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DOI:
10.1038/s41586-022-05233-8

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Citation for published version (Harvard):

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Spiny chondrichthyan from the lower Silurian of South China

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Modern representatives of chondrichthyans (cartilaginous fishes) and osteichthyans (bony fishes and tetrapods) exhibit contrasting skeletal anatomy and development that underscore the distant evolutionary split of the two clades. Recent work on upper Silurian and Devonian jawed vertebrates has exposed similar skeletal conditions that blur conventional distinctions between osteichthyans, chondrichthyans and their jawed gnathostome ancestors. Here we describe the remains (dermal plates, scales and fin spines) of a chondrichthyan, *Fanjingshania renovata* gen. et sp. nov., from the lower Silurian of China that predates the earliest articulated fossils of jawed vertebrates. *Fanjingshania* possesses dermal shoulder girdle plates and a complement of fin spines of striking anatomical similarity to those recorded in a subset of stem chondrichthyans (climatiid 'acanthodians'). Uniquely among chondrichthyans, however, it demonstrates osteichthyan-like resorptive shedding of scale odontodes and absence of odontogenic tissues in spines. Our results identify independent acquisition of these conditions in the chondrichthyan stem group, adding *Fanjingshania* to an increasing number of taxa nested within traditionally-defined 'acanthodians'. The discovery of *Fanjingshania* provides the strongest support yet for a proposed early Silurian radiation of jawed vertebrates prior to their widespread appearance in the fossil record in the Lower Devonian.
Hypotheses of skeletal evolution within the principal divisions of early jawed vertebrates (osteichthyans, chondrichthyans and stem-gnathostome 'placoderms') have recently come under scrutiny following reports of traditionally recognised crown-group conditions (e.g. endochondral bone, marginal jaw bones) in the stem lineage among 'placoderms' as well as 'placoderm'-like dermal scales in chondrichthyans. In concert with these data from upper Silurian and Devonian specimens, phylogenies of early jawed vertebrates expose gaps in the fossil record that extend back well into the Upper Ordovician and predict significant range extensions for a number of important lineages. Upper Ordovician (Sandbian) and lower Silurian (Llandovery) remains of isolated dermal scales and spines attributed to acanthodian-grade stem chondrichthyans and enigmatic groups such mongolepids, sinacanthids and elegestolepids provide further evidence of early diversity. Nevertheless, due to the absence of articulated fossils and characters unequivocally linking them to established groups, the incorporation of these specimens into existing phylogenetic schemes of early vertebrates remains problematic.

Here we describe a c. 439-million-year-old chondrichthyan from the middle Llandovery of South China, whose remains were extracted from bone bed samples of the Rongxi Formation at Shiqian (Extended Data Fig. 1). The new taxon is based on abundant isolated remains and fragments of fused skeletal components and represents the stratigraphically oldest jawed vertebrate with a clearly established dermoskeletal anatomy. This discovery provides the first substantive morphological and developmental data from a chondrichthyan occurring c. 20 million years prior to the earliest chondrichthyan body fossils and supports early estimates for the timing of the initial evolutionary radiation of jawed vertebrates.
Systematic palaeontology

Chondrichthyes Huxley, 1889

Fanjingshania renovata gen. et sp. nov.

Etymology. 'Fanjingshania', after Mount Fanjingshan, situated c. 100 km northeast of the type locality; 'renovata', Latin for renewal (renovatus), alluding to the remodelling in the dermal skeleton of the species.

Holotype. Portion of a ventral (pinnal) shoulder girdle dermal plate fused to a fragment of a pectoral fin spine, IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V27433.1 (Figs. 1g, 2a–c and Extended Data Fig. 4c).

Referred material. Over 1000 isolated specimens including: head (tectal and postorbital) tesserae (Fig. 1s and Extended Data Fig. 2a, b), trunk scales, fused sclerotic plates (Fig. 1r), an incomplete branchiostegal plate (Fig. 1q), pectoral, prepelvic, pelvic, dorsal and anal fin spines (Fig. 1e, f, h–o, u–w and Extended Data Fig. 3), incomplete lorical (median) and pinnal (paired) shoulder girdle plates fused to complete or partial spines (Fig. 1a–d, g, p, t and Extended Data Fig. 4).

Locality and horizon. Shiqian-Tunping section at Leijiatun village (Shiqian County), Guizhou Province, China (Extended Data Fig. 1). Rongxi Formation, Ozarkodina guizhouensis conodont biozone (c. 439 Ma; late Aeronian, Llandovery, Silurian).

Diagnosis (as for genus). Jawed vertebrate with paired (pinnal) dermal shoulder girdle plates, each fused to a pair of prepectoral spines, a pectoral and a prepelvic (admedian) fin spine; ventral and ascending laminae of the pinnal plates extended to the posterior edge of pectoral fin spines; median (lorical) shoulder girdle plate with a
low conical spine; fin spines are laterally compressed and broad-based and carry
ornamenting ridges studded with fine tubercles; trunk scale crowns possess a linear
array of primary odontodes sculpted by discontinuous nodose ridges; the anterior of
trunk scale crows features a conspicuous pustule or a large, dome-shaped
replacement odontode; dentine developed only in scale/tesserae crowns.

Remarks. Attribution of dermoskeletal elements to *Fanjingshania* is based on their
tissue composition (cellular bone and/or atubular dentine), surface sculpture (nodose
ridges and fine tuberculate ornament), developmental features (hard-tissue
resorption and scale crown growth), as well as direct evidence from fused elements.
In turn, the assignment of fin spines, dermal plates and tesserae to specific body
positions (Fig. 2x, y and Extended Data Fig. 7) rests on similarities with the
dermoskeletal anatomy of climatiids\(^{13,14,27,28}\), particularly that of *Climatius
reticulatus*\(^{27,28}\).

Isolated tooth whorls were also recovered from our Rongxi samples from
Shiqian (Extended Data Fig. 1). The disarticulated nature and the yet uncertain
tissue composition of the tooth whorls result in the absence of direct morphological
and histological evidence that could support their attribution to *Fanjingshania*. This is
further complicated by the co-occurrence of whorls with the fragmentary remains of
other, still to be described, chondrichthyans that are recognised on the basis of
distinct fin spines and scales. We therefore formally described the tooth whorl
material elsewhere, following established practice\(^{29}\) to erect a new taxon for
disarticulated vertebrate remains that can be distinguished by a unique set of
features.

Elements of the dermal skeleton
The holotype of *Fanjingshania* (Figs. 1g, 2a–c) and other figured material (Figs. 1t, 2j and Extended Data Figs. 4a, b, d, 5d, e) represent articulated dermal scales fused together by a basal plate that are fused to a fragment of a spine wall. The latter is either level with the basal plate or makes contacts with it at an angle. These specimens are recognised as remnants of pectoral fin spines fused to paired ventral plates of the shoulder girdle (pinnal plates) of a compound type documented in a number of stem chondrichthyans (e.g. *Ptomacanthus*\(^{30}\), *Sabrinacanthus*\(^{28}\) and *Diplacanthus*\(^{31}\)). Within total-group Chondrichthyes the pectoral girdle is the only site where large (macromeric) dermal ossifications are associated with spines\(^{32}\).

'Placoderm' or osteichthyan origin of these elements is considered unlikely as there are no known examples of pinnal-like multi-component dermal plates in either of the two groups\(^{33-35}\).

The scales carried by the pinnal plates vary in size (Fig. 2a) and have irregular rhomboid to oblong crowns ornamented with nodose ridges adorned by fine tubercles. The pectoral fin spine fragments of V27433.1–V27433.7 preserve up to 13 flat-topped nodose ridges studded with tubercles. The spine ridges are of variable width and can bifurcate as well as assume a 'string of pearls' appearance near the junction with the plate (Fig. 1t).

Other partial plates (Figs. 1c, d, 2d, e) with the basal plate/dermal scale structure of the pinnal elements fuse around the periphery of a low, broad-based spine with recurved, posteriorly offset apex. The spines are longer than high and possess up to 11 nodose ridges per lateral side that become discontinuous basally. These features are also seen in climatiid 'acanthodians' (e.g. *Erriwacanthus*\(^{28,36}\), *Sabrinacanthus*\(^{28}\) and *Climatius*\(^{27}\)) and where there is a fusion of the posterior
margin of the pinnal plates with a pair of prepelvic (admedian) fin spines formed medially of the pectoral fin spines.

Two fragmentary specimens (Fig. 1a, b and Extended Data Fig. 4j–l) possess laterally compressed pairs of fused spines of unequal size. The spines are nearly symmetrical, ornamented with rows of tubercules that extend on to incompletely preserved dermal plates that are continuous with the spine margins. In both specimens, one of the lateral plate laminae is angled and tapers towards as well as extends beyond the smaller of the spine pair (Fig. 1a). These elements morphologically correspond to the prepectoral spines integrated into the anterior pinnal plates of stem chondrichthyans (e.g. in Parexus, Climatius, Ptomacanthus, Brachyacanthus and Euthacanthus)\textsuperscript{14,27,28,30}, with the dermal shelves of V27436.1, 2 representing the remnants of ascending and ventral pinnal laminae (Fig. 1a, b and Extended Data Fig. 4j, l).

A partial plate (V27441.1, Fig. 1p) is distinguished from other Fanjingshania material by a low conical spine aligned to a prominent bulge of the plate margin. The spine is flanked by two basal plate-supported scales of the type observed in the pinnal elements of Fanjingshania. The distinct plate margins and spine of V27441.1 are features of the median ventral (lorical) plates of Climatius\textsuperscript{27,28} and Parexus\textsuperscript{14} and identify the specimen as such.

Incomplete isolated fin spines (Fig. 1e, f, h–o, u–w and Extended Data Fig. 3) attributed to Fanjingshania possess the nodose ridge sculpture seen in the fin spine fragments fused to plates of the dermal pectoral girdle (Fig. 1t). Their assignment to specific positions in the body (Fig. 1x, y) is dictated by close morphological similarity to the fin spine types of Climatius reticulatus\textsuperscript{27,28}. Pectoral fin spines (Fig. 1e, f)
exhibit strong lateral compression and broad, recured profiles. Their anterior edge is shaped into a well-developed rib, whereas the posterior one bears a deep sulcus. Spines recognised as anterior dorsal (Fig. 1n, o) resemble in overall appearance the pectoral fin spines but are distinguished by a more upright apex. More acuminate and less recurved spine types are identified as posterior dorsal (Fig. 1l, m), pelvic (Fig. 1h, i) and anal (Fig. 1j, k) fin spines. Other spine material assigned to *Fanjingshania* comprises low, laterally flattened spines with an acutely sloped, uneven anterior edge and a second incipient apex in a posterior position (Fig. 1u–w). Differences in size and angle of curvature between these allow to differentiate three morphologies representing paired ventral (prepelvic) spines of the type developed posterior of the pectoral girdle in a range of stem chondrichthyans (e.g. in diplacanthids\textsuperscript{31} and climatiids\textsuperscript{14,27,28}).

Isolated trunk scales belonging to *Fanjingshania* have deltoid to ovoid crowns with symmetric and asymmetric outlines (Fig. 2f, h and Extended Data Fig. 2c–k). Crown surfaces reveal the margins of apposed odontodes (Fig. 2f, h) of increasing size ornamented in non-abraded specimens by tuberculated ridges. The scale crowns extend posteriorly over rhombic bases with substantially smaller footprints and a prominent neck-like constriction. In some specimens the anterior odontodes are truncated or fully excavated and replaced by a large acuminate odontode raised above the crown surface (Fig. 2f, g).

**Dermoskeletal growth and tissue structure**

Pinnal plate scales and isolated trunk scales possess a row of appositionally arranged crown odontodes as well as an anterior cluster of secondary odontodes (Fig. 2b, h). Atubular dentine with incremental depositional lines and dispersed
mineralised spherites is seen in thin sections as the sole component of the odontodes (Fig. 2g, i and Extended Data Figs. 2p, q, 5e). The crowns are supported by bases of lamellar bone harbouring densely packed cell lacunae and pervaded by apically converging fibre spaces (Fig. 2g, i).

The pinnal plates share the cellular bone composition of the bases of the scales to which they are fused (Fig. 2c, e, j). The plates' cellular bone is continuous with the walls of pectoral and admedian spines (Fig. 2c, j and Extended Data Fig. 4a, h) that consist entirely of this tissue, including an outer vascular zone and the ornamenting ridges (Fig. 1c, d and Extended Data Fig. 4a, d). Cellular bone composition is also recognised in isolated fin spines (Extended Data Fig. 3v, w), where globular calcified cartilage is present apically inside the spines' central cavity.

Scale resorption is evidenced in the pinnal plate material by longitudinally truncated crowns at different states of completeness (Fig. 1a, d and Extended Data Fig. 5f–i). Resorption surfaces are also observed in isolated trunk scales (Fig. 1i and Extended Data Fig. 5a, c, e) but form only anteriorly where a deep cavity marks the partial removal or shedding of odontodes and the apical portion of the base. The resorption cavity is covered by a large acuminate replacement odontode (Fig. 2g and Extended Data Fig. 5a, c) at a later stage of scale development.

*Fanjingshania* is an outlier among early vertebrates in presenting a unique mix of jawed vertebrate plesiomorphies and apomorphies pertaining to dermoskeletal development (Fig. 3). Of these, only the formation of a single row of consecutive scale-odontode generations has been recognised in stem chondrichthyans described from articulated material (in *Parexus*14, *Brochoadmones*37, *Seretolepis*38 and *Kathemacanthus*38). The atubular dentine of
Fanjingshania conforms to the characteristics of a tissue type known as lamellin$^{22,24}$, with distribution previously restricted to enigmatic scale- and spine-based chondrichthyan (mongolepids$^{22-24,39}$ and sinacanthids$^{23,24,40}$) the majority of which occur in the Telychian (lower Silurian). Intriguingly, other chondrichthyan-like remains recovered from mongolepid/sinacanthid assemblages, such as the scale-based Yuanolepis bachunensis$^{23}$ and spine morphology A$^{24}$, share scale and spine structure and histology with Fanjingshania.

The dermoskeletal remodelling in Fanjingshania has not previously been recognised within the total-group Chondrichthyes$^{1,17}$. In trunk scales this is evident by the shedding of odontodes through resorptive removal of dentine and dermal bone and the deposition of new odontode generations on the exterior surface (Fig. 1f, g and Extended Data Fig. 5a, c, e) The closest examples of this replacement mechanism are identified in the oral and extra-oral dermal skeleton of some stem and crown osteichthyans$^{41-45}$. Odontode resorption in Fanjingshania, however, is not site specific as in osteichthyans but instead proceeds areally by episodic removal of multiple odontode generations. Its odontode replacement pattern also deviates from that of other vertebrates$^{3}$ by reducing the number of scale odontodes as shedding proceeds.

**Phylogenetic results**

On the basis of limited character data determined by the fragmentary nature of the material, Fanjingshania was resolved under parsimony and Bayesian optimality criteria (Fig. 3 and Extended Data Fig. 6) as a derived stem chondrichthyan nested within climatiid 'acanthodians'$^{14,30}$. A consequence of this placement is a c. 20 million year age increase to internal nodes of the chondrichthyan stem relative to recent
estimates\textsuperscript{5,7}. These results pull back the earliest occurrence date for climatiids to the early Silurian and similarly extend the ghost ranges of other conventional 'acanthodian' groupings\textsuperscript{14,31,38,46,47} away from their first documented appearances in the late Silurian–Early Devonian (Fig. 3). A corresponding extension of the osteichthyan stem deep into the Silurian is also predicted by our analysis (Fig. 3), which is in accordance with morphological clock estimates\textsuperscript{6} for the divergence of osteichthysans and chondrichthysans. The absence of recognisable osteichthyan remains from samples coeval with Fanjingshania might be explained by preservation bias against isolated teeth and body-fossils in strata of comparable age.

\textit{Fanjingshania}, and potentially lamellin-forming chondrichthysans at large (including mongolepids\textsuperscript{22-24} and sinacanthids\textsuperscript{23,25,40}), provide evidence for the existence of taxa with a climatiid-type dermoskeletal anatomy in the lower Silurian. This infers a protracted diversification model for the climatiids as well as for the remainder of the 'acanthodian' lineages, for which direct fossil evidence from the Upper Ordovician–lower Silurian is still missing\textsuperscript{39,48,49}. A possible factor contributing to this discrepancy, akin to the barren osteichthyan record, could be the under-sampling of pre-Devonian vertebrate assemblages.

\textit{Fanjingshania} adds a number of jawed vertebrate homoplasies (e.g. resorptive odontode shedding and absence of odontogenic tissues in dermal spines) to the chondrichthyan stem within a phylospace occupied by traditionally defined 'acanthodians'\textsuperscript{16}. These results are in conflict with the current view\textsuperscript{3} of total-group Chondrichthyes as primitively lacking competence to grow dermoskeletal tissues through resorption and remodelling. They increase the disparity of character combinations in early chondrichthysans and provide much needed data on the
sequence of evolutionary changes leading up to the emergence of crown chondrichthyans.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/XXXXX


Methods

The fossil material assigned to Fanjingshania consists of over 1000 isolated fin spines, spines, tesserae, scales and plates (Table S1). The specimens were recovered from residues of sediment samples (35SQTP) disaggregated with buffered 8% acetic acid. The 35SQTP samples were collected from the upper beds of the Rongxi Formation exposed in the Shiqian-Tunping section (Extended Data Fig. 1) near the village of Leijiatun, Shiqian County, Guizhou Province, China50. All
studied specimens were reposited at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

**X-ray tomography**

Synchrotron X-ray tomography was used to image seven specimens (V26641, V27433.1, V27434.1, 3, V27435.1, 13, 14, 26 and V27437.15) at beamlines BL01A1 and BL01B1 of the Taiwan Light Source (TLS), National Synchrotron Radiation Research Center (NSRRC), Taiwan. Radiograph data were acquired with a parallel semi-white-light hard X-ray beam at ≥ 4 keV over a 180° rotation arc at 0.3° increments. The resultant datasets contain 601 radiographs of 1600 X 1200-pixel size and 2.76 μm per pixel resolution. Radiograph alignment was enhanced in Matlab R2014b by processing the data with the fast projection matching (Faproma) algorithm developed by Wang. Reconstructions of tomographic slices from radiograph projections was performed in VGSTUDIO MAX 3.0 and produced sets of 1200 slices per specimen.

Over 600 specimens, including illustrated material (V27435.7, V27437.4, 8–14, V27439.1, V27438.4, V27440.2, V27441.1, 2, 4–6, V27443.1), were examined at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences with the X-ray micro-computed tomography scanner (225-3D-μCT) designed by the Institute of High Energy Physics, Chinese Academy of Sciences. Another 6 scales, a pair of prepectoral spines and a fin spine fragment (V27435.15–20, V27436.1, V27437.16) were imaged with a Zeiss Xradia Versa 520 micro-CT scanner at the Yunnan Key Laboratory for Palaeobiology, Yunnan University, China and six scales (V27435.2, 21, 23–26) were imaged with a
Skyscan1172 micro-CT scanner at the School of Dentistry, University of Birmingham. The IVPP analyses produced radiograph datasets acquired over 360° rotation cycles that were converted in VGSTUDIO MAX 3.0 to 1748 x 556-pixel tomograms with a 5.33 μm per pixel resolution. The Zeiss Xradia Versa 520 radiograph data were generated over a 360° rotation arc at 50 keV and reconstructed in VGSTUDIO MAX 3.0 to produce 984 X 1009 pixel tomograms with pixel size of 3.63 μm. Radiographs from the Skyscan1172 analysis were acquired at 70 keV with the use of X-ray attenuating 0.5 mm Al filter and rotation set to 180°. Resultant tomograms are 1332 x 2000 pixels with resolution of 2.06 μm per pixel.

Volumetric reconstructions of specimens from tomographic slices was performed in Mimics 19.0.

Scanning electron microscopy

Surface features of 4 partial and complete fin spines, 29 scales, 5 pectoral plate fragments and a tectal tessera, including the illustrated V27433.5, V27435.6, 9, 11, 12, 27, V27441.3 and V27442.1, were documented uncoated with a Phenom ProX Desktop SEM at 5 keV at the School of Geography, Earth and Environmental Sciences, University of Birmingham.

Light microscopy

A pair of prepectoral spines (V27436.2), an admedian fin spine fused to a pinnal plate (V27434.2) and four fin spines (V27437.3, 5–7) were imaged with a GXM
XTL3101 stereo microscope at the School of Geography, Earth and Environmental
Sciences, University of Birmingham.

A total of 40 specimens (tesserae, incomplete pinnal plates fused to pectoral
fin spine fragments and partial and complete fin spines) were thin sectioned at
Qujing Normal University, China. Nomarski DIC polarized light micrographs of the
sections (including figured material V27433.2, 3, 6, V27434.4, V27435.4, 5, 8, 10,
V27437.1, 2, 14, V27438.5) were imaged with an Olympus D12 digital camera
mounted on an Olympus BX51 Fluorescent Microscope.

Phylogenetic analyses

We performed phylogenetic analyses under parsimony and Bayesian optimality
criteria using a data matrix of 105 taxa and 292 characters (see Supplementary Data
7, 8). The matrix was compiled from characters and character codings from Brazeau
et al.8, Coates et al.7, Dearden53, Dearden et al.30, Qiao54 and Vaškaninová et al.55
(see also List of characters and Supplementary Data).

The parsimony analysis was conducted in TNT version 1.556 under parsimony
criteria by running a traditional search with TBR swapping algorithm set to save 100
trees per replication and limited to 1000 addition-sequence replicates. Trees were
rooted by designating Galeaspida as an outgroup and a maximum of 100000 trees
was kept in the memory. The analysis returned 5639 most parsimonious trees (920
steps each) from which we calculated 50 percent majority-rule consensus (926
steps) and strict consensus (1099 steps) trees (Supplementary Data 7). All
characters were unordered and of equal weights with character states at internal
nodes reconstructed as MPR sets in PAUP version 4.0a (build 169)57.
Bootstrap values for the 50 percent majority-rule and strict consensus trees were calculated in TNT by resampling the data matrix over 100 bootstrap replicates using the traditional search option (Supplementary Data 7). The 50 percent majority-rule consensus tree (Fig. 3 and Extended Data Fig. 6a) and its branch length values was imported into R (version 4.0.2) and time adjusted with the R package paleotree 3.3.25. The analysis was performed using the timePaleoPhy function of paleotree with mbl-type time scaling and pre-assigned taxon and tree root ages taken from King et al.6 and other studies (Table S2).

A Bayesian analysis was conducted in MrBayes version 3.2.7a59 using a MCMC statistical model, gamma-distribution rates and variable character-coding bias. The analysis was run for 10 million generations with a tree sampling frequency of 1000. Burn-in for tree samples was set at 25% and tree topology was constrained by designating Galeaspida as an outgroup and jawed gnathostomes as monophyletic (Supplementary Data 8).

Note on Figure 3

The line drawings and interpretation of dermoskeletal features of early jawed gnathostomes depicted in Fig. 3 based on data from: Béchard et al.60 (Bothriolepis), Pearson and Westoll61 (Cheirolepis), Miles28 and Burrow et al.5 (Climatius), Zhu et al.19 (Entelognathus), Zhu et al.35 (Guiyu), Hanke and Wilson38 (Kathemacanthus) and Dupret62 (Kujdanowiaspis).

Data availability
Investigated *Fanjingshania* specimens were assigned accession numbers (IVPP V27433–V27443) and deposited at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing. Supplementary information nex, zip and ply format files are currently available at https://www.dropbox.com/sh/or0zqqt4seheael/AADZmI2kNWcJ77WI0a5zXePOa?dl=0 and will be published online in a publicly accessible repository (ADMorph) upon acceptance of the manuscript.


**Acknowledgements** We thank Y.-M. Hou for the acquisition of the micro-CT X-ray data, Y. Hwu (Academia Sinica) and Y.-T. Weng (NSRRC) for performing and
assisting with the synchrotron X-ray analyses, and Y.Z. Hu for her comments and advice during the volumetric reconstructions of the specimens. This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA19050102, XDB26000000), the National Natural Science Foundation of China (41530102), the Key Research Program of Frontier Sciences, CAS (QYZDJ-SSW-DQC002), an Open Project Grant of the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, CAS (LVEHO19001), MOST 108-2116-M-213-001 (Taiwan), Chinese Postdoctoral Science Foundation grant (2019M663440) and the National Synchrotron Radiation Research Center, Taiwan (beamtime Projects No 2019-3-083-1 and 2019-3-185-1).


Competing interests The authors declare no competing interests.
Fig. 1 | Dermoskeletal elements of *Fanjingshania renovata*. Volume renderings based on synchrotron (g) and microcomputed X-ray tomography data (f, n, o, q–s, u, v), scanning electron micrographs (p, t, w) and optical micrographs (a–e, h–m). Incomplete pinnal plate carrying two prepectoral spines (V27436.2) in a, external and b, visceral views. Incomplete pinnal plate fused to an admedian spine (V27434.2) in c, visceral and d, ventral views. e, Partial pectoral fin spine (V27437.3) in lateral view. f, Incomplete pectoral spine (V27437.4) in posterior view. g, Ventral oblique view of a pectoral fin spine fragment fused to a partial ventral lamina of a pinnal plate (V27433.1, holotype). h, Lateral and i, posterior views of an incomplete pelvic fin spine (V27437.7). Incomplete anal fin spine (V27437.6) in j, lateral and k, posterior views. Incomplete posterior dorsal fin spine (V27437.5) in l, lateral and m, posterior views. n, Lateral and o, posterior views of an incomplete anterior dorsal fin spine (V27437.8). p, Incomplete anterior loricale plate (V27442.1) in ventral view. q, Partial branchiostegal plate (V27439.1) in visceral view. r, Incomplete fused sclerotic plates (V27443.1) in lateral view. s, Postorbital tessera (V27440.2) in crown view. t, Pectoral plate fragment fused to a partial pinnal plate (V27433.4) in external view. (u–w), Lateral views of prepelvic fin spines (V27441.1–3) of increasingly more posterior positions. Schematic reconstruction of the dermal skeleton of *Fanjingshania renovata* in x, ventral and y, lateral views based on similarities of the material assigned to the new taxon (see also Supplementary Information) with the anatomy of climatiid stem chondrichthycans\textsuperscript{14,27}. Line art adapted from Denison 1979\textsuperscript{16}. Arrowheads point to anterior. adfs, anterior dorsal fin spine; admfs, admedian fin spine; afs, anal fin spine; al, ascending lamina; alor, anterior loricale plate; bst, branchiostegal plates; pdfs, posterior dorsal fin spine; pelfs, pelvic fin spines; ppelfs1–3, prepelvic fin spines 1–4; ppms, pfs, pot, postorbital tessera; pi, pinnal
plate; pps, prepectoral spines; sp, sclerotic plates; tt, tectal tesserae; vl, ventral lamina. Scale bars, 1 mm.

**Fig. 2** | Histological and developmental features of the pectoral shoulder girdle and trunk

**scales of *Fanjingshania renovata***. Volume renderings generated from X-ray synchrotron (a–e) and microcomputed tomography (f, h) data and optical micrographs (g, i, j). 

- **a**, A fragment of a pectoral fin spine fused to a partial ventral lamina of a pinnal plate depicted in external (ventral) view (V27433.1, holotype). 
- **b**, Detail of a pinnal plate scale (s2) in V27433.1 with colour-coded secondary and primary odontodes. 
- **c**, Virtual slice through the pinnal plate and pectoral fin spine wall of the holotype (V27433.1). 
- **d**, Lateral view of an incomplete admedian fin spine fused to a fragment of pinnal ventral lamina (V27434.1). 
- **e**, Virtual slice through the partial pinnal plate of V27434.1. 
- **f**, Lateral crown aspect of a trunk scale with a large replacement odontode (V27435.2). 
- **g**, Longitudinal section of an isolated trunk scale with an anterior replacement odontode (V27435.5). 
- **h**, Asymmetrical trunk scale (V27435.1) in anterior crown view. 
- **i**, Part of a longitudinally sectioned trunk scale (V27435.22). 
- **j**, Section through a partial pinnal plate fused to a fragment of pectoral spine wall (V27433.2). 

Squares correspond to colour-coded odontodes in (b) and (h). Red dashed lines mark scale base/basal plate boundary. White dashed lines mark resorption surfaces. ad, atubular dentine; admfs, admedian fin spine; bp, basal plate; cb, cellular bone; pfs, pectoral fin spine; pi, pinnal plate; ro, replacement odontode; sb, scale base; s1–5, scale 1–5; sc, scale crown. Scale bars, 1mm (a–f, h, j), 0.5 mm (g, i).
Fig. 3 | Phylogenetic placement of *Fanjingshania renovata* within early jawed vertebrates.

Simplified 50 percent majority-rule consensus tree from a parsimony analysis of a data matrix of 105 taxa and 292 characters. Diagrams to the right of the tree illustrate the distribution of dermoskeletal characters possessed by *Fanjingshania* in select chondrichthyans, osteichthyans and 'placoderms' (see also Supplementary Information). Circles at internal nodes represent parsimony reconstructions of a select set of anatomical and developmental/histological characters coded for *Fanjingshania*. Circles opposite taxon labels show presence of these characters at terminal nodes. Character number in the data matrix is given in parentheses (see Supplementary Information).
Extended Data Fig. 1 | The Shiqian-Tunping section at Leijiatun (Shiqian County, Guizhou Province, China). Diagram revealing the relationship of the Rongxi to the other Silurian lithostratigraphic units (color coded) exposed at Shiqian-Tunping and the location of the *Fanjingshania*-bearing beds (depicted in grey, sample 3SQT0) within the sequence.
Extended Data Fig. 2 | Head and trunk dermoskeletal elements of Fanjingshania renovata.

Volume renderings based on X-ray microcomputed tomography data (a–c, i, j, l, m), scanning electron micrographs (d, k, n, o) and optical micrographs (p, q). Fused tectal tesserae (V27438.4) in a, crown and b, basal views. c, Broad asymmetrical trunk scale in crown view (V27435.23). d, Asymmetrical trunk scale (V27435.6) in crown view. Incomplete symmetrical trunk scale (V27435.7) in e, crown and f, base views. g, Crown view of an asymmetrical trunk scale (V27435.12). h, Crown view of a symmetrical trunk scale (V27435.24) with a large anterior tubercle. i, Basal view of V27435.24. j, Crown view of a trunk scale (V27435.11) with an anterior replacement odontode. k, Incomplete trunk scale (V27435.9) with an anteriorly excavated crown. l, Section through two fused tectal tesserae (V27438.5). m, Longitudinal section through a trunk scale (V27435.8). Arrowheads point to anterior. ad, atubular dentine; cb, cellular bone; po, primary odontodes; ro, replacement odontode; sb, scale base; sc, scale crown; so, secondary odontodes, tt, tectal tesserae. Scale bars, 1 mm.
Extended Data Fig. 3 | Fin spines of *Fanjingshania renovata*. Volume renderings based on X-ray microcomputed tomography data (a–t) and optical micrographs (u–x). Incomplete pectoral fin spine (V27437.9) in a, lateral and b, apical lateral view. Incomplete pectoral spine (V27437.10) in (c, d) lateral and e, posterior lateral views. Pelvic fin spine (V27437.11) in f, lateral and g, posterior views. Partial anterior dorsal fin spine (V27437.12) in (h, j) and i, posterior views. Incomplete posterior dorsal fin spine (V27437.13) in k, lateral and l, posterior views. Incomplete anal fin spine (V27437.14) in m, lateral and n, posterior views. (o, p) Incomplete prepelvic fin spine (V27441.4) in lateral views. Prepelvic fin spine (V27441.5) in q, lateral and r, basal lateral views. (s, t) Incomplete prepelvic fin spine (V27441.6) in lateral apical views. u, Transversely sectioned fin spine fragment (V27437.2) shown in part. v, Transversely sectioned apical fragment of a fin spine (V27437.1). w, Enlarged anterior of v, showing detail of the spine’s tissue structure. Portion of a longitudinally sectioned pectoral fin spine (V27437.14). cc, calcified cartilage; cb, cellular bone; lz, lamellar zone; vz, vascular zone. Scale bars, 1 mm (a–t), 0.5 mm (v), 0.25 mm (u), 0.2 mm (x) and 0.05 mm.
Extended Data Fig. 4 | Elements of the dermal shoulder girdle of *Fanjingshania renovata*.

Optical micrographs (a, d, i), scanning electron micrograph (b) and volume renderings based on synchrotron (e–h) and microcomputed (j–l) X-ray tomography data. a, Section through a fragment of a pectoral fin spine wall fused to a partial pinnal plate (V27433.3). b, Fragment of a pectoral fin spine wall fused to a partial pinnal plate (V27433.5) in external view. c, Horizontal virtual section through a partial pinnal plate fused to a pectoral fin spine fragment (V27433.1, holotype). d, Detail of a pectoral fin spine wall (from a sectioned pectoral fin spine fragment fused to a partial pinnal plate, V27433.6). e, Lateral view of an admedian fin spine fused to a pinnal plate fragment (V27434.3). f, Transverse virtual slice through V27434.3 shown in anterior view. g, Lateral view of an incomplete admedian fin spine fused to a fragment of pinnal plate (V27434.1). h, Virtual transverse section through V27434.1 in posterior view. i, Portion of basal wall of an admedian fin spine (V27434.4) sectioned along its long axis, apical to the left. j, Lateral view of two prepectoral spines fused to a partial pinnal plate (V27436.1). k, Vertical virtual slice through V27436.1 in ventral view. l, Lateral view of V27436.1 showing ventral pinnal plate lamina (downturned due to a post-mortem fracture). l, Horizontal virtual slice through the prepectoral spines of V27436.1. Arrowheads point to anterior. admfs, admedian fin spine; al, ascending lamina; bp, basal plate; cb, cellular bone; pfs, pectoral fin spine; pi, pinnal plate; pps, prepectoral spines; s1–4, scales 1–4; sc, scale crown; vl, ventral lamina. Scale bars, 1 mm (a–c, e–h, j–l), 0.5 mm (d) and 0.2 mm (i).
Extended Data Fig. 5 | Resorption features in the dermal skeleton of *Fanjingshania renovata*.

Volume renderings based on synchrotron X-ray tomography data (a–d, f–i), optical micrograph (e) and scanning electron micrograph (i). a, Trunk scale (V27435.10) with an anterior replacement odontode and ‘exploded view’ of the same specimen revealing the resorption surfaces in the scale crown and base. b, Basal view of an asymmetrical trunk scale (V27435.1) and the crown and base of the same specimen in crown aspect demonstrating absence of resorption surfaces in contrast to V27435.10. c, Transverse virtual slice through V27435.10 at the level of the replacement odontode. d, Transverse virtual slice through V27435.1 at the level of the primordial odontode. e, Longitudinally sectioned trunk scale (V27435.4) with an anterior resorption surface. f, A partially resorbed pinnal plate scale highlighted in a dermal shoulder girdle fragment (V27433.1, partial admedian fin spine fused to a fragment of a pinnal plate) shown in external (ventral) view. g, Horizontal virtual slice through the pinnal plate and fin spine wall of V27433.1. h, Vertical virtual slice through the pinnal plate and fin spine wall of V27433.1. i, Partially resorbed pinnal plate scale shown in (f–h) superimposed onto an isolated trunk scale (V27433.27). Image of resorbed scale reflected and magnified 1.5x the scale in (i). ad, atubular dentine; admfs, admedian fin spine; bp, basal plate; cb, cellular bone; pi, pinnal plate; po, primary odontodes; ro, replacement odontode; rs, resorption surface; sb, scale base; sc, scale crown; so, secondary odontodes. Scale bars, 1 mm (a–d, f–i) and 0.5 mm (e).
Extended Data Fig. 6 | Phylogenetic reconstructions of early gnathostomes based on a data matrix of 105 taxa and 292 characters. a, 50 percent majority-rule and b, strict consensus trees from an analysis performed under parsimony optimality criteria (numbers in (a) and (b) represent 50 percent and above bootstrap support for internal nodes). c, 50 percent majority-rule consensus tree from a Bayesian phylogenetic analysis (numbers represent posterior probability values).
*Extended Data Fig. 7* | Life reconstruction of *Fanjingshania renovata*. Artwork by Fu Boyuan and Fu Baozhong.
Supplementary Information for:

Spiny chondrichthyan from the lower Silurian of South China

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Horizon and locality

Vertebrate-bearing samples (35SQTP) containing the *Fanjingshania* material were collected from a recently exposed road section (Shiqian-Tunping) of the Rongxi Formation located near the village of Leijiatun in Shiqian County, Guizhou Province, China. The samples come from a unit of interbedded mudstone and limestone conglomerate beds from the upper part of the Rongxi Formation (Extended Data Fig. 1). Present in 35SQTP are also platform elements of the conodont *Ozarkodina guizhouensis* that is indicative of the upper Aeronian–lower Telychian *Ozarkodina guizhouensis* Biozone. The Rongxi Formation at Shiqian has been dated to the upper Aeronian, within the *Ozarkodina parahassi* division of the *O. guizhouensis* Biozone, using biostratigraphic evidence from the underlying Majiaochong and the overlying Xiushan Formations. Alternative, lower Telychian, age estimates can be explained by the recently proposed diachronous nature of the Rongxi Formation at localities across South China. We therefore consider the Aeronian age of the Rongxi Formation as most plausible.

Specimen descriptions

**Holotype.** Isolated specimen (V27433.1) preserving a fragment of a spine wall fused along its basal margin to articulated dermal scales supported by a basal plate (Fig. 2a, c and Extended Data Figs. 4c, 5a–c). The exterior surface of the partial spine is ornamented by six tubercle-studded ridges of varying width. The ridges are flat-topped with scalloped lateral sides and extend to contact the scales at an acute angle (Figs. 1g, 2a). The spine preserves an undamaged posterior edge that bears a deep longitudinal indentation. Surface renderings and virtual slices reveal in situ
fusion of scale bases by a common basal plate. The latter is best preserved in the posterior of the specimen where it is seen to be continuous with the inner portion of the spine wall (Fig. 2c). The scales have a staggered arrangement, forming an anterior (incompletely preserved) and posterior pairs oriented obliquely in relation to the spine base (Fig. 2a). A partial scale is present between the posterior-most spine ridge and the scale pairs (Fig. 2a). Scale crowns have a rhomboid appearance and possess irregular margins accentuated by an enlarged lateral lobe. The crown surfaces show signs of post-mortem abrasion and preserve deep grooves separating high relief nodose ridges. A prominent button-shaped tubercle is a consistent feature of the crown anterior where the ornament changes to disorganised short ridges and tubercles. Volumetric reconstructions reveal concave scale bases with low profiles that do not extend beyond the crown margins.

The tomography data demonstrate a clear density contrast between the tissue of the basal plate and the more radiotransparent scales fused to it (Fig. 2c). The basal plate extends to occupy the spaces between the scales and is continuous with the inner portion of the spine wall (Fig. 2c and Extended Data Figs. 4c, 5h). Radiopaque material is present inside the spine ridges whose tissue displays a faint lamellar texture in horizontal virtual slices (Fig. 2c and Extended Data Fig. 4c). Scales possess compound crowns of appositionally deposited odontode generations of increasingly larger size (Fig. 2b). The crowns' primordial odontode surmounts the apex of the base and is bounded anteriorly by a cluster of vermiform and tuberculate secondary odontodes. Scale bases consist of lamellar bone with plywood-like architecture pervaded by vertically oriented fibres (Fig. 2c). In the partial scale, the crown and base are truncated by irregular resorption surfaces along which the scale makes contact with the spine (Fig. 2b).
Other fused elements. Represented by incomplete shoulder girdle plates fused to spines and spine fragments, fused sclerotic plates and fused head tesserae.

Type 1 dermal elements (*partial pectoral fin spines fused to fragments of a pinnal plates*). These constitute partial spine bases fused to a basal plate carrying dermal scales of the type possessed by the holotype. Investigated specimens (V27433.1–V27433.9) preserve up to 13 spine ridges of variable width adorned by nodose ornament (Fig. 1t and Extended Data Fig. 4b). The spine wall of these is either level with (Fig. 2c, j) or joins at an angle (Fig. 1t and Extended Data Fig. 4a) the basal plate/scales units. Specimens of the latter type show fragmentation of the spine's ridged ornament into strings of independent nodes (Fig. 1t) near the contact with the base.

The plates' scales arrange with an offset and organise in rows that are directed obliquely relative to the spine ridges. As observed in the holotype, some of the scales proximal to the spine represent resorbed remnants of regular-sized scales exhibiting truncated crown ornament along a ruffled longitudinal margin facing the spine (Extended Data Fig. 4b). In some specimens the spine ridges develop between the proximal scales or even extend beyond their anterior edge. Scale crowns are asymmetrical with ovoid to rhomboid appearance and possess an ornament of prominent nodose ridges that anteriorly become discontinuous and organise around a conspicuous medial pustule. In less abraded specimens the crown surface is studded with tubercles formed on top of the main sculpting features.

Thin-sectioned specimens (V27433.2, V27433.3, V27433.6 and V27433.7) demonstrate extensive diagenetic replacement of hard tissues inside scale crowns.
and the nodose sculpture of the spine ridges (Fig. 2j and Extended Data Fig. 4a, d).

Optically faint depositional lines and rudiments of pulp canals are however preserved in the scale crowns of V27433.3 (Extended Data Fig. 4a). Other sectioned material (V27433.2 and V27433.7) shows evidence of partial and/or complete removal of odontodes and basal tissue along the oblique resorption surfaces of partial scales. Scale bases consist of compact lamellar bone harbouring fusiform cell lacunae and vertically oriented fibre spaces (Fig. 2j and Extended Data Fig. 4a, d). The lamellar bone continues below the bases without an optically distinct boundary and forms a basal palate that fuses the scales together. It also extends into the inner spine wall with no break in its lamellar structure. The same tissue architecture is maintained across the thickness of the spine wall, including inside the ornamenting ridges.

Similar to the lamellar bone of the scale bases and basal plate, the tissue exhibits flattened cell lacunae and fibre spaces directed orthogonal to the spine's outer surface (Extended Data Fig. 4d).

Type 2 dermal elements (complete and partially preserved admendian spines fused to pinnal plate fragments). Specimens consisting of a low, laterally compressed spine with a broad elliptical base fused to a partial dermal lamina (Figs. 1c, d, 2d, e, and Extended Data Fig. 4e–i). The spine apex is posteriorly offset due to an acutely angled anterior margin that bears a strong keel connected to an ornament of equally spaced nodose ridges. The posterior spine edge has a slightly concave, near vertical profile and does not develop a noticeable longitudinal sulcus. Around its perimeter the spine base flares out into a shelf-like extension where the ornamenting ridges fragment into series of individual nodes. The examined fragmentary material demonstrates ovoid or kidney-shaped scales (Fig. 2d and Extended Data Fig. 4g) fused to the lateral and/or posterior margins of spine bases. In less abraded
specimens (Fig. 1d) the scale crowns are ornamented by tuberculate ridges aligned in an antero-posterior direction. Some of the scales in contact with the spine wall possess crowns truncated by irregular resorption surfaces developed primarily along their long axis. All scales fuse to a basal plate with irregular outer margins that follows the scales' contour and is clearly delineated from them around its periphery by a recessed border.

A longitudinally sectioned specimen preserves a portion of the original structure of the outer spine wall where a lamellar bone is identified to harbour fusiform cell lacunae aligned with the tissue's lamellae (Extended Data Fig. 4i). Tomographic slices show this outer zone of the spine to be pervaded by a vascular network of canals present inside the ornamenting ridges as well deeper within the tissue (Extended Data Fig. 4f). In V27434.3 the vascular zone is separated internally by a radiotransparent boundary from a compact tissue developed in the apical portion of the spine (Extended Data Fig. 4f). The lamellar bone of the spine wall extends to form the basal plate that fuses together the scales to the spine periphery. This lamellar architecture is also developed inside the scale bases with a perceptible change in radiodensity marking the transition between the two in V27434.1 (Extended Data Fig. 4h). A prominent pustule-shaped crown primordium surmounts the base apically and is the first in a row of appositionally deposited primary odontodes (Fig. 2e). A smaller component of the scale crowns is a cluster of vermiform secondary odontodes deposited anteriorly and laterally to the primordium. Many of the scales in proximity of the spine wall are in various stages of resorption evidenced in the synchrotron data by irregular surfaces truncating the odontode generations (Fig. 2d, e and Extended Data Figs. 4g, h).
Type 3 dermal elements (prepectoral spines fused to pinnal plate fragments). Two specimens (V27436.1 and V27436.2) possessing a pair of spines of unequal size that fused laterally to partially preserved dermal plates (Fig. 1c, d and Extended Data Fig. 4j–l). The spines are squat, laterally flattened and near symmetrical elements fused together along their long axes. The larger of the two spines shows a slight bend towards one of its lateral sides. Both spines possess ridged ornament that is continuous with rows of tubercules carried by the dermal plate laminae. In either specimen, intact plate margins are preserved only on one side of the spines and demonstrate an undulating edge indented by a deep uninterrupted groove as well as broadening of the plate in direction of the larger spine.

Tomography data from V27436.1 show fusion of the spine walls at their bases as well as canal spaces rimmed by concentric depositional lines formed within the ornamenting ridges and deep inside the spine wall.

Type 4 dermal element (anterior lorical plate fused to a median prepectoral spine). A single specimen comprising of a diminutive spine fused to a partially preserved basal plate (Fig. 1p). The spine has a stubby, conical appearance with nodose ridges radiating down from its apex. Around most of its circumference the spine is fused to a fragment of a basal plate bearing a coarse tuberculate ornament. Only one of the plate's free margins is largely intact and demonstrates a recessed edge arched into a prominent medial bulge that aligns with the spine. Preserved portions of the basal plate flanking the spine also possess deeply grooved margins and carry partial scale crowns ornamented with disjointed ridges and tubercles.

Type 5 dermal elements (fused sclerotic plates). A single specimen (Fig. 1r) displaying one partial and one complete plate with curved profiles fused along a
linear contact surface. A fragment of a third element is fused to each of the better preserved plates. The complete plate is polygonal and possesses a dome-like raised area that is located near its junction with the partial plate where a similar acuminate region is also present. The plates possess an ornament of thick radiating ridges that descend from their apical areas and become discontinuous towards the periphery. One side of the plates' margins is shaped into a well-defined, continuous arc with a characteristic 'lip' not developed elsewhere around their perimeter. The visceral surface of the complete plate is concave and divided longitudinally by a low ridge.

Type 6 dermal elements (fused tectal tesserae). Six specimens representing fused in articulation polygonal tesserae exhibiting flattened profiles and planar lower surfaces. The largest of these aggregates consists of 8 tesserae (Extended Data Fig. 2a, b) of varying sizes and shapes adorned by branching ridges anastomosing to a medial ridge. Differences in tessera shape and size are also observed in compound two- and three-tessera elements.

A thin-sectioned specimen (Extended Data Fig. 2l) comprising of two fused tesserae reveals basal lamellar bone harbouring cell lacunae aligned with the tissue's lamellae. The base is pervaded by extrinsic fibre space that converge towards its apex. Histological detail of tessera crowns is lacking due to extensive diagenetic alteration of original tissue structure.

Disarticulated material

Spine morphology A (pectoral fin spines). Incomplete specimens (Fig. 1e, f and Extended Data Fig. 3a–e) constituting laterally compressed, elongate spines with broad sides and strongly recurved profiles. The spines exhibit a gradual apical taper accompanied by apical convergence of the spine ornament. The latter is developed
on the spines' lateral sides as flat-topped nodose ridges of variable width that
bifurcate basally. In non-abraded specimens (Fig. 1e) the ridges are studded with
fine tubercles also present on the anterior spine edge where they are carried on an
enlarged rib-like ridge. A deep sulcus runs the length of the posterior spine edge.

The wall of pectoral and other fin spine morphologies consists of a cellular
bone tissue organised into an outer vascular and inner lamellar zone (Extended Data
Fig. 3v, w). The thicker outer zone is extensively recrystalised in all examined
specimens and contains diagenetically infilled canals running parallel the spine
surface (Extended Data Fig. 3u, v). Concentric deposition of the cellular bone around
the canals is identified optically in thin sectioned spines. The inner zone has a
compact appearance and harbours densely packed fusiform cell spaces infilled by
optically opaque diagenetic material (Extended Data Fig. 3w). The cell spaces align
with the bone lamellae of the inner zone tissue that arrange circumferentially around
the spine core. Apically, the central spine cavity is occupied by calcified cartilage
consisting of aggregates of mineralised globules and wavy growth increments
(Extended Data Fig. 3w, x). Arrested growth surfaces are evident in globules in
contact with the inner cellular bone.

Spine morphology B (pelvic fin spines). Partial and nearly complete spines (Fig. 1h, i
and Extended Data Fig. 3f, g) with acuminate, moderately arched profiles and
flattened lateral sides. Some specimens preserve the basal portion of the spine that
broadens noticeably in respect to its apical part (Fig. 1h, i). Flat-topped nodose
ridges of varying width adorn the spines' lateral sides with some of the ridges
bifurcating in proximity of the spine base. A progressively widening and deeply
incised sulcus marks the posterior spine edge.
Spine morphology C (anterior dorsal fin spines). Represented by incomplete spines (Fig. 1n, o and Extended Data Fig. 3h–j) exhibiting extreme lateral compression and broad profiles with an arched anterior and slightly curved posterior margins. The spines' lateral sides bear ornamenting ridges of the kind recorded in morphologies A and B and a posterior sulcus along the length of preserved portions of specimens.

Spine morphology D (posterior dorsal fin spines). Partially preserved acuminate spines (Fig. 1l, m and Extended Data Fig. 3k, l) possessing straight to lightly depressed anterior and posterior edges that diverge rapidly to form a broad base. The spines exhibit moderate lateral compaction and carry the vertical ridged ornament observed in the other spine morphologies (A to C). A deep and basally widening sulcus is present along the preserved apical portions of the spines’ posterior edge. The core of the spines is occupied by a large-diameter cavity that tapers off in the apical portion of the spine.

Spine morphology E (anal fin spines). Incomplete spines demonstrating acuminate profiles with a gently arched anterior edge and a straight posterior margin (Fig. 1j, k and Extended Data Fig. 3m, n). The lateral sides of the spine trunk bear nodose ridges of variable width that bifurcate in the apical and basal portions of the spines. A basally widening sulcus is a feature of the posterior spine edge.

Spine morphology F (prepelvic fin spines). Complete and partially preserved stubby spines (Fig. 1u–w and Extended Data Fig. 3o–t) with lengths exceeding two times or more the height of their apices. The spines exhibit strong lateral compression that produces an elliptical base with a narrow footprint. Three morphological variants of these spines are distinguished on the basis of differences in the angle of slope of the anterior spine edge. Specimens with a low anterior margin possess an apex with an
extreme posterior offset (Fig. 1u and Extended Data Fig. 3o, p). The other two variants (Fig. 1v, w and Extended Data Fig. 3q–t) have steeper anterior margins and develop a diminutive accessory cusp posterior of the spine apex. Spine ornament is represented by evenly spaced nodose ridges that bifurcate basally and converge towards the spine apex and accessory cusps when present. Complete specimens display an excavated basal surface throughout the antero-posterior length of the spine.

Type 7 dermal elements (a branchiostegal plate). A plate fragment (Fig. 1q) of elongate appearance preserving a wedge-shaped margin at its intact end. The external plate surface carries a thick medial ridge from which radiates finer ornament of nodose ridges. The visceral (basal) face of the plate is smooth and deeply excavated.

Type 8 dermal elements (postorbital tesserae). Tall and elongate tesserae with a vaulted appearance possessing a wide medial crest that connects to deeply engraved vertical ridges developed on their lateral sides (Fig. 1s). These ridges carry secondary nodose ornament and bifurcate as well as become discontinuous in a basal direction. In the figured specimen (Fig. 1s) two polygonal tectal tesserae are fused to one side the periphery of the tessera.

Type 9 dermal elements (isolated trunk scales). Partially preserved and complete scales (Fig. 2f, h and Extended Data Figs. 2c–k, 5a–e, i) possessing rhomboid to ovoid crowns supported by a low base. The specimens display symmetrical as well as asymmetrical crowns with moderate to extreme extension posterior of the scale base. Crown surfaces bear elaborate ornament of fine tubercles and discontinuous nodose ridges with antero-posterior alignment. The crowns' anterior develops a
conspicuous pustule-like tubercle (Extended Data Fig. 2c–e, g, h) and deep furrows that carve a complex array of vermiform ridges and tubercles (Fig. 1g and Extended Data Fig. 2d, e). In rare specimens this area of the crown and part of the underlying base are excavated by a smooth-walled depression that cuts through the surface ornament (Extended Data Figs. 2k, 5e). In a number of scales, the depression is occupied by an outsized replacement odontode that protrudes above the rest of the crown (Extended Data Figs. 2j, 5a, c). The replacement odontode is an elongate, dome-shaped element with a strong medial crest and sides ornamented by fine nodose ridges.

Scale bases have rhomboid outlines and flat or concave lower surfaces (Extended Data Figs. 2f, i, 5b, d, e). An exception to this are specimens possessing a replacement odontode where the lower base develops a conspicuous central bulge (Extended Data Fig. 5a, c).

Scale crowns consist of a row of appositionally arranged primary odontodes that increase in size in progressively more posterior positions (Extended Data Figs. 2m, 5e). Anteriorly these are bounded by vermiform and tuberculate secondary odontodes of irregular distribution (Extended Data Figs. 2c–e, g, h, m, 5e). Sectioned scales with an anterior depression reveal resorptive removal of early generations of primary and secondary odontodes as well as the apex of the scale base (Extended Data Figs. 2k, 5e). A similarly shaped resorption surface supports the large replacement odontode in all histologically examined specimens (Fig. 2g and Extended Data Fig. 5a, c).

The scale crown odontodes are formed of atubular dentine that possesses vestigial pulp cavity spaces occupied by diagenetic material. The tissue exhibits
wavy depositional lines and isolated clusters of mineralised globules (Extended Data Figs. 2m, 5e). Compact lamellar bone with closely packed cell spaces forms the scale base. Its matrix is pervaded by vertical fibre spaces that converge vertically towards the apex of the base (Extended Data Figs. 2m, 5e, d).

Remarks on the dermoskeletal characters of *Fanjingshania*

Assignment of *Fanjingshania* spine/fin spine morphologies to specific body positions is based on close similarities with the spine/fin spine complements of the climatiids (sensu Burrow et al.7) *Climatius*8-10 and *Vernicomacanthus*9,11-13. Comparison with the head dermoskeleton of the latter two taxa, and that of another climatiid, *Brachyacanthus*11,14, allowed to identify in *Fanjingshania* tectal and postorbital tesserae, as well as sclerotic and branchiostegal plates.

Recognition of dermal plate fragments belonging to *Fanjingshania* as pinnal and lorical plates is supported by their fusion to an array of spines and fin spines (median/paired prepectoral, pectoral and admedian). Some or all of these spine types are also documented to coalesce with paired (pinnal) and median (lorical) plates in the shoulder girdles of climatiids7-9,15, diplacanthids16 and other stem chondrichthyans17. Similar to *Fanjingshania*, histological data from *Climatius*8 and *Diplacanthus*16 expose pinnal and lorical plates as compound elements composed of dermal scales fused together by a basal plate.

List of characters

   0 absent
   1 present

2. [B:2] Prismatic calcified cartilage.
   0 single layered
   1 multi-layered

3. [B:3] Perichondral bone.
   0 present
   1 absent

   0 absent
   1 present

5. [B:5] Enamel(oid) present on dermal bones and scales.
   0 absent
   1 present

   0 single-layered
   1 multi-layered

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

   0 absent
0 absent
1 present

10. [B:10] Dentine kind (modified).
Character 10 of Brazeau et al. was modified by introducing an extra state to account for the atubular dentine (lamellin) possessed by Fanjingshania.
0 mesodentine
1 semidentine
2 orthodentine
3 lamellin

0 present
1 absent

0 osteodentine
1 orthodentine

13. [B:13] Longitudinal scale alignment in fin webs.
0 absent
1 present

0 absent
1 present

Character 15 of Brazeau et al.\textsuperscript{18} was reformulated to describe mono- and poly-
odontode scale crowns on the basis of odontode number without alluding to their
patterning.

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

16. [B:16] **Concentric addition of trunk scale odontodes (modified).**

Modified character 16 of Brazeau et al.\textsuperscript{18} distinguished from the original formulation
by specifying that the concentric growth of scales refers to their odontode
generations.

0 absent
1 present

17. [B:17] **Buried odontode generations (modified).**

We split character 17 of Brazeau et al.\textsuperscript{18} in order to code separately for overgrowth
of odontode generations (character 17) and odontode resorption (character 291).

0 present
1 absent

18. [B:18] **Trunk scales with peg-and-socket articulation.**

0 absent
1 present

19. [B:19] **Scale peg.**

0 broad
1 narrow

20. [B:20] **Anterodorsal process on scale.**

0 absent
1 present

21. [B:21] **Trunk scale profile.**
<table>
<thead>
<tr>
<th>Question</th>
<th>Answer</th>
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<tbody>
<tr>
<td>22. Profile of scales with constriction between crown and base.</td>
<td></td>
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<tr>
<td>23. Trunk scales with bulging base.</td>
<td></td>
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<tr>
<td>24. Trunk scales with flattened base.</td>
<td></td>
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<tr>
<td>25. Basal pore in scales.</td>
<td></td>
</tr>
<tr>
<td>26. Flank scale alignment.</td>
<td></td>
</tr>
<tr>
<td>27. Scute-like ridge scales (basal fulcra).</td>
<td></td>
</tr>
<tr>
<td>28. Sensory line canal.</td>
<td></td>
</tr>
<tr>
<td>0 distinct crown and base demarcated by a constriction (&quot;neck&quot;)</td>
<td></td>
</tr>
<tr>
<td>1 flattened</td>
<td></td>
</tr>
<tr>
<td>0 neck similar in width to crown</td>
<td></td>
</tr>
<tr>
<td>1 neck greatly constricted, resulting in anvil-like shape</td>
<td></td>
</tr>
<tr>
<td>23. Trunk scales with bulging base.</td>
<td></td>
</tr>
<tr>
<td>24. Trunk scales with flattened base.</td>
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</tr>
<tr>
<td>28. Sensory line canal.</td>
<td></td>
</tr>
<tr>
<td>0 absent</td>
<td></td>
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<tr>
<td>1 present</td>
<td></td>
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<tr>
<td>0 present</td>
<td></td>
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<tr>
<td>1 absent</td>
<td></td>
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<tr>
<td>0 absent</td>
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</tr>
<tr>
<td>1 present</td>
<td></td>
</tr>
<tr>
<td>0 vertical rows oblique rows or hexagonal</td>
<td></td>
</tr>
<tr>
<td>1 rhombic packing</td>
<td></td>
</tr>
<tr>
<td>2 disorganised</td>
<td></td>
</tr>
<tr>
<td>0 absent</td>
<td></td>
</tr>
<tr>
<td>1 present</td>
<td></td>
</tr>
<tr>
<td>0 perforates scales</td>
<td></td>
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</table>
1 passes between scales
2 C-shaped scales

29. [B:29] **Dermal ornamentation.**
0 smooth
1 parallel, vermiform ridges
2 concentric ridges
3 tuberculate

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

32. [B:32] **Jugal portion of infraorbital canal joins supramaxillary canal.**
0 present
1 absent

33. [B:33] **Dermal skull roof (modified).**
State 2 was added from character 25 of Coates el al.¹⁹
0 includes large dermal plates
1 consists of undifferentiated plates, tesserae or scales
2 naked or largely scale free

34. [B:34] **Anterior pit line of dermal skull roof.**
0 absent
1 present
   0 large interlocking polygonal plates
   1 microsquamose, not larger than trunk squamation

36. [B:36] Cranial spines.
   0 absent
   1 present

37. [B:37] Cranial spines.
   0 monocuspid
   1 multicupsid

38. [B:38] Extent of dermatocranial cover.
   0 complete
   1 incomplete (limited to skull roof)

   0 present
   1 absent

40. [B:40] Endolymphatic ducts with oblique course through dermal skull bones.
   0 absent
   1 present

41. [B:41] 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)
42. [B:42] Pineal opening perforation in dermal skull roof.
0 present 1 absent

43. [B:43] Dermal plate associated with pineal eminence or foramen.
0 contributes to orbital margin (plate(s) excluded from orbital margin by skull roofing bones.)
1 plate bordered laterally by skull roofing bones

44. [B:44] Broad supraorbital vaults.
0 absent 1 present

45. [B:45] Median commissure between supraorbital sensory lines.
0 absent 1 present

46. [B:46] Dermal cranial joint at level of sphenoid-otic junction.
0 absent 1 present

47. [B:47] Otic canal extends through postparietals.
0 absent 1 present

48. [B:48] Number of bones of skull roof lateral to postparietals.
0 two 1 one 2 more than two
49. [B:49] Suture between paired skull roofing bones (centrals of placoderms postparietals of osteichthyans).

0 straight
1 sinusoidal

50. [B:50] Medial processes of paranuchal wrapping posterolateral corners of nuchal plate.

0 absent
1 present

51. [B:51] Paired pits on ventral surface of nuchal plate.

0 absent
1 present

52. [B:52] Sclerotic ring.

0 absent
1 present

53. [B:53] Consolidated cheek plates.

0 absent
1 present

54. [B:54] Cheek plate.

0 undivided
1 divided (i.e., squamosal and preopercular)

55. [B:55] Subsquamosals in taxa with divided cheek.

0 absent
1 present

56. [B:56] Preopercular shape.
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 ('arthrodire'-type)
2   reverse ginglymoid ('antiarch'-type)
3   longitudinal

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. [B:63] Branchiostegal plate series along ventral margin of lower jaw.
   0 absent
   1 present

64. [B:64] Branchiostegal ossifications.
   0 plate-like
   1 narrow and ribbon-like
   2 filamentous

   0 ornamented
   1 unornamented

66. [B:66] Imbricated branchiostegal ossifications.
   0 absent
   1 present

   0 absent
   1 present

68. [B:68] Lateral gular.
   0 absent
   1 present

   0 absent
   1 present
70. [B:70] Shape of opercular (submarginal) ossification.
0 broad plate that tapers towards its proximal end
1 narrow, rod-shaped

71. [B: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)

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

73. [B:73] Basihyal.
0 absent
1 present

74. [B:74] Interhyal.
0 absent
1 present

75. [B:75] Hypohyal.
0 absent
1 present

76. [B:76] Endoskeletal urohyal.
0 absent
1 present

77. [B:77] Oral dermal tubercles borne on jaw cartilages or at margins of the mouth.
78. [B:78] Oral dermal tubercles patterned in organised rows (teeth).

79. [B:79] Enamel(oid) on teeth.

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

81. [C:79] Tooth families/whorls.

82. [B:82] Bases of tooth whorls.

83. [B:83] Distribution of tooth whorls.

84. [B:84] Distribution of tooth whorls.
2 upper jaws only

85. [B:85] Teeth ankylosed to dermal bones.
0 absent
1 present

86. [B:86] Plicidentine.
0 absent
1 present

87. [B:87] Dermal jaw plates on biting surface of jaw cartilages.
0 absent
1 present

0 absent
1 present

89. [B:89] Premaxilla.
0 extends under orbit
1 restricted anterior to orbit

0 splint-shaped
1 cleaver-shaped

91. [B:91] Pair of tooth plates (anterior supragnathals or vomers) on ethmoidal plate.
0 absent
1 present
92. [B:92] Strong posterior flexion of dentary symphysis.

0 absent
1 present


0 along much of ventral margin of dentary
1 restricted to posterior half of dentary

94. [B:94] Coronoid fangs.

0 absent
1 present

95. [B:95] Position of upper mandibular arch cartilage (and associated cheek plate where present).

0 entirely suborbital
1 with a postorbital extension

96. [B:96] Position of mandibular arch articulations.

0 terminal
1 subterminal


0 comineralized
1 separate mineralizations

98. [B:98] Large otic process of the palatoquadrate.

0 absent
1 present

99. [B:99] Insertion area for jaw adductor muscles on palatoquadrate.

0 ventral or medial
1 lateral

100. [B:100] Palatoquadrate fused with neurocranium.

0 absent
1 present

101. [B:101] Oblique ridge or groove along medial face of palatoquadrate.

0 absent
1 present

102. [B:102] Fenestration of palatoquadrate at basipterygoid articulation.

0 absent
1 present

103. [B:103] Perforate or fenestrate anterodorsal (metapterygoid) portion of palatoquadrate.

0 absent
1 present

104. [B:104] Pronounced dorsal process on Meckelian bone or cartilage.

0 absent
1 present

105. [B:105] Number of coronoids.

0 four or more
1 three or fewer

106. [B:106] Preglenoid process.

0 absent
1 present

0 absent
1 present


0 absent
1 present


0 absent
1 present

110. [B:110] Parasphenoid.

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


0 absent
1 present


0 absent
1 present

113. [B:113] Buccohypophysial canal in parasphenoid.

0 single
1 paired

114. [B:114] Nasal opening(s).
0 dorsal, placed between orbits
1 ventral and anterior to orbit

115. [B:115] **External opening of posterior nostril and orbit.**
0 separated by dermal bone(s)
1 confluent

116. [B:116] **Olfactory tracts.**
0 short, with olfactory capsules situated close to telencephalon cavity
1 elongate and tubular (much longer than wide)

117. [B:117] **Prominent pre-orbital rostral expansion of the neurocranium.**
0 present, formed of subethmoidal platform ('upper lip')
1 absent
2 present, formed of rhinocapsular block

118. [B:118] **Pronounced sub-ethmoidal keel.**
0 absent
1 present

119. [B:119] **Internasal vacuities.**
0 absent
1 present

120. [B:120] **Discrete division of the ethmoid and more posterior braincase at the level of the optic tract canal.**
0 absent
1 present

121. [B:121] **Position of myodome for superior oblique eye muscles.**
0 posterior and dorsal to foramen for nerve II
1. anterior and dorsal to foramen

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<tbody>
<tr>
<td><strong>122. [B:122]</strong></td>
<td><strong>Endoskeletal intracranial joint.</strong></td>
</tr>
<tr>
<td>0</td>
<td>absent</td>
</tr>
<tr>
<td>1</td>
<td>present</td>
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<tbody>
<tr>
<td><strong>123. [B:123]</strong></td>
<td><strong>Spiracular groove on basicranial surface</strong></td>
</tr>
<tr>
<td>0</td>
<td>absent</td>
</tr>
<tr>
<td>1</td>
<td>present</td>
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<tr>
<td><strong>124. [B:124]</strong></td>
<td><strong>Transverse otic process.</strong></td>
</tr>
<tr>
<td>0</td>
<td>present</td>
</tr>
<tr>
<td>1</td>
<td>absent</td>
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<tr>
<td><strong>125. [B:125]</strong></td>
<td><strong>Jugular canal.</strong></td>
</tr>
<tr>
<td>0</td>
<td>long (invested in otic region along length of skeletal labyrinth)</td>
</tr>
<tr>
<td>1</td>
<td>short (restricted to short portion of region of skeletal labyrinth, or anterior to it)</td>
</tr>
<tr>
<td>2</td>
<td>absent (jugular vein uninvested in otic region)</td>
</tr>
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<tr>
<td><strong>126. [B:126]</strong></td>
<td><strong>Spiracular groove on lateral commissure.</strong></td>
</tr>
<tr>
<td>0</td>
<td>absent</td>
</tr>
<tr>
<td>1</td>
<td>present</td>
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<tr>
<td><strong>127. [B:127]</strong></td>
<td><strong>Subpituitary fenestra.</strong></td>
</tr>
<tr>
<td>0</td>
<td>absent</td>
</tr>
<tr>
<td>1</td>
<td>present</td>
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<tr>
<td><strong>128. [B:128]</strong></td>
<td><strong>Supraorbital shelf broad with convex lateral margin.</strong></td>
</tr>
<tr>
<td>0</td>
<td>absent</td>
</tr>
<tr>
<td>1</td>
<td>present</td>
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</table>
129. [B:129] Orbit dorsal or facing dorsolaterally, surrounded laterally by endocranium.

0 present
1 absent

130. [B:130] Eyestalk attachment area.

0 absent
1 present

131. [B:131] Postorbital process.

0 absent
1 present


0 absent
1 present

133. [B:133] Series of perforations for innervation of supraorbital sensory canal in supraorbital shelf.

0 absent
1 present

134. [B:134] Extended prehypophysial portion of sphenoid.

0 absent
1 present

135. [B:135] Narrow interorbital septum, with outer walls in contact along midline forming a single sheet.

0 absent
1 present
136. 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

137. 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

138. Glossopharyngeal nerve (N. IX) exit.
0 foramen situated posterolateral to otic capsule and anterior to metotic fissure
1 through metotic fissure

139. Relationship of cranial endocavity to basisphenoid.
0 endocavity occupies full depth of sphenoid
1 enodcavity dorsally restricted

140. Subcranial ridges.
0 absent
1 present

141. Ascending basisphenoid pillar pierced by common internal carotid.
0 absent
1 present

142. Canal for lateral dorsal aorta within basicranial cartilage.
0 absent
1 present
143. [B:143] 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

144. [B:144] Canal for efferent pseudobranchial artery within basicranial cartilage.
0 absent
1 present

0 same anteroposterior level as hypophysial opening
1 anterior to hypophysial opening
2 posterior to hypophysial opening

146. [B:146] Articulation between neurocanium and palatoquadrate posterodorsal to orbit (suprapterygoid articulation).
0 absent
1 present

147. [B:147] Labyrinth cavity.
0 separated from the main neurocranial cavity by a cartilaginous or ossified capsular wall
1 skeletal capsular wall absent

0 absent
1 present

149. [B:149] Pituitary vein canal.
0 dorsal to level of basipterygoid process
1 flanked posteriorly by basipterygoid process
150. [B:150] **External (horizontal) semicircular canal.**

0 absent
1 present

151. [B:151] **Sinus superior.**

0 absent or indistinguishable from union of anterior and posterior canals with saccular chamber
1 present

152. [B:152] **External (horizontal) semicircular canal.**

0 joins the vestibular region dorsal to posterior ampulla
1 joins level with posterior ampulla

153. [B:153] **Horizontal semicircular canal in dorsal view.**

0 medial to path of jugular vein
1 dorsal to jugular vein

154. [B:154] **Lateral cranial canal.**

0 absent
1 present

155. [B:155] **Posterior dorsal fontanelle.**

0 absent
1 present

156. [B:156] **Shape of posterior dorsal fontanelle.**

0 approximately as long as broad
1 much longer than wide, slot-shaped

157. [B:157] **Synotic tectum.**
158. [B:158] **Dorsal ridge.**

0 absent
1 present

159. [B:159] **Shape of median dorsal ridge anterior to endolymphatic fossa.**

0 developed as a squared-off ridge or otherwise ungrooved
1 bears a midline groove

160. [B:160] **Endolymphatic ducts in neurocranium.**

0 posteriodorsally angled tubes
1 tubes oriented vertically through median endolymphatic fossa

161. [B:161] **Position of hyomandibula articulation on neurocranium.**

0 below or anterior to orbit, on ventrolateral angle of braincase
1 on otic capsule, posterior to orbit

162. [B:162] **Position of hyomandibula articulation relative to structure of skeletal labyrinth.**

0 anterior or lateral to skeletal labyrinth
1 at level of posterior semicircular canal

163. [B:163] **Hyoid arch articulation on braincase.**

0 single
1 double

164. [B:164] **Branchial ridges.**

0 present
1 reduced to vagal process
2 absent (articulation made with bare cranial wall)

165. [B:165] Craniospinal process.
0 absent
1 present

166. [B:166] Ventral cranial fissure.
0 absent
1 present

0 absent
1 present

0 absent
1 present

0 absent
1 present

0 absent
1 present

171. [B:171] Spino-occipital nerve foramina.
0 two or more, aligned horizontally
1 one or two, dorsoventrally offset
0 present or entirely unfused
1 absent

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

0 absent
1 present

175. [B:175] Paired occipital facets.
0 absent
1 present

176. [B:176] Size of aperture to notochordal canal.
0 much smaller than foramen magnum
1 as large, or larger, than foramen magnum

177. [B:177] Canal for median dorsal aorta within basicranium.
0 absent
1 present

0 absent
1 present

0 present
0 ventral and dorsal (scapular) components
1 ventral components only

181. [B:181] Shape of dorsal blade of dermal shoulder girdle (either cleithrum or anterolateral plate).
0 spatulate
1 pointed

182. [B:182] Dermal shoulder girdle forming a complete ring around the trunk.
0 present
1 absent

183. [B:183] Pectoral fenestra completely encircled by dermal shoulder armour.
0 present
1 absent

0 absent
1 present

185. [B:185] Posterior dorsolateral (PDL) plate or equivalent.
0 absent
1 present

186. [B:186] Pronounced internal median keel on dorsal shoulder girdle (i.e., crista of median dorsal plate).
0 absent
1 present
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</table>
| 187. [B:187] | **Crista internalis of dermal shoulder girdle.** | 0 absent  
|   |   | 1 present |
| 188. [B:188] | **Scapular infundibulum.** | 0 absent  
|   |   | 1 present |
| 189. [B:189] | **Scapular process of shoulder endoskeleton.** | 0 absent  
|   |   | 1 present |
| 190. [B:190] | **Ventral margin of separate scapular ossification.** | 0 horizontal  
|   |   | 1 deeply angled |
| 191. [B:191] | **Cross sectional shape of scapular process.** | 0 flattened or strongly ovate  
|   |   | 1 subcircular |
| 192. [B:192] | **Flange on trailing edge of scapulocoracoid.** | 0 absent  
|   |   | 1 present |
| 193. [B:193] | **Scapular process with posterodorsal angle.** | 0 absent  
|   |   | 1 present |
| 194. [B:194] | **Endoskeletal postbranchial lamina on scapular process.** |
1805 0 present
1806 1 absent
1807
1809 0 mineralised all around
1810 1 unmineralised on internal face forming a hemicylindrical cross-section
1811
1812 196. [B:196] Coracoid process.
1813 0 absent
1814 1 present
1815
1816 197. [B:197] Procoracoid mineralisation.
1817 0 absent
1818 1 present
1819
1821 0 deeper than wide (stenobasal)
1822 1 wider than deep (eurybasal)
1823
1824 199. [B:199] Pectoral fin articulation.
1825 0 monobasal
1826 1 polybasal
1827
1828 200. [B:200] Number of basals in polybasal pectoral fins.
1829 0 three or more
1830 1 two
1831
1832 201. [B:201] Branching radials in paired fins.
1833 0 absent
1834 1 present
0 five or fewer
1 seven or more

0 absent
1 present

204. [B:204] Perforate propterygium.
0 absent
1 present

205. [B:205] Filamentous extension of pectoral fin from axillary region.
0 absent
1 present

0 absent
1 present

207. [B:207] Pelvic claspers.
0 absent
1 present

208. [B:208] Dermal pelvic clasper ossifications.
0 absent
1 present

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<td>1867</td>
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<td>1868</td>
<td><strong>210. [B:210]</strong> Pectoral fin base has large, hemispherical dermal component.</td>
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<td>1869</td>
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<td>1870</td>
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<td><strong>211. [B:211]</strong> Dorsal fin spines.</td>
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<td>1875</td>
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<td>1876</td>
<td><strong>212. [B:212]</strong> Anal fin spine.</td>
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<tr>
<td>1877</td>
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<td>1878</td>
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<td>1879</td>
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<td>1880</td>
<td><strong>213. [B:213]</strong> Paired fin spines.</td>
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<tr>
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<td>1882</td>
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<td>1883</td>
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<td>1884</td>
<td><strong>214. [B:214]</strong> Median fin spine insertion.</td>
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<tr>
<td>1885</td>
<td>0 shallow, not greatly deeper than dermal bones/scales</td>
<td></td>
</tr>
<tr>
<td>1886</td>
<td>1 deep</td>
<td></td>
</tr>
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<td>1887</td>
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<td>1889</td>
<td>We follow Burrow et al.\textsuperscript{21} and Hanke &amp; Wilson\textsuperscript{22} in labelling the fin spine pairs developed between the pectoral and pelvic fin spines as 'prepelvic' instead of the 'intermediate' used by Brazeau et al.\textsuperscript{18}</td>
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<td>1891</td>
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<td>1892</td>
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<td>1895</td>
<td><strong>216. [B:216]</strong> Fin spine cross-section.</td>
<td></td>
</tr>
</tbody>
</table>
0 Round or horseshoe shaped
1 Flat-sided, with rectangular profile

217. [B:217] Prepelvic spines when present (modified).
See comments on character 215.
0 one pair
1 multiple pairs

218. [B:218] Paired prepectoral spines (modified).
Modified to enable coding for lateral pairs of prepectoral spines.
0 absent
1 present

0 absent
1 present

220. [B:220] Fin spines with nodes.
0 absent
1 present

221. [B:221] Fin spines with rows of large retrorse denticles.
0 absent
1 present

222. [B:222] Expanded spine rib on leading edge of spine.
0 absent
1 present

223. [B:223] Spine ridges
1926 0 converging at the distal apex of the spine
1927 1 converging on leading edge of spine
1928
1929 **224. [B:224]** Synarcual.
1930 0 absent
1931 1 present
1932
1933 **225. [B:225]** Series of thoracic supraneurals.
1934 0 absent
1935 1 present
1936
1937 **226. [B:226]** Number of dorsal fins, if present.
1938 0 one
1939 1 two
1940
1941 **227. [B:227]** Posterior dorsal fin shape.
1942 0 base approximately as broad as tall, not broader than all of other median fins
1943 1 base much longer than the height of the fin, substantially longer than any of the other dorsal fins
1944
1945 **228. [B:228]** Basal plate in dorsal fin.
1946 0 absent
1947 1 present
1948
1949 **229. [B:229]** Branching radial structure articulating with dorsal fin basal plate.
1950 0 absent
1951 1 present
1952
1954 0 absent
1955 1 present
1956
0 absent
1 present

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

0 absent
1 present

0 absent
1 present

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

236. [B:236] Canal-bearing bone of skull roof extends far past posterior margin of parietals.
0 no
1 yes

0 absent
1 present

1988 0 on postparietal
1989 1 on parietal
1990
1993 0 absent
1994 1 present
1995
1997 0 absent
1998 1 present
1999
2001 0 absent
2002 1 present
2003
2005 0 absent
2006 1 present
2007
2009 0 imperforate
2010 1 perforate
2011
2012 244. [B:244] Urohyal shape.
2013 0 absent
2014 1 vertical plate
2015
2017 0 present
2018 1 absent
246. [B:246] Length of dentary.
  0 constitutes a majority of jaw length
  1 half the length of jaw or less

  0 absent
  1 present

  0 absent
  1 present

  0 extends through infradentaries
  1 extends through infradentaries and dentary

250. [B:250] Extensive flange composed of prearticular and Meckelian bone
  that extends beyond ventral edge of outer dermal series.
  0 absent
  1 present

251. [B:251] Posterior coronoid.
  0 similar to anterior coronoids
  1 forms expanded coronoid process

  0 absent
  1 present

253. [B:253] Inturned medial process of premaxilla.
2050 0 absent
2051 1 present

2053 **254.** Anteriorly directed adductor fossae between neurocranium and skull roof.
2055 0 absent
2056 1 present

2058 **255.** Vomerine fangs.
2059 0 absent
2060 1 present

2062 **256.** Number of dermopalatines.
2063 0 multiple
2064 1 one

2066 **257.** Entopterygoids.
2067 0 separated
2068 1 contact along midline

2070 **258.** Rostral tubuli.
2071 0 absent
2072 1 present

2074 **259.** Position of anterior nostril.
2075 0 facial
2076 1 at oral margin

2078 **260.** Posterior nostril.
2079 0 facial
2080 1 at margin of oral cavity
261. [B:261] Three large pores (in addition to nostrils) associated with each side of ethmoid.

0 absent
1 present

262. [B:262] Ventral face of nasal capsule in taxa with mineralized ethmoid.

0 complete
1 fenestra ventrolateralis
2 entire floor unmineralized

263. [B:263] Size of profundus canal in postnasal wall.

0 small
1 large


0 absent
1 present


0 restricted to ethmosphenoid region
1 extends to otic region

266. [B:266] Endoskeletal spiracular canal.

0 open
1 spiracular bar
2 complete enclosure in canal


0 absent
268. [B:268] Relative position of jugular groove/canal and hyomandibular articulation.
0 hyomandibula dorsal
1 hmd straddles
2 hmd ventral

269. [B:269] Optic lobes.
0 narrower than cerebellum
1 same width or wider than cerebellum

270. [B:270] Hypophyseal chamber.
0 projects posterodorsally
1 projects ventrally or anteroventrally

0 dorsal to braincase endocavity roof
1 ventral to braincase endocavity roof

272. [B:272] Horizontal semicircular canal.
0 obliquely oriented
1 horizontally oriented

0 absent
1 present

274. [B:274] Pelvic girdle with substantial dermal component.
0 present
1 absent
275. [B:275] Pelvic fin spines.
0 absent
1 present

276. [B:276] Pelvic fin.
0 monobasal
1 polybasal

0 absent
1 present

278. [B:278] Condition of postparietals/centrals.
0 do not meet in midline
1 meet in midline
2 single midline bone

279. [B:279] Parietals.
0 absent
1 present

0 do not meet in midline
1 meet in midline

0 absent
1 present
282. [B:282] **Pituitary vein canal.**
- 0 discontinuous, enters the cranial cavity
- 1 discontinuous, enters hypophysial recess
- 2 continuous transverse vein

283. [B:283] **Sutures between dermal bones.**
- 0 absent
- 1 present

284. [B:284] **Interolateral/clavicular margin.**
- 0 angled anterolaterally
- 1 mediolaterally straight

285. **Scale odontodes added in a linear sequence within rows (linear odontocomplexes) (new character).**
- 0 absent
- 1 present

286. **Number of linear odontocomplexes in scale crowns (new character).**
- 0 one
- 1 more than one

287. [D:262] **Anteriormost prepelvic fin spine (admedian fin spine) associated with the shoulder girdle (modified).**
We agree with Dearden et al.\(^\text{17}\) in recognising the shoulder girdle spines positioned medially of the pectoral fin spines in a number of stem chondrichthians (e.g. climatiids\(^\text{8,9}\), diplacanthids\(^\text{16}\) and gyracanthids\(^\text{23}\)) as the first prepelvic fin spine pair. Here these are labelled admedian after Burrow et al.\(^\text{7,8,16}\), who contrary to this and other studies\(^\text{17,24}\) consider them separate from the prepelvic series.
- 0 absent
- 1 present
288. [K:482] **Median ventral prepectoral spine.**
0 absent
1 present

289. [K:447] **Median ventral trunk plates.**
0 absent
1 present

290. **Direction of tooth addition within tooth families relative to the jaw ramus (new character).**
0 lingual
1 mesial
2 distal

291. [B:17] **Odontode resorption in the extra-oral dermal skeleton (modified).**
See comments on character 17.
0 absent
1 present

292. **Pinnal plates of the dermal shoulder girdle (new character).**
Pinnal plates are distinguished from the dermal plates of jawed stem gnathostomes ('placoderms')\(^{25,26}\) and osteichthyans\(^{27-29}\) due to developmental differences. The latter form as a single unit through areal growth unlike the pinnals where independent dermal scales are integrated into discrete elements fused together by a basal plate\(^{8,16,30}\) (see also this study). On this basis, and in accordance with previous research\(^{31}\), we code for presence/absence of pinnal plates independently of the pectoral ventral plate pairs of 'placoderms' (ventrolateral plates) and osteichthyans (clavicles).
0 absent
1 present

**Table S1.** Relative abundance of *Fanjingshania* dermoskeletal elements estimated from a subsample (c. 500 specimens) of the material recovered from the Rongxi
Formation at Leijiatun (Extended Data Fig. 1). Relative abundance: X, very low; XX, low; XXX, medium; XXXX, high.

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<td>trunk scales</td>
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</tr>
<tr>
<td>head tesserae</td>
<td>XXX</td>
</tr>
<tr>
<td>branchiostegal plates</td>
<td>X</td>
</tr>
<tr>
<td>pinnal plate fragments</td>
<td>XX</td>
</tr>
<tr>
<td>loral plate fragments</td>
<td>X</td>
</tr>
<tr>
<td>prepectoral spines</td>
<td>X</td>
</tr>
<tr>
<td>pectoral fin spines</td>
<td>XX</td>
</tr>
<tr>
<td>prepelvic fin spines</td>
<td>XXX</td>
</tr>
<tr>
<td>pelvic fin spines</td>
<td>X</td>
</tr>
<tr>
<td>anterior dorsal fin spines</td>
<td>XX</td>
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<tr>
<td>posterior dorsal fin spines</td>
<td>XX</td>
</tr>
<tr>
<td>anal fin spines</td>
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Table S2. Tip (taxon) ages for the time-scaled 50 percent majority-rule tree shown in part in Fig. 3 (full tree available in Supplementary data 7).

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<th>Taxon</th>
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<th>Reference</th>
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<td>Acanthodes</td>
<td>298</td>
<td>King et al.20</td>
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<tr>
<td>Achoania</td>
<td>412</td>
<td>King et al.20</td>
</tr>
<tr>
<td>Akmonistion</td>
<td>327</td>
<td>King et al.20</td>
</tr>
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<td>Austroptyctodus</td>
<td>327</td>
<td>King et al.20</td>
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<tr>
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<td>383</td>
<td>King et al.20</td>
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<td>King et al.20</td>
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<tr>
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<td>415</td>
<td>King et al.20</td>
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<td>Buchanosteus</td>
<td>408</td>
<td>King et al.20</td>
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<td>Campbellodus</td>
<td>383</td>
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<tr>
<td>Cassidiceps</td>
<td>415</td>
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<td>Cheiracanthus</td>
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<td>383</td>
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**Descriptions of supplementary files**

**Supplementary Data 1.** A set of tomographic slices from a synchrotron X-ray radiation analysis of the holotype specimen of *Fanjingshania* (V27433.1). Tomographic slices generated in Mimics 19.0.

**Supplementary Data 2.** A set of tomographic slices from a synchrotron X-ray radiation analysis of *Fanjingshania* specimen V27434.1. Tomographic slices generated in Mimics 19.0.

**Supplementary Data 3.** A set of tomographic slices from a synchrotron X-ray radiation analysis of *Fanjingshania* specimen V27435.1. Tomographic slices generated in Mimics 19.0.

**Supplementary Data 4.** Volume rendering of *Fanjingshania* V27433.1 with colour coded features (see Fig. 2 for interpretation). 3D reconstruction and segmentation of synchrotron tomography data performed in Mimics 19.0.

**Supplementary Data 5.** Volume rendering of a *Fanjingshania* specimen V27434.1 with colour coded features (see Fig. 2 for interpretation). 3D reconstruction and segmentation of synchrotron tomography data performed in Mimics 19.0.

**Supplementary Data 6.** Volume rendering of the holotype of a *Fanjingshania* specimen V27435.1 with colour coded features (see Fig. 2 for interpretation). 3D reconstruction and segmentation of synchrotron tomography data performed in Mimics 19.0.

**Supplementary Data 7.** Parsimony analysis files. Character-taxon matrix in TNT (.tnt) and nexus (.nex) file formats. Most parsimonious trees (.tre) produced by the parsimony analysis. 50 percent majority-rule consensus tree (.tre) and strict consensus tree (.tre) for the set of most parsimonious trees. TNT log in rich text format (.rtf) of the parsimony and the bootstrap resampling analyses. PAUP log file (.log) of reconstructed character states at internal nodes of the 50 percent majority-rule consensus tree. R script in rich text format (.rtf) used in the calculation of the time-scaled 50 percent majority-rule consensus tree.
Supplementary Data 8. Bayesian analysis files. Character-taxon matrix (.nex), consensus tree (.tre) and other output files (.ckp, .mcmc, .parts, .t, .tprobs, .tstat and .vstat) generated in MrBayes version 3.2.7a.

Supplementary references


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