia eos* sp. nov.

Etymology. Generic name after Meemann Chang for her contributions to paleoichthyology. Specific name from Greek *eos*, ‘dawn’, indicating the rudimentary condition of the cosmine-like surface covering.

Holotype. V14536.1, a fairly complete skull roof, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing.

Age and locality. Early Devonian (late Lochkovian), Xitun Formation, Qujing, East Yunnan, China.

Description. *Meemannia eos* gen. et sp. nov. (Fig. 1) is represented by three fairly complete skull roofs (V14536.1–3) and one posterior portion of the skull roof (V14536.4) with incompletely preserved

oto-occipital structures. The skull roof surface is punctured by coarse pore openings (though smaller than those in primitive sarcopterygians *Psarolepis*⁴, *Achoania*⁵ and *Styloichthys*¹⁴) often arranged in parallel grooves with intervening smooth ridges.

Meemannia manifests skull roof features variously found in primitive actinopterygians such as *Dialipina*^{1,15}, *Cheirolepis*^{16,17}, *Moythomasia*¹⁸ and *Howqualepis*¹⁹ (Fig. 1a–d, g, h). The parietal is flanked by an elongated dermosphenotic traversed by the anterior portion of the otic canal before it exits at a point close to the posterior corner of the orbital margin. The postparietal is flanked by a large supratemporal with a postero-laterally protruding flange that contributes to a markedly embayed posterior margin of the skull roof. As in *Howqualepis*, the anterior portion of the parietal carries an elongated indentation representing an opening of the supraorbital canal. As in *Dialipina*, the large shield-shaped postrostral anteriorly separates the parietals, the supraorbital canal traverses the anterior portion of the parietal without contacting the otic canal, the middle and posterior pit-lines lie close to the median line, and the rostral part of the skull roof (though unpreserved) seems easily separable from the rest of the skull during preservation, a condition also found in some placoderms (for example, acanthothoracids)^{13,20} and in ‘loose-nosed’ lungfishes²⁰.

Meemannia’s endocranial features revealed in the oto-occipital region (Fig. 1e, f) resemble those in both basal actinopterygians (for example, *Ligulalepis*^{2,3}) and basal sarcopterygians (for example, *Psarolepis*²¹), such as the position and shape of the semicircular canals and utricular recess, a large lozenge-shaped myelencephalic portion of the brain cavity (cav.cr) posteriorly closed off by medially converging ridges, paired lateral cranial canals (lcc), a large supraotic cavity (cav.so) with anteriorly diverging extensions, and a large posterior dorsal fontanelle (pdf). The last two may be general gnathostome features because they also exist in some chondrichthyans²².

The most remarkable feature of *Meemannia* is a unique histological condition bearing on the origin of cosmine, an enigmatic vertebrate hard tissue unknown in living forms but widely spread among fossil sarcopterygians^{13,23}. As revealed by 15 transverse sections of specimen V14534.3 (Fig. 2a–c), the upper portion consists of three or four superimposed layers of enamel (e1–e4) and odontodes (od1–od4) separated by flask-shaped pore cavities (pc), interconnecting horizontal canals (hc), and pore openings (p). The middle portion consists of vascular bone and is poorly developed, whereas the lower portion consisting of lamellar bone is well developed and often directly underlies the upper portion.

The enamel of the most superficial layer dips slightly into the pore openings, whereas the enamel of each underlying layer dips slightly into the side wall of the pore cavities at different levels. This arrangement, together with the superimposition of three or four enamel–odontode layers, indicates that each layer (or successive generation)

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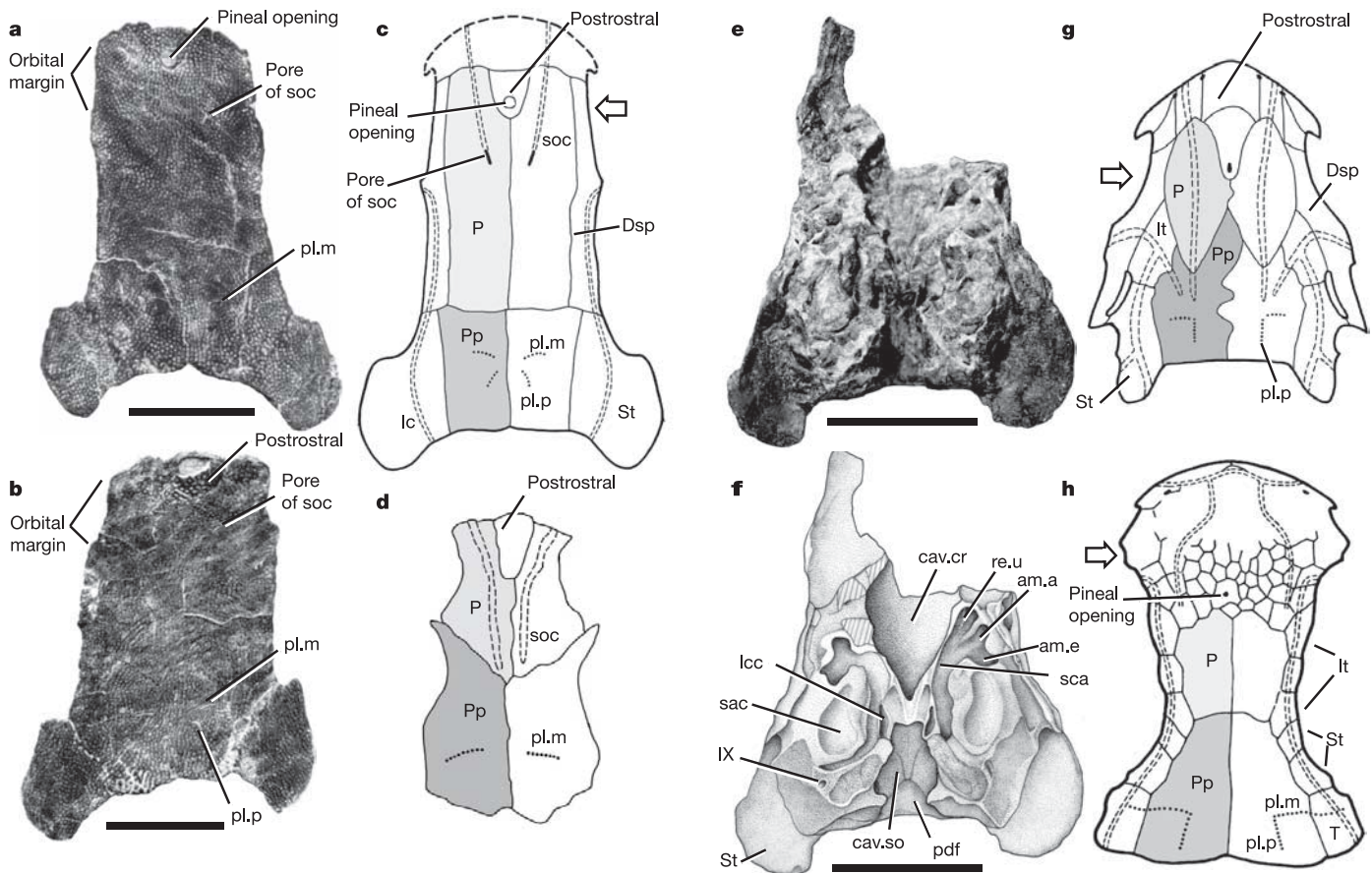


Figure 1 | *Meemannia eos* gen. et sp. nov. This 405-Myr-old fish shows a mixture of basal actinopterygian and sarcopterygian features. **a, b**, Dorsal view of skull roof (**a**, holotype, V14536.1; **b**, V14536.2). **e, f**, Ventral view of posterior portion of the skull roof with incompletely preserved oto-occipital structures (**e**, V14536.4; **f**, illustrative drawing). **c, d, g, h**, Reconstruction of skull roof (**c**) compared with two actinopterygians, *Dialipina*¹⁵ (**d**) and *Cheirolepis*¹⁶ (**g**), and one sarcopterygian, *Powichthys*³⁰ (**h**). Abbreviations: am.a, am.e, anterior and external ampullae; cav.cr, cranial cavity; cav.so,

supraotic cavity; Dsp, dermosphenotic; It, intertemporal; lc, otic portion of the main lateral line canal; lcc, lateral cranial canal; P, parietal; pdf, posterior dorsal fontanelle; pl.m, pl.p, middle and posterior pit-lines; Pp, postparietal; re.u, utricular recess; sac, sacculus; sca, anterior semicircular canal; soc, supraorbital canal; St, supratemporal; T, tabular; IX, exit of the ninth cranial nerve. Open arrow in **c, g** and **h** indicates the position of the orbit. Scale bar, 5 mm (**a, b, e, f**).

might be deposited without resorbing previously deposited layers and that the pore cavities grow in depth with the successive deposition of each layer.

The pore cavities, horizontal canals and pore openings in *Meemannia* represent typical components of a pore–canal network characteristic of cosmine found in many crown-group sarcopterygians. However, the superimposition of enamel–odontode layers as well as the weak development of the vascular bone resembles the dermal bone features found in actinopterygians (for example, *Andreolepis*¹¹) and some acanthodians¹². Cosmine in crown-group sarcopterygians has one single layer of odontodes and enamel, and a process of resorption preceding each event of cosmine redeposition prevents the formation of overlapping layers⁷. Although isolated cases of buried odontodes have been reported in *Porolepis*²⁴ (a porolepiform) and *Uranolophus*²⁵ (a lungfish), these occur below the level of the cosmine layer and no superimposed layers are formed. Continuing histological work reveals that *Psarolepis* and *Styloichthys* also possess a pore–canal network embedded in superimposed layers of odontodes and enamel (Fig. 2d, e). However, the superimposed layers occur less frequently than in *Meemannia* and the number of superimposed layers varies in neighbouring regions, indicating the possible initial development of partial resorption in these two forms.

To explore the phylogenetic position of *Meemannia*, we constructed a data matrix of 125 characters (with 25 available characters for *Meemannia*) and 19 taxa representing both actinopterygians

and sarcopterygians. Phylogenetic analysis²⁶ (see Supplementary Information) yields two most parsimonious trees, both showing *Meemannia* as the most basal sarcopterygian below the node of *Psarolepis* (Fig. 3). The two trees differ only in the position of *Ligulalepis*, which forms the sister-group of either *Dialipina* or *Osorioichthys*²⁷. However, this result should be treated with caution because the node below *Meemannia* and the nodes in the actinopterygian lineage have low Bremer support values.

Despite the tentative nature of *Meemannia*'s position, its unique character combination has wide implications for studying deep osteichthyan phylogeny and the early divergence of actinopterygians and sarcopterygians.

First, *Meemannia* makes it possible to interpret features found in basal members of both lineages in the common framework of deep osteichthyan phylogeny. For instance, the apparent separation of the rostral part of the skull roof from the rest of the skull (in *Dialipina* and *Meemannia*), the *Psarolepis*-like endocranial features (in *Ligulalepis*^{2,3} and *Meemannia*), the actinopterygian-like skull roof pattern (in *Meemannia*, *Dialipina* and other actinopterygians), the absence of a dermal joint between the parietal and the postparietal (in *Meemannia*, *Dialipina* and other actinopterygians), and the superimposition of enamel–odontode layers (in *Meemannia* and *Andreolepis*¹¹, as well as in *Psarolepis* and *Styloichthys*) should now be viewed as general osteichthyan features existing in the common ancestor of actinopterygians and sarcopterygians.

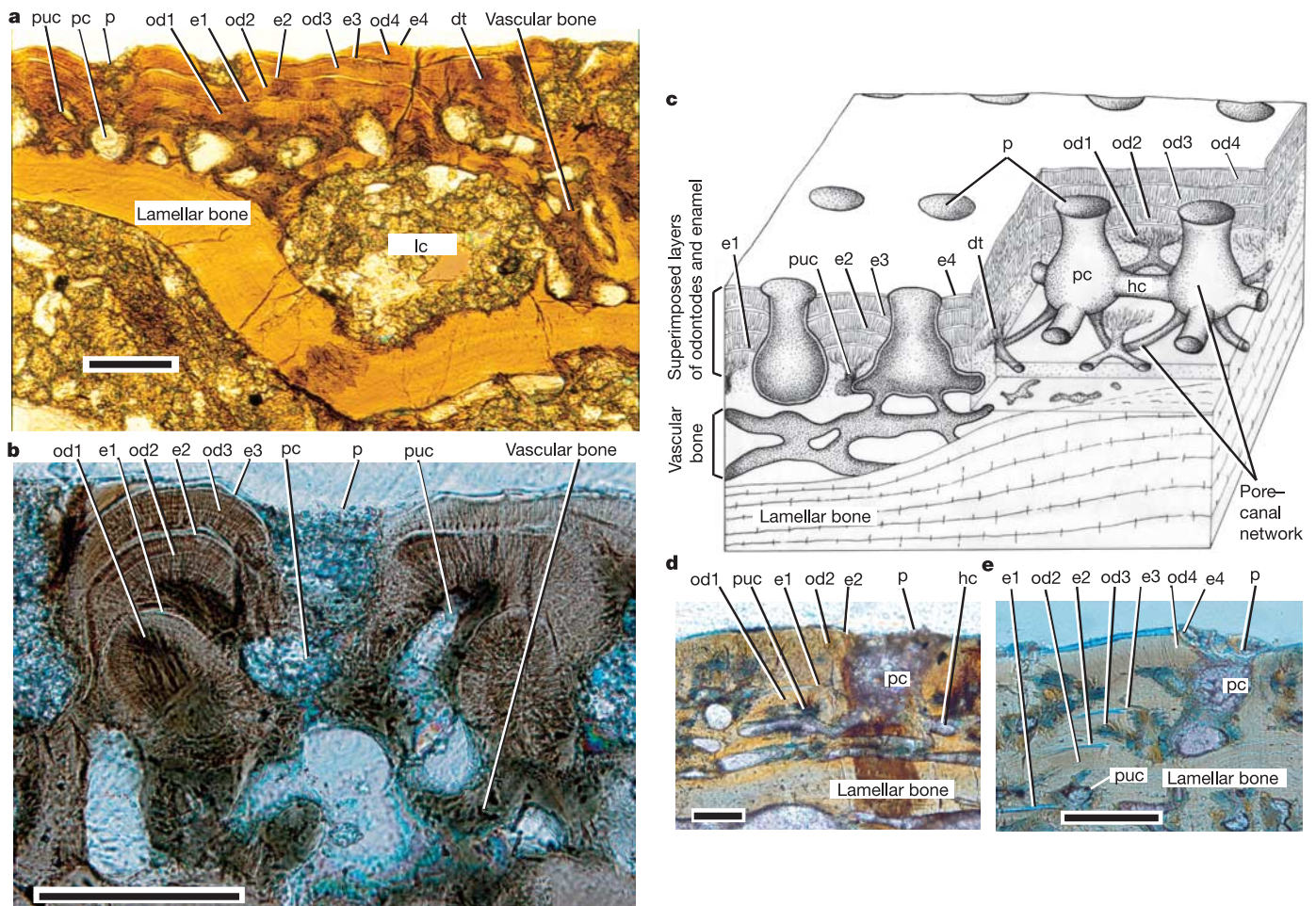


Figure 2 | *Meemannia* possesses a pore-canal network combined with three or four layers of odontodes and enamel in dermal bone surface. This condition preceded the appearance of typical cosmine found in crown-group sarcopterygians. *Psarolepis* and *Styloichthys* present an intermediate condition between *Meemannia* and crown-group sarcopterygians. **a**, **b**, Two transverse sections of *Meemannia* skull roof (V14534.3). **c**, Reconstruction

based on transverse sections of V14534.3. **d**, Transverse section of *Psarolepis* (V14600.5, skull roof). **e**, Transverse section of *Styloichthys* (V14599.4, cleithrum). Abbreviations: dt, dentine tubules; e1–e4, layers of enamel; hc, horizontal canal; lc, otic portion of the main lateral line canal; od1–od4, layers of odontodes; p, pore opening; pc, pore cavity; puc, pulp cavity. Scale bar, 100 μ m.

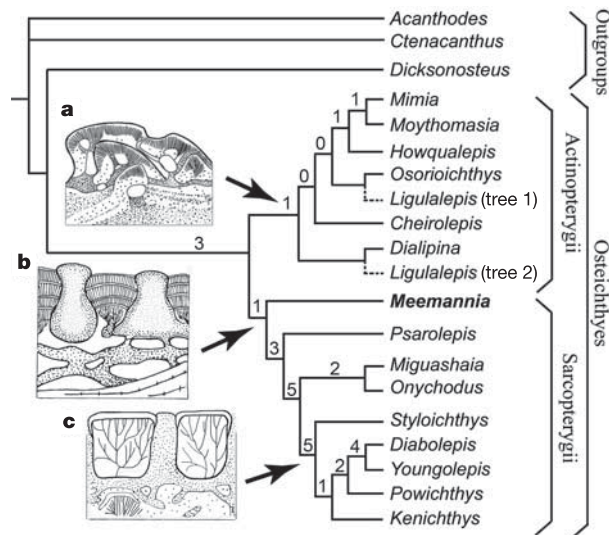


Figure 3 | Cladogram showing the tentative position of *Meemannia* as the most basal sarcopterygian and the step-by-step origin of cosmine in crown-group sarcopterygians. The figure is based on two most parsimonious trees that differ in the positions of *Ligulalepis*. Bremer support values are shown at nodes. Tree length 222, consistency index

0.6216, homoplasy index 0.3784, retention index 0.7807, rescaled consistency index 0.4853. See Supplementary Information for details. Insets compare the histological features of *Meemannia* (**b**) with those found in actinopterygians (*Andreolepis*¹¹, **a**) and crown-group sarcopterygians (*Porolepis*²⁴, **c**).

Second, *Meemannia* indicates that cosmine in crown-group sarcopterygians might have developed step by step, first through the acquisition of a pore–canal network (in *Meemannia*) and subsequently through the development of increased ability to resorb previously deposited enamel–odontode layers (in *Psarolepis*, *Styloichthys* and crown-group sarcopterygians). *Psarolepis* and *Styloichthys* may represent an intermediate stage in which the ability to resorb previous layers was initially developed before it became fully established in crown-group sarcopterygians.

Last, *Meemannia* may shed light on long-standing controversies about the biology of cosmine^{6,7}. With three or four superimposed layers of odontodes and enamel associated with only one pore–canal network, *Meemannia* shows that there is no one-to-one association between the deposition of each layer of odontodes and enamel and the formation of a pore–canal system. On the contrary, the slight dipping of successive enamel layers into the side wall of pore cavities indicates that the space known as pore cavities increases in depth as each enamel–odontode layer is deposited. Although opinions still differ on the biological interpretation of the pore–canal network^{6,7,28,29}, *Meemannia* seems to lend support to the theory that the pore–canal network might represent vascular structures involved in the deposition of odontodes and enamel¹⁰, rather than a network of cutaneous sensory or glandular structures^{7,9,20}.

METHODS

Phylogenetic analysis was performed with the phylogenetic package PAUP*4.0b10 (ref. 26). See Supplementary Information for the list of 125 characters with sources of reference, the data matrix, the two most parsimonious trees and the characters defining major clades. As the position of *Meemannia* is based on only 25 available characters, the phylogenetic result is subject to future changes when more characters become available.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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