

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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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

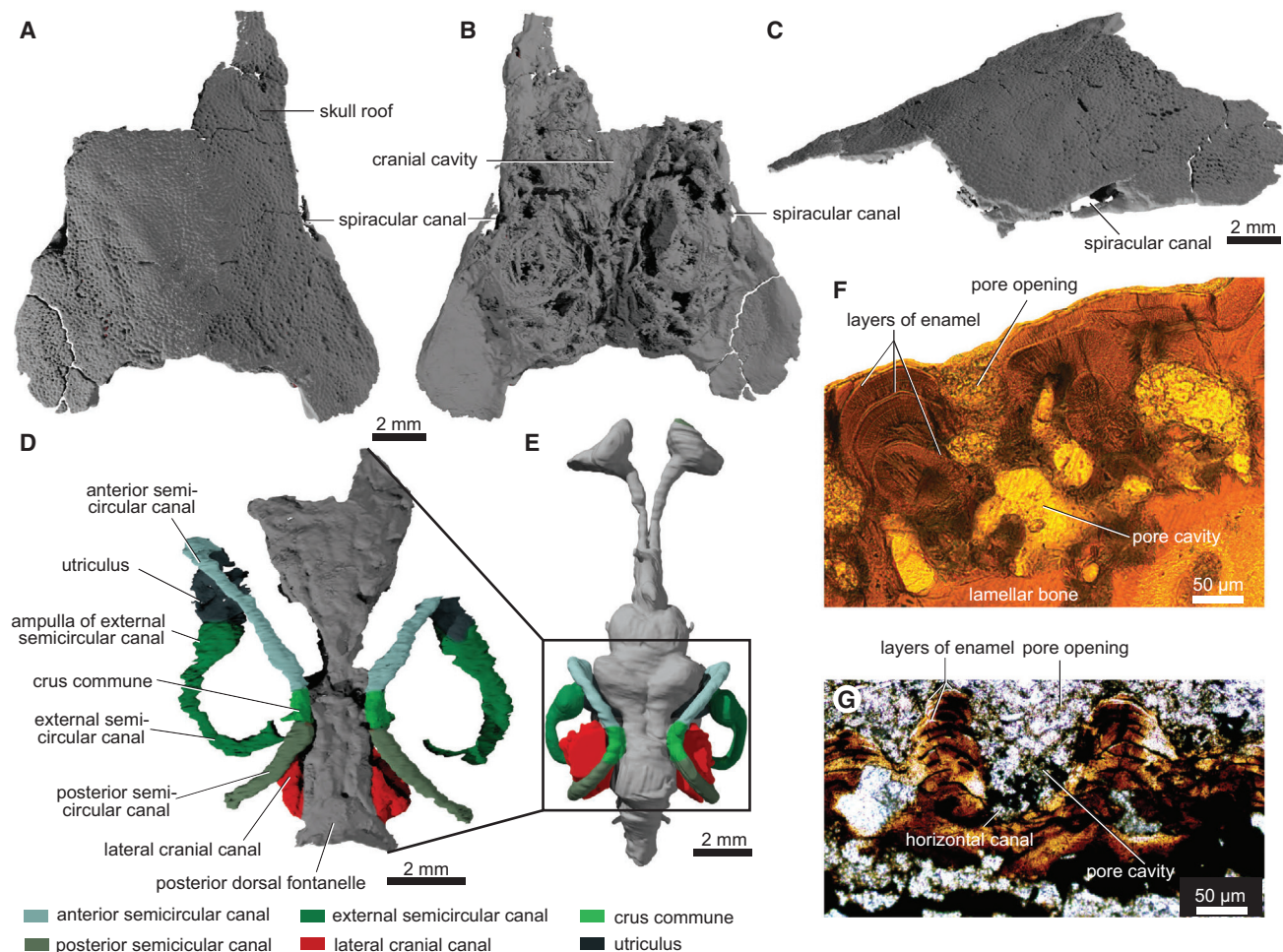


Figure 1. Cranial Anatomy of *Meemannia eos* Based on High-Resolution Computed Tomography of IVPP V14536.4

(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 crus 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 crus 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

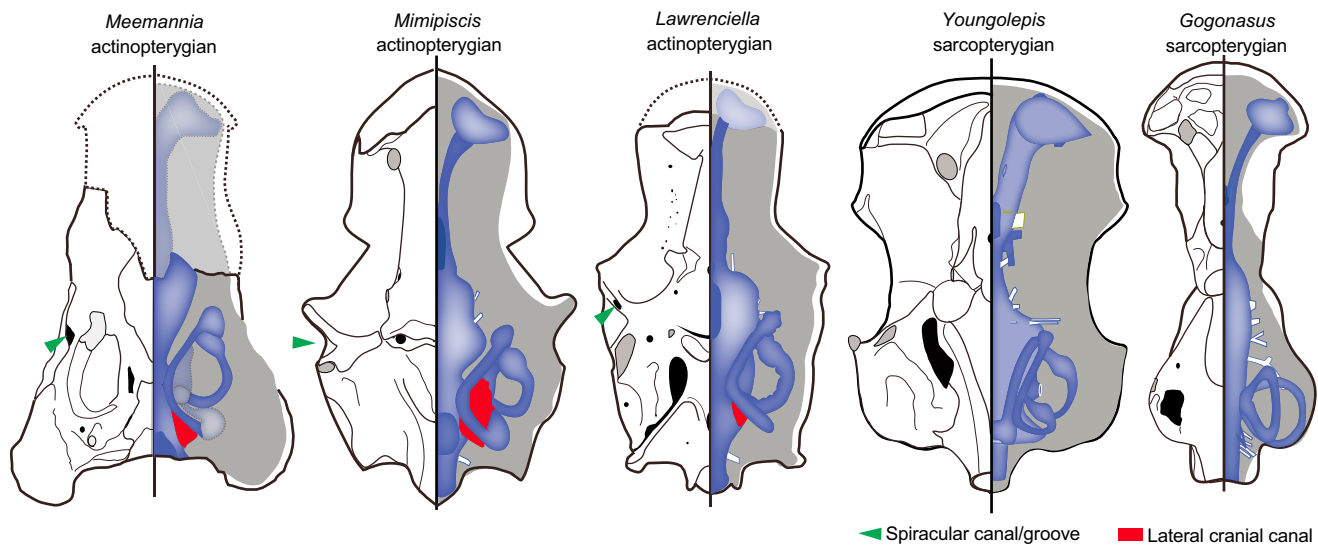


Figure 2. Comparative Braincase and Endocast Morphology of Selected Osteichthyans

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

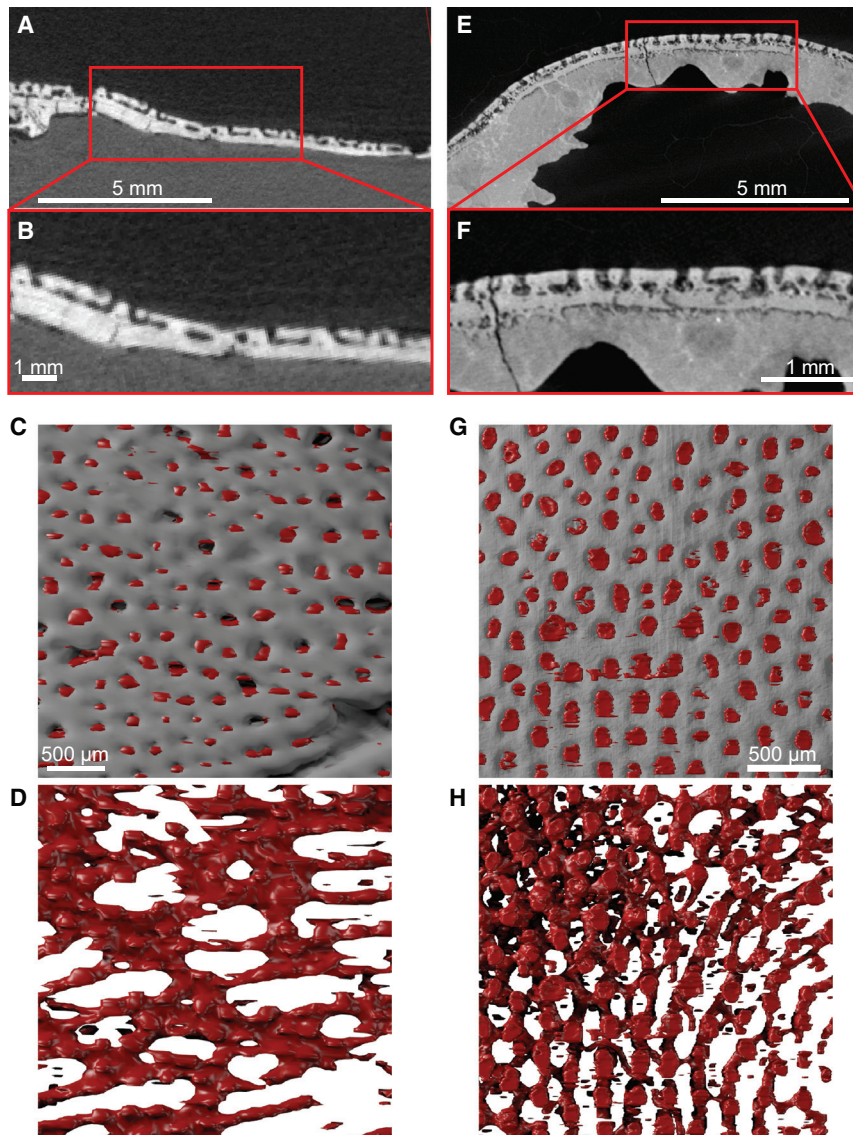


Figure 3. Comparison of Pore Canal System in *Cheirolepis* NHMUK PV P.12508 and *Psarolepis* IVPP V6796

(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 *Ligulalepis* 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 '*Ligulalepis*' 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., *Pteroniscus* [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 *Ligulalepis* 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.

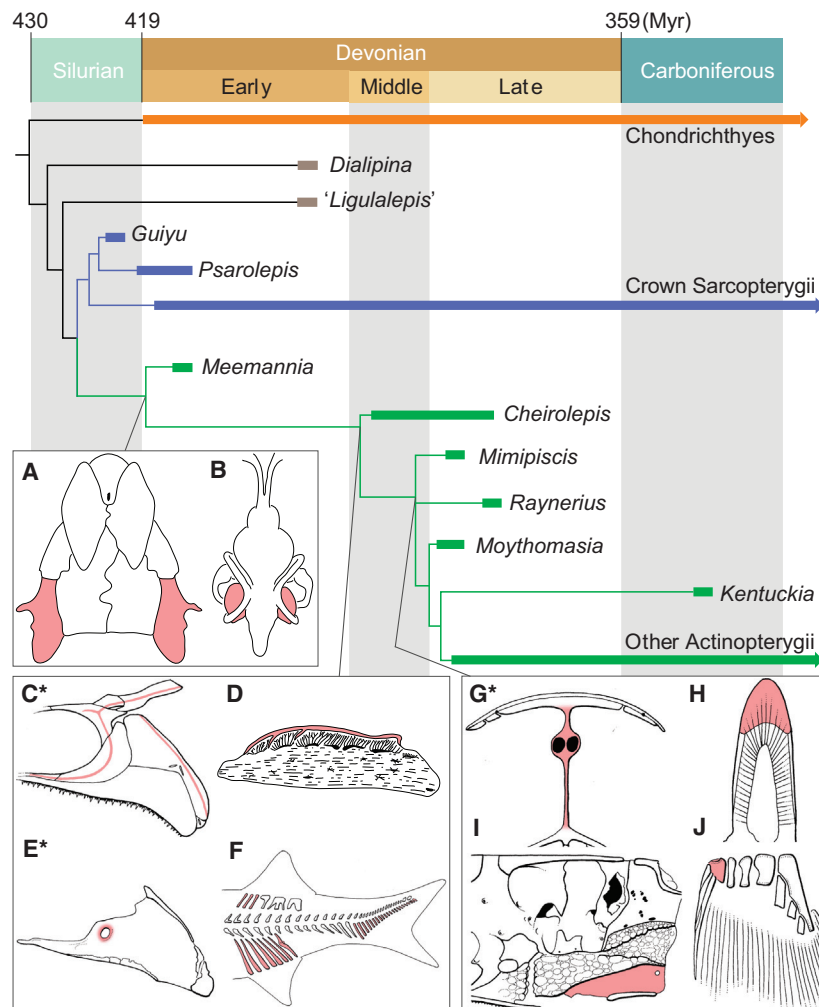


Figure 4. Summary Phylogeny, Simplified from the Strict Consensus Tree, and the Evolution of Key Actinopterygian Features

(A) Posteriorly expanded supratemporals (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) Basipterygoid 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., *Paphosiscus* [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.

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Supplemental Information

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

Jing Lu, Sam Giles, Matt Friedman, Jan L. den Blaauwen, and Min Zhu

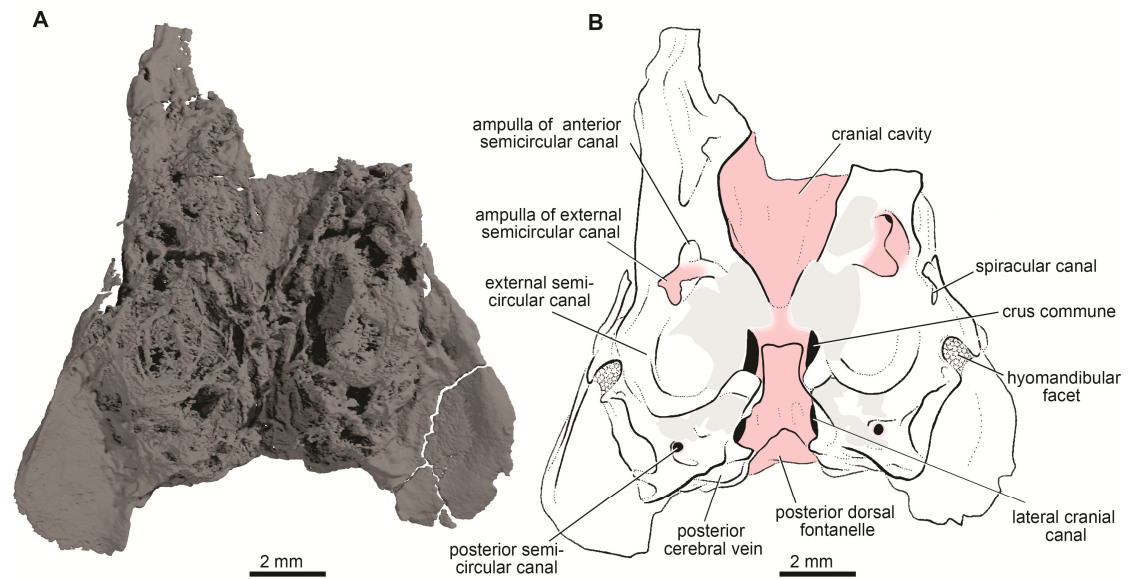


Figure S1. The braincase of *Meemannia eos* (IVPP V14536.4). Related to Figure 1.

(A) Rendering of braincase in ventral view.

(B) Interpretive drawing of braincase in ventral view.

Grey shading indicates areas where the perichondral bone is missing or badly broken; red indicates the extent of the endocast as reconstructed in Figure 1.

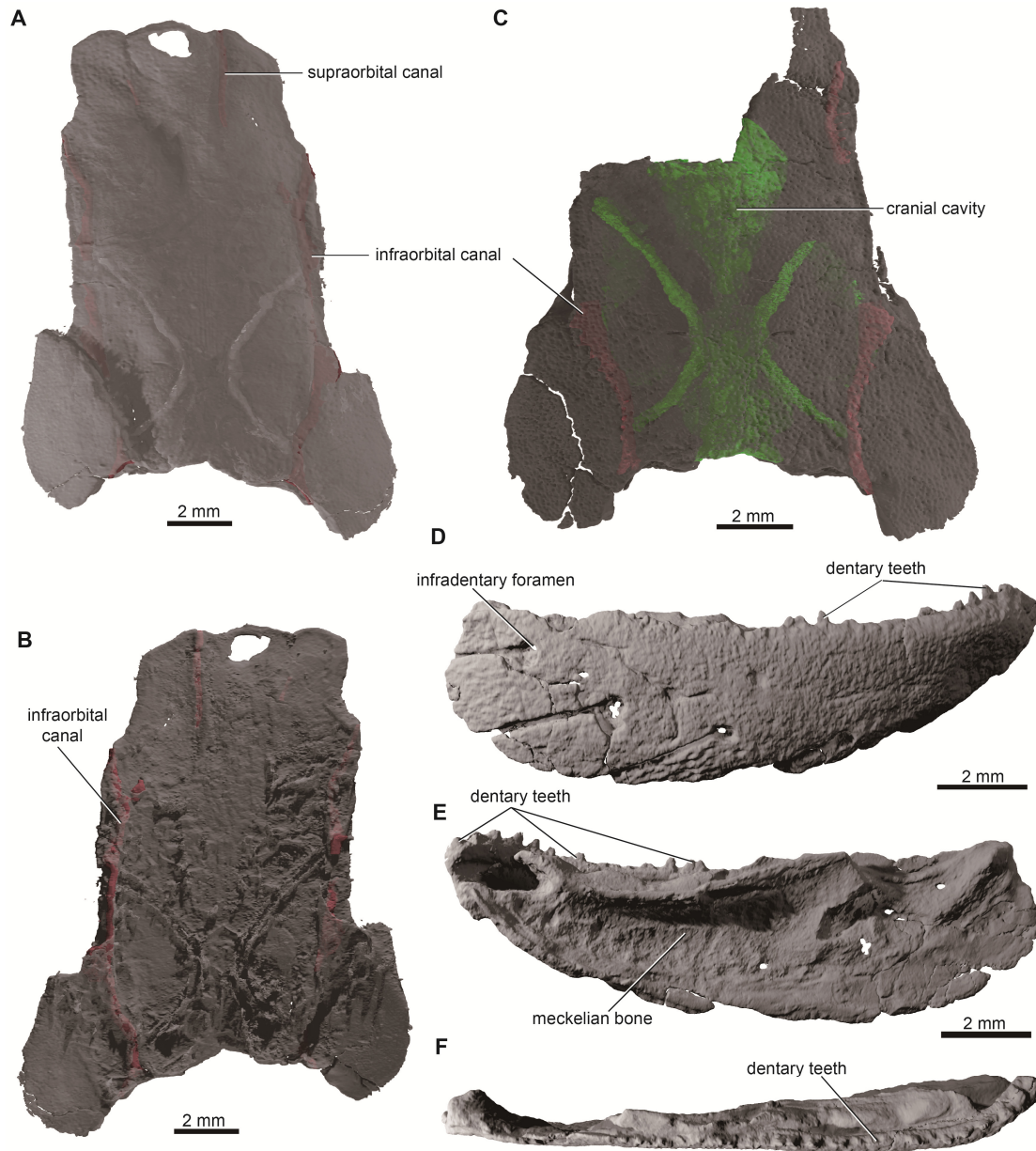


Figure S2. Skull and lower jaw of *Meemannia eos*. Related to Figure 1.

- (A) Semi-transparent rendering of IVPP V14536.2 showing path of sensory canals (dark red) in dorsal view.
- (B) Semi-transparent rendering of IVPP V14536.2 showing path of sensory canals (dark red) in ventral view.
- (C) Semi-transparent rendering of IVPP V14536.4 in dorsal view showing the endocast (dark green) and sensory canals (dark red).
- (D) Rendering of lower jaw (IVPP V14536.5) showing the dentary teeth extending to the anterior end of the jaw in external view.
- (E) Rendering of lower jaw (IVPP V14536.5) showing the dentary teeth extending to the anterior end of the jaw in internal view.
- (F) Rendering of lower jaw (IVPP V14536.5) showing the dentary teeth extending to the anterior end of the jaw in dorsal view.

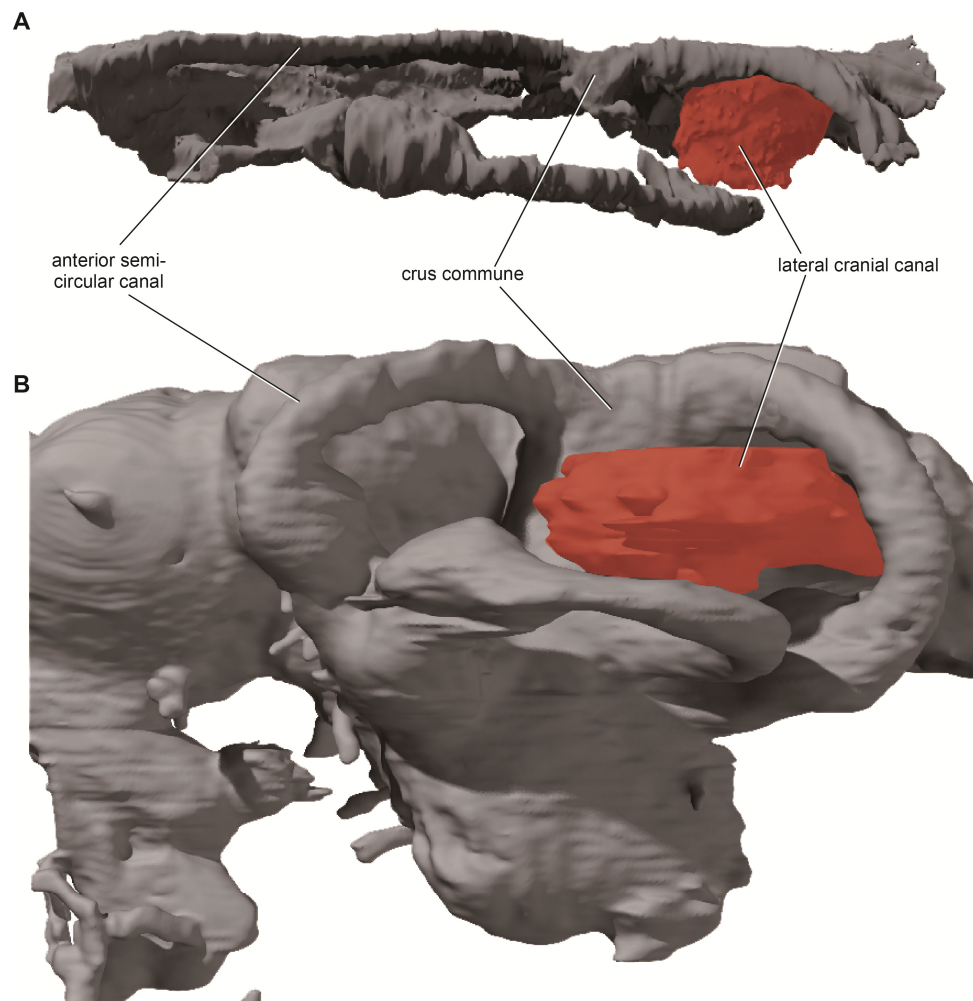


Figure S3. Comparison of labyrinth and associated structures in left lateral view. Related to Figures 1 and 2.

(A) *Meemannia* (IVPP V14536.4).

(B) *Mimipiscis* (NHMUK PV P.53247) [S1].

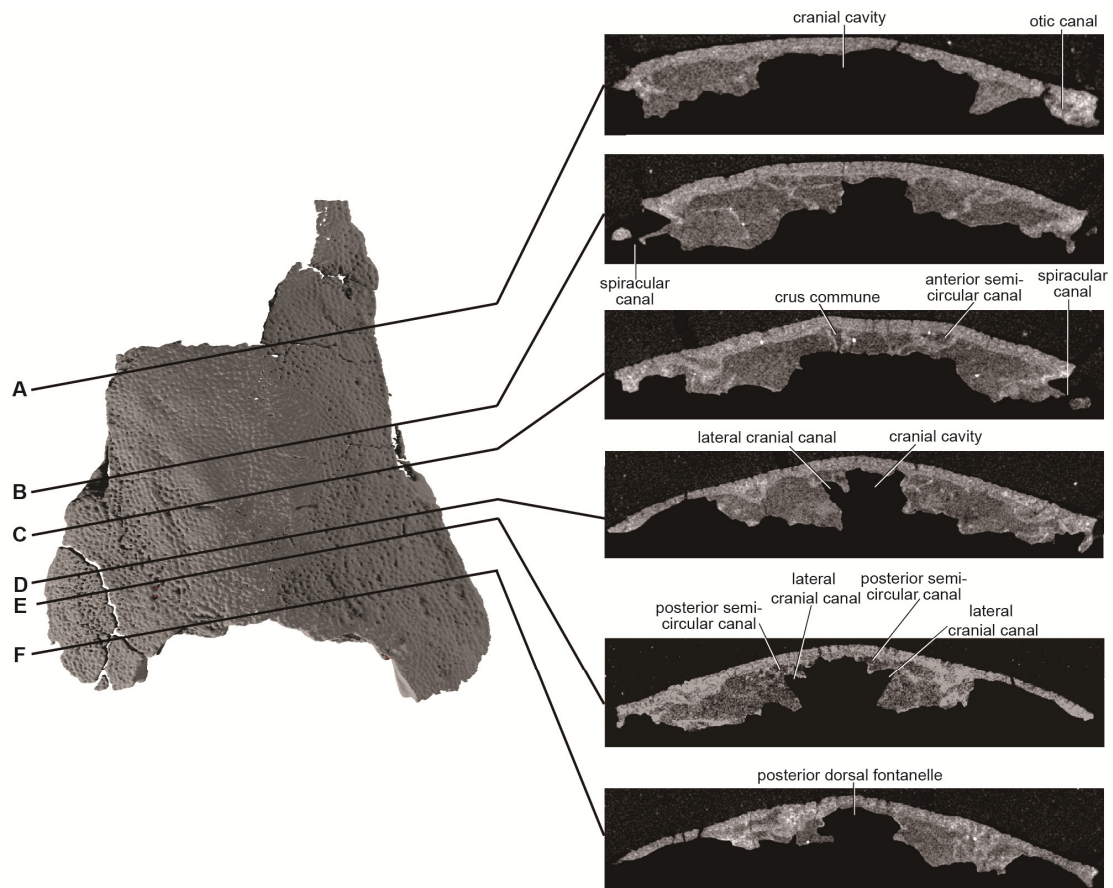


Figure S4. Transverse tomographs of *Meemannia eos* (IVPP V14536.4). Related to Figure 1.

- (A) Section through the anterior part of the cranial cavity.
- (B) Section through the spiracular canal and the cranial cavity.
- (C) Section through the crus commune of the cranial cavity.
- (D) Section through the lateral cranial canal of the cranial cavity.
- (E) Section bisecting the left and right lateral cranial canal of the cranial cavity
- (F) Section through the posterior dorsal fontanelle of the cranial cavity.

Matrix is dark grey, bone (both dermal and endoskeletal) is light grey, air is black; fixing putty (dorsal to skull roof) is speckled black and grey.

Supplemental Experimental Procedures

Supplemental notes

A re-description of the neurocranium of *Meemannia* has been performed based on HRCT scanning at IVPP. *Meemannia* was originally described as the most primitive sarcopterygian, on the basis of its combining an actinopterygian-like skull roof with a cosmine-like dermal surface and a pore–canal network [S2]. Our re-study of *Meemannia* based on HRCT reveals endoskeletal enclosure of the spiracle and a lateral cranial canal. Identification of the second feature casts doubt on the presence of this structure in *Psarolepis* and ‘*Ligulalepis*’. These traits, in combination with actinopterygian-like aspects of the dermal skull roof, support re-interpretation of *Meemannia* as a ray-finned fish. This new placement is bolstered by the presence of an extensive pore–canal network in *Cheirolepis*, which indicates that this character is a probable osteichthyan symplesiomorphy that cannot be used to align *Meemannia* with sarcopterygians to the exclusion of ray-finned fishes.

High-resolution computed tomography

We analysed two detached crania and one lower jaw element (IVPP V14534.2, IVPP V14534.4, and IVPP V14534.5) of *Meemannia eos* at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS), Beijing, China using 225 kV micro-CT (developed by the Institute of High Energy Physics, CAS). A skull roof of *Psarolepis* (IVPP V6796) was also scanned. IVPP V14534.2 was scanned with an energy of 130 kV and 100 mA, at a detector resolution of 15.68 μm per pixel. IVPP V14534.4 was scanned with a voltage of 140 kV and current of 100 mA, at a detector resolution of 9.41 μm per pixel. IVPP V14534.5 was scanned with a voltage of 110 kV and current of 120 mA, at a detector resolution of 8.62 μm per pixel. IVPP V6796 was scanned with a voltage of 120 kV and current of 120 mA, at a detector resolution of 7.48 μm per pixel. All scans were conducted using a 1440° rotation with a step size of 0.25° and an unfiltered aluminium reflection target. 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 with a 2000 x 2000 pixel detector. A voltage of 120 kV and current of 155 mA were used, with a resultant voxel size of 36.32 μm . Scan data were analysed using Mimics (<http://biomedical.materialise.com/mimics>; Materialise). After segmenting, surface meshes were exported into and imaged in Blender (<http://blender.org>; Stitching Blender Foundation).

Phylogenetic Analysis:

1) Phylogenetic notes

Analyses were performed in PAUP* v.4.0b10 [1] using a dataset modified from that of ref. [S3], with 90 taxa and 269 characters (seven ordered: 64, 126, 136, 166, 262, 264, 268). We follow Giles [S4] in only coding characters relating to the braincase and skull roof of *Janusiscus* and ‘*Ligulalepis*’. We conducted a heuristic search using 1,000 random addition sequence replicates, holding 5 trees at each step, with the tree bisection and reconnection (TBR) strategy

enabled and maxtrees set to automatically increase by 500. The constraint [Galeaspida[Osteostraci[Ingroup]]] was enforced. Bootstrap values were calculated using 1,000 replicates of a heuristic search, five trees held at each step, TBR enabled, 10 reps, rearrlimit=20,000,000, limitperrep=yes. Bremer support values were calculated using PRAP2 [S5].

The analysis resulted in 815,616 shortest trees with a length of 768 steps. A summary strict consensus tree, showing a subset of taxa with an emphasis on actinopterygians is shown in Figure 4; the full tree is given in DRYAD Figure S5. The optimization tree, showing all unambiguous character changes, is given in supplementary data 1. *Meemannia* is recovered as the sister taxon of all remaining actinopterygians, with a Bremer decay index of 2 and a bootstrap support of 76%, and three unambiguous characters, two of which have a consistency index of 1. The large number of shortest trees is largely due to polychotomous branching on the chondrichthyan stem, with varying relationships between placoderm lineages and within the sarcopterygian crown contributing to a more minor degree.

2) List of Taxa

Taxa included in the analyses with associated references

Taxon	References
Galeaspida	Donoghue et al. 2000 [S6]; Wang et al. 2005 [S7]; Gai et al. 2011 [S8].
Osteostraci	Denison 1947 [S9]; Janvier 1985 [S10]; Sansom 2009 [S11].
<i>Acanthodes</i>	Gross 1947 [S12]; Miles 1968 [S13], 1973 [S14, S15]; Coates 1994 [S16]; Valiukevicius 1995 [S17]; Davis et al. 2012 [S18].
<i>Akmonistion</i>	Coates & Sequeira 1998 [S19]; Coates et al. 1998 [S20]; Coates & Sequeira 2001 [S21].
<i>Austroptyctodus</i>	Long, 1997 [S22]; Miles & Young 1977 [S23].
<i>Bothriolepis</i>	Denison 1978 [S24]; Young 1986 [S25]; Young 1988 [S26].
<i>Brachyacanthus</i>	Watson 1937 [S27]; Denison 1979 [S28].
<i>Brindabellaspis</i>	Young 1980 [S29], 1986 [S25]; Burrow & Turner 1998 [S30], 1999 [S31].
<i>Brochoadmones</i>	Bernacsek & Dineley 1977 [S32]; Gagnier & Wilson 1996 [S33]; Hanke & Wilson 2006 [S34].
<i>Buchanosteus</i>	Young 1979 [S35], 1986 [S25]; Young et al. 2001 [S36].
<i>Campbellodus</i>	Miles & Young 1977 [S23]; Long 1997 [S22].
<i>Cassidiceps</i>	Gagnier & Wilson 1996 [S37].
<i>Cheiracanthus</i>	Watson 1937 [S27]; Miles 1973 [S14]; Denison 1979 [S28].
<i>Cheirolepis</i>	Ørvig 1967 [S38]; Pearson & Westoll 1979 [S39]; Arratia & Cloutier 1996 [S40]; Giles et al. 2015 [S41].
<i>Chondrenchelys</i>	Moy-Thomas 1935 [S42]; Lund 1982 [S43]; Finarelli & Coates 2014 [S44].
<i>Cladodoides</i>	Gross 1937 [S45], 1938 [S46]; Maisey 2005 [S47].
<i>Cladoselache</i>	Hussakof & Bryant 1918 [S48]; Woodward & White 1938 [S49]; Bendix-Almgreen 1975 [S50]; Schaeffer 1981 [S51]; Zangerl 1981 [S52]; Maisey 2007 [S53].
<i>Climatius</i>	Watson 1937 [S27]; Ørvig 1967 [S38]; Miles 1973 [S14, S54].

<i>Cobelodus</i>	Zangerl & Case 1976 [S55]; Maisey 2007 [S53].
<i>Coccosteus</i>	Stensiö 1963 [S56]; Miles & Westoll 1968 [S57].
<i>Cowralepis</i>	Ritchie 2005 [S58]; Carr et al. 2009 [S59]; Long et al. 2009 [S60].
<i>Culmacanthus</i>	Long, 1983 [S61]; Burrow & Young 2012 [S62].
<i>Debeerius</i>	Grogan & Lund 2000 [S63].
<i>Diabolepis</i>	Chang & Yu 1984 [S64]; Chang 1995 [S65].
<i>Dialipina</i>	Schultze 1968 [S66]; Schultze & Cumbaa 2001 [S67].
<i>Dicksonosteus</i>	Goujet 1975 [S68], 1984 [S69].
<i>Diplacanthus</i>	Watson 1937 [S27]; Miles 1973 [S14]; Gagnier 1996 [S70].
<i>Diplocercides</i>	Forey 1998 [S71].
<i>Dipterus</i>	Parrington 1950 [S72]; White 1965 [S73]; Challands 2015 [S74].
<i>Doliodus</i>	Miller et al. 2003 [S75]; Turner 2004 [S76]; Maisey et al. 2009 [S77]; Maisey et al. [S78].
<i>Entelognathus</i>	Zhu et al. 2013 [S79].
<i>Eurycaraspis</i>	Liu 1991 [S80].
<i>Eusthenopteron</i>	Jarvik 1980 [S81].
<i>Euthacanthus</i>	Watson, 1937 [S27]; Newman et al. 2011 [S82].
<i>Gavinia</i>	Long, 1999 [S83].
<i>Gemuendina</i>	Gross 1963 [S84].
<i>Gladiobranchus</i>	Bernacsek & Dineley 1977 [S32]; Hanke & Davis 2008 [S85]; Newman et al. 2012 [S86].
<i>Glyptolepis</i>	Andrews & Westoll 1970 [S87]; Jarvik 1972 [S88]; Cloutier & Schultze 1996 [S89]; Ahlberg 1989 [S90].
<i>Gogonasus</i>	Long et al. 1997 [S91]; Long et al. 2006 [S92]; Holland 2014 [S93].
<i>Guiyu</i>	Zhu et al. 2009 [S94]; Qiao & Zhu 2010 [S95].
<i>Gyracanthides</i>	Warren et al. 2000 [S96]; Turner et al. 2005 [S97].
<i>Hamiltonichthys</i>	Maisey, 1989 [S98].
<i>Helodus</i>	Moy-Thomas 1936 [S99].
<i>Homalacanthus</i>	Watson 1937 [S27]; Gagnier 1996 [S70].
<i>Howqualepis</i>	Long 1988 [S100]; Giles et al. 2015 [S101].
<i>Incisoscutum</i>	Johanson & Smith 2005 [S102]; Ahlberg et al. 2009 [S103].
<i>Ischnacanthus</i>	Watson 1937 [S27]; Gross 1947 [S12]; Miles 1973 [S14]; Blais et al. 2011 [S104].
<i>Jagorina</i>	Stensiö 1969 [S105].
<i>Janusiscus</i>	Giles et al. 2015 [S4].
<i>Kansasiella</i>	Poplin 1974 [S106].
<i>Kathemacanthus</i>	Gagnier & Wilson 1996 [S37]; Hanke & Wilson 2010 [S107].
<i>Kentuckia</i>	Rayner 1951 [S108]; Giles & Friedman 2014 [S1].
<i>Kujdanowiaspis</i>	Stensiö 1969 [S105]; Dupret 2010 [S109].
<i>Latviacanthus</i>	Schultze & Zidek 1982 [S110].
<i>Lawrenciella</i>	Hamel & Poplin 2008 [S111].
<i>‘Ligulalepis’</i>	Basden et al. 2000 [S112]; Basden & Young 2001 [S113].
<i>Lunaspis</i>	Heintz 1937 [S114]; Gross 1961 [S115].

<i>Lupopsyrus</i>	Bernacsek & Dineley 1977 [S32]; Hanke & Davis 2012 [S116].
<i>Macropetalichthys</i>	Stensiö 1925 [S117], 1969 [S105]; Gross 1935 [S118]; Denison 1978 [S24]; Young, 1978 [S119].
<i>Meemannia</i>	Zhu et al. 2006 [S2]; Zhu et al. 2010 [S120].
<i>Mesacanthus</i>	Watson 1937 [S27]; Gross 1947 [S12]; Miles 1973 [S14].
<i>Miguashaia</i>	Cloutier 1996 [S121]; Forey 1998 [S71].
<i>Mimipiscis</i>	Gardiner & Bartram 1977 [S122]; Gardiner 1984 [S123]; Giles & Friedman 2014 [S1].
<i>Moythomasia</i>	Gardiner 1984 [S123].
<i>Obtusacanthus</i>	Hanke & Wilson 2004 [S124].
<i>Onychodus</i>	Andrews et al. 2006 [S125].
<i>Onychoselache</i>	Dick & Maisey 1980 [S126]; Coates & Gess 2007 [S127].
<i>Orthacanthus</i>	Schaeffer 1981 [S51]; Maisey 1983 [S128].
<i>Parayunnanolepis</i>	Zhang et al. 2001 [S129]; Zhu et al. 2012 [S130].
<i>Parexus</i>	Watson 1937 [S27]; Miles 1973 [S14].
<i>Poracanthodes</i>	Valiukevicius 1992 [S131]; Denison 1979 [S28].
<i>Porolepis</i>	Jarvik 1972 [S88]; Clément 2004 [S132].
<i>Powichthys</i>	Jessen 1975 [S133], 1980 [S134].
<i>Promesacanthus</i>	Hanke 2008 [S135].
<i>Psarolepis</i>	Zhu & Schultze 1997 [S136]; Yu 1998 [S137]; Zhu et al. 1999 [S138]; Qu et al. 2013 [S139].
<i>Pterichthyodes</i>	Hemmings 1978 [S140].
<i>Ptomacanthus</i>	Miles 1973 [S14]; Denison 1979 [S28]; Brazeau 2009 [S141], 2012 [S142].
<i>Pucapampella</i>	Maisey 2001 [S143]; Maisey & Anderson 2001 [S144]; Janvier & Maisey 2010 [S145]; Maisey & Lane 2010 [S146].
<i>Ramirosuarezia</i>	Pradel et al. 2009 [S147].
<i>Raynerius</i>	Giles et al. 2015 [S148].
<i>Rhamphodopsis</i>	Miles 1967 [S149]; Long 1997 [S22]; Miles & Young 1977 [S23].
<i>Romundina</i>	Goujet & Young 2004 [S150]; Giles et al. 2013 [S151].
<i>Styloichthys</i>	Zhu & Yu 2002 [S152], 2004 [S153]; Friedman 2007 [S154]; Lu & Zhu 2008 [S155].
<i>Tamiobatis</i>	Schaeffer 1981 [S51]; Williams 1998 [S156].
<i>Tetanopsyrus</i>	Gagnier & Wilson 1995 [S157]; Gagnier et al. 1999 [S158]; Hanke et al. 2001 [S159].
<i>Tristychius</i>	Dick 1978 [S160]; Coates & Gess 2007 [S127].
<i>Uranolophus</i>	Denison 1968 [S161]; Campbell & Barwick 1988 [S162].
<i>Vernicomacanthus</i>	Miles 1973 [S14].
<i>Youngolepis</i>	Chang & Yu 1981 [S163]; Chang 1982 [S164], 1991 [S165], 2004 [S166].
<i>Yunnanolepis</i>	Zhu 1996 [S167]; Zhang 1980 [S168]; Giles et al. 2013 [S151].

2) List of Characters

Characters 1–236 taken from Giles et al. (2015; see for character notes and provenance) [S5], which in turn is modified from Davis et al. [S18] and Brazeau [S141]. Changes in coding and the source of additional characters (c.237–269) is noted in the description. Characters have especially benefitted from new, detailed treatments of *Cheirolepis* [S101], *Chondrenchelys* [S44], and *Gogonasus* [S93], and references on the squamation of *Styloichthys* [S155]. Ordered multistate characters are indicated with an asterisk (*).

Histology

1. Tessellate prismatic calcified cartilage:

- 0. absent
- 1. present

2. Prismatic calcified cartilage:

- 0. single layered
- 1. multi-layered

3. Perichondral bone:

- 0. present
- 1. absent

4. Extensive endochondral ossification:

- 0. absent
- 1. present

5. Enamel(oid) present on dermal bones and scales:

- 0. absent
- 1. present

6. Enamel:

- 0. single-layered
- 1. multi-layered

7. Enamel layers:

- 0. applied directly to one another (ganoine)
- 1. separated by layers of dentine

8. Pore canal network (sensu Zhu et al. [S118]):

The previous formulation of this character referenced an extensive pore canal network. However, this leaves assessment of presence and absence ambiguous based on subjective interpretations of when such a network might be considered ‘extensive’. Instead, we have reformulated this character to capture those instances in which cavities connect with the

outer surface of the bone via pores. Changed from ‘?’ to ‘0’ for *Cassidiceps*, *Euthacanthus*, *Helodus*, *Homalacanthus*, *Ischnacanthus*, *Janusiscus*, *Kathemacanthus*, *Kentuckia*, *Latviacanthus*, ‘*Ligualepis*’, *Mesacanthus*, *Onychodus*, *Pterichthyodes*, *Tristychius*; from ‘1’ to ‘0’ in *Dialipina*, *Poracanthodes*; from ‘0’ to ‘?’ in *Guiyu*, *Jagorina*, *Moythomasia*.

- 0. absent
- 1. present

9. Dentinous tissue:

- 0. absent
- 1. present

10. Dentine kind:

- 0. mesodentine
- 1. semidentine
- 2. orthodentine

11. Bone cell lacunae in body scale bases:

- 0. present
- 1. absent

12. Main dentinous tissue forming fin spine:

Changed from ‘-’ to ‘0’ in *Pterichthyodes*.

- 0. osteodentine
- 1. orthodentine

Squamation

13. Longitudinal scale alignment in fin webs:

Changed from ‘-’ to ‘0’ in *Pterichthyodes*.

- 0. present
- 1. absent

14. Differentiated lepidotrichia:

- 0. absent
- 1. present

15. Body scale growth pattern:

- 0. comprising single odontode unit/generation ("monodontode")
- 1. comprising a complex of multiple odontode generations/units ("polyodontode")

16. Body scale growth concentric:

- 0. absent
- 1. present

- 17. Generations of odontodes:**
0. buried
1. areally growing
2. resorbed
- 18. Body scales with peg-and-socket articulation:**
Changed from '?' to '1' in *Styloichthys*.
0. absent
1. present
- 19. Scale peg:**
Changed from '?' to '0' in *Styloichthys*.
0. broad
1. narrow
- 20. Anterodorsal process on scale:**
Changed from '?' to '1' in *Styloichthys*.
0. absent
1. present
- 21. Body scale profile:**
Changed from '?' to '1' in *Styloichthys*.
0. distinct crown and base demarcated by a constriction ("neck")
1. flattened
- 22. Profile of scales with constriction between crown and base:**
0. neck similar in width to crown
1. neck greatly constricted, resulting in anvil-like shape
- 23. Body scales with bulging base:**
Changed from '?' to '0' in *Styloichthys*.
0. absent
1. present
- 24. Body scales with flattened base:**
Changed from '?' to '1' in *Styloichthys*.
0. present
1. absent
- 25. Basal pore in scales:**
0. absent
1. present

- 26. Flank scale alignment:**
Changed from ‘-‘ to ‘?’ for *Chondrenchelys*.
0. vertical rows oblique rows or hexagonal
 1. rhombic packing
 2. disorganised

- 27. Scute-like ridge scales (basal fulcra):**
0. absent
 1. present

- 28. Sensory line canal:**
0. perforates scales
 1. passes between scales
 2. C-shaped scales

Dermal bones of the skull

- 29. Dermal ornamentation:**
Changed from ‘1’ to ‘3’ for *Glyptolepis*, from ‘3’ to ‘-‘ for *Onychoselache*, from ‘3’ to ‘0’ for *Psarolepis*.
0. smooth
 1. parallel, vermiform ridges
 2. concentric ridges
 3. tuberculate

- 30. Sensory line network:**
0. preserved as open grooves (sulci) in dermal bones
 1. sensory lines pass through canals in dermal bones (open as pores)

- 31. Sensory canals/grooves:**
0. contained within the thickness of dermal bones
 1. contained in prominent ridges on visceral surface of bone

- 32. Jugal portion of infraorbital canal joins supramaxillary canal:**
0. present
 1. absent

- 33. Dermal skull roof:**
0. includes large dermal plates
 1. consists of undifferentiated plates or tesserae

- 34. Anterior pit line of dermal skull roof:**
Changed from ‘1’ to ‘0’ for *Cheirolepis*.
0. absent

1. present
- 35. Tessera morphology:**
0. large interlocking polygonal plates
 1. microsquamose, not larger than body squamation
- 36. Cranial spines:**
0. absent
 1. present, multicuspid
 2. present, monocuspid
- 37. Extent of dermatocranial cover:**
0. complete
 1. incomplete (limited to skull roof)
- 38. Openings for endolymphatic ducts in dermal skull roof:**
Changed from '0' to '-' for *Ischnacanthus*.
0. present
 1. absent
- 39. Endolymphatic ducts with oblique course through dermal skull bones:**
0. absent
 1. present
- 40. Endolymphatic duct relationship to median skull roof bone (i.e. nuchal plate):**
0. within median bone
 1. on bones flanking the median bone (e.g. paranuchals)
- 41. Pineal opening perforation in dermal skull roof:**
0. present
 1. absent
- 42. Dermal plate associated with pineal eminence or foramen:**
0. contributes to orbital margin
 1. plate bordered laterally by skull roofing bones
- 43. Series of paired median skull roofing bones that meet at the dorsal midline of the skull (rectilinear skull roof pattern):**
0. absent
 1. present
- 44. Broad supraorbital vaults:**
0. absent
 1. present

- 45. Median commissure between supraorbital sensory lines:**
0. absent
1. present
- 46. Dermal cranial joint at level of sphenoid-otic junction:**
Changed from '?' to '-' for *Chondrenchelys*.
0. absent
1. present
- 47. Otic canal extends through postparietals:**
0. absent
1. present
- 48. Number of bones of skull roof lateral to postparietals:**
We have modified this character to take into account the condition in *Powichthys* and lungfishes (new additions to the matrix), which show more than two bones lateral to the postparietals.
0. two
1. one
2. more than two
- 49. Suture between paired skull roofing bones (centrals of placoderms; postparietals of osteichthyans):**
0. straight
1. sinusoidal
- 50. Medial processes of paranuchal wrapping posterolateral corners of nuchal plate:**
0. absent
1. present
2. paranuchals precluded from nuchal by centrals
3. no median posterior skull roof bone
- 51. Paired pits on ventral surface of nuchal plate:**
0. absent
1. present
- 52. Sclerotic ring:**
0. absent
1. present
- 53. Consolidated cheek plates:**
0. absent
1. present

- 54. Cheek plate:**
0. undivided
1. divided (i.e., squamosal and preopercular)
- 55. Subsquamosals in taxa with divided cheek:**
Changed from '?' to '-' for *Chondrenchelys*.
0. absent
1. present
- 56. Preopercular shape:**
Changed from '?' to '-' for *Chondrenchelys*.
0. rhombic
1. bar-shaped
- 57. Vertical canal associated with preopercular/suborbital canal:**
0. absent
1. present
- 58. Enlarged postorbital tessera separate from orbital series:**
0. absent
1. present
- 59. Extent of maxilla along cheek:**
0. to posterior margin of cheek
1. cheek bones exclude maxilla from posterior margin of cheek
- 60. Dermal neck joint:**
0. overlap
1. ginglymoid
- 61. Sensory line scales/plates on head:**
0. unspecialized
1. apposed growth
2. paralleling canal
3. semicylindrical C-shaped ring scales
- 62. Bony hyoidean gill-cover series (branchiostegals):**
0. absent
1. present
- 63. Branchiostegal plate series along ventral margin of lower jaw:**
0. absent
1. present

64. Branchiostegal ossifications*:

- 0. plate-like
- 1. narrow and ribbon-like
- 2. filamentous

65. Branchiostegal ossifications:

Changed from '1' to '0' for *Porolepis*, *Gogonasus*.

- 0. ornamented
- 1. unornamented

66. Imbricated branchiostegal ossifications:

- 0. absent
- 1. present

67. Median gular:

- 0. absent
- 1. present

68. Lateral gular:

- 0. absent
- 1. present

69. Opercular (submarginal) ossification:

- 0. absent
- 1. present

70. Shape of opercular (submarginal) ossification:

- 0. broad plate that tapers towards its proximal end
- 1. narrow, rod-shaped

71. Size of lateral gular plates:

- 0. extending most of length of the lower jaw
- 1. restricted to the anterior third of the jaw (no longer than the width of three or four branchiostegals)

Ventral hyoid arch and gill skeleton

72. Gill arches:

Changed from '?' to '0' in *Chondrenchelys*.

- 0. largely restricted to region under braincase
- 1. extend far posterior to braincase

73. Basihyal:

- 0. absent
- 1. present

74. Interhyal:

- 0. absent
- 1. present

75. Hypohyal:

- 0. absent
- 1. present

76. Endoskeletal urohyal:

- 0. absent
- 1. present

Dentition and jaw bones

77. Oral dermal tubercles borne on jaw cartilages or at margins of the mouth:

- 0. absent
- 1. present

78. Oral dermal tubercles patterned in organised rows (teeth):

- 0. absent
- 1. present

79. Enamel(oid) on teeth:

- 0. absent
- 1. present

80. Cap of enameloid restricted to upper part of teeth (acrodin):

- 0. absent
- 1. present

81. Tooth whorls:

- 0. absent
- 1. present

82. Bases of tooth whorls:

- 0. single, continuous plate
- 1. some or all whorls consist of separate tooth units

83. Distribution of tooth whorls:

- Changed from '1' to '0' for *Debeerius*; from '-' to '0' for *Chondrenchelys*.
- 0. entire length of tooth row

1. restricted to symphysial region
- 84. Distribution of tooth whorls:**
Changed from '1' to '0' for *Helodus*.
0. upper and lower jaws
 1. lower jaws only
 2. upper jaws only
- 85. Teeth ankylosed to dermal bones:**
0. absent
 1. present
- 86. Plicidentine:**
0. absent
 1. present
- 87. Dermal jaw plates on biting surface of jaw cartilages:**
0. absent
 1. present
- 88. Maxillary and dentary marginal bones of mouth:**
0. absent
 1. present
- 89. Premaxilla:**
0. extends under orbit
 1. restricted anterior to orbit
- 90. Maxilla shape:**
0. splint-shaped
 1. cleaver-shaped
- 91. Pair of tooth plates (anterior supragathals or vomers) on ethmoidal plate:**
Changed from '1' to '0' for *Onychodus*, *Chondrenchelys*.
0. absent
 1. present
- 92. Strong posterior flexion of dentary symphysis:**
Changed from '1' to '0' for *Chondrenchelys*.
0. absent
 1. present
- 93. Extent of infradentaries:**
0. along much of ventral margin of dentary

1. restricted to posterior half of dentary
- 94. Coronoid fangs:**
0. absent
 1. present
- 95. Position of upper mandibular arch cartilage (and associated cheek plate where present):**
0. entirely suborbital
 1. with a postorbital extension
- 96. Position of mandibular arch articulations:**
Changed from '0' to '1' for *Cheirolepis*; '0' to '?' in *Chondrenchelys*, *Debeerius*.
0. terminal
 1. subterminal
- 97. Autopalatine and quadrate:**
Changed from '-' to '0' for *Debeerius*.
0. comineralized
 1. separate mineralizations
- 98. Large otic process of the palatoquadrate:**
Changed from '1' to '?' for *Chondrenchelys*.
0. absent
 1. present
- 99. Insertion area for jaw adductor muscles on palatoquadrate:**
0. ventral or medial
 1. lateral
- 100. Palatoquadrate relationship to dermal cheek bones:**
0. articulation narrow and restricted
 1. broad articulation
- 101. Palatoquadrate fused with neurocranium:**
0. absent
 1. present
- 102. Oblique ridge or groove along medial face of palatoquadrate:**
0. absent
 1. present
- 103. Fenestration of palatoquadrate at basipterygoid articulation:**
Changed from '0' to '-' for *Chondrenchelys*.

- 0. absent
- 1. present

104. Perforate or fenestrate anterodorsal (metapterygoid) portion of palatoquadrate:

- 0. absent
- 1. present

105. Pronounced dorsal process on Meckelian bone or cartilage:

- 0. absent
- 1. present

106. Number of coronoids:

- 0. four or more
- 1. three or fewer

107. Preglenoid process:

Changed from ‘?’ to ‘1’ for *Helodus*.

- 0. absent
- 1. present

108. Jaw articulation located on rearmost extremity of mandible:

- 0. absent
- 1. present

Neurocranium and associated dermal ossifications

109. Precerebral fontanelle:

- 0. absent
- 1. present

110. Median dermal bone of palate (parasphenoid):

- 0. absent
- 1. present

111. Parasphenoid:

- 0. lozenge-shaped
- 1. splint-shaped
- 2. diamond-shaped

112. Multifid anterior margin of parasphenoid denticle plate:

- 0. absent
- 1. present

113. Enlarged ascending processes of parasphenoid:

- 0. absent
 - 1. present
- 114. Buccohypophysial canal in parasphenoid:**
- 0. single
 - 1. paired
- 115. Nasal opening(s):**
- 0. dorsal, placed between orbits
 - 1. ventral and anterior to orbit
- 116. Posterior nostril:**
- 0. separated from orbital fenestra
 - 1. confluent with orbital fenestra
- 117. Olfactory tracts:**
- 0. short, with olfactory capsules situated close to telencephalon cavity
 - 1. elongate and tubular (much longer than wide)
- 118. Prominent pre-orbital rostral expansion of the neurocranium:**
- 0. present
 - 1. absent
- 119. Pronounced sub-ethmoidal keel:**
- 0. absent
 - 1. present
- 120. Internasal vacuities:**
- 0. absent
 - 1. present
- 121. Discrete division of the ethmoid and more posterior braincase at the level of the optic tract canal:**
- 0. absent
 - 1. present
- 122. Position of myodome for superior oblique eye muscles:**
- 0. posterior and dorsal to foramen for nerve II
 - 1. anterior and dorsal to foramen
- 123. Endoskeletal intracranial joint:**
- 0. absent
 - 1. present

124. Spiracular groove on basicranial surface:

- 0. absent
- 1. present

125. Transverse otic process :

- 0. present
- 1. absent

126. Jugular canal*:

In the previous formulation, a 'short' jugular canal was described as being anterior to the skeletal labyrinth. However, most taxa with a short jugular canal have this somewhere along the length of the labyrinth rather than exclusively anterior to it. We have therefore modified the terminology to accommodate this pattern. Changed from '?' to '2' for *Chondrenchelys*.

- 0. long (invested in otic region along length of skeletal labyrinth)
- 1. short (restricted to short portion of region of skeletal labyrinth, or anterior to it)
- 2. absent (jugular vein uninvested in otic region)

127. Spiracular groove on lateral commissure:

- 0. absent
- 1. present

128. Subpituitary fenestra:

Onychodus changed from '?' to '0'.

- 0. absent
- 1. present

129. Supraorbital shelf broad with convex lateral margin:

- 0. absent
- 1. present

130. Orbit dorsal or facing dorsolaterally, surrounded laterally by endocranium:

- 0. present
- 1. absent

131. Eyestalk attachment area:

- 0. absent
- 1. present

132. Postorbital process:

Changed from '?' to '1' for *Chondrenchelys*.

- 0. absent
- 1. present

- 133. Canal for jugular in postorbital process:**
 Changed from ‘?’ to ‘1’ for *Chondrenchelys*.
 0. absent
 1. present
- 134. Series of perforations for innervation of supraorbital sensory canal in supraorbital shelf:**
 0. absent
 1. present
- 135. Extended prehypophysial portion of sphenoid:**
 0. absent
 1. present
- 136. Narrow interorbital septum, with outer walls in contact along midline forming a single sheet:**
 The previous formulation of this character distinguished ‘narrow’ and ‘broad’ interorbital septa. This lacks precision, and is subject to differing opinions. We therefore have reformulated this character to refer to distinguish cases where the lateral walls of the braincase are separate in the orbital region from those where they join as a single sheet along the midline.
 0. absent
 1. present
- 137. The main trunk of facial nerve (N. VII):**
 0. elongate and passes anterolaterally through orbital floor
 1. stout, divides within otic capsule at the level of the transverse otic wall
- 138. Course of hyoid ramus of facial nerve (N. VII) relative to jugular canal:**
 0. traverses jugular canal, with separate exit in otic region
 1. intersects jugular canal, with exit through posterior jugular foramen
- 139. Glossopharyngeal nerve (N. IX) exit:**
 0. foramen situated posteroventral to otic capsule and anterior to metotic fissure
 1. through metotic fissure
- 140. Relationship of cranial endocavity to basisphenoid:**
 0. endocavity occupies full depth of sphenoid
 1. endocavity dorsally restricted
- 141. Subcranial ridges:**
 0. absent
 1. present

- 142. Ascending basisphenoid pillar pierced by common internal carotid:**
- 0. absent
 - 1. present
- 143. Canal for lateral dorsal aorta within basicranial cartilage:**
- 0. absent
 - 1. present
- 144. Entrance of internal carotids:**
- 0. through separate openings flanking the hypophyseal opening or recess
 - 1. through a common opening at the central midline of the basicranium
- 145. Canal for efferent pseudobranchial artery within basicranial cartilage:**
- 0. absent
 - 1. present
- 146. Position of basal/basipterygoid articulation:**
Changed from '1' to '?' for *Debeerius*.
- 0. same anteroposterior level as hypophysial opening
 - 1. anterior to hypophysial opening
 - 2. posterior to hypophysial opening
- 147. Articulation between neurocanium and palatoquadrate posterodorsal to orbit (suprapterygoid articulation):**
- 0. absent
 - 1. present
- 148. Labyrinth cavity:**
- 0. separated from the main neurocranial cavity by a cartilaginous or ossified capsular wall
 - 1. skeletal capsular wall absent
- 149. Basipterygoid process (basal articulation) with vertically oriented component:**
- 0. absent
 - 1. present
- 150. Pituitary vein canal:**
- 0. dorsal to level of basipterygoid process
 - 1. flanked posteriorly by basipterygoid process
- 151. External (horizontal) semicircular canal:**
- 0. absent
 - 1. present

- 152. Sinus superior:**
 0. absent or indistinguishable from union of anterior and posterior canals with saccular chamber
 1. present
- 153. External (horizontal) semicircular canal:**
 Changed from '1' to '?' for *Moythomasia*.
 0. joins the vestibular region dorsal to posterior ampulla
 1. joins level with posterior ampulla
- 154. Horizontal semicircular canal in dorsal view:**
 0. medial to path of jugular vein
 1. dorsal to jugular vein
- 155. Lateral cranial canal:**
 0. absent
 1. present
- 156. Trigemino-facial recess:**
 Changed from '1' to '0' for *Eusthenopteron*, *Gogonasus*, *Jagorina*, *Ramirosuarezia*; from '?' to '0' for *Psarolepis*, *Styloichthys*; from '?' to '1' for *Tamiobatis*.
 0. absent
 1. present
- 157. Posterior dorsal fontanelle:**
 Changed from '?' to '0' for *Chondrenchelys*.
 0. absent
 1. present
- 158. Shape of posterior dorsal fontanelle:**
 Changed from '?' to '-' for *Chondrenchelys*.
 0. approximately as long as broad
 1. much longer than wide, slot-shaped
- 159. Synotic tectum:**
 Changed from '?' to '-' for *Chondrenchelys*.
 0. absent
 1. present
- 160. Dorsal ridge:**
 0. absent
 1. present
- 161. Shape of median dorsal ridge anterior to endolymphatic fossa:**

- 0. developed as a squared-off ridge or otherwise ungrooved
 - 1. bears a midline groove
- 162. Endolymphatic ducts in neurocranium:**
 Changed code from '?' to '1' for *Chondrenchelys*.
- 0. posteriodorsally angled tubes
 - 1. tubes oriented vertically through median endolymphatic fossa
- 163. Position of hyomandibula articulation on neurocranium:**
 Changed code from '?' to '1' for *Ligulalepis*.
- 0. below or anterior to orbit, on ventrolateral angle of braincase
 - 1. on otic capsule, posterior to orbit
- 164. Position of hyomandibula articulation relative to structure of skeletal labyrinth:**
- 0. anterior or lateral to skeletal labyrinth
 - 1. at level of posterior semicircular canal
- 165. Hyoid arch articulation on braincase:**
- 0. single
 - 1. double
- 166. Branchial ridges*:**
- 0. present
 - 1. reduced to vagal process
 - 2. absent (articulation made with bare cranial wall)
- 167. Craniospinal process:**
 Changed from '?' to '0' for *Chondrenchelys*.
- 0. absent
 - 1. present
- 168. Ventral cranial fissure:**
 Changed from '?' to '0' for *Chondrenchelys*.
- 0. absent
 - 1. present
- 169. Basicranial fenestra:**
 Changed from '?' to '-' for *Chondrenchelys*.
- 0. absent
 - 1. present
- 170. Metotic (otic-occipital) fissure:**
- 0. absent
 - 1. present

171. Vestibular fontanelle:

Changed from '1' to '?' for *Porolepis*; '?' to '0' for *Chondrenchelys*.

- 0. absent
- 1. present

172. Occipital arch wedged in between otic capsules:

Changed from '?' to '0' for *Psarolepis*.

- 0. absent
- 1. present

173. Spino-occipital nerve foramina:

- 0. two or more, aligned horizontally
- 1. one or two, dorsoventrally offset

174. Ventral notch between parachordals:

- 0. present or entirely unfused
- 1. absent

175. Parachordal shape:

- 0. forming a broad, flat surface as wide as the otic capsules
- 1. mediolaterally constricted relative to the otic capsules

176. Stalk-shaped parachordal/occipital region:

- 0. absent
- 1. present

177. Paired occipital facets:

- 0. absent
- 1. present

178. Size of aperture to notochordal canal:

- 0. much smaller than foramen magnum
- 1. as large, or larger, than foramen magnum

179. Canal for median dorsal aorta within basicranium:

Changed from '?' to '0' for *Chondrenchelys*.

- 0. absent
- 1. present

180. Hypotic lamina (and dorsally directed glossopharyngeal canal):

Changed from '?' to '-' for *Chondrenchelys*.

- 0. absent
- 1. present

Paired fins and girdles

- 181. Macromeric dermal shoulder girdle:**
- 0. present
 - 1. absent
- 182. Dermal shoulder girdle composition:**
- 0. ventral and dorsal (scapular) components
 - 1. ventral components only
- 183. Shape of dorsal blade of dermal shoulder girdle (either cleithrum or anterolateral plate):**
- 0. spatulate
 - 1. pointed
- 184. Dermal shoulder girdle forming a complete ring around the trunk:**
- 0. present
 - 1. absent
- 185. Pectoral fenestra completely encircled by dermal shoulder armour:**
- 0. present
 - 1. absent
- 186. Median dorsal plate:**
- 0. absent
 - 1. present
- 187. Posterior dorsolateral (PDL) plate or equivalent:**
- 0. absent
 - 1. present
- 188. Pronounced internal median keel on dorsal shoulder girdle (i.e., crista of median dorsal plate):**
- 0. absent
 - 1. present
- 189. Crista internalis of dermal shoulder girdle:**
- 0. absent
 - 1. present
- 190. Scapular infundibulum:**
- 0. absent
 - 1. present

- 191. Scapular process of shoulder endoskeleton:**
0. absent
1. present
- 192. Ventral margin of separate scapular ossification:**
0. horizontal
1. deeply angled
- 193. Cross sectional shape of scapular process:**
0. flattened or strongly ovate
1. subcircular
- 194. Flange on trailing edge of scapulocoracoid:**
0. absent
1. present
- 195. Scapular process with posterodorsal angle:**
0. absent
1. present
- 196. Endoskeletal postbranchial lamina on scapular process:**
0. present
1. absent
- 197. Mineralisation of internal surface of scapular blade:**
0. mineralised all around
1. unmineralised on internal face forming a hemicylindrical cross-section
- 198. Coracoid process:**
0. absent
1. present
- 199. Procoracoid mineralisation:**
0. absent
1. present
- 200. Fin base articulation on scapulocoracoid:**
0. deeper than wide (stenobasal)
1. wider than deep (eurybasal)
- 201. Pectoral fin articulation:**
0. monobasal
1. polybasal

- 202. Number of basals in polybasal pectoral fins:**
0. three or more
1. two
- 203. Branching radials in paired fins:**
0. absent
1. present
- 204. Number of mesomeres in metapterygial axis:**
0. five or fewer
1. seven or more
- 205. Biserial pectoral fin endoskeleton:**
0. absent
1. present
- 206. Perforate propterygium:**
Changed from ‘-’ to ‘0’ for *Chondrenchelys*.
0. absent
1. present
- 207. Filamentous extension of pectoral fin from axillary region:**
0. absent
1. present
- 208. Pelvic fins:**
Changed from ‘?’ to ‘0’ for Galeaspida.
0. absent
1. present
- 209. Pelvic claspers:**
0. absent
1. present
- 210. Dermal pelvic clasper ossifications:**
0. absent
1. present
- 211. Pectoral fins covered in macromeric dermal armour:**
0. absent
1. present
- 212. Pectoral fin base has large, hemispherical dermal component:**

Changed from ‘?’ to ‘0’ for *Styloichthys*.

- 0. absent
- 1. present

Axial skeleton including median fins and their supports

213. Dorsal fin spines:

- 0. absent
- 1. present

214. Anal fin spine:

- 0. absent
- 1. present

215. Paired fin spines:

- 0. absent
- 1. present

216. Median fin spine insertion:

- 0. shallow, not greatly deeper than dermal bones/scales
- 1. deep

217. Intermediate fin spines:

- 0. absent
- 1. present

218. Fin spine cross-section:

- 0. Round or horseshoe shaped
- 1. Flat-sided, with rectangular profile

219. Intermediate spines when present:

- 0. one pair
- 1. multiple pairs

220. Prepectoral fin spines:

- 0. absent
- 1. present

221. Fin spines with ridges:

- 0. absent
- 1. present

222. Fin spines with nodes:

- 0. absent

1. present
- 223. Fin spines with rows of large retrorse denticles:**
0. absent
 1. present
- 224. Expanded spine rib on leading edge of spine:**
0. absent
 1. present
- 225. Spine ridges:**
0. converging at the distal apex of the spine
 1. converging on leading edge of spine
- 226. Synarcual:**
0. absent
 1. present
- 227. Series of thoracic supraneurals:**
0. absent
 1. present
- 228. Number of dorsal fins, if present:**
0. one
 1. two
- 229. Posterior dorsal fin shape:**
0. base approximately as broad as tall, not broader than all of other median fins
 1. base much longer than the height of the fin, substantially longer than any of the other dorsal fins
- 230. Basal plate in dorsal fin:**
0. absent
 1. present
- 231. Branching radial structure articulating with dorsal fin basal plate:**
0. absent
 1. present
- 232. Anal fin:**
0. absent
 1. present
- 233. Basal plate in anal fin:**

- 0. absent
- 1. present

234. Caudal radials:

- 0. extend beyond level of body wall and deep into hypochordal lobe
- 1. radials restricted to axial lobe

235. Supraneurals in axial lobe of caudal fin:

- 0. absent
- 1. present

236. Epichordal lepidotrichia in caudal fin:

- 0. absent
- 1. present

Additional characters:

237. Enamel and pore canals:

Zhu & Schultze [S169]; Zhu et al. [S170]; Zhu & Yu [S152]; Zhu et al. 2006 [S2]; Friedman [S154]. Taxa that lack pore openings are coded as inapplicable for this character.

- 0. enamel absent from inner surface of pores
- 1. enamel lines portions of pore canal

238. Canal-bearing bone of skull roof extends far past posterior margin of parietals:

New character.

- 0. no
- 1. yes

239. Pineal eminence (in taxa lacking pineal foramen):

Friedman [S154]; Zhu et al. [S94]; Giles et al. [S148].

- 0. absent
- 1. present

240. Position of anterior pitline:

Cloutier & Ahlberg [S171]; Zhu & Schultze [S169]; Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].

- 0. on postparietal
- 1. on parietal

241. Opening in dermal skull roof for spiracular bounded by bones carrying otic canal:

Friedman [S154]; Zhu et al. [S94]; Giles et al. [S148].

- 0. absent

1. present
- 242. Median skull roof bone between postparietals (B-bone):**
Cloutier & Ahlberg [S171]; Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].
0. absent
 1. present
- 243. Westoll lines:**
Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].
0. absent
 1. present
- 244. Preoperculosubmandibular:**
Cloutier & Ahlberg [S171]; Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].
0. absent
 1. present
- 245. Hyomandibula:**
Friedman [S154]; Zhu et al. [S94]; Friedman & Brazeau [S172]; Xu & Gao [S173]; Zhu et al. [S79]; Brazeau & Friedman [S174]; Xu et al. [S175]; Giles et al. [S148].
0. imperforate
 1. perforate
- 246. Urohyal shape:**
Modified from Friedman [S154].
0. absent
 1. vertical plate
- 247. Maxilla (in taxa with marginal jaw bones):**
Cloutier & Ahlberg [S171]; Zhu & Yu [S152]; Friedman [S154]; Giles et al. [S148].
0. present
 1. absent
- 248. Length of dentary:**
Cloutier & Ahlberg [S171]; Ahlberg & Johanson [S176]; Zhu et al. [S170]; Zhu & Yu [S152]; Zhu & Ahlberg [S177]; Friedman [S154]; Zhu et al. [S94]; Giles et al. [S148].
0. constitutes a majority of jaw length
 1. half the length of jaw or less
- 249. Labial pit:**
Cloutier & Ahlberg [S171]; Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].
0. absent
 1. present

- 250. Prearticular symphysis:**
 Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].
 0. absent
 1. present
- 251. Mandibular sensory canal:**
 Patterson [S178]; Cloutier & Ahlberg [S171]; Coates [S179]; Schultze & Cumbaa [S67];
 Zhu & Schultze [S169]; Zhu et al. [S170]; Zhu & Yu [S152]; Cloutier & Arratia [S180];
 Zhu et al. 2006 [S2]; Friedman [S154]; Zhu et al. [S94]; Zhu et al. [S79]; Giles et al.
 [S148].
 0. extends through infradentaries
 1. extends through infradentaries and dentary
- 252. Extensive flange composed of prearticular and Meckelian bone that extends beyond ventral edge of outer dermal series:**
 Friedman [S154]; Zhu et al. [S94].
 0. absent
 1. present
- 253. Posterior coronoid:**
 Cloutier & Ahlberg [S171]; Ahlberg & Johanson [S176]; Zhu & Ahlberg [S177]; Giles et al. [S148].
 0. similar to anterior coronoids
 1. forms expanded coronoid process
- 254. Retroarticular process:**
 Friedman [S154]; Giles et al. [S148].
 0. absent
 1. present
- 255. Inturned medial process of premaxilla:**
 Friedman [S154].
 0. absent
 1. present
- 256. Anteriorly directed adductor fossae between neurocranium and skull roof:**
 Cloutier & Ahlberg [S171].
 0. absent
 1. present
- 257. Vomerine fangs:**
 Ahlberg & Johanson [S176]; Zhu & Ahlberg [S177]; Zhu et al. [S170]; Zhu & Yu [S152];
 Friedman [S154].
 0. absent

1. present
- 258. Number of dermopalatines:**
Friedman [S154].
0. multiple
 1. one
- 259. Entopterygoids:**
Friedman [S181].
0. separated
 1. contact along midline
- 260. Rostral tubuli:**
Cloutier & Ahlberg [S171]; Ahlberg & Johanson [S176]; Zhu & Ahlberg [S177];
Schultze & Cumbaa [S67]; Zhu & Schultze [S169]; Zhu et al. [S170]; Zhu & Yu [S152];
Zhu et al. [S2]; Friedman 2007 [S154, S181].
0. absent
 1. present
- 261. Position of anterior nostril:**
Modified from Zhu et al. [S170]; Zhu & Yu [S152]; Friedman 2007 [S154, S181].
0. facial
 1. at oral margin
- 262. Posterior nostril*:**
Modified from Cloutier & Ahlberg [S171]; Schultze & Cumbaa [S67]; Zhu & Schultze
[S169]; Zhu et al. [S170]; Zhu & Yu [S152]; Zhu et al. 2006 [S2]; Friedman 2007 [S154,
S181].
0. facial
 1. at margin of oral cavity
 2. palatal
- 263. Three large pores (in addition to nostrils) associated with each side of ethmoid (rostral organ):**
Cloutier & Ahlberg [S171]; Friedman [S154].
0. absent
 1. present
- 264. Ventral face of nasal capsule in taxa with mineralized ethmoid*:**
Modified from Schultze & Cumbaa [S67]; Zhu & Schultze [S169]; Zhu et al. [S170]; Zhu
& Yu [S152]; Zhu et al. 2006 [S2]; Friedman [S154, S181]; Zhu et al. [S94]; Zhu et al.
[S79]; Giles et al. [S148].
0. complete
 1. fenestra ventrolateralis

2. entire floor unmineralized
- 265. Size of profundus canal in postnasal wall:**
Modified from Zhu et al. [S170]; Zhu & Yu [S152]; Friedman [S154].
0. small
 1. large
- 266. Paired pineal and parapineal tracts:**
Friedman [S181].
0. absent
 1. present
- 267. Posterior of parasphenoid:**
Zhu et al. [S170]; Zhu & Yu [S152]; Friedman 2007 [S154, S181].
0. restricted to ethmosphenoid region
 1. extends to otic region
- 268. Endoskeletal spiracular canal*:**
Patterson [S178]; Gardiner [S123]; Gardiner & Schaeffer [S182]; Taverne [S183]; Coates [S179]; Gardiner et al. [S184]; Xu & Gao [S173]; Xu et al. [S175]; Giles et al. [S148].
0. open
 1. partial enclosure or spiracular bar
 2. complete enclosure in canal
- 269. Barbed lepidotrichial segments:**
Friedman [S154].
0. absent
 1. present

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