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Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome

Sam Giles¹, Matt Friedman¹ & Martin D. Brazeau^{2,3}

The phylogeny of Silurian and Devonian (443–358 million years (Myr) ago) fishes remains the foremost problem in the study of the origin of modern gnathostomes (jawed vertebrates). A central question concerns the morphology of the last common ancestor of living jawed vertebrates, with competing hypotheses advancing either a chondrichthyan^{1–3} or osteichthyan-like^{4,5} model. Here we present *Janusiscus schultzei* gen. et sp. nov., an Early Devonian (approximately 415 Myr ago) gnathostome from Siberia previously interpreted as a ray-finned fish⁶, which provides important new information about cranial anatomy near the last common ancestor of chondrichthyans and osteichthyans. The skull roof of *Janusiscus* resembles that of early osteichthyans, with large plates bearing vermiform ridges and partially enclosed sensory canals. High-resolution computed tomography (CT) reveals a braincase bearing characters typically associated with either chondrichthyans (large hypophyseal opening accommodating the internal carotid arteries) or osteichthyans (facial nerve exiting through jugular canal, endolymphatic ducts exiting posterior to the skull roof) but lacking a ventral cranial fissure, the presence of which is considered a derived feature of crown gnathostomes^{7,8}. A conjunction of well-developed cranial processes in *Janusiscus* helps unify the comparative anatomy of early jawed vertebrate neurocrania, clarifying primary homologies in ‘placoderms’, osteichthyans and chondrichthyans. Phylogenetic analysis further supports the chondrichthyan affinities of ‘acanthodians’, and places *Janusiscus* and the enigmatic *Ramirosuarezia*⁹ in a polytomy with crown gnathostomes. The close correspondence between the skull roof of *Janusiscus* and that of osteichthyans suggests that an extensive dermal skeleton was present in the last common ancestor of jawed vertebrates⁴, but ambiguities arise from uncertainties in the anatomy of *Ramirosuarezia*. The unexpected contrast between endoskeletal structure in *Janusiscus* and its superficially osteichthyan-like dermal skeleton highlights the potential importance of other incompletely known Siluro-Devonian ‘bony fishes’ for reconstructing patterns of trait evolution near the origin of modern gnathostomes.

Gnathostomata Gegenbaur, 1874

Janusiscus schultzei gen. et sp. nov.

Etymology. Generic name refers to double-sided nature of the specimen, with an osteichthyan-like dorsal skull roof, but a braincase that displays an array of plesiomorphic gnathostome characters (Latin *Ianus*, the god of doorways and transitions, often depicted as having two faces; [*p*] *iscis*, fish). Specific name in honour of Hans-Peter Schultze (University of Kansas), who first described these specimens⁶.

Holotype. GIT (Institute of Geology, Tallinn, Estonia) 496-6 (Pi.1384), skull roof and braincase, both missing anterior region (Fig. 1 and Extended Data Figs 1a, 3).

Referred material. We refer a second, more complete skull roof (GIT 496-7 (Pi. 1383); Extended Data Fig. 1c) from the type locality to *Janusiscus*. Rhombic scales lacking clear dorsal pegs are also known from this deposit (GIT 496-8–496-16; Extended Data Fig. 2a–c), but cannot be definitively associated with cranial material. All of these remains were previously

attributed⁶ to *Dialipina markae*, the type of which is an isolated scale bearing a modest peg from the Lower Devonian of Kotelnny Island, New Siberian Islands¹⁰ (approximately 1,500 km from the Sida River site). **Locality and horizon.** Lower member, Kureika Formation, Sida River, Kotui Basin, Siberia. The presence of the zone fossil *Rhinopteraspis crouchi* in a lateral equivalent of the Kureika Formation¹¹ restricts the age of this deposit to middle Lochkovian (approximately 415 Myr ago)¹². This is consistent with evidence drawn from other biostratigraphic markers (Supplementary Notes).

Diagnosis. A jawed vertebrate characterized by a rectilinear pattern of skull roof bones bearing vermiform ridges but lacking endochondral bone, a ventral cranial fissure and vestibular fontanelles. Skull roof differs from those attributed to the type species of *Dialipina* (*Dialipina salgueiroensis*)¹³ in having postparietals longer than parietals, and parietals lacking anterolateral extensions. Principal autapomorphy of *Janusiscus* is a boundary between parietals and postparietals that slopes posteriorly towards the midline, with the postparietals forming distinct anterolateral processes (as per the original description⁶). Braincase with broad otic region, and narrow sphenoid pierced by large hypophyseal opening and bearing pronounced ventrolateral ridges.

Description. The skull roof comprises paired parietals and postparietals, and a median pineal plate (Fig. 1a and Extended Data Fig. 1). The anterior part of the skull roof, including the pineal, is not preserved in the holotype. All bones are ornamented with vermiform ridges, although the histological structure of these ridges is not preserved (Extended Data Fig. 2h–j). The supraorbital sensory canals extend across the parietals and postparietals in open grooves but are enclosed in bony tubes posteriorly (Extended Data Fig. 3). The postparietal bears a middle pit-line behind the termination of the supraorbital canal. The pattern of dermal ornament in the posterior part of the skull suggests the presence of posteriorly placed pitlines (as in *Ligulalepis*¹⁴).

High-resolution CT scanning of GIT 496-6 reveals a nearly complete perichondrally ossified neurocranium, lacking evidence of endochondral mineralization (Fig. 1 and Extended Data Figs 4, 5). The incompletely preserved ethmoid is co-mineralized with the remainder of the braincase. The basisphenoid is elongate and mediolaterally narrow, resembling conditions in *Acanthodes*³ and osteichthyans^{15,16}. The basisphenoid bears a large, diamond-shaped hypophyseal opening but no evidence of a parasphenoid. Subcranial ridges like those of *Doliodus*¹⁷ define the lateral margins of the basisphenoid and extend posteriorly to the otic region (Extended Data Fig. 5). The modest basiptyergoid processes emerge as slight flanges posterior to the level of the hypophysis. Like ‘placoderms’^{18,19} and many chondrichthyans^{20,21}, *Janusiscus* lacks a ventral cranial fissure. The gently concave parachordal region tapers towards the occiput, where its edges form ventral cristae that border grooves for the lateral dorsal aortae. The occipital margin bears a notch that is aligned with a midline thickening of the parachordal surface.

Two prominent transverse processes are present (Fig. 1a, b). The postorbital process defines the rear margin of the orbit. The passage of the jugular vein through the postorbital process is unclear. It bears a ventral notch and a posterodorsal opening, either of which may have

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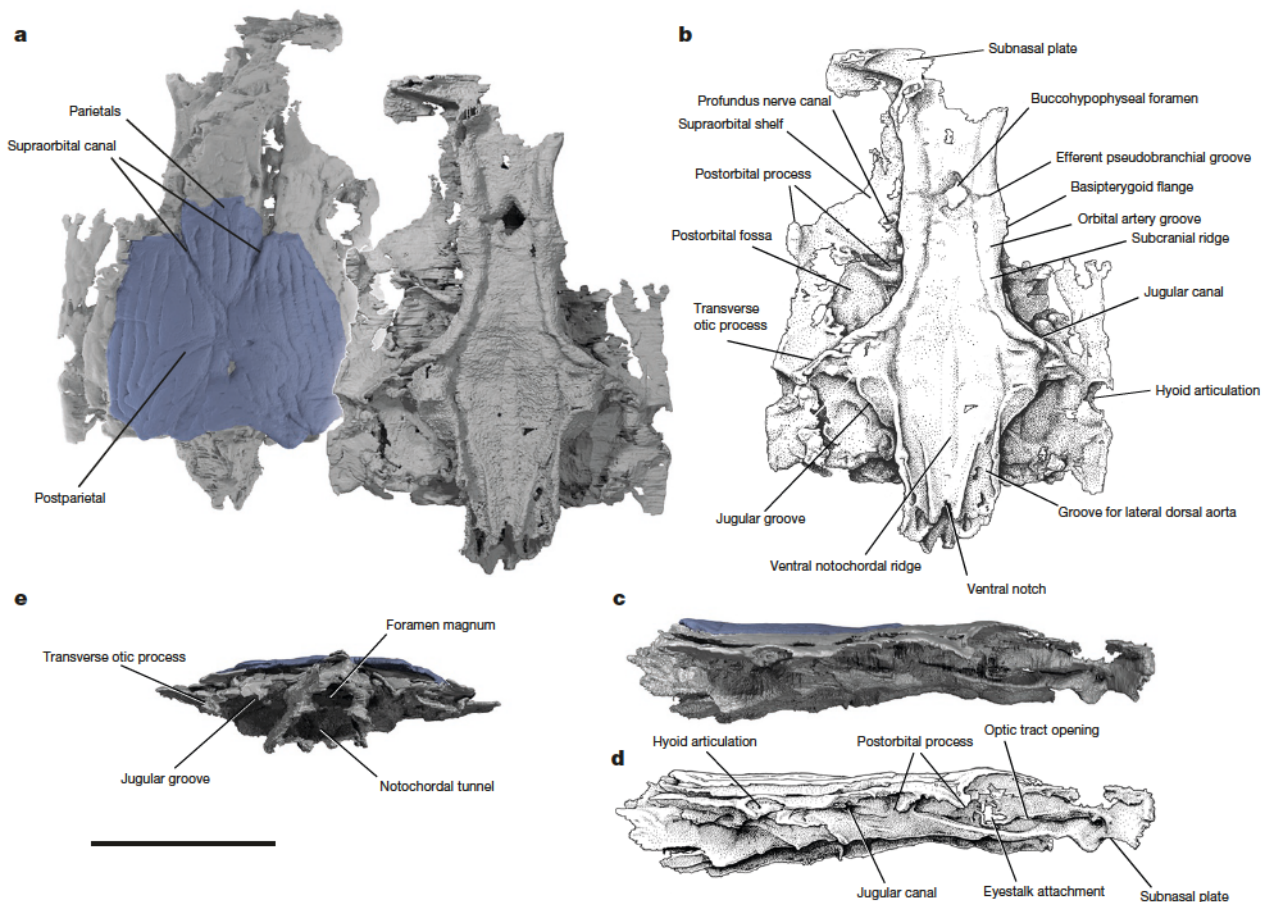


Figure 1 | The skull of *Janusiscus schultzei* gen. et sp. nov. based on high-resolution CT of GIT 496-6 (Pi.1384). **a**, Dorsal (left) and ventral views. **b**, Interpretive drawing of ventral view. **c**, Right lateral view. **d**, Interpretive drawing of right lateral view. **e**, Posterior view. Scale bar, 5 mm.

accommodated the jugular vein. The transverse otic process is separated from the postorbital process by a wide postorbital fossa. This process terminates distally in a single hyomandibular facet, and is pierced by the jugular canal. An enclosed canal for the hyomandibular branch of the facial nerve intersects that of the jugular (Extended Data Fig. 3).

The suborbital and supraorbital shelves are well developed. The orbital wall is interrupted by a large eyestalk attachment with a raised posteroventral rim (Fig. 1c, d and Extended Data Fig. 6c–e). The optic nerve exited through a foramen anterior to the eyestalk area. Foramina for the oculomotor, profundus and abducens nerves, along with associated myodomes, are present along an arc in the rear of the orbit (Extended Data Fig. 6).

The otic capsules are broad, protruding well beyond the lateral margins of the basicranium (Extended Data Fig. 3). Paired endolymphatic ducts emerge from the roof of the braincase immediately posterior to the skull roof (Extended Data Figs 2j and 3). Vestibular fontanelles are absent, but the condition of the metotic fissure is unclear. The narrow occipital region extends well behind the otic capsules. A mineralized shelf separates the cavum cranii from the notochordal canal (Fig. 1e).

Janusiscus presents an unexpected suite of osteichthyan, chondrichthyan and generalized gnathostome traits. A rectilinear pattern of skull roof bones bearing vermiform ornament, partially buried sensory canals, endolymphatic ducts opening posterior to the dermal skull roof, and the exit of the hyomandibular branch of the facial nerve into the jugular canal are features typically associated with osteichthyans^{22,23}. However, the combination of a flat-based braincase, weakly developed basipterygoid processes, the absence of vestibular fontanelles, and the absence of a ventral cranial fissure are inconsistent with *Janusiscus* as a crown-group osteichthyan and therefore also with the original actinopterygian

diagnosis⁶ and its current use as a fossil calibration in ray-finned fish molecular clocks²⁴.

Janusiscus possesses some chondrichthyan-like features, including the absence of paired openings for the internal carotids, a condition also shared with *Acanthodes*. Instead, the internal carotids entered the braincase through the large hypophyseal opening. The subcranial ridges flanking the ventrolateral angle of the braincase in *Janusiscus* strongly resemble those in the early chondrichthyan *Doliodus*¹⁷.

At least four pairs of transverse cranial processes are present on the braincases of some early gnathostomes (Supplementary Notes, Fig. 2 and Extended Data Fig. 7). The prominent transverse walls in *Janusiscus* allow us to address the primary homology of the anterior two processes. Comparison with crown-group osteichthyans and placoderms reveals that the so-called ‘supraorbital process’ of arthrodires corresponds to the postorbital process of crown-group gnathostomes (including the postorbital pila of sarcopterygians²⁵) and the postorbital pila of *Entelognathus*⁴. The ‘anterior postorbital process’ of placoderms can be homologized with the transverse otic process of osteichthyans. The transverse otic process appears to be substantially reduced or lost in *Acanthodes*³ and the earliest chondrichthyans^{7,8,17}, although it may correspond to the prominent lateral otic process of later chondrichthyans such as *Orthacanthus* and *Tamiobatis* (Extended Data Fig. 7). This further corroborates recent anatomical reinterpretations of *Acanthodes*³ and its placement in the chondrichthyan total group^{4,5}.

Phylogenetic analysis recovers *Janusiscus* in a polytomy with *Ramiroisuareszia* and the gnathostome crown. This corroborates our removal of the Siberian material from the genus *Dialipina*, which we recover as a stem osteichthyan^{2–5}. Our result provides the first analytical placement for the enigmatic *Ramiroisuareszia*, which has previously been

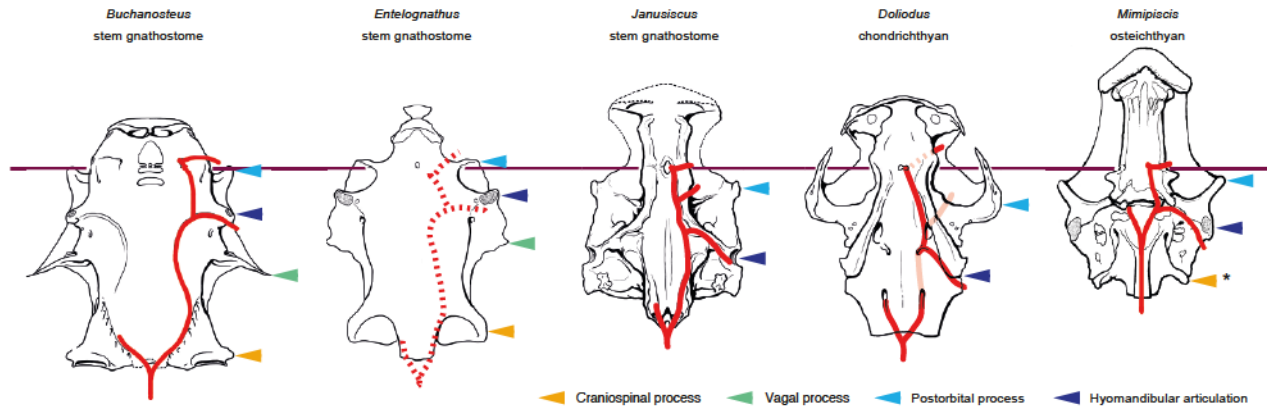


Figure 2 | Comparative braincase morphology of selected Palaeozoic gnathostomes. Braincases are aligned on the hypophyseal opening, the position of which is indicated by the horizontal purple line. The path of the major cranial blood vessels is shown in red, with inferred paths represented by

compared with 'placoderm'-grade stem gnathostomes^{9,26} and holocephalan chondrichthyans⁹.

Although our analysis favours the stem gnathostome hypothesis for *Janusiscus*, we consider stem chondrichthyan and stem osteichthyan placements to be reasonable alternatives: both require only one additional step. Placement of *Janusiscus* on the chondrichthyan stem may seem provocative, but the hypothesis of micromery as a derived chondrichthyan trait predicts macromeric stem chondrichthyans. While there is ambiguity in the position of *Janusiscus* relative to the three branches incident to the gnathostome crown node, we reject an actinopterygian interpretation⁶, which requires seven additional steps.

The new anatomical details of *Janusiscus* and our phylogenetic result corroborate the recently revived hypothesis that 'acanthodians' are, in fact, total-group chondrichthyans. The osteichthyan-like skull roof of *Janusiscus* strongly implies that the continuous dermal armour common to 'placoderms' and bony fishes is a gnathostome symplesiomorphy^{4,5}. However, uncertainty about conditions of the exoskeleton in *Ramiro-suarezia* precludes more definitive statements about the nature of the

dotted lines. Character distributions reject the homology of craniospinal processes in 'placoderms' and actinopterygians. Illustrations are redrawn with permission from refs 4, 16, 17 (Wiley), 29 (Wiley).

dermal skeleton in the earliest crown gnathostomes. We find that chondrichthyans (including all 'acanthodians') and osteichthyans are united to the exclusion of *Janusiscus* by the presence of a ventral cranial fissure separating the otic and sphenoid regions of the braincase (Fig. 3). The revised comparative framework for gnathostome braincases provided by *Janusiscus* highlights substantial neurocranial modifications uniting total-group chondrichthyans (for example, loss of the jugular vein canal in the otic region, hyomandibular articulation at the level of the posterior semicircular canal; Fig. 3)²³, while casting doubt on the validity of some supposed osteichthyan synapomorphies (for example, exit of the hyomandibular branch of the facial nerve through the jugular canal; Extended Data Fig. 3).

This work reinforces an emerging consensus for osteichthyan-like anatomical conditions in stem gnathostomes and also in the last common ancestor of crown-group gnathostomes^{4,5}. The recognition that many features of the bony fish dermal skeleton might be general traits of modern jawed vertebrates highlights the need to revisit the roughly half-dozen supposed stem osteichthyans known only from isolated

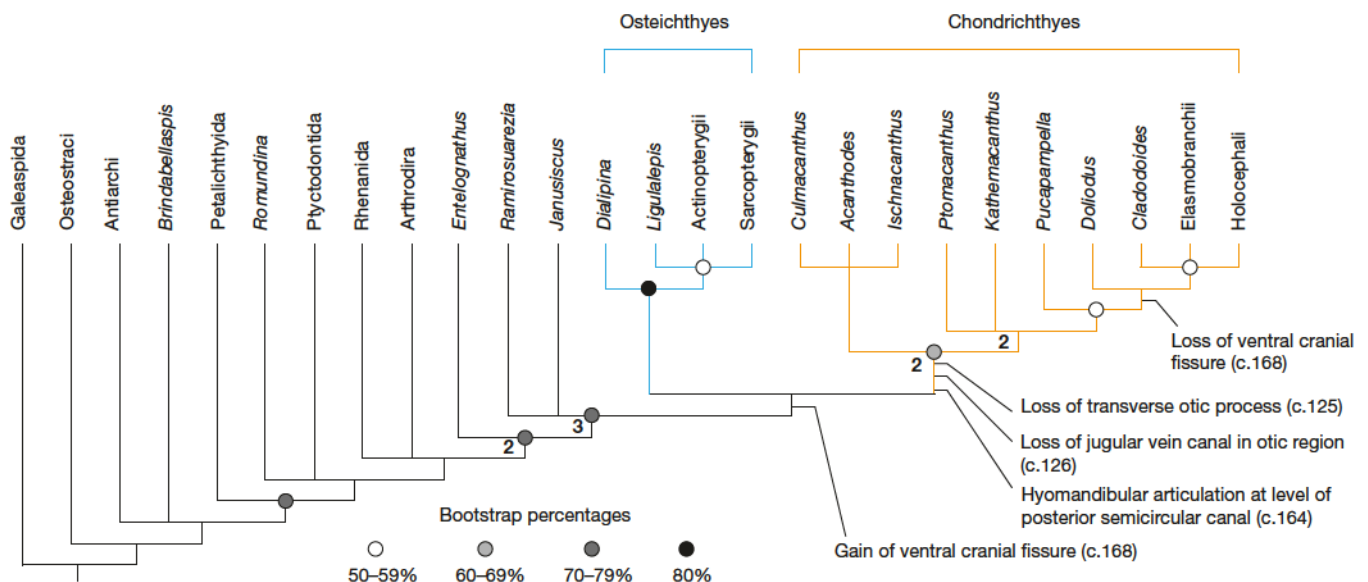


Figure 3 | Summary result of phylogenetic analyses. Some clades are collapsed or omitted for simplicity. Shaded disks represent ranges of bootstrap support, numbers at nodes are decay indices. Numbers refer to characters in

character list (Supplementary Notes). Full cladograms are provided in Extended Data Figs 8, 9 and Supplementary Fig. 1.

dermal fragments^{22,27,28}. Notably, our results suggest the plausibility of alternative placements for some of these taxa as either stem gnathostomes or even stem chondrichthyans.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions The project was conceived by M.D.B. and M.F. CT scanning was conducted by M.F. and M.D.B. S.G. generated the CT renderings. Figs 1–3 were produced by M.D.B. and S.G. with input from M.F. All authors participated in the generation of phylogenetic data. M.D.B. conducted the phylogenetic analyses. All authors participated in the interpretation of the specimen data and writing the manuscript, and generating Extended Data Figs 1–9, Supplementary Fig. 1 and Supplementary Notes.

Author Information The Life Science Identifiers (LSIDs) [urn:lsid:zoobank.org:pub:CFD16449-8A34-4401-9E01-289EA91C2C77](http://zoobank.org/pub:CFD16449-8A34-4401-9E01-289EA91C2C77) (article), [urn:lsid:zoobank.org:act:652A7405-164B-4D58-B5AF-F21EDF552303](http://zoobank.org:act:652A7405-164B-4D58-B5AF-F21EDF552303) (genus), and [urn:lsid:zoobank.org:act:3BD31DC4-11E1-4510-A185-B295CC626C07](http://zoobank.org:act:3BD31DC4-11E1-4510-A185-B295CC626C07) (species) have been deposited in ZooBank. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to M.D.B. (m.brazeau@imperial.ac.uk).

METHODS

X-ray computed microtomography. GIT 496-6 was scanned using a SkyScan1172, combining two vertically overlapping scan series of 7,200 projections with an energy of 100 kV and 100 μ A and 4.75 s exposure. Scan data were analysed using Mimics (<http://biomedical.materialise.com/mimics>; Materialise). After segmenting, surface meshes were exported into and imaged in Blender (<http://blender.org>; Stitching Blender Foundation).

Phylogenetic analysis. Phylogenetic analysis was performed in PAUP* v.4.0b10 (ref. 30) using a data set with 236 characters (three of which were ordered: 64, 126 and 166) and 78 taxa. The data set is based on ref. 3. In addition to a number of coding changes, one highly incomplete taxon (*Rhadinacanthus*) and four characters were deleted from the matrix of ref. 3; full justification for excluded characters is given in the character list. Additional characters were taken from a variety of sources, and are referenced in the character list. In addition to *Janusiscus* and taxa carried forward from the data set of ref. 3, we added 18 taxa spanning most taxonomic assemblages of Palaeozoic gnathostomes. In the case of *Janusiscus*, we coded as unknown any characters relating to scale morphology and histology; the Siberian scales originally referred to *D. markae* were not directly associated with the braincase, and their affinity is thus uncertain (for further details, see Supplementary Notes). We follow a similar convention with the braincase attributed to *Ligulalepis*, and hence scale and histology characters are coded as uncertain. We assessed taxonomic equivalence³¹ using the software package TAXEQ3 (ref. 32). No taxa showed non-unique combinations of character states that would permit safe taxonomic reduction, so analyses were executed with a complete taxon set. Although several taxa are highly incomplete, we followed previous recommendations^{33,34} by maximizing the absolute number of characters instead of deleting incomplete or fragmentary taxa.

We conducted a heuristic search using 1,000 random addition sequence replicates, holding 5 trees at each step, and the tree bisection and reconnection (TBR) strategy. Maxtrees was set to automatically increase by 100. To prevent outgroup taxa from moving to the ingroup or collapsing of the ingroup node, we employed a rooted constraint tree, keeping only trees consistent with the following general topology: (Galeaspida (Osteostraci (Ingroup))).

Bootstrap values were calculated using 15,000 replicates of a heuristic search using random addition sequence, 10 replicates, holding 5 trees at each step, using the TBR strategy. To speed up the search, we set a limit of 20 million rearrangements per addition sequence replicate (options: rearrlimit = 20000000 limitperrep = yes in the hsearch command in PAUP*).

Node decay values (that is, Bremer support) were calculated manually using 20 random addition sequence replicates of a heuristic search, rearrlimit = 20000000, limitperrep = yes, and by incrementing the KEEP score by 1 over the length of the shortest tree found. Nodes retained in the strict consensus tree had their decay index incremented by one.

We conducted a set of further searches using the protocols outlined earlier with the following modifications. First, we conducted an equally weighted analysis minus *Janusiscus* to assess whether inferred patterns of relationships among early gnathostomes were robust to exclusion of the genus. To test whether the tree topology was sensitive to the removal of random taxa, we conducted an additional five searches each following the removal of a randomly selected terminal. Random selection was conducted using Microsoft Excel's RANDBETWEEN function with parameters set to 3 and 78 (we excepted the outgroup from random pruning) and used the first five results obtained to draw taxa from the list following their order in the Nexus

file. To speed up these searches, we used rearrlimit = 10000000 and limitperrep = yes. Finally, we reweighted all characters by their retention indices in the shortest trees recovered by our initial analysis that applied equal character weights.

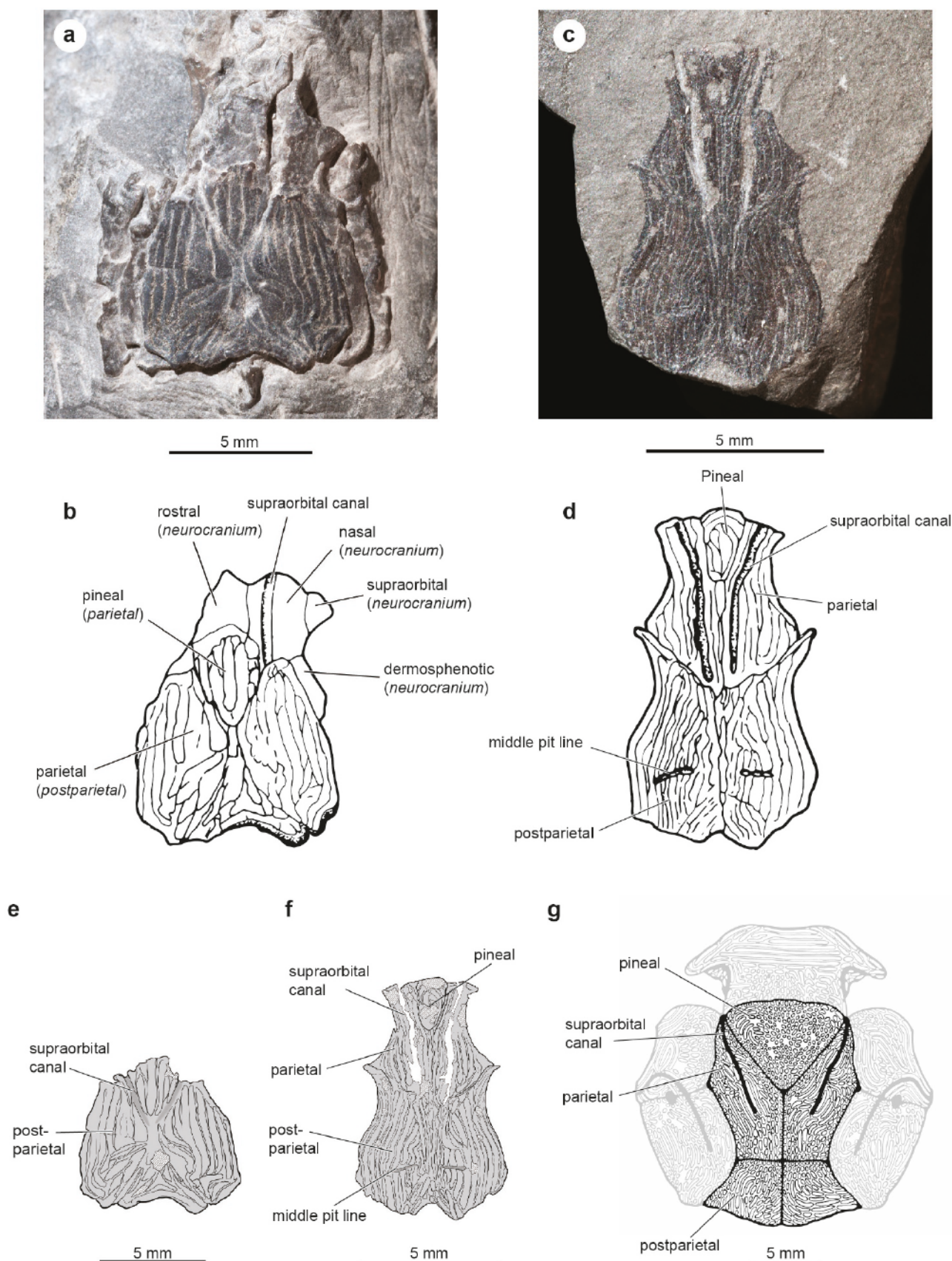
Phylogenetic results. The phylogenetic search resulted in 522,936 trees of 639 steps. A summary strict consensus tree with some clades omitted or collapsed is shown in Fig. 3. The complete result is shown in Extended Data Fig. 8a. The Adams consensus tree is shown in Extended Data Fig. 8b. All unambiguous character state transformations are shown in Supplementary Fig. 1. A summary strict consensus tree of an analysis of the data set with characters reweighted by retention index is shown in Extended Data Fig. 9a. It preserves all major branching patterns found in the analysis of equally weighted characters, but shows greater resolution within some clades.

Inferred interrelationships are not changed when *Janusiscus* is removed from the analysis (Extended Data Fig. 9b), as its influence on how cranial processes are recognized and coded pervades large parts of the data set. The removal of an additional five taxa at random (*Cladodelache*, *Tristychius*, *Acanthodes*, *Kentuckia*, *Lupopsyrus*) each had no considerable impact on the overall tree topology, excepting differences in the degree of resolution.

The overall large number of trees results in polychotomous branchings primarily concentrated in the chondrichthyan stem compounded with a smaller number of polychotomous branchings in the gnathostome and osteichthyan stems. The Adams consensus shows two principal branching patterns that are consistent within the results. One is a clade of stem chondrichthyans comprising acanthodiforms, ischnacanthids, some diplacanthids, as well as *Latviacanthus* and *Euthacanthus*. The other branching consisted of most *Climatius*-like taxa and conventionally defined chondrichthyans (including the crown group).

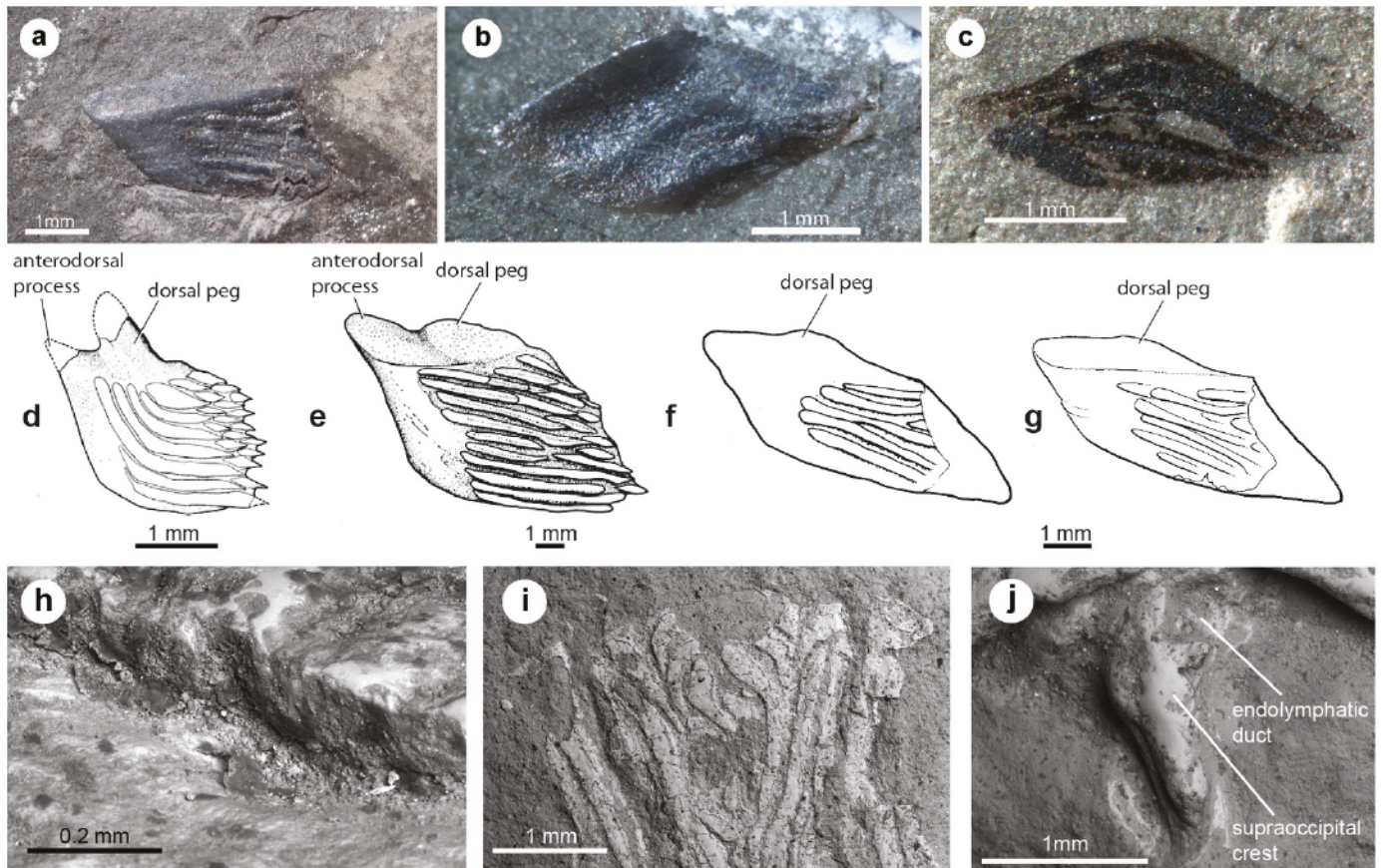
Support for key nodes is summarized in Fig. 3, with full details given Extended Data Fig. 8a. Unsurprisingly, most are quite low. The highest values are found within well-studied groups (for example, sarcopterygians and actinopterygians) or associated with clades with numerous specializations (for example, holocephalans, bothriolepidid antiarchs). A decay index of 2 and a bootstrap support of 68% are recovered for the clade comprising all chondrichthyans and acanthodians. A decay index greater than 1 is consistent with the very long branch subtending this clade (Supplementary Fig. 1). The low bootstrap value might be explained by the fact that more than half of the transformations along this branch are homoplasious and have a consistency index of 0.5 or less. In spite of this, the branch is supported by five invariant, unambiguous synapomorphies (see Supplementary Fig. 1).

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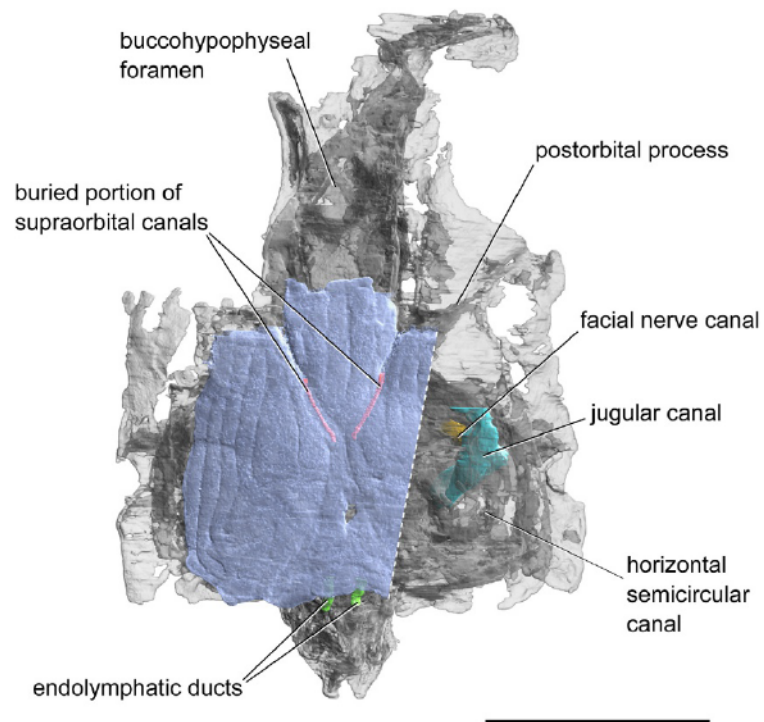
Extended Data Figure 1 | Dermal skull roofing bones of *Janusiscus* and *Dialipina salgueiroensis*. **a**, Photograph of the holotype (GIT 496-6 (Pi.1384)). **b**, Original interpretation modified with permission from ref. 6. Reinterpretation of bones italicized in brackets (where applicable). **c**, Photograph of the referred skull roof (GIT 496-7 (Pi.1383)). **d**, Original

interpretation modified with permission from ref. 6. **e**, New interpretive drawing of the holotype (GIT 496-6 (Pi.1384)). **f**, New interpretive drawing of the referred skull roof (GIT 496-7 (Pi.1383)). **g**, *Dialipina salgueiroensis*, modified with permission from ref. 13.

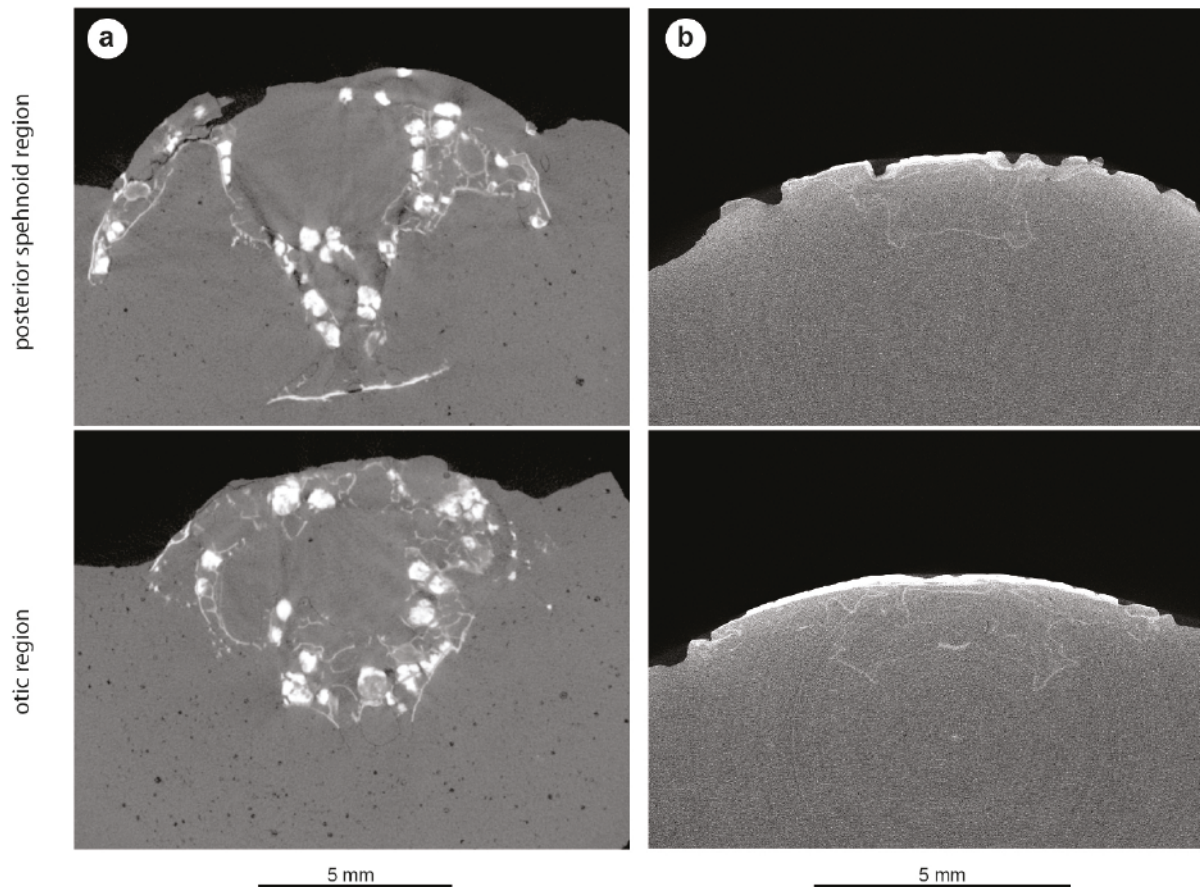


Extended Data Figure 2 | Scales attributed to *Dialipina* and scanning electron micrograph images of *Janusiscus schultzei* gen. et sp. nov. Scales from the localities of the Kureika Formation along the Sida River, Kotui Basin, Siberia, previously referred to *D. markae*, in: a, external view (GIT 496-8 (Pi.1384a)), previously figured by Schultze⁶ (plate 1, figure 3); b, internal view (GIT 496-10 (Pi.1385b)); c, external view (GIT 496-16 (Pi.1387)), ventral margin at upper right. d, e, Gross-scale morphology of *D. salgueiroensis* and referred species of *Dialipina*. d, Holotype of *D. salgueiroensis*, from the Emsian of Canada. Reproduced from ref. 10 (Fig. 3h) (with kind permission from Springer Science and Business Media). e, Holotype of *D. markae*, from the Lochkovian of the New Siberian Islands. Reproduced from ref. 10 (Fig. 3a) (with kind permission from Springer Science and Business Media). f, Scale from the Kureika Formation, Siberia, referred to *D. markae* and figured previously

(reproduced with permission from figure 4 in ref. 6). This scale is the same specimen as in a⁶. g, New interpretive drawing of scale in a. h, Broken edge of the skull roof in the holotype (GIT 496-6 (Pi.1384)). The histological structure is not preserved. i, The anterior part of the referred skull roof (GIT 496-7). The dermal bone is poorly preserved, with the bone in the centre of each ridge missing. The histological structure is not preserved. j, The holotype (GIT 496-6 (Pi.1384)) in dorsal view, showing the endoskeletal supraoccipital crest and openings of the endolymphatic ducts. Images in a, b, and c are modified slightly with permission from those by the Institute of Geology at Talinn University of Technology and licensed by CC 3.0 (http://geokogud.info/git/specimen_image/496/496-8.jpg; http://geokogud.info/git/specimen_image/496/496-10.jpg; http://geokogud.info/git/specimen_image/496/496-16.jpg).

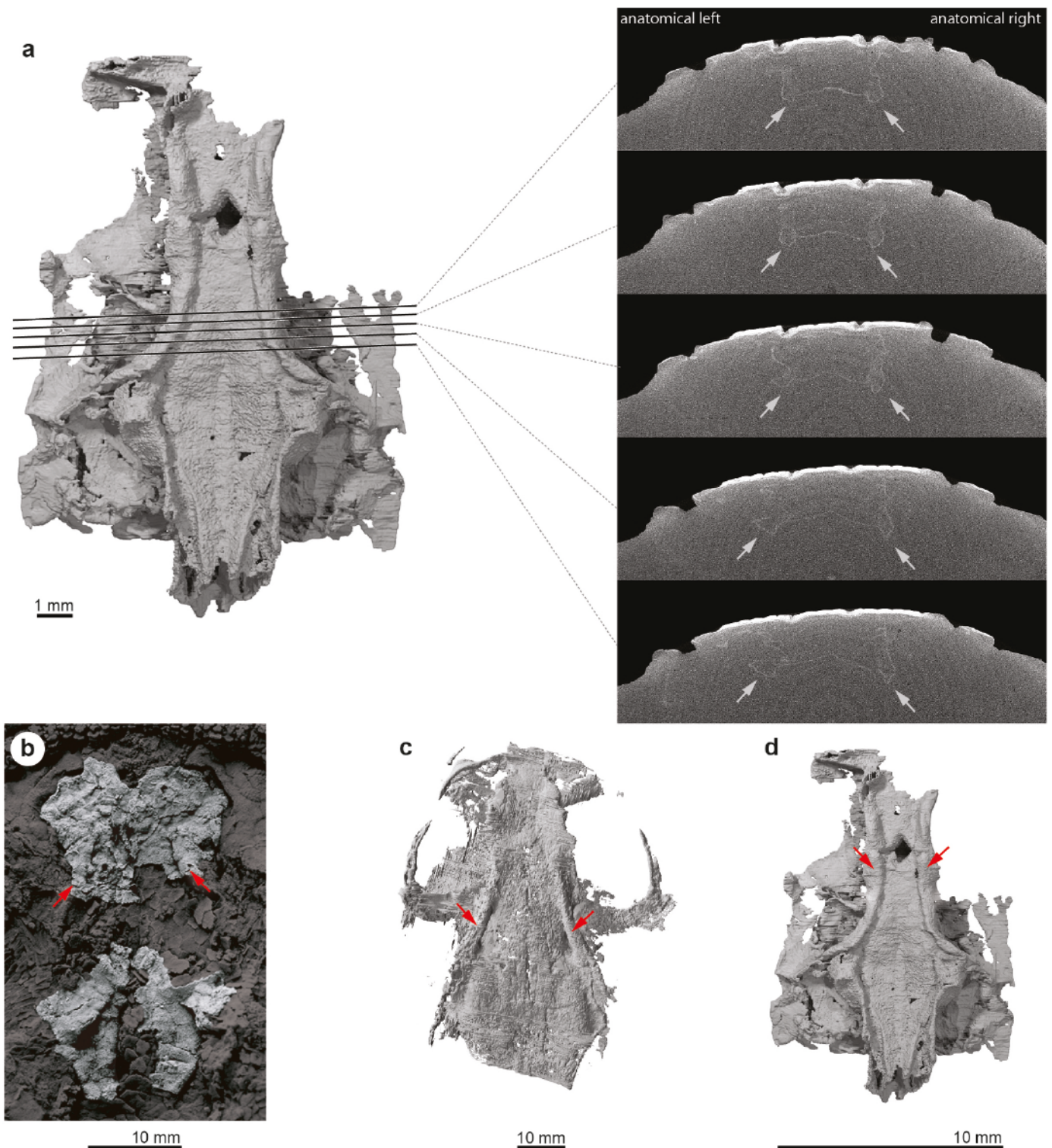


Extended Data Figure 3 | Semi-transparent rendering of the skull of *Janusiscus schultzei* gen. et sp. nov. showing osteichthyan-like traits not visible externally. Scale bar, 5 mm.



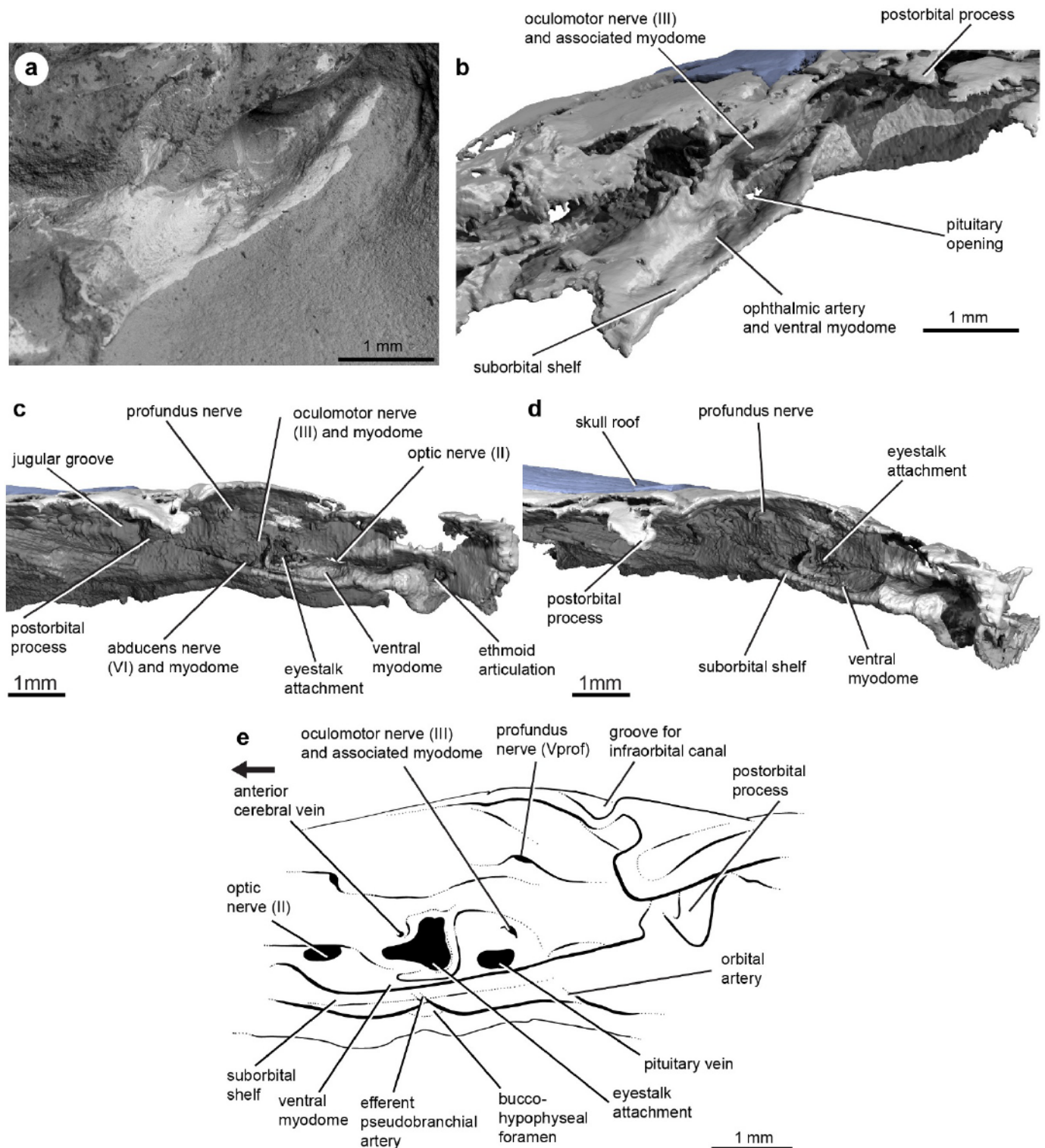
Extended Data Figure 4 | *Janusiscus* lacks endochondral ossification. a, The actinopterygian *Kentuckia deani* MCZ 5226; tomographs showing extensive and well-developed endochondral ossification in both the sphenoid (top) and otic (bottom) regions. Bright white objects are voids within spongy endochondral bone that have been diagenetically infilled with dense (probably

iron) minerals. b, *Janusiscus schultzei* gen. et sp. nov. GIT 496-6 (Pi.1384); tomographs showing lack of obvious endochondral ossification in either the sphenoid (top) or otic (bottom) regions. There is also no visual indication of endochondral bone in a break across the ethmoid region of this same specimen.



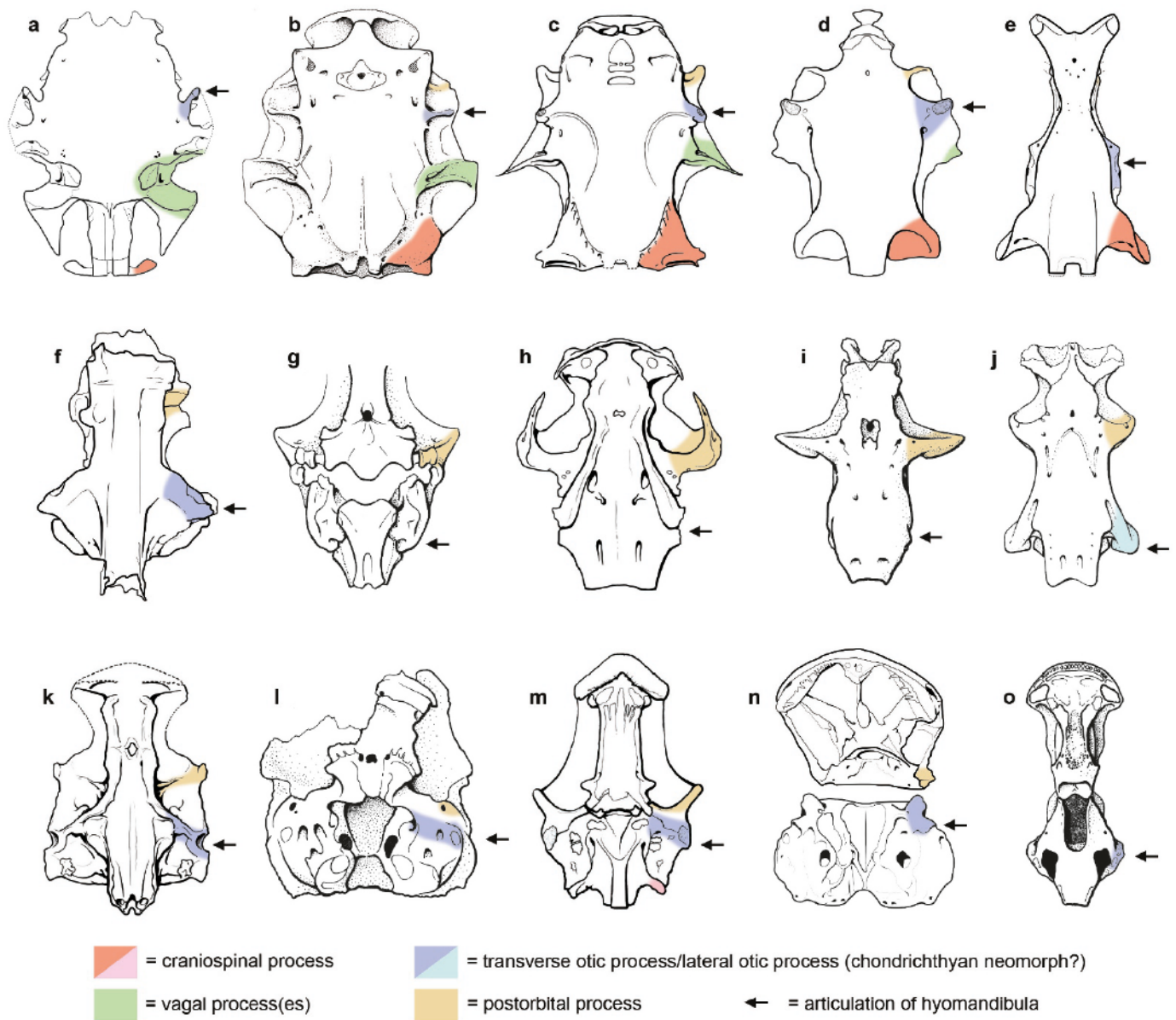
Extended Data Figure 5 | Subcranial ridges in *Janusiscus* and early crown gnathostomes. a, Reconstructed tomographs showing that the thickenings along the lateral margins of the sphenoid region of *Janusiscus* do not represent artefacts of post-mortem compression. b, The 'acanthodian' *Ptomacanthus anglicus* NHMUK PV P 24919a; a silicone peel of the specimen preserved in negative, dusted with ammonium chloride. Portions of the skull other than the

neurocranium are partially masked for clarity. c, The chondrichthyan *Doliodus problematicus* NBMG 10127/1a; a reconstruction of the neurocranium based on CT data. d, *Janusiscus schultzei* gen. et sp. nov. GIT 496-6 (Pi.1384); a reconstruction of the neurocranium based on CT data. Red arrows in each panel indicate subcranial ridges.



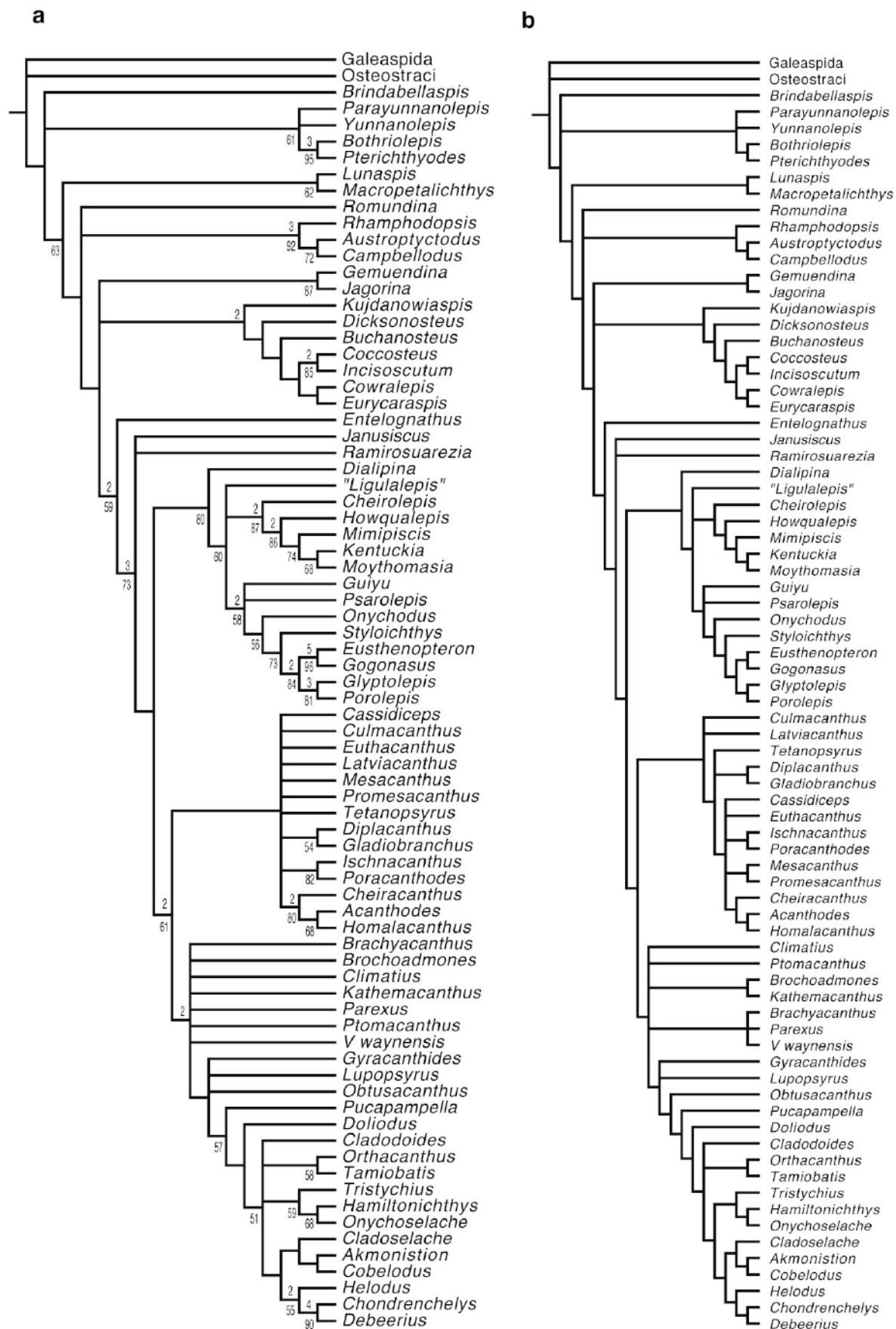
Extended Data Figure 6 | Orbit anatomy of *Janusiscus schultzei* gen. et sp. nov. a, Scanning electron micrograph image into left orbit showing endoskeletal bone and surrounding matrix. b, Image based on X-ray computed microtomography scan with matrix digitally removed. c, Lateral view into right

orbit, with matrix digitally removed. d, Anterolateral view into right orbit, with matrix digitally removed. e, Interpretive drawing of the orbit, based on a composite of the left and right orbits of the holotype (GIT 496-6 (Pi.1384)). Arrow points to anterior.



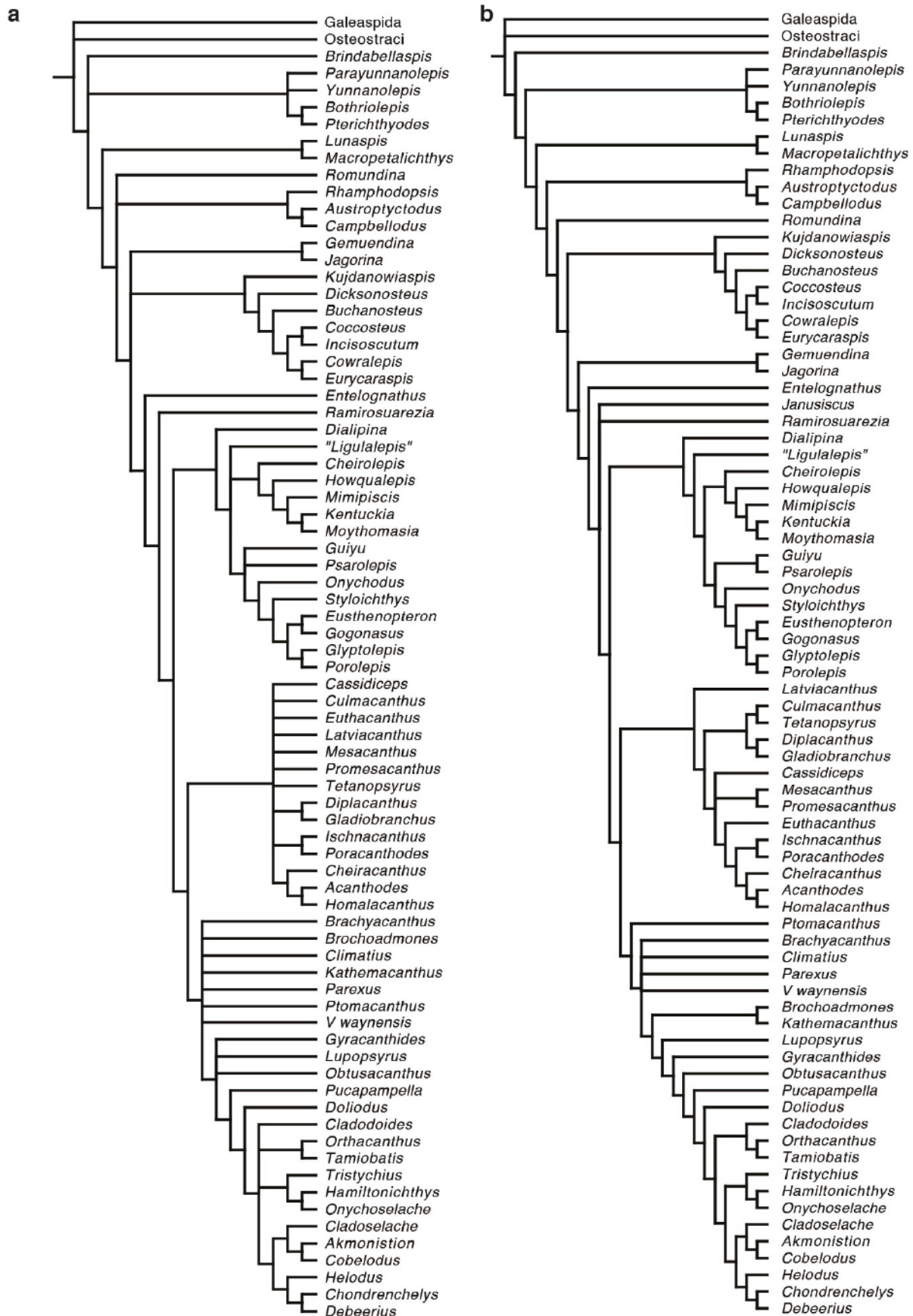
Extended Data Figure 7 | Comparison of transverse processes in the braincases of early gnathostomes. a, *Macropetalichthys* (redrawn from ref. 18). b, *Dicksonosteus* (redrawn from ref. 19). c, *Buchanosteus* (redrawn from ref. 29). d, *Entelognathus* (redrawn from ref. 4). e, *Jagorina* (redrawn from ref. 19). f, *Ramiroisuareszia* (redrawn from ref. 9). g, *Acanthodes* (redrawn from

ref. 3). h, *Doliodus* (redrawn from ref. 17). i, *Cladodoides* (redrawn from ref. 21). j, *Orthacanthus* (redrawn from ref. 20). k, *Janusiscus*. l, *'Ligulalepis'* (redrawn from ref. 14). m, *Mimipiscis* (redrawn from ref. 16). n, *Psarolepis* (redrawn from ref. 25). o, *Gogonassus* (redrawn from ref. 35).



Extended Data Figure 8 | Results of phylogenetic analysis. **a**, Strict consensus of the 522,936 shortest trees (639 steps) for 78 taxa and 236 equally weighted characters. Digits above nodes indicate Bremer decay indices above 1.

Digits below nodes indicate percentage bootstrap support. **b**, Adams consensus tree of the 522,936 shortest trees for 78 taxa and 236 equally weighted characters.



Extended Data Figure 9 | Results of modified phylogenetic analyses. **a**, Strict consensus tree of 216 trees with a score of 452.52565 resulting from analysis of characters reweighted according to retention index. **b**, Strict consensus of the

128,395 shortest trees for 77 taxa and 236 equally weighted characters, with *Janusiscus* removed from the data set.