

The Oldest Actinopterygian Highlights the Cryptic Early History of the Hyperdiverse Ray-Finned Fishes

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DOI:

[10.1016/j.cub.2016.04.045](https://doi.org/10.1016/j.cub.2016.04.045)

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Document Version

Publisher's PDF, also known as Version of record

Citation for published version (Harvard):

Jing, L, Giles, S, Friedman, M, den Blauuwen, J & Zhu, M 2016, 'The Oldest Actinopterygian Highlights the Cryptic Early History of the Hyperdiverse Ray-Finned Fishes', *Current Biology*, vol. 26, no. 12, pp. 1602-1608. <https://doi.org/10.1016/j.cub.2016.04.045>

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Current Biology

The Oldest Actinopterygian Highlights the Cryptic Early History of the Hyperdiverse Ray-Finned Fishes

Highlights

- Once considered a lobe-fin, *Meemannia* is the oldest ray-finned fish
- MicroCT reveals ray-fin characters including lateral cranial and spiracular canals
- *Meemannia* revises hypotheses of bone histology in the ancestor of bony fishes
- “Cosmine”-like tissues are also present in the ray-fin *Cheirolepis*

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In Brief

Lu et al. show that *Meemannia*, once interpreted as a primitive lobe-fin, is the oldest ray-finned fish. Evidence includes a lateral cranial canal and endoskeletal enclosure of the spiracle. “Cosmine”-like tissues, previously thought to unite *Meemannia* with lobe-fins, are widely distributed among early bony fishes, including the ray-fin *Cheirolepis*.



The Oldest Actinopterygian Highlights the Cryptic Early History of the Hyperdiverse Ray-Finned Fishes

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<http://dx.doi.org/10.1016/j.cub.2016.04.045>

SUMMARY

Osteichthyans comprise two divisions, each containing over 32,000 living species [1]: Sarcopterygii (lobe-finned fishes and tetrapods) and Actinopterygii (ray-finned fishes). Recent discoveries from China highlight the morphological disparity of early sarcopterygians and extend their origin into the late Silurian [2–4]. By contrast, the oldest unambiguous actinopterygians are roughly 30 million years younger, leaving a long temporal gap populated by fragments and rare body fossils of controversial phylogenetic placement [5–10]. Here we reinvestigate the enigmatic osteichthyan *Meemannia* from the Early Devonian (~415 million years ago) of China, previously identified as an exceptionally primitive lobe-finned fish [3, 7, 11, 12]. *Meemannia* combines “cosmine”-like tissues taken as evidence of sarcopterygian affinity with actinopterygian-like skull roof and braincase geometry, including endoskeletal enclosure of the spiracle and a lateral cranial canal. We report comparable histological structures in undoubted ray-finned fishes and conclude that they are general osteichthyan features. Phylogenetic analysis places *Meemannia* as an early-diverging ray-finned fish, resolving it as the sister lineage of *Cheirolepis* [13] plus all younger actinopterygians. This brings the first appearance of ray-fins more in line with that of lobe-fins and fills a conspicuous faunal gap in the otherwise diverse late Silurian-earliest Devonian vertebrate faunas of the South China Block [4].

RESULTS

Despite comprising half of living vertebrate richness—some 32,000 species [1]—actinopterygians have an obscure early evolutionary history. The earliest definitive actinopterygian is the Middle Devonian (Eifelian) *Cheirolepis* [13, 14], with earlier candidates generally represented by fragments [6, 10] subject to differing phylogenetic interpretations [3, 6, 8–10, 15]. By contrast, earliest Devonian deposits yield a diversity of lobe-finned fishes [4, 16, 17]. The Lochkovian Xitun Formation of

Yunnan, China, illustrates this general trend, providing remarkable fossils instrumental in documenting the evolutionary origins of individual sarcopterygian lineages [4, 18] but apparently lacking any actinopterygians. *Meemannia* is the newest—and least understood—member of this fauna [11, 12]. Represented by four isolated skull roofs and a referred jaw (Figures 1, S1, and S2), *Meemannia* presents an intriguing mosaic of characters: histology interpreted as a precursor to the “cosmine” of rhipidistian sarcopterygians (lungfishes plus tetrapods) combined with an undivided braincase and skull roof resembling that of actinopterygians [11–13, 19] (Dryad Figure S1, available at <http://dx.doi.org/10.5061/dryad.t6j72>). Initial phylogenetic analyses placed *Meemannia* as the earliest-diverging sarcopterygian based on histological features, interpreting correspondences with ray-fins as crown osteichthyan generalities [3, 7, 11, 12].

Subsequent studies suggest ambiguity in the phylogenetic position of *Meemannia*. Although placement near the last common ancestor of crown osteichthyans is universally agreed, specific hypotheses vary; in addition to the initial lobe-fin identification [3, 7, 11, 12], *Meemannia* has been recovered in a polytomy with actinopterygians and sarcopterygians [20] and as a stem osteichthyan [21]. An additional placement of *Meemannia* as an actinopterygian has also been reported, but low nodal support [9], a principal focus on other regions of gnathostome phylogeny [22], and highly unorthodox tree shapes [10] cast some doubt on the reliability of these results.

The failure to resolve a consistent placement for this taxon partly reflects uncertainty surrounding the morphology of *Meemannia*. Here we use high-resolution computed tomography to re-examine the most complete remains of *Meemannia* (skull roofs: IVPP [Institute of Vertebrate Paleontology and Paleoanthropology] V14536.2 and V14536.4, Figures 1, S1, and S2A–S2C; referred jaw: V14536.5, Figures S2D–S2F), presenting new details of the internal skeleton and providing one of the earliest osteichthyan endocasts.

Description

Braincase

Our results confirm many past interpretations of anatomy (e.g., geometry of buried sensory canals; Figures S2A–S2C) but reveal unexpected features. Surprisingly, the braincase of *Meemannia* bears an enclosed bony canal for the spiracle (Figures 1A–1C) consisting of a narrow bridge located on the lateral margin of the otic region. It is present in a specimen with extensively mineralized otic capsules (V14536.4; Figure 1) but absent in those in

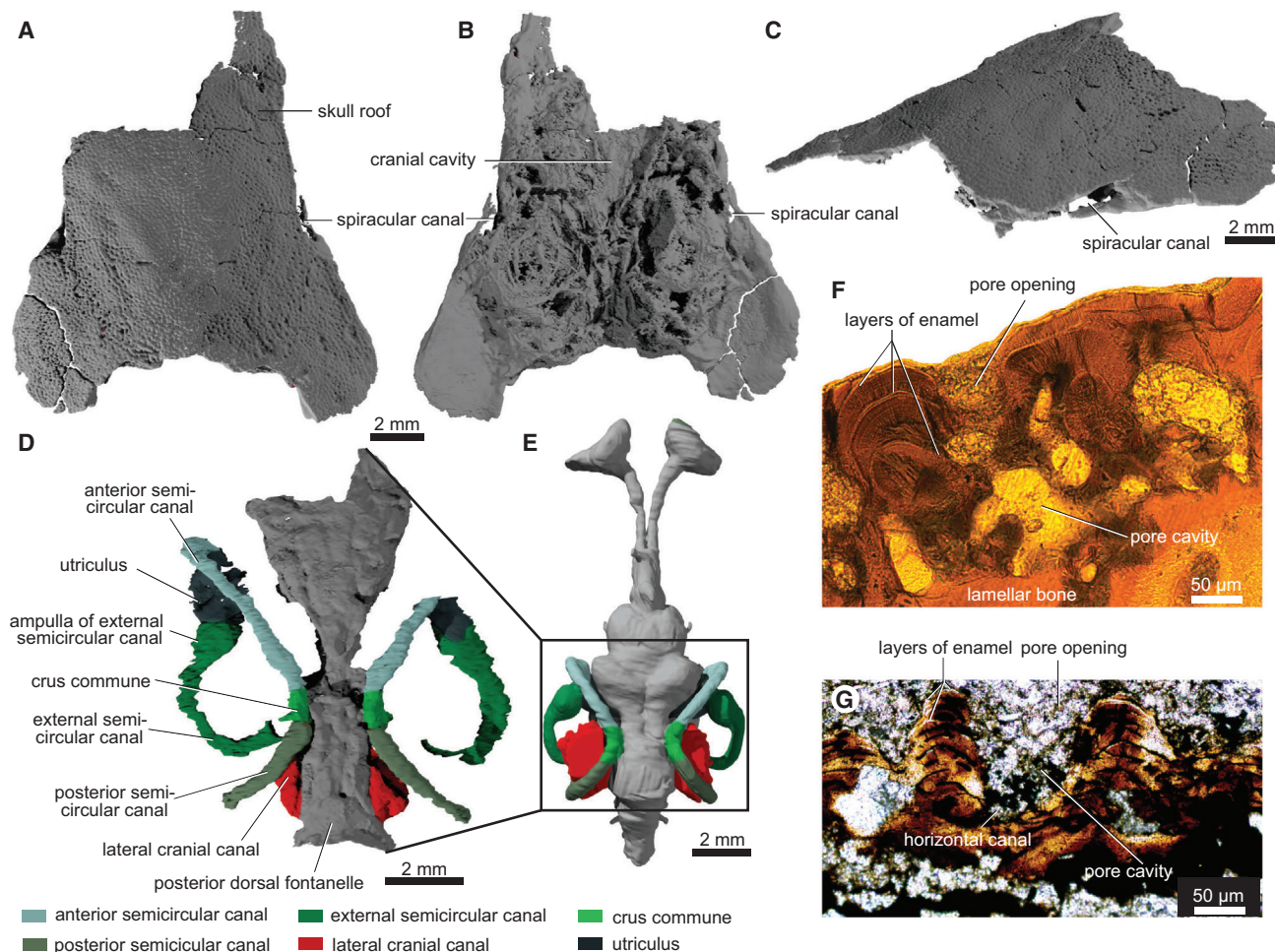


Figure 1. Cranial Anatomy of *Meemannia eos* Based on High-Resolution Computed Tomography of IVPP V14536.4

(A) Dorsal view.
 (B) Ventral view.
 (C) Dorsolateral view of left side.
 (D) Endocast in dorsal view.
 (E) Endocast of *Mimipiscis* in dorsal view.
 (F) Transverse section through *Meemannia* skull roof (V14534.3).
 (G) Transverse section through dermal skull plate of *Cheirolepis* (G.2014.7.38).
 See also Figures S1–S4.

which dermal bone is preserved but endocranial ossification is weak or absent (V14536.2; Figures S2A and S2B), indicating that the bridge is endoskeletal rather than dermal in origin. The aperture of this canal aligns with the spiracular notch, lateral to the anterior part of the supratemporal (Figure 1A; Dryad Figure S1). We reinterpret the bone flanking the lateral side of the frontal as the intertemporal rather than dermosphenotic [11, 12] and regard its anterior extent as uncertain based on thin sections [12] and our own tomographs. As the dermosphenotic and cheek bones of *Meemannia* are unknown, it is unclear whether a dermal spiracular opening was present. However, the spiracular notch corresponds to those of early actinopterygians including *Cheirolepis* [14] and *Mimipiscis* [23] (Dryad Figure S1).

Endocast

Three pairs of semicircular canals are present. The anterior and posterior canals join in a crura commune that extends above the

dorsal roof of the cavum cranii (Figure 1D), manifest as a large embayment in the dorsal roof of the endocavity anterolateral to the posterodorsal fontanelle and previously interpreted as the lateral cranial canal [12]. The endocast of *Meemannia* bears paired, ear-shaped projections of the lateral walls between the crura commune and the level of the otoccipital fissure, extending through the loop of the posterior semicircular canal. These correspond precisely to the lateral cranial canals of undoubted actinopterygians [24, 25] (Figures 2, S3, and S4) in both morphology and position. Other features appear to be primitive for osteichthyans, lacking specializations associated with either sarcopterygians (e.g., supraotic cavity [25]) or actinopterygians (e.g., expanded optic lobes [24]).

Dermal Skeleton and Histology

Endocranial features are joined by previously described actinopterygian-like attributes of *Meemannia*, most notably

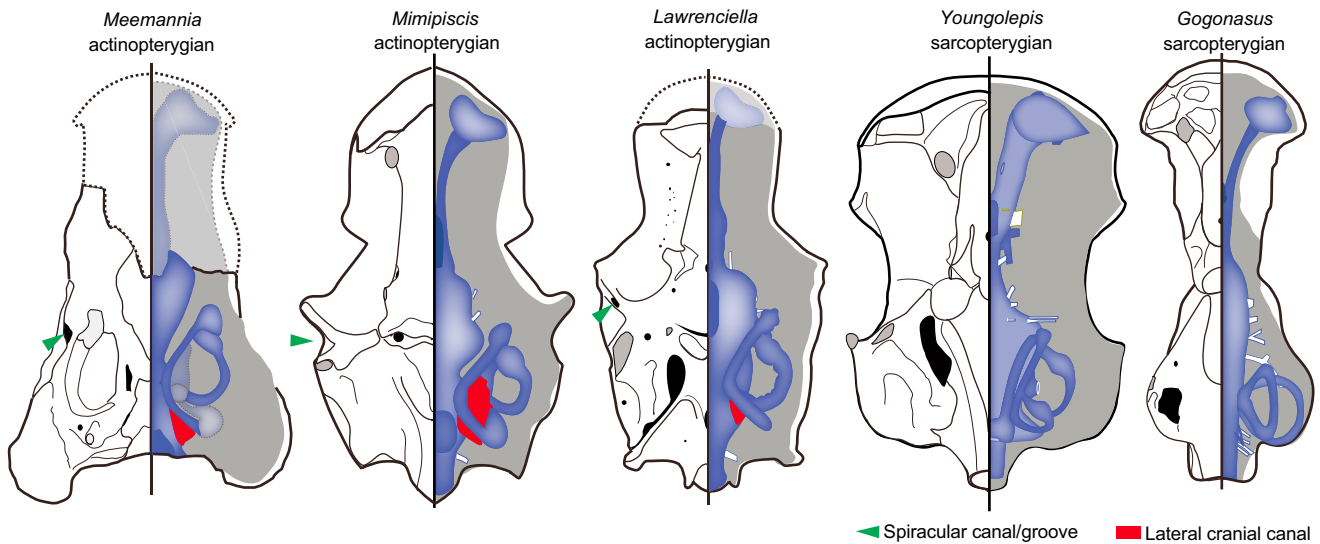


Figure 2. Comparative Braincase and Endocast Morphology of Selected Osteichthyans

Ventral view of braincase (left half) showing the endoskeletal spiracular canal or groove (green arrow) in actinopterygians and dorsal view of endocast (right half, in blue) showing the lateral cranial canal (in red) in actinopterygians. Gray shading (right half) indicates extent of endocranial roof. Illustrations are redrawn from [11, 19, 24–26]. See also Figure S3.

supratemporals that extend far posterior to the hind margin of the parietals (cf. *Cheirolepis* [13], *Moythomasia* [23], *Raynerius* [19]; Figure 1A); we apply conventional actinopterygian skull roof terminology [19] (Dryad Figure S1) and the absence of any surface on the referred lower jaw for the attachment of whorl-like parasymphysial plate (Figures S2D and S2F). Comparison with non-osteichthyan outgroups indicates that both features might be actinopterygian synapomorphies rather than gnathostome symplesiomorphies [3, 20]. Although some early actinopterygians bear enlarged parasymphysial teeth [27], these are members of the principal tooth row of the dentary and not homologous with the separate parasymphysial tooth whorls of other gnathostomes.

The phylogenetic signal of these skeletal traits seems strongly at odds with histological attributes of *Meemannia* regarded as sarcopterygian characters. However, this conflict might stem from a limited understanding of histological structure and diversity within actinopterygians; dermal bone histology of many actinopterygians is understudied, with preference instead given to scale histology [23, 28]. *Cheirolepis*, the earliest unequivocal ray-finned fish, shows dermal bone surface ornament resembling the so-called “large-pore cosmine” of early sarcopterygians and *Meemannia* (Figures 3 and Dryad Figures S2–S4). These pores are not readily visible in specimens from productive localities such as Tynet Burn and Lethen Bar, where the bone surfaces are typically damaged (as noted by [13]). However, material from Edderton (e.g., NHMUK [Natural History Museum, London] PV P.60553, Figure 6c in [15]; PV P.12508, Figure 3 and Dryad Figures S2 and S3; BGS [British Geological Survey] G.2015.25.9, Dryad Figure S2), Cromarty (e.g., BGS T.3577A, Dryad Figure S2D), and Achanarras (e.g., G.2014.7.38, Figure 1G) shows porous surface ornament. Pore openings on the surface of the bone are continuous with pore cavities and are linked by horizontal canals, with a composite dentine and

enamel stratum overlying the basal lamellar bone (Figures 1F and 1G and Dryad Figures S2D and S2E).

Phylogenetic Results

We included *Meemannia* in a revised version of a recent gnathostome data matrix, augmented with further osteichthyan characters and taxa to avoid spurious groupings among bony fishes reported in some past analyses [7, 10, 20–22, 29]. We find strong support for the placement of *Meemannia* as an actinopterygian (Figure 4; phylogenetic tree available at <http://dx.doi.org/10.5061/dryad.t6j72>; Dryad Figure S5), including three unambiguous synapomorphies: a lateral cranial canal, a spiracular canal, and supratemporals that extend far posterior to the hind margin of the parietals. *Dialipina*, which has been previously recovered as an actinopterygian [3, 6, 11] and stem osteichthyan [7–9, 20, 21, 29], is resolved here as the sister lineage of all other bony fishes, but with weak support.

DISCUSSION

Spiracular Canal Evolution

A long endoskeletal spiracular canal is classically regarded as a character uniting a clade of post-Devonian ray-finned fishes [23]. However, the Devonian *Cheirolepis* [14], *Mimipiscis*, and *Moythomasia* [23] bear a thin bony commissure partially or completely enclosing the spiracle against the lateral wall of the braincase. This bar is anatomically and topologically consistent with the structure in *Meemannia* and represents the precursor of the elongated canal of younger taxa (Figure 2). Endocranial enclosure of the spiracle is generally absent in sarcopterygians (excluding the highly nested *Powichthys* [17] and *Eusthenopteron* [25]), the braincase referred to *Ligulalepis* [6], *Acanthodes* [29], early chondrichthyans [25], and ‘placoderms’ [20, 25]. The stem gnathostome *Janusiscus* bears symmetrical endocranial

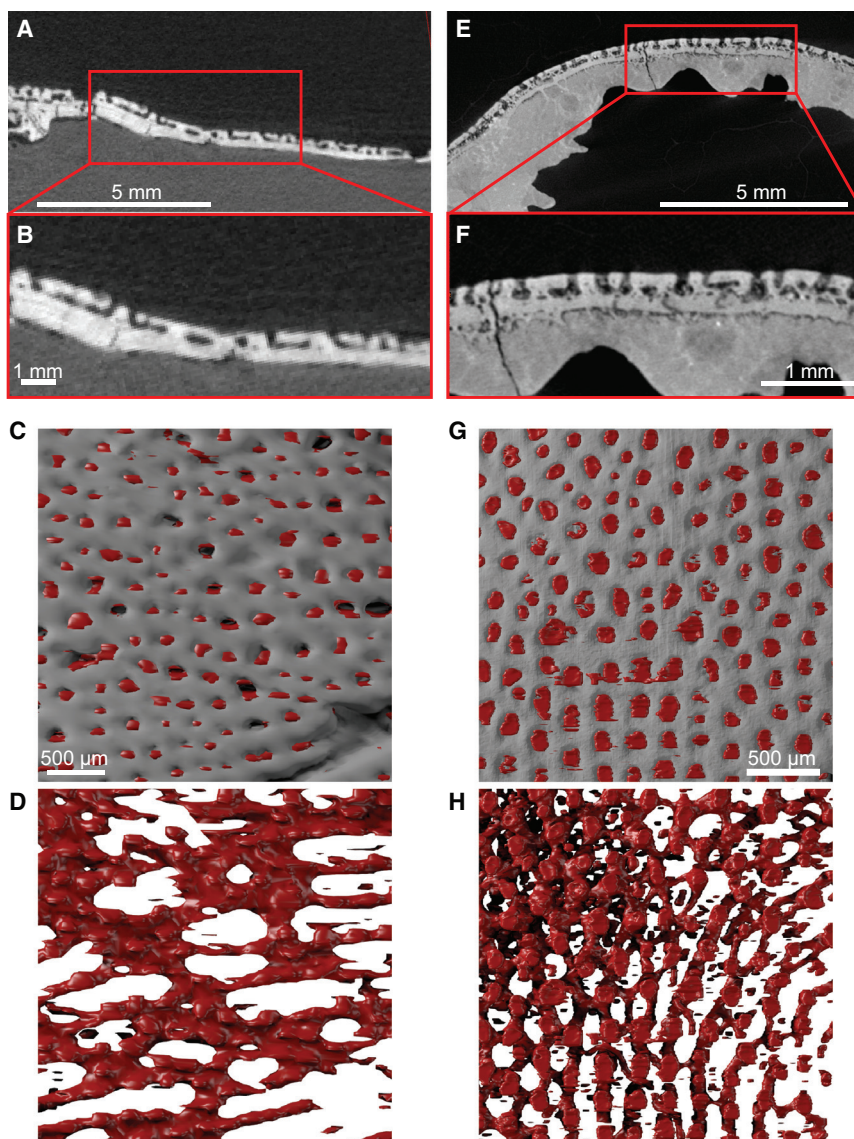


Figure 3. Comparison of Pore Canal System in *Cheirolepis* NHMUK PV.P.12508 and *Psarolepis* IVPP V6796

(A) Tomographs through maxilla of *Cheirolepis*. (B) Tomographs through maxilla of *Cheirolepis* in larger scale. (C) Rendering showing close up of dermal ornament on maxilla of *Cheirolepis*. (D) Rendering of pore canal system only of *Cheirolepis* with bone removed. (E) Tomographs through postparietal of *Psarolepis*. (F) Tomographs through postparietal of *Psarolepis* in larger scale. (G) Rendering showing close up of dermal ornament on postparietal of *Psarolepis*. (H) Rendering of pore canal system only of *Psarolepis* with bone removed. (C–H) Dermal bone in gray, pore canal system in red.

abundant fossil evidence that the absence in the latter two groups is secondary [23, 34]. Absence of a canal in polypterids is conventionally regarded as primary, making the structure a synapomorphy of a subset of crown actinopterygians (Actinopteri) [23, 31]. However, the posterior semicircular canal is incompletely enclosed within bone and cartilage in polypterids [35], questioning whether it is logically possible for a lateral cranial canal of the sort detectable in fossils to be present. Significantly, the nature of absence in *Polypterus* differs from the condition in actinopterygian outgroups [25], where the relevant portions of the endocavity are enclosed in bone but there is no projection through the loop of the posterior semicircular canal.

Zhu et al. [12] identified a dorsal embayment in the braincase of *Meemannia*, *Psarolepis*, and *Ligulelepis* as a lateral cranial

fenestrations aligned with its spiracular grooves [9], although the absence of similar features in both early sarcopterygians and the stem osteichthyan '*Ligulelepis*' argues against homology between the bridge in *Janusiscus* and actinopterygians (see optimizations in the phylogenetic tree available at <http://dx.doi.org/10.5061/dryad.t6j72>).

Lateral Cranial Canal Evolution

A lateral cranial canal is known only in actinopterygians [23, 24, 31]. It is primitively a perichondrally lined diverticulum that exits the lateral wall of the cavum cranii at the level of the hindbrain and passes through the loop of the posterior semicircular canal. It may end blindly (e.g., *Mimipiscis* [24] and *Lepisosteus* [25]), pierce the wall of the braincase and exit into the fossa bridgei (e.g., *Pteronisculus* [32]), or rejoin the cranial cavity through the loop of the anterior semicircular canal (e.g., *Caturus* [33]). Among living taxa, a lateral cranial canal is present in gars, sturgeons, and paddlefishes but is absent in polypterids, *Amia*, and teleosts. There is

canal, casting doubt that the feature is restricted to ray-finned fishes. However, these candidates differ from conventional lateral cranial canals. Most significantly, they are dorsally—rather than laterally—oriented and lie anterior to the usual position of the lateral cranial canal. Tomographic study of *Meemannia* shows that this feature is actually the crus commune, with a genuine lateral cranial canal situated more posteriorly and laterally (Figure 1D) but not easily visible in published figures [11, 12]. Although the presence of a lateral cranial canal in *Psarolepis* and *Ligulelepis* cannot be entirely ruled out without further investigation, it seems unlikely.

Primitive Dermal Bone Histology in Osteichthyans

Presence of a “cosmine”-like tissue in *Cheirolepis* suggests that the histological traits argued to link *Meemannia* with sarcopterygians are general features of bony fishes [10, 36]. These findings also highlight the ambiguity that often surrounds the use of terms such as “cosmine” and “ganoine” and present an opportunity to review the ways by which these tissues are identified.

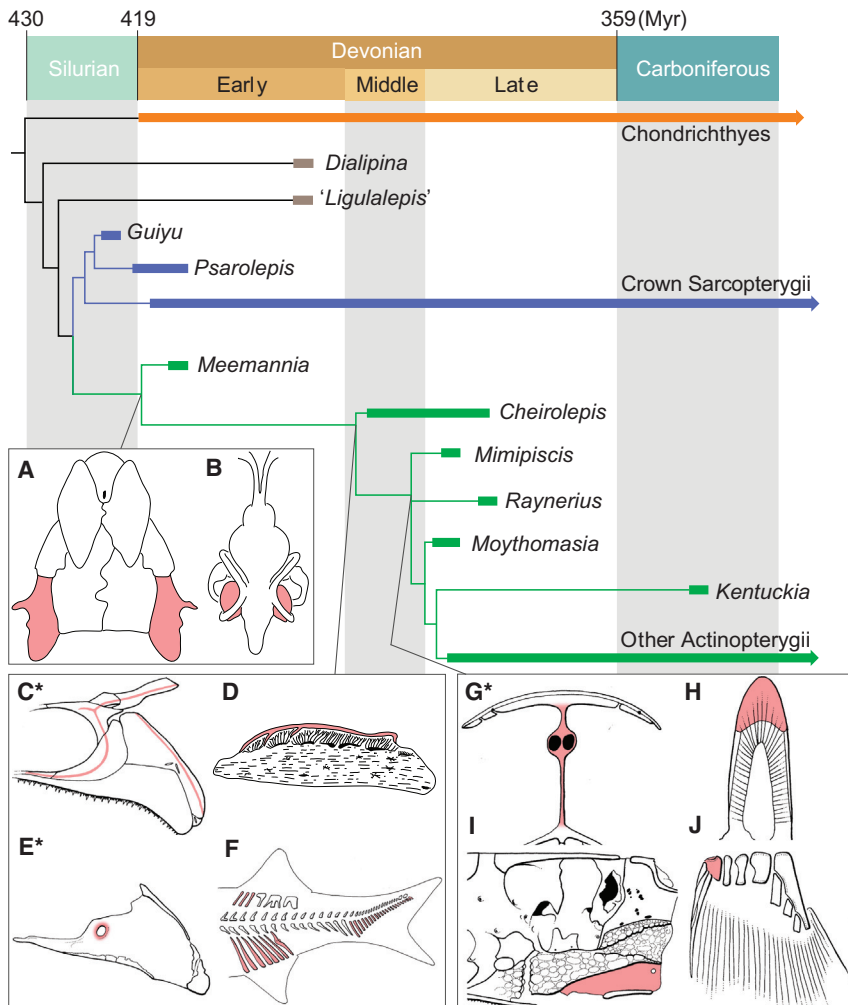


Figure 4. Summary Phylogeny, Simplified from the Strict Consensus Tree, and the Evolution of Key Actinopterygian Features

(A) Posteriorly expanded supratorpals (c.238).
 (B) Lateral cranial canal (c.155).
 (C) Absence of jugal sensory canal (c.32).
 (D) Multiple superimposed layers of enamel (“ganoine”; c.5–8).
 (E) Basiptyergoid fenestra (c.103).
 (F) Absence of basal plates (c.230 and c.233).
 (G) Interorbital septum comprising a single sheet of bone (c.136).
 (H) Acrodin (c.80).
 (I) Enclosed dorsal aorta (c.179).
 (J) Perforate pectoral propterygium (c.206).
 Asterisks refer to characters that cannot be optimized to a particular node due to missing data from proximate taxa. Illustrations (C) and (E–J) are redrawn and modified from [13, 24, 30]. See also Dryad Figures S1–S5.

Actinopterygians above *Cheirolepis* show modifications to this ancestral tissue type: loss of pore canals and underlying network and retention of multiple layers of enamel, but with loss of intervening dentine. Large, irregular pores are visible on the lower jaw, gulars, and scales of certain Devonian (e.g., *Moythomasia* [23] and *Raynerius* [19]) and Carboniferous (e.g., *Paphosisiscus* [15]) actinopterygians but appear to be absent in taxa such as *Tegeolepis* [39], *Howqualepis* [27], and *Mimipiscis* [23]. It is not possible to say whether they are homologous with the pore canal network of sarcopterygians and the earliest actinopterygians without

“Cosmine” is a complex tissue type, the identification of which is contingent on the presence of enamel on dermal bones and scales, enamel being present as a single layer (indicating that resorption is active), dentine underlying the enamel layer, regular pore openings (“pore canals”) on the surface of the enamel, and pore canals extending to pore cavities under the surface of the bone and connected horizontally by horizontal or mesh canals (a “pore canal network”). “Cosmine” is often contrasted with “ganoine,” itself a composite tissue generally considered an actinopterygian character [10, 37], identified by the presence of multiple layers of enamel without intervening dentine layers and the absence of pore canals or a pore canal network.

Meemannia has been described as displaying the first step toward the evolution of “cosmine” proper [11, 12], possessing only some of the tissue’s identifying features: pore openings on the dermal surface, a pore-canal network, dentine, and superimposed layers of enamel, suggesting that resorption was absent. New histological data for *Cheirolepis* indicate that a precursor of both “cosmine” and “ganoine” was present in the last common ancestor of actinopterygians and sarcopterygians. This hypothesis gains support if interpretations of *Psarolepis* as a stem osteichthyan rather than stem sarcopterygian are corroborated by subsequent analyses [2, 36, 38].

more complete histological investigation. Younger species of *Cheirolepis* appear to lack porous ornament, possessing the ridges more typically associated with actinopterygians [40], although dermal bone histology is unknown. These species nest within *Cheirolepis*, suggesting that a primitively present pore canal system may have been secondarily lost. The stepwise evolution of “cosmine” proper is well documented in sarcopterygians [12, 38], and the combination of characters that diagnoses the tissue is restricted to a subset of sarcopterygians: rhipidistians (lungfishes plus tetrapods).

Recognition of *Meemannia* as an actinopterygian punctuates a puzzling stratigraphic gap for half of the bony fish tree of life. Despite numerous reports of candidate ray-finned fishes from the Early Devonian and late Silurian [5, 10, 41], few of these remains can be placed with confidence [8]. Characters recently proposed as indicating actinopterygian affinity for this material [10]—an anterodorsal process on the scale, peg and socket articulation, and multilayered enamel—only diagnose membership of total-group Osteichthyes. While considerable sarcopterygian diversity is known from the earliest Devonian, and increasingly the late Silurian, the oldest unequivocal actinopterygian material is some 30 million years younger [41]. By this point, even deep-diverging ray-fin lineages like *Cheirolepis* had acquired

considerable specializations, pointing to an extensive—but as yet unsampled—evolutionary history [41]. It has been hypothesized that this gap stems from low actinopterygian richness and abundance [8], a pattern apparent throughout the Devonian record [42, 43]. *Meemannia* reinforces this pattern; in contrast to hundreds of sarcopterygian and placoderm fossils known from the shallow marine Xitun Formation, it is represented by only five specimens. The mandibles of co-occurring sarcopterygians point to considerable early trophic specialization in that group, with examples like toothplates and a palatal bite in *Diabolepis* [44] and the combination of a long adductor fossa, short dentary, and double jaw joint in *Styloichthys* [16]. By contrast, the lower jaws attributed to *Meemannia* lack such extreme modifications and, like those of other early ray-finned fishes, fall near the center of a function space for early gnathostome mandibles [43].

The rarity of *Meemannia*, and early ray-fins more generally, supports a “long-fuse” model for actinopterygian diversification [41, 42], by which the clade persisted at low levels of numerical abundance, taxonomic richness, and morphological disparity for millions of years before undergoing apparently explosive diversification in the early Carboniferous after the end-Devonian Hangenberg Event [42]. *Meemannia* provides an anatomical snapshot of the earliest stages of ray-finned fish evolution, at a time when their rarity and limited ecological variety gave no indication of the dominant role they would play in aquatic vertebrate ecosystems of the future.

EXPERIMENTAL PROCEDURES

High-Resolution Computed Tomography

We analyzed two detached crania and one lower-jaw element (IVPP V14534.2, V14534.4, and V14534.5) of *Meemannia eos* at the IVPP, Chinese Academy of Sciences (CAS), Beijing, China, using 225 kV microCT (developed by the Institute of High Energy Physics, CAS). A skull roof of *Psarolepis* (IVPP V6796) was also scanned. One specimen of *Cheirolepis* (NHMUK PV P.12508) was scanned at the Imaging and Analysis Centre of NHMUK using a Metris X-Tek HMX ST 225 CT system. Additional parameters are given in the [Supplemental Experimental Procedures](#). Scan data were analyzed using Mimics (<http://biomedical.materialise.com/mimics>; Materialise).

Phylogenetic Analysis

Analyses were performed in PAUP* v.4.0b10 [45] using a dataset modified from that of [9], with 90 taxa and 269 characters (seven ordered: 64, 126, 136, 166, 262, 264, 268). Additional settings are given in the [Supplemental Experimental Procedures](#).

ACCESSION NUMBERS

The Nexus format file and a large-format PDF of a phylogenetic tree depicting all character state transformations on internal nodes, together with all input data and output files, are available on DRYAD: <http://dx.doi.org/10.5061/dryad.t6j72>.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.04.045>.

AUTHOR CONTRIBUTIONS

The project was conceived by M.Z. All authors performed the research. S.G., J.L., and M.F. generated the computed tomography renderings. Figures were

produced by J.L., S.G., and M.F. M.F., S.G., and J.L. conducted the phylogenetic analyses. J.L.d.B. and S.G. prepared the *Cheirolepis* sections. All authors participated in the interpretation of the specimen data and writing the manuscript.

ACKNOWLEDGMENTS

We thank Y.-M. Hou, R. Close, and D. Sykes for assistance with CT scanning. We are grateful to C. Rogers for help with thin sectioning. This work was supported by the Major Basic Research Projects of China (2012CB821902), the National Natural Science Foundation of China (41472016 and 41530102), and the National Major Scientific Instrument and Equipment Development Project of China (2011YQ03012) to J.L. and M.Z.; NERC Cohort NE/J500045/1 grant to S.G.; and the Phillip Leverhulme Prize and John Fell Fund, both to M.F.

Received: February 16, 2016

Revised: March 29, 2016

Accepted: April 18, 2016

Published: May 19, 2016

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