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Hidden morphological diversity among early tetrapods

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Phylogenetic analysis of early tetrapod evolution has achieved a consensus across diverse datasets[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 became increasingly terrestrial[4,5], whereas the crown group demonstrates marked morphological diversity and disparity[6]. The oldest fossil attributed to the tetrapod crown group is the highly-specialized aïstopod *Lethiscus stocki*[7,8], which shows 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 provide new information on the only known specimen of *Lethiscus* from micro-Computed Tomography (µCT) that dramatically challenges this consensus. Digital dissection reveals extremely primitive cranial morphology, including a spiracular notch, large remnant of the notochord within the braincase, open ventral cranial fissure, anteriorly

restricted parasphenoid, and Meckelian ossifications. The braincase is elongate and lies atop a dorsally projecting septum of the parasphenoid, similar to stem tetrapods such as embolomeres. This morphology is consistent in a second aïstopod, *Coloraderpeton*, although different in detail. Phylogenetic analysis, including critical new braincase data, places aïstopods deep on the tetrapod stem, whereas another major lepospondyl lineage is displaced into 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, Supplemental Videos 1-4). It has large orbits and a fenestra in the cheek region enclosed by the postorbital, jugal, quadratojugal, squamosal, and supratemporal. Overall skull morphology demonstrates underlying similarities with the morphology of both phlegethontiid[9] and oestocephalid[10,11] aïstopods of the Carboniferous and Permian.

The skull has a pointed, foreshortened antorbital region (Extended Data Fig. 2). The nasals and frontals are mediolaterally narrow, but anteroposteriorly long, struts spanning from the rostrum to the posterior orbital margin, where they overlap the parietals, 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 parietals, extending posteriolaterally into the postparietals to contact the tabulars, as seen in oestocephalids[10,11], *Eoherpeton*[12], and embolomeres[13]. The postparietals are medially-restricted rectangular bones except for a triangular process that projects into the posterior margin of the parietal. The tabulars are also elongate, and their posterior margin possess a slight hook-like process similar to that seen in some embolomeres[13] and *Acanthostega*[14], the lateral margin of which forms, with the squamosal, a spiracular notch. The supratemporal 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 by a lateral flange of the parietal.

The premaxilla has an anteroposteriorly foreshortened maxillary ramus, but an elongate nasal process. The lacrimal is a thin, dorsoventrally-reduced ossification at the base of a triangular prefrontal and spans from the anteroventral margin of the orbit to the external naris. An orbital process of the frontal precludes contact between the prefrontal and postorbital. The postorbital and jugal articulate in a tongue-in-groove joint like that seen in phlegethontiids. The jugal is posteriorly elongated, forming the ventral margin of the temporal fenestra with the quadratojugal and squamosal. The maxilla spans from the external naris to the midpoint of the postorbital cheek. The quadratojugal articulates dorsally with a triangular squamosal, 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*. The walls of the sphenethmoid extend posteriorly to meet the pila antotica but a large lateral portion remains unossified. A foramen within the contact between the sphenethmoid and parasphenoid represents the passage of the optic nerves. A patent buccohypophyseal canal passes through the parasphenoid posterior to the optic foramen, but well anterior to the pila antotica (also in *Coloraderpeton*; Extended Data Fig. 4b and c). The small triangular basal plate of the parasphenoid 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, as well as other tetrapods crownward of whatcheeriids. Large dorsal recesses are present in the antotic-prootic 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 prootic from otoccipital. The basicranial fissure is more tightly sutured in *Coloraderpeton* but fully co-ossified in phlegethontiids[9]. The otoccipital 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 exoccipitals. The occipital articulation is notochordal, forming a recess into the otoccipital ossification rather than a condyle. A partially-enclosed channel within the basioccipital may have housed a remnant of the notochord that would have extended anteriorly into a recess within the basisphenoid region (Fig. 2g-i), and has a similar relationship with the saccular region of the otic endocast as reported for the notochordal recess in the stem-tetrapod *Ichthyostega*[15]. The occiput of *Coloraderpeton* (Extended Data Figs. 4-5, Supplementary Videos 5-6) has the same notochordal pit characteristic of aïstopods 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. 2b,c,e, Extended Data Fig. 1j). No foramen for the stapedial artery is present.

The remaining palate morphology is relatively similar to most stem tetrapods. The pterygoids have a modest interpterygoid vacuity, and anteriorly approach each other at the midline but do not suture. Relatively long ectopterygoids appear to be toothless; 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 is small and triangular, and bears a shallow trochlear 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 palatine and ectopterygoid parallel to the marginal tooth row.

The lower jaws (Extended Data Fig. 6a-h) resemble other stem tetrapods in preserving an elongate dorsal opening into the Meckelian canal. The elongate dentary 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, approximately half the length of

the lower jaw. The angular is extensive in lateral view but lacks a lingual lamina; contact with the prearticular is edge-to-edge as in whatcheeriids and Devonian tetrapods[16]. The prearticular occupies most of the posteromedial surface of the jaw, and a small Meckelian foramen is present. The articular 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.

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

To test whether the plesiomorphic anatomy observed in our μCT reconstructions of *Lethiscus* and *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 Figure 3 and Extended Data Figure 7. Two results are immediately striking. One, aïstopods are securely placed on the tetrapod stem, at least as stemward of the whatcheeriid taxa *Whatcheeria* and *Pederpes*. This result eliminates long ghost lineages 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 taxon to captorhinids and diapsids. This result is both consistent with early understandings of microsaur relationships[17,18] and reflects historical difficulties in differentiating between recumbirostrans and early eureptiles[19].

Monophyly of all[1-2] or most lepospondyls including aïstopods[3] 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 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 sharing convergent reductions in cranial anatomy (e.g. loss of spiracular notch, loss of palatal fangs) and simplification of the axial skeleton. This 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 datasets.

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, accomplishing a scale of reduction in the dermal skull seen only in recumbirostrans[22-23] and amniotes[24].

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 Ma)[27].

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Author Contributions

Project instigated by JSA and JDP. CT volumetric data compiled by JDP, MS, PEA, and JSA. Phylogenetic analysis by JDP, MS, PEA, and JSA. Paper written by JSA, JDP, MS, and PEA.

Author Information

The authors declare no competing financial interest.

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Figure Captions

Figure 1. Skull (a-c) and lower jaw (d, e) of *Lethiscus stocki*, MCZ 2185. Skull shown in dorsal (a), right lateral (b), and ventral (c) views. Lower jaw shown in medial (d) and lateral (e) views. All are to scale. **Abbreviations:** 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, otoccipital; 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.

Figure 2. Braincase and endocast of *Lethiscus stocki*, MCZ 2185. Braincase (a-d) shown in lateral (a), ventral (b), anterior (c), and occipital (d) views. Endocast shown in lateral (e), ventral (f), and lateral oblique (g) views. All are to scale. **Abbreviations:** an, anterior process of notochord; asc, anterior semicircular canal; bcf, basicranial fissure; bhyc, buccohypophyseal canal; cere, cerebellar fossa; crb, cerebral fossa; fm, foramen magnum; hsc, horizontal semicircular canal; hyp, hypophyseal fossa; nI, passage of olfactory nerve; nII, passage of optic nerve; nV_1, passage of profundus nerve; nV_{2+3}, passage of maxillomandibular branch of trigeminal nerve; nr, intracranial notochordal remnant; occ, occipital cotyle; ocn, occipital notochordal remnant; otoc, otoccipital complex; pa, pila antotica; po, passage for pineal organ; pop, paroccipital process; por, ossification of preoptic root; pro, prootic-sphenoid complex; psph, parasphenoid; sacc, saccular recess of inner ear; stap, stapes; stf, location of stapedial footplate; syn, synotic tectum.

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 the arrows. Grey interval represents a hiatus in tetrapod sampling ('Romer's Gap') during the Early Carboniferous. Species previously assigned to the Lepospondyli are indicated in purple. Numbered scale at bottom is in millions of years (Ma); all resolved nodes represent 100% appearance in all most parsimonious trees unless otherwise indicated.

Methods

Computed tomography

Scan parameters for the primary skull block and rostral block of *Lethiscus stocki* (MCZ 2185) have been previously reported in the literature[8]. 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/61 μA, and a 0.25 mm brass filter was used to reduce beam hardening artifacts. 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 artifacts. 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 in *Lethiscus*.

Data availability

CT image slice data are available upon request.

Phylogenetic analysis

We conducted a phylogenetic analysis to test overall patterns of tetrapod diversity and whether *Lethiscus* remains within the tetrapod crown. We modified a recently-published analysis of crown tetrapod relationships[28] with addition of middle ear characters[29] by adding a number of characters related to the braincase recently described[22-24,28]. In order to test the position of aïstopods and recumbirostrans more broadly in early tetrapod phylogeny, we combined this matrix with an updated form[30] of an early tetrapod phylogeny[16]. 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 datasets (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.

EXTENDED DATA FIGURES

Extended Data Figure 1. Skull (a-j) and lower jaw (k, m) of *Lethiscus stocki*, MCZ 2185, and lower jaw (l, n) of *Coloraderpeton brilli*, CM 47687. Skull shown in dorsal (a-b), right lateral (c-d), ventral (e-f), anterior (g, i), and occipital (h, j) views. Lower jaws shown in medial (k-l) and lateral (l, n) views. All are to scale. **Abbreviations:** ad, adsymphyseal; ang, angular; art, articular; bchy, buccohypophyseal canal; ch choana; d, dentary; ecpt, ectopterygoid; f, frontal; fm, foramen magnum; inf, internarial fontanelle; j, jugal; l, lacrimal; mb, Meckelian bone; mllc, mandibular lateral line canal; mx, maxilla; n, nasal; occ, occipital cotyle; otoc, otoccipital; p, parietal; pal, palatine; part, prearticular; pin, pineal foramen; plf, palatine fang; pmx, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal,

prf, prefrontal; psph, parasphenoid; pt, pterygoid; q, quadrate; qrpt, quadrate ramus of pterygoid; sp, splenial; sq, squamosal; st, supratemporal; stap, stapes; sur, surangular; t, tabular; v, vomer.

Extended Data Figure 2. Skull of *Lethiscus stocki*, MCZ 2185, main block. Specimen figured in dorsal (**a**), right lateral (**b**), ventral (**c**), and left lateral (**d**) views. All are to scale. **Abbreviations:** ang, angular; art, articular; d, dentary; ecpt, ectopterygoid; j, jugal; l, lacrimal; mx, maxilla; otoc, otoccipital; pal, palatine; po, postorbital; pp, postparietal; prf, prefrontal; psph, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal; sur, surangular; v, vomer.

Extended Data Figure 3. Skull of *Lethiscus stocki*, MCZ 2185, skull roof (a) and snout (b,c). All are to scale. **Abbreviations:** ad, adsymphyseal; d, dentary; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; pal, palatine; pmx, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; q, quadrate; sq, squamosal; st, supratemporal; stap, stapes.

Extended Data Figure 4. Skull of *Coloraderpeton brilli*, CM 47687. Specimen figured in dorsal (**a**), lateral (**b**), and ventral (**c**) views. All are to scale. **Abbreviations:** ang, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; mllc, mandibular lateral line canal; otoc, otoccipital; p, parietal; pal, palatine; part, prearticular; pin, pineal foramen; pof, postfrontal; prat, proatlas; ?preop, possible preopercular; prf, prefrontal; psph, parasphenoid; pt, pterygoid; q, quadrate; sp, splenial; sq, squamosal; sur, surangular.

Extended Data Figure 5. Braincase of *Coloraderpeton brilli*, CM 47687. Specimens figured in left lateral (**a**), dorsal (**b**), ventral (**c**), and right lateral (**d**) view. All are to scale. **Abbreviations:** bcf, basicranial fissure; bchy, buccohypophyseal canal; fme, foramen metoticum; fv, fenestra vestibularis; nV_1, foramen serving profundus branch of the trigeminal; nV_{2+3}, foramen serving maxillomandibular branches of the trigeminal nerve; occ, occipital cotyle; pit, foramen serving pituitary artery; psph, parasphenoid; sphen, sphenethmoid; stap, stapes.

Extended Data Figure 6. Lower jaws of *Lethiscus stocki*, MCZ 2185 (a-h), and *Coloraderpeton brilli*, CM 47687 (i-p). CT volumes on left, line drawings on right. Left lower jaw of *Lethiscus* shown in dorsal

(**a,b**), medial (**c,d**), lateral (**e,f**), and ventral (**g,h**) views. Left lower jaw of *Coloraderpeton brilli* shown in dorsal (**i,j**), medial (**k,l**), lateral (**m,n**), and ventral (**o,p**) views. Not to scale. **Abbreviations**: ad, adsymphyseal; ang, angular; art, articular; c, coronoid; c1, first coronoid; cf, coronoid foramen; d, dentary; mb, Meckelian bone; mf, Meckelian foramen; mllc, mandibular lateral line canal; part, prearticular; sp, splenial; sur, surangular.

Extended Data Figure 7. Phylogenetic analysis showing relationships of the aïstopods *Lethiscus stocki* and *Coloraderpeton brilli*, and selected 'lepospondyls.' Consensus (**a**) and bootstrap (**b**) trees, showing relationships of 58 tetrapod and tetrapodomorph taxa. Consensus tree represents majority rule consensus of 36 most parsimonious trees (1684 steps). Node values indicate percent frequency this topology appears among the most parsimonious trees. Bootstrap tree shows majority rule consensus of trees produced via 1000 bootstrap replicates resampled with replacement. Node values indicate bootstrap support.