

Hidden morphological diversity among early tetrapods

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Phylogenetic analysis of early tetrapod evolution has resulted in a consensus across diverse data sets^{1–3} in which the tetrapod stem group is a relatively homogenous collection of medium- to large-sized animals showing a progressive loss of ‘fish’ characters as they become increasingly terrestrial^{4,5}, whereas the crown group demonstrates marked morphological diversity and disparity⁶. The oldest fossil attributed to the tetrapod crown group is the highly specialized aïstopod *Lethiscus stocki*^{7,8}, which shows a small size, extreme axial elongation, loss of limbs, spool-shaped vertebral centra, and a skull with reduced centres of ossification, in common with an otherwise disparate group of small animals known as lepospondyls. Here we use micro-computed tomography of the only known specimen of *Lethiscus* to provide new information that strongly challenges this consensus. Digital dissection reveals extremely primitive cranial morphology, including a spiracular notch, a large remnant of the notochord within the braincase, an open ventral cranial fissure, an anteriorly restricted parasphenoid element, and Meckelian ossifications. The braincase is elongate and lies atop a dorsally projecting septum of the parasphenoid bone, similar to stem tetrapods such as embolomeres. This morphology is consistent in a second aïstopod, *Coloraderpeton*, although the details differ. Phylogenetic analysis, including critical new braincase data, places aïstopods deep on the tetrapod stem, whereas another major lepospondyl lineage is displaced into the amniotes. These results show that stem group tetrapods were much more diverse in their body plans than previously thought. Our study requires a change in commonly used calibration dates for molecular analyses, and emphasizes the importance of character sampling for early tetrapod evolutionary relationships.

We reconstructed the entire skull of *Lethiscus* (Fig. 1, Extended Data Figs 1–3, Supplementary Videos 1–4). It has large orbits and a fenestra in the cheek region enclosed by the postorbital, jugal, quadratojugal, squamosal, and supratemporal bones. Overall, the skull morphology demonstrates underlying similarities with the morphologies of both phlegetontiid⁹ and oestocephalid^{10,11} aïstopods of the Carboniferous and Permian periods.

The skull has a pointed, foreshortened antorbital region (Extended Data Fig. 3). The nasal and frontal bones are mediolaterally narrow but anteroposteriorly long struts that span from the rostrum to the posterior orbital margin, where they overlap the parietal bones, which bear a large foramen on their median suture located just posterior to the mid-point of the skull. The parietal–postparietal suture is deeply W-shaped, with two posterolateral processes, one from each of the parietal bones, extending posterolaterally into the postparietal bones to contact the tabular bones, as seen in oestocephalids^{10,11}, *Eoherpeton*¹², and embolomeres¹³. The postparietal bones are medially restricted and rectangular, except for a triangular process that projects into the posterior margin of the parietal bone. The tabular bones are also elongate, and their posterior margins possess a slight hook-like process similar to that seen in some embolomeres¹³ and *Acanthostega*¹⁴, the

lateral margin of which forms, with the squamosal bone, a spiracular notch. The supratemporal bone is an elongate structure that forms most of the dorsal margin of the temporal fenestra, and is prevented from contacting the posterior process of the postorbital bone by a lateral flange of the parietal bone.

The premaxilla has an anteroposteriorly foreshortened maxillary ramus, but an elongate nasal process. The lacrimal bone is a thin, dorsoventrally reduced ossification at the base of a triangular prefrontal bone and spans from the anteroventral margin of the orbit to the external naris. An orbital process of the frontal bone precludes contact between the prefrontal and postorbital bones. The postorbital and jugal bones articulate in a tongue-in-groove joint like that seen in phlegetontiids. The jugal bone is posteriorly elongated, forming the ventral margin of the temporal fenestra with the quadratojugal and squamosal bones. The maxilla spans from the external naris to the midpoint of the postorbital cheek. The quadratojugal bone articulates dorsally with a triangular squamosal bone, whose dorsoposterior margin is incised into a spiracular notch.

The braincase (Fig. 2) and its dermal investing bones are strongly indicative of a very basal position among stem tetrapods. The entire sphenethmoid complex is vaulted high above the surface of the palate, and sits atop a dorsally expanded cultriform process. A similar dorsal lamina of the cultriform process is also present in *Coloraderpeton* (Extended Data Figs 4, 5, Supplementary Videos 5, 6). The walls of the sphenethmoid ossification extend posteriorly to meet the pila antotica but a large lateral portion remains unossified. A foramen within the contact between the sphenethmoid and parasphenoid bones represents the passage of the optic nerves. A patent buccohypophyseal canal passes through the parasphenoid bone posterior to the optic foramen, but well anterior to the pila antotica (also in *Coloraderpeton*; Extended Data Fig. 5b, c). The small triangular basal plate of the parasphenoid bone is restricted to the anterior (antotic) region. The basal plate is slightly more expanded posteriorly in *Coloraderpeton*, but is still much more anteriorly restricted than in other lepospondyls and other tetrapods crownward of whatcheeriids. Large dorsal recesses are present in the antotic–prootic elements, accommodating the auricles. Two foramina pierce this region, possibly serving the profundus and maxillomandibular branches of the trigeminal nerve. Ventrally, there is a well-developed basicranial fissure separating the prootic and otoccipital bones. The basicranial fissure is more tightly sutured in *Coloraderpeton* but fully co-ossified in phlegetontiids⁹. The otoccipital bone is fused into one solid unit. Metotic and hypoglossal foramina are present in the area where the suture would be located between the opisthotic and exoccipital bones. The occipital articulation is notochordal, forming a recess into the otoccipital ossification rather than a condyle. A partially enclosed channel within the basioccipital bone may have housed a remnant of the notochord that would have extended anteriorly into a recess within the basisphenoid region (Fig. 2f, g), and has a similar relationship with the saccular region of the otic endocast as reported for the notochordal recess in the stem tetrapod

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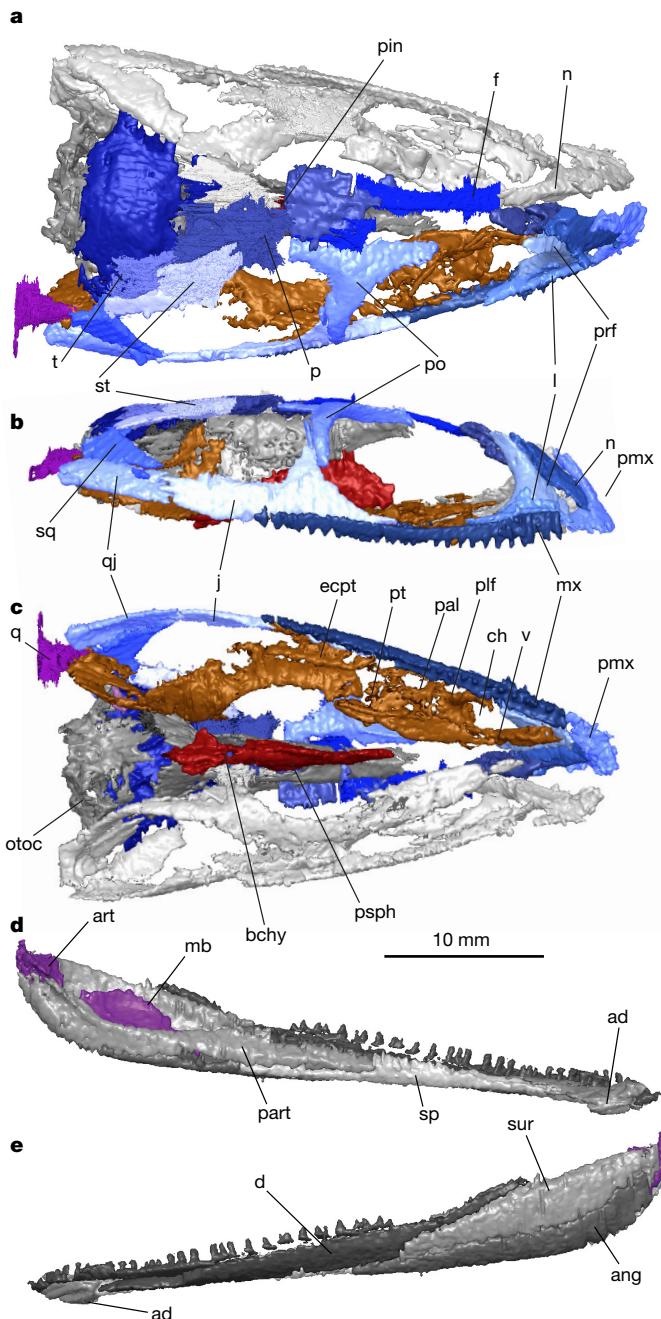


Figure 1 | Skull and lower jaw of *L. stocki*, MCZ 2185. **a–c**, Skull shown in dorsal (a), right lateral (b), and ventral (c) views. **d, e**, Lower jaw shown in medial (d) and lateral (e) views. All are to scale. ad, adsymphyseal; ang, angular; art, articular; bchy, buccohypophyseal canal; ch, choana; d, dentary; ecpt, ectopterygoid; f, frontal; j, jugal; l, lacrimal; mb, Meckelian bone; mx, maxilla; n, nasal; otoc, otocapital complex; p, parietal; pal, palatine; part, prearticular; pin, pineal foramen; plf, palatine fang; pmx, premaxilla; po, postorbital; prf, prefrontal; psph, parasphenoid; pt, pterygoid; q, quadrate; sp, splenial; sq, squamosal; st, supratemporal; sur, surangular; t, tabular; v, vomer.

*Ichthyostega*¹⁵. The occiput of *Coloraderpeton* has the same notochordal pit characteristic of aistopods and is suggestive of having a similar, but shorter, internal recess for a continuation of the notochord, but the braincase is too crushed to fully reconstruct its extent. A stapes is present within the fenestra vestibularis in *Lethiscus*, with a columella that extends laterally to slightly dorsolaterally from the braincase into the spiracular lumen towards the spiracular notch (Fig. 2a–c, Extended Data Fig. 1j). No foramen for the stapedial artery is present.

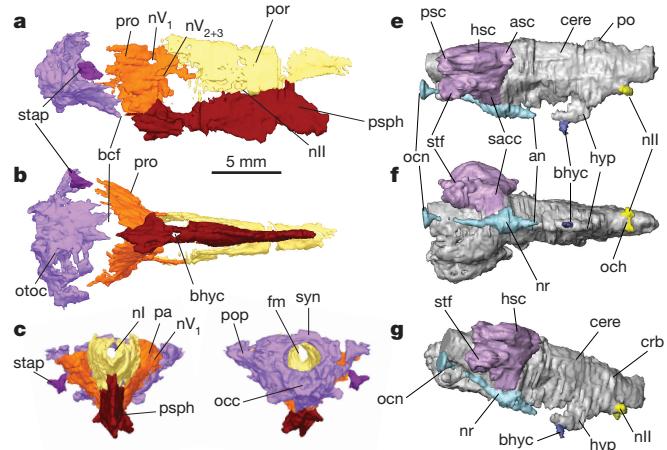


Figure 2 | Braincase and endocast of *L. stocki*, MCZ 2185. **a–d**, Braincase shown in lateral (a), ventral (b), anterior (c), and occipital (d) views. **e–g**, Endocast shown in lateral (e), ventral (f), and lateral oblique (g) views. All are to scale. an, anterior process of notochord; asc, anterior semicircular canal; bcf, basicranial fissure; cere, cerebellar fossa; crb, cerebral fossa; fm, foramen magnum; hsc, horizontal semicircular canal; hyp, hypophyseal fossa; nl, passage of olfactory nerve; nII, passage of optic nerve; nV₁, passage of profundus nerve; nV₂₊₃, passage of maxillomandibular branch of trigeminal nerve; nr, intracranial notochordal remnant; occ, occipital cotyle; ocn, occipital notochordal remnant; pa, pila antotica; po, passage for pineal organ; pop, paroccipital process; por, ossification of preoptic root; pro, prootic–sphenoid complex; sacc, saccular recess of inner ear; stap, stapes; stf, location of stapedial footplate; syn, synotic tectum

The remaining palate morphology is relatively similar to those of most stem tetrapods. The pterygoid bones have a modest interpterygoid vacuity, and anteriorly approach each other at the midline but do not suture. Relatively long ectopterygoid bones appear to be toothless; the palatines bear a single fang-pit pair posterior to the margin of the choana. The vomers are thin elongate structures that span from the premaxillae to the posterior margin of the choanae, and bear a single row of teeth along their length. The quadrate bone is small and triangular, and bears a shallow troclear articulation for the lower jaw. The palate of *Coloraderpeton*, where preserved (Extended Data Fig. 4), is largely similar, but exhibits a row of equally sized teeth on the palatine and ectopterygoid bones parallel to the marginal tooth row.

The lower jaws (Extended Data Fig. 6a–h) resemble those of other stem tetrapods in preserving an elongate dorsal opening into the Meckelian canal. The elongate dentary bone appears to be the only tooth-bearing element, despite the presence of a massive adsymphyseal ossification (forming most of the symphysis) and a single coronoid bone. A single splenial ossification is located on the medial surface, extending from the posterior limit of the adsymphyseal to the angular bone, approximately half the length of the lower jaw. The angular bone is extensive in lateral view but lacks a lingual lamina; contact with the prearticular bone is edge-to-edge, as in whatcheeriids and Devonian tetrapods¹⁶. The prearticular bone occupies most of the posteromedial surface of the jaw, and a small Meckelian foramen is present. The articular bone is present in the posterodorsal portion of the jaw, and has a dorsal, hook-like process on its posterior surface—no retroarticular process is present. A second, blade-like Meckelian ossification can be found inside the jaw anterior to the articular bone.

Coloraderpeton has consistent lower jaw anatomy (Extended Data Fig. 6i–p), although the prearticular and articular elements are coossified. Several small Meckelian foramina pierce the prearticular bone, and a long coronoid series bears at least three large foramina that open into the mandibular canal. A series of pits along the angular bone connect to an at least partially enclosed mandibular lateral line canal.

To test whether the plesiomorphic anatomy observed in our micro-computed tomography reconstructions of *Lethiscus* and

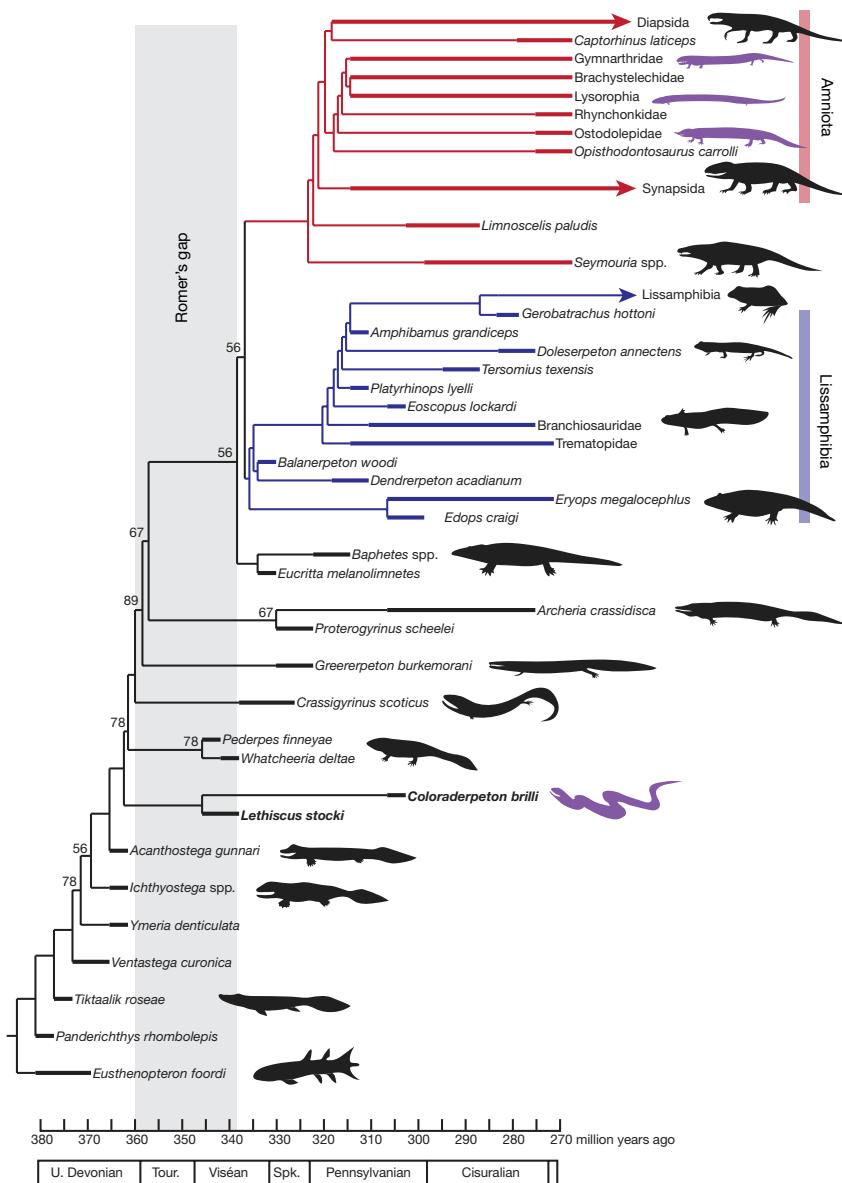


Figure 3 | Time-calibrated phylogeny (majority-rule consensus tree) of major Palaeozoic tetrapod lineages illustrating the relationships of aïstopods and trends in early tetrapod body plan evolution. Blue lineages represent the lissamphibian (frog, salamander, and caecilian) total group, whereas red lineages represent the amniote (mammals, reptiles, and birds) total group. Extant lineages are indicated by arrows. Grey shading

represents a hiatus in tetrapod sampling (Romer's gap) during the Early Carboniferous period. Species previously assigned to the Lepospondyli are indicated in purple. All resolved nodes represent 100% appearance in all most parsimonious trees unless otherwise indicated. U. Devonian, Upper Devonian; Tour., Tournaisian; Spk, Serpukhovian.

Coloraderpeton supports a revision of the phylogenetic relationships of aïstopods, we conducted a phylogenetic analysis of early tetrapod relationships. The result produced 36 most parsimonious trees, the consensus of which is presented in Fig. 3 and Extended Data Fig. 7. Two results are immediately striking. First, aïstopods are securely placed on the tetrapod stem, at least stemward of the whatcheeriid taxa *Whatcheeria* and *Pederpes*. This result eliminates the long ghost lineages that have been hypothesized for several stem amphibian and stem amniote lineages by placing *Lethiscus* among contemporary Early Carboniferous taxa, rather than among taxa from the Carboniferous–Permian transition. Second, recumbirostrans and lysorophians are found to be amniotes, sister taxa to captorhinids and diapsids. This result is consistent with early understandings of microsaur relationships^{17,18} and also reflects historical difficulties in differentiating between recumbirostrans and early eureptiles¹⁹.

Monophyly of all^{1,2} or most lepospondyls, including aïstopods³, has been a finding of a majority of early tetrapod phylogenetic studies

since computer-assisted methods were first introduced. Our analysis unambiguously confirms polyphyly of the group by showing that the aïstopod braincase was organized in a manner distinct from those of other lepospondyls but consistent with that seen in Devonian stem tetrapods. Rather than representing a major diversification of stem amniotes, lepospondyls seem to be an assemblage of small-bodied early tetrapods that share convergent reductions in cranial anatomy (for example, loss of the spiracular notch and palatal fangs) and simplification of the axial skeleton. This conclusion underscores the importance of intensive sampling of internal, particularly neurocranial, anatomy in phylogenetic inference, and the volatility of even well-established consensus topologies when exposed to new data sets.

Importantly, placing *Lethiscus* deep on the tetrapod stem demonstrates that, rather than being relatively conservative in body plan and ecology, the earliest tetrapods exhibited functional and ecological diversity much more extensive than previously appreciated. Under the previous hypothesis, the relatively morphologically conservative

Crassigyrinus (a basal stem tetrapod with reduced limbs)²⁰ and *Spathicephalus*²¹ (a baphetoid with an extremely broad skull) were the most specialized stem tetrapods. *Lethiscus* demonstrates extreme small size in the tetrapod stem group and, for the first time in the tetrapod fossil record, complete limblessness and elongation of both the presacral and caudal vertebral series relatively quickly after tetrapods first emerged on land. Moreover, the highly fenestrated skull indicates cranial specialization not otherwise seen until the Late Carboniferous and Permian periods, accomplishing a scale of reduction in the dermal skull seen only in recumbirostrans^{22,23} and amniotes²⁴.

The placement of *Lethiscus* firmly on the tetrapod stem also has implications for molecular calibration. Molecular clock calibrations for the tetrapod crown should now shift to other taxa, notably the stem lissamphibian *Balanerpeton*²⁵ and stem amniote *Westlothiana*²⁶ from the uppermost Viséan East Kirkton locality (332.9–330.9 million years ago)²⁷.

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.

Received 12 October 2016; accepted 5 May 2017.

Published online 21 June 2017.

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

Acknowledgements We thank S. Pierce, J. Cundiff, the late F. A. Jenkins, C. Schaff, the late W. Amaral, D. Berman, A. Henrici, P. Holroyd, A. C. Milner, J. A. Clack, J. Bolt and W. Simpson for access to specimens, and J. Bolt, R. Carroll, J. A. Clack, M. Coates, N. Fröbisch, D. Germain, A. Huttenlocker, M. Laurin, H. Maddin, D. Marjanović, J. Olori, R. R. Reisz, and R. Schoch for discussions. We particularly thank D. Germain for first suggesting reanalysis of the *Lethiscus* data set with current computational tools. This research was supported in part by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to J.S.A.

Author Contributions Project instigated by J.S.A. and J.D.P. Micro-CT volumetric data compiled by J.D.P., M.S., P.E.A. and J.S.A. Phylogenetic analysis by J.D.P., M.S., P.E.A. and J.S.A. Paper written by J.S.A., J.D.P., M.S. and P.E.A.

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Reviewer Information *Nature* thanks S. Sumida and the other anonymous reviewer(s) for their contribution to the peer review of this work.

METHODS

Computed tomography. Scan parameters for the primary skull block and rostral block of *L. stocki* (MCZ 2185) have been previously reported⁸. The skull roof of *L. stocki* (MCZ 2185) was scanned using a Skyscan 1173 at the Museum of Comparative Zoology, Harvard University. The scan was conducted at 130 kV and 61 µA, and a 0.25 mm brass filter was used to reduce beam hardening artefacts. The resulting image stack had a voxel size of 22.03 µm. Tomographic stacks were imported into Amira 5 (Visage, Inc.). Elements were segmented using the LabelField module. Labels were then exported as individual surface files using the Arithmetic module and imported into Maya (Autodesk, Inc.) for assembly.

An attributed skull of *Coloraderpeton brilli* (CM 47687) from Interval 300 of the Sangre de Cristo Formation outside Howard, Colorado, was scanned using a Skyscan 1173 at the McCaig Bone and Joint Institute, University of Calgary. The scan was conducted at 100 kV and 60 µA with a 0.1 mm aluminium filter to reduce beam hardening artefacts. The resulting image stack had a voxel size of 21.6 µm. Tomographic stacks were cropped and downsampled by a factor of 3 in the z-plane to reduce computational time using ImageJ. Segmentation and assembly of the skull were completed as for *Lethiscus*.

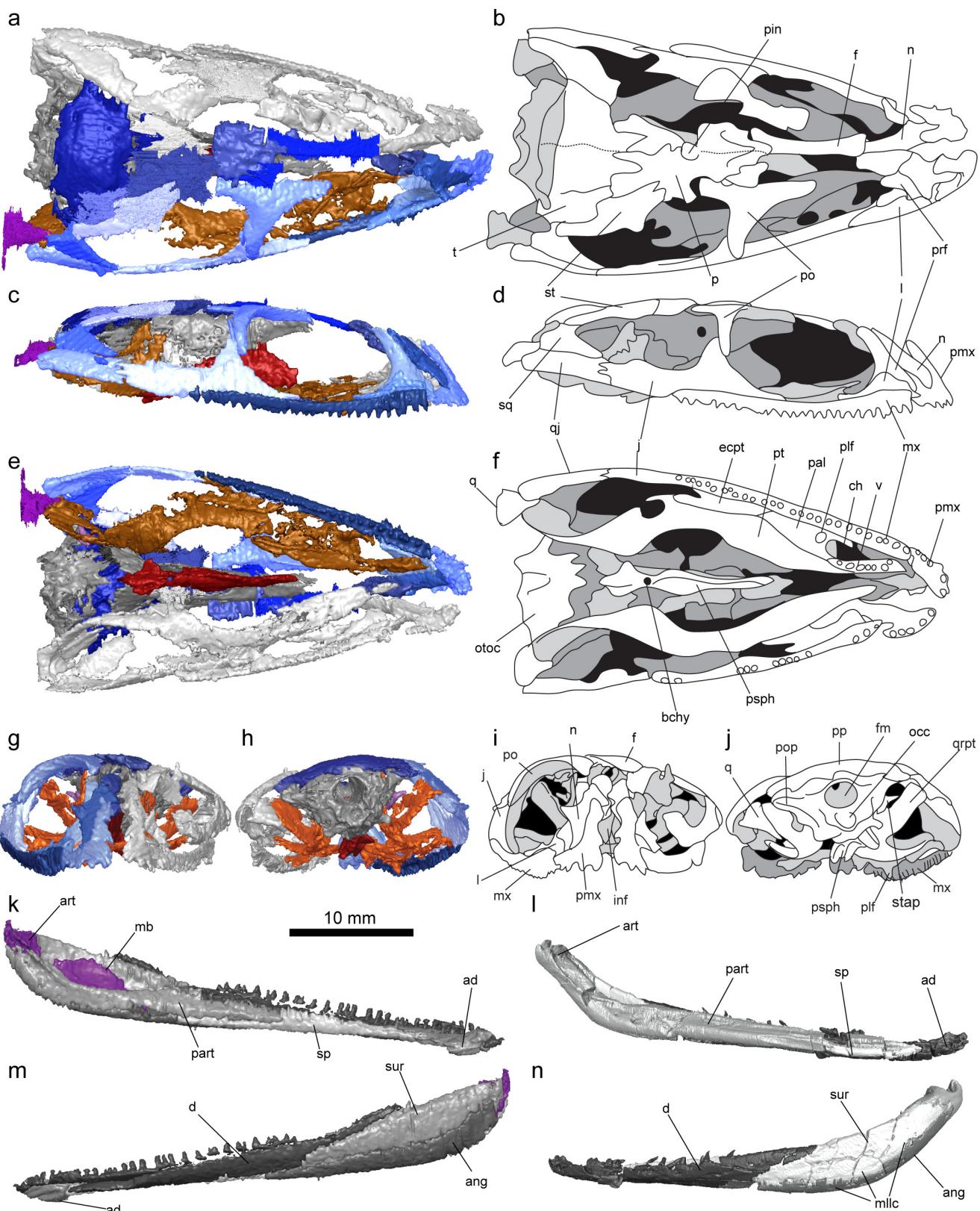
Phylogenetic analysis. We conducted a phylogenetic analysis to test overall patterns of tetrapod diversity and to investigate whether *Lethiscus* remains within the tetrapod crown. We modified a recently published analysis of crown tetrapod relationships²⁸ with the addition of middle ear characters²⁹ by adding a number of characters related to the braincase recently described^{22–24,28}. In order to test the position of aistopods and recumbirostrans more broadly in early tetrapod

phylogeny, we combined this matrix with an updated form³⁰ of an early tetrapod phylogeny¹⁶. Nonoverlapping data were coded from specimens or CT where possible, and the literature where necessary, and selected characters were modified to reduce redundancy either between or within data sets (Supplementary Information). The taxon coverage was then reduced to reflect only specimens with well-preserved and completely described neurocranial anatomy. The resulting phylogenetic analysis consisted of 57 ingroup taxa, one outgroup (*Eusthenopteron*) and 370 characters, 340 of which are parsimony informative for this sample of taxa.

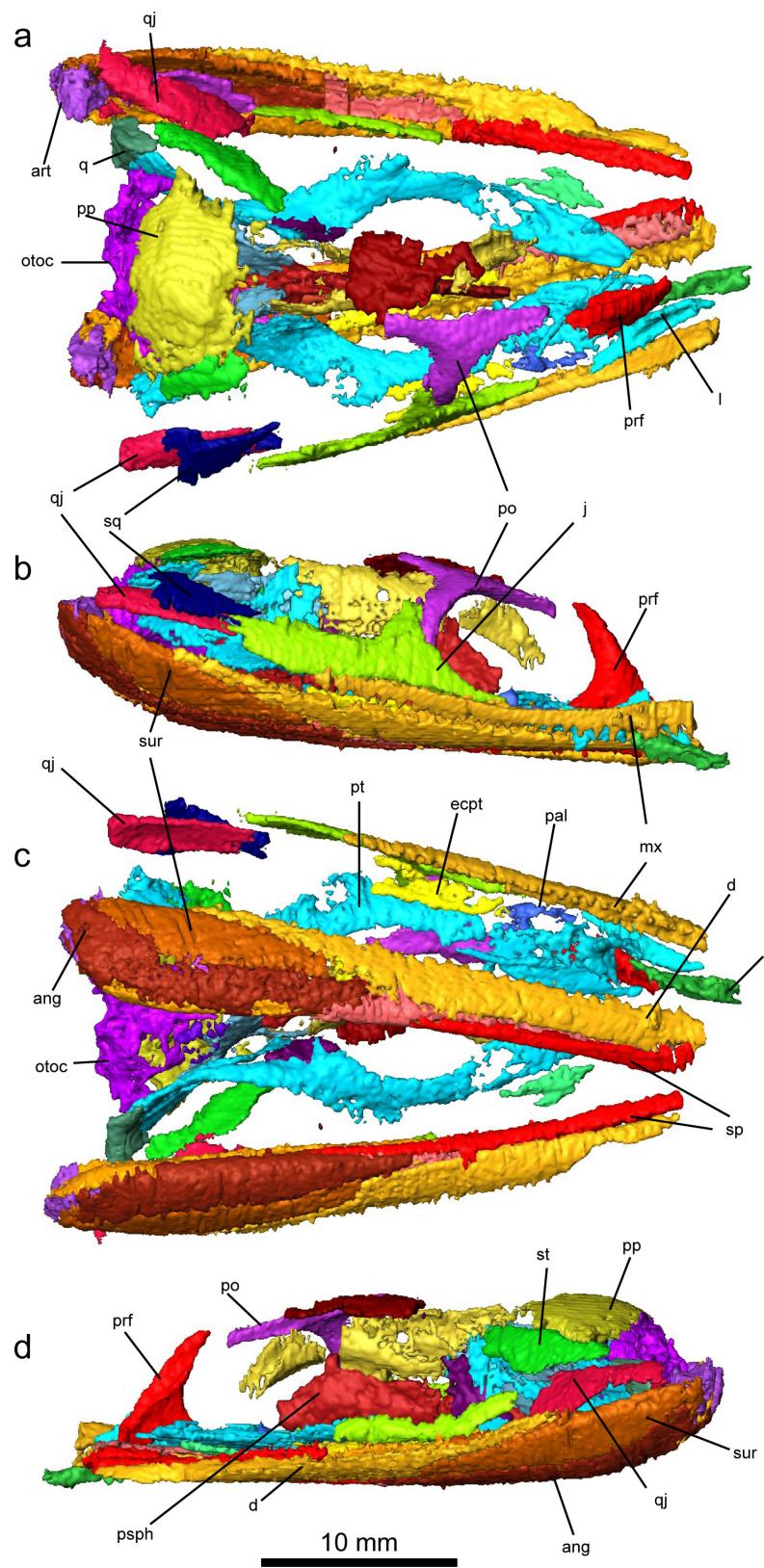
We assessed phylogeny using a maximum parsimony criterion. Parsimony analysis was conducted in PAUP 4.0a151. We searched for trees using the heuristic algorithm (hsearch) using one hundred thousand random addition replicates and a TBR branch-swapping algorithm.

Data availability. CT image slice data and all other data are available from the corresponding author upon reasonable request.

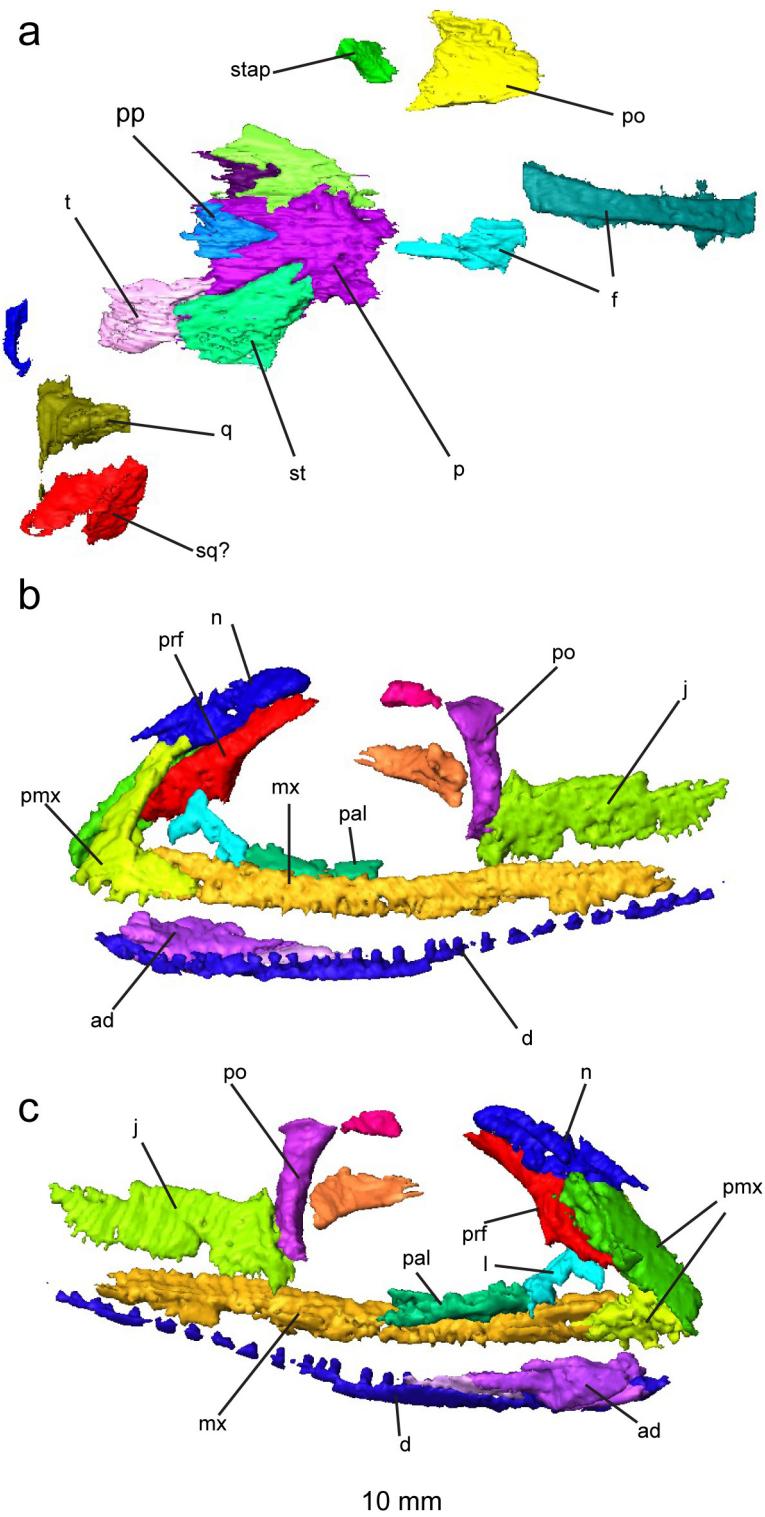
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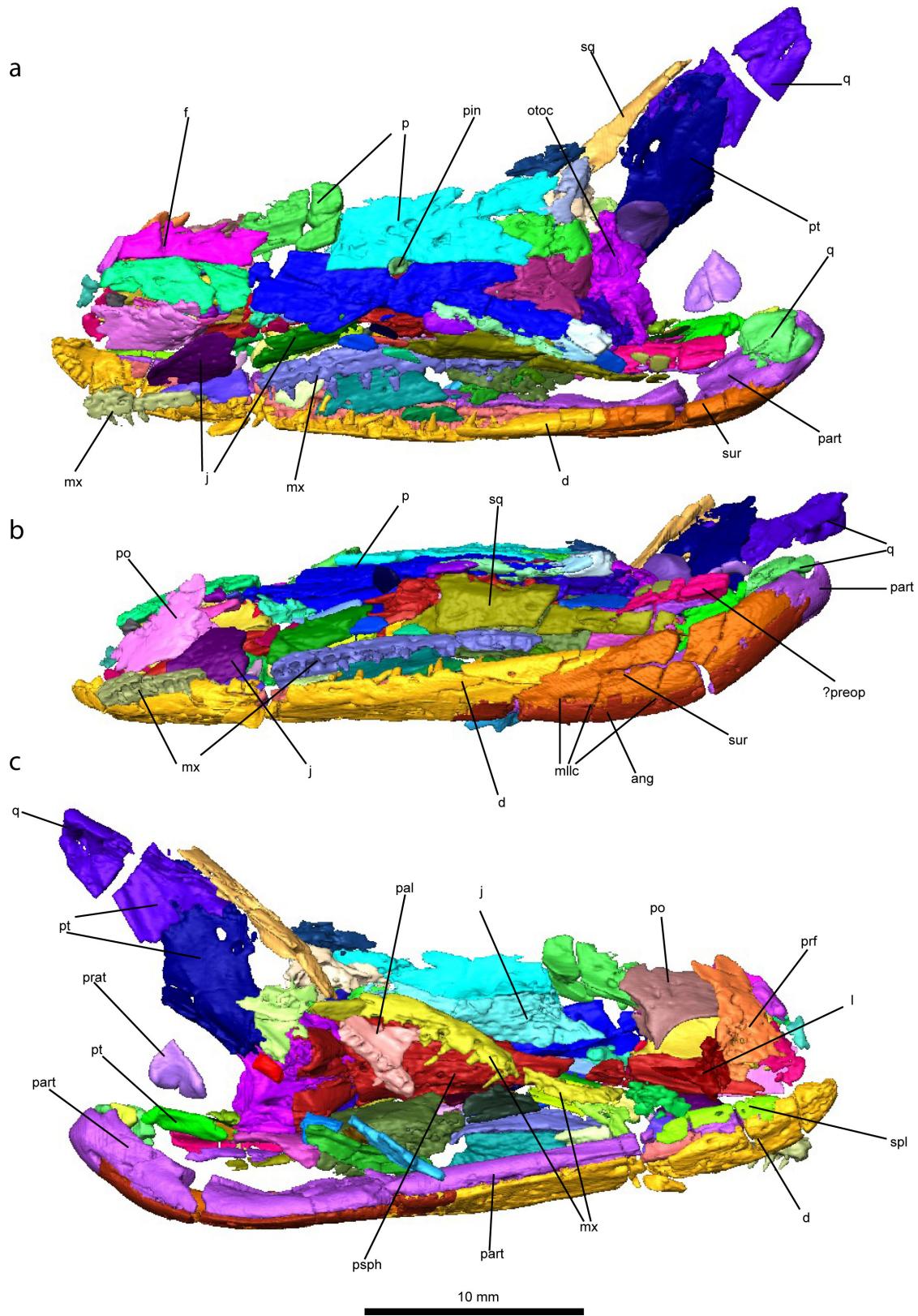
Extended Data Figure 1 | Skull and lower jaw of *L. stocki*, MCZ 2185, and lower jaw of *C. brilli*, CM 47687. a–j, Skull shown in dorsal (a, b), right lateral (c, d), ventral (e, f), anterior (g, i), and occipital (h, j) views. k–n, Lower jaws shown in medial (k, l) and lateral (m, n) views. All are to scale. inf, internarial fontanelle; mlrc, mandibular lateral line canal; pp, postparietal; qrpt, quadrate ramus of pterygoid.



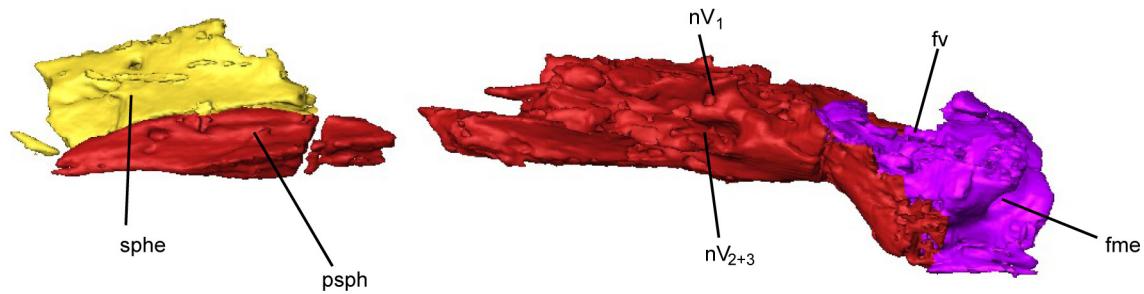
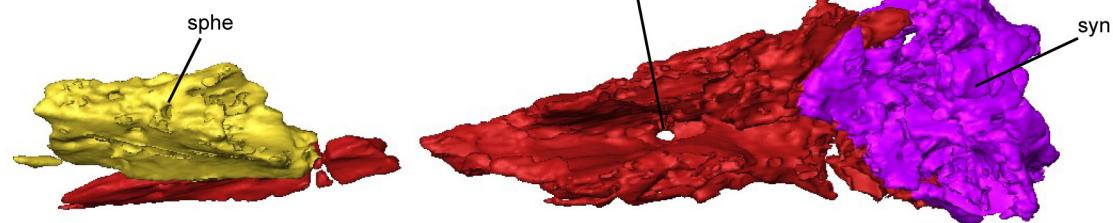
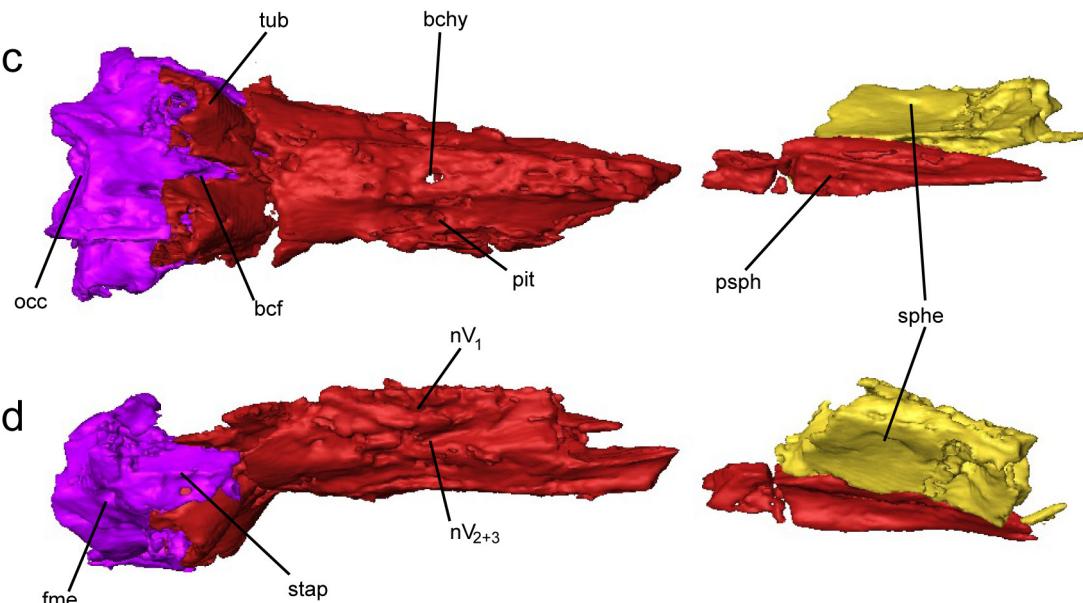
Extended Data Figure 2 | Skull of *L. stocki*, MCZ 2185, main block. a–d, Specimen figured in dorsal (a), right lateral (b), ventral (c), and left lateral (d) views. All are to scale.



Extended Data Figure 3 | Skull of *L. stocki*, MCZ 2185. a, Skull roof. b, c, Snout. All are to scale.

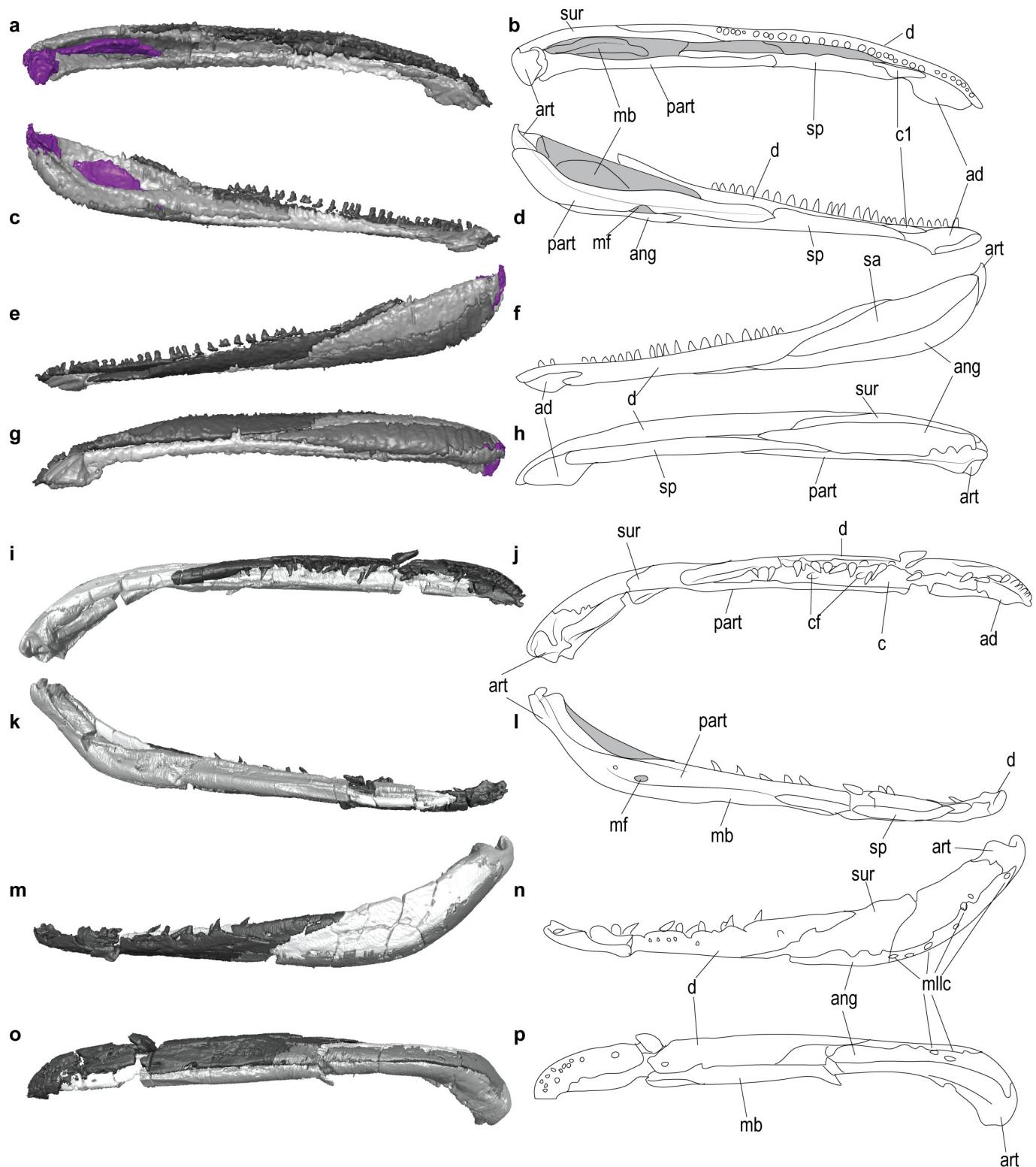


Extended Data Figure 4 | Skull of *C. brilli*, CM 47687. a–c, Specimen figured in dorsal (a), lateral (b), and ventral (c) views. All are to scale. po, postfrontal; prat, proatlas; ?preop, possible preopercular.

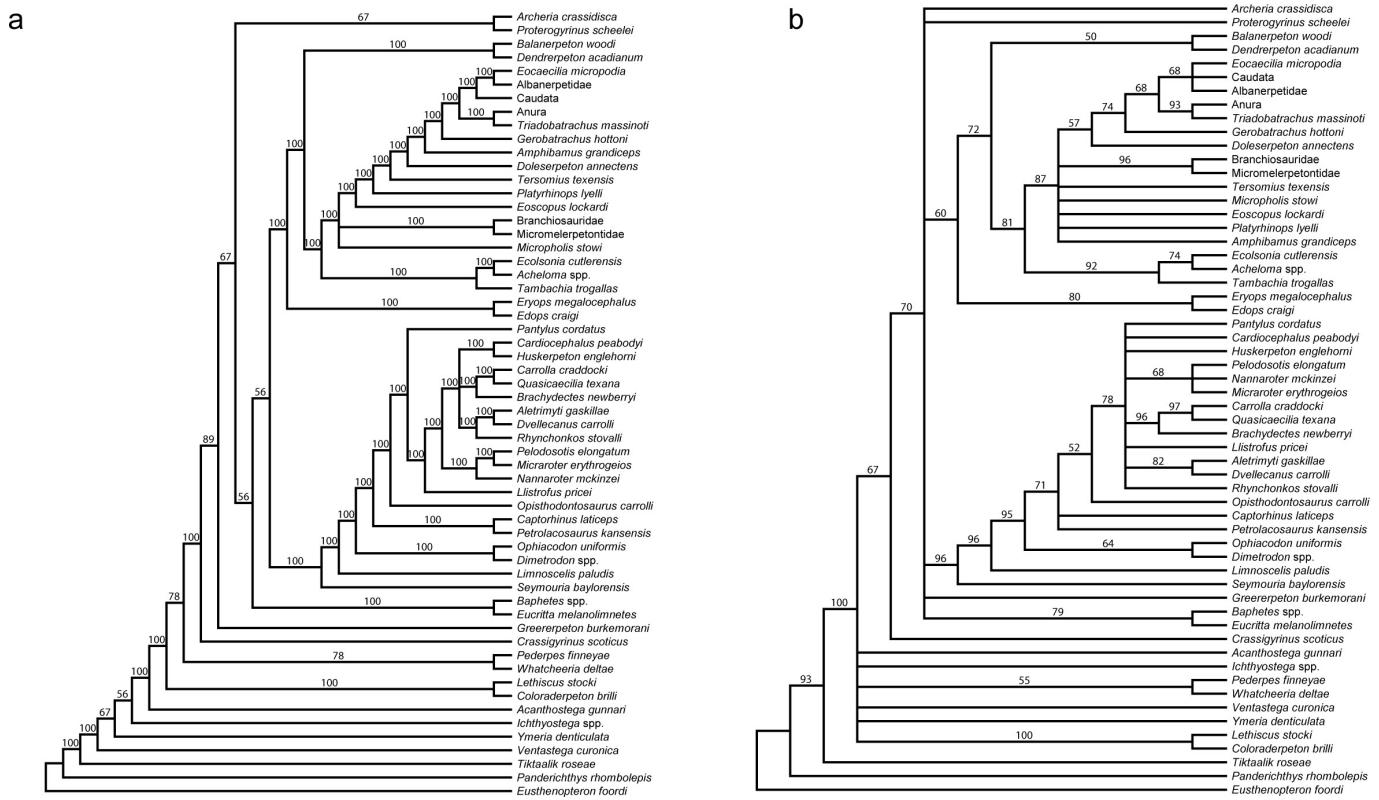
a**b****c**

10 mm

Extended Data Figure 5 | Braincase of *C. brillii*, CM 47687. **a–d**, Specimens figured in left lateral (a), dorsal (b), ventral (c), and right lateral (d) views. All are to scale. fme, foramen metoticum; fv, fenestra vestibularis; pit, foramen serving pituitary artery; sphe, sphenethmoid.



Extended Data Figure 6 | Lower jaws of *L. stocki*, MCZ 2185 and *C. brilli*, CM 47687. CT volumes on left, line drawings on right. **a–h**, Left lower jaw of *Lethiscus* shown in dorsal (**a**, **b**), medial (**c**, **d**), lateral (**e**, **f**), and ventral (**g**, **h**) views. **i–p**, Left lower jaw of *C. brilli* shown in dorsal (**i**, **j**), medial (**k**, **l**), lateral (**m**, **n**), and ventral (**o**, **p**) views. Not to scale. **c**, coronoid; **c1**, first coronoid; **cf**, coronoid foramen; **mf**, Meckelian foramen.



Extended Data Figure 7 | Phylogenetic analysis showing relationships of the aïstopods *L. stocki* and *C. brillii*, and selected lepospondyls.
Consensus (a) and bootstrap (b) trees, showing relationships of 58 tetrapod and tetrapodomorph taxa. a, Consensus tree represents majority rule consensus of 36 most parsimonious trees (1,684 steps). Node values

indicate per cent frequency for this topology appearing among the most parsimonious trees. b, Bootstrap tree shows majority rule consensus of trees produced via 1,000 bootstrap replicates resampled with replacement. Node values indicate bootstrap support.