

Research



Cite this article: Stocker MR, Nesbitt SJ, Kligman BT, Paluh DJ, Marsh AD, Blackburn DC, Parker WG. 2019 The earliest equatorial record of frogs from the Late Triassic of Arizona. *Biol. Lett.* **15**: 20180922.

<http://dx.doi.org/10.1098/rsbl.2018.0922>

Received: 29 December 2018

Accepted: 1 February 2019

Subject Areas:

palaeontology, evolution, taxonomy and systematics

Keywords:

Chinle Formation, frog, ilium, microfossils, Norian, evolution

Author for correspondence:

Michelle R. Stocker

e-mail: stockerm@vt.edu

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4395908>.

The earliest equatorial record of frogs from the Late Triassic of Arizona

Michelle R. Stocker¹, Sterling J. Nesbitt¹, Ben T. Kligman^{1,2}, Daniel J. Paluh³, Adam D. Marsh², David C. Blackburn³ and William G. Parker²

¹Department of Geosciences, Virginia Tech, Blacksburg, VA 24061, USA

²Petrified Forest National Park, 1 Park Road, Petrified Forest, AZ 86028, USA

³Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA

ID MRS, 0000-0002-6473-8691; SJN, 0000-0002-7017-1652; BTK, 0000-0003-4400-8963; DJP, 0000-0003-3506-2669; ADM, 0000-0002-3223-8940; DCB, 0000-0002-1810-9886; WGP, 0000-0002-6005-7098

Crown-group frogs (Anura) originated over 200 Ma according to molecular phylogenetic analyses, though only a few fossils from high latitudes chronicle the first approximately 60 Myr of frog evolution and distribution. We report fossils that represent both the first Late Triassic and the earliest equatorial record of Salientia, the group that includes stem and crown-frogs. These small fossils consist of complete and partial ilia with anteriorly directed, elongate and distally hollow iliac blades. These features of these ilia, including the lack of a prominent dorsal protuberance and a shaft that is much longer than the acetabular region, suggest a closer affinity to crown-group Anura than to Early Triassic stem anurans *Triadobatrachus* from Madagascar and *Czatkobatrachus* from Poland, both high-latitude records. The new fossils demonstrate that crown anurans may have been present in the Late Triassic equatorial region of Pangea. Furthermore, the presence of Early Jurassic anurans in the same stratigraphic sequence (*Prosalirus bitis* from the Kayenta Formation) suggests that anurans survived the climatic aridification of this region in the early Mesozoic. These fossils highlight the importance of the targeted collection of microfossils and provide further evidence for the presence of crown-group representatives of terrestrial vertebrates prior to the end-Triassic extinction.

1. Background

Many components of the living vertebrate fauna originated as small-bodied clades in the Triassic Period, including the first records of mammaliaforms, squamates, turtles, crocodylomorphs, dinosaurs (as birds today) and lissamphibians [1–4]. Some of these clades originated by the Early Triassic but remained exceptionally rare, with their next appearances in the fossil record in the Jurassic. Thus, chronologic gaps in the records of many taxa are a major problem for recognizing morphological and functional transformations in these groups. Furthermore, a more accurate understanding of this diversity is hampered in that Triassic terrestrial small-bodied tetrapods are best known from high palaeolatitudes, specifically eastern North America and Europe [2,5–7]. However, small-bodied tetrapods should also be present in equatorially sourced Triassic rocks, such as in the southwestern USA. Research from the past 20 years has significantly increased the sampled diversity of small-bodied tetrapods from the Chinle Formation, aided by methods such as screen washing [8,9], and that work is key to building a broader and more detailed picture of evolution across Pangea.

Among the small-bodied tetrapods that originated in the Triassic are the anurans and the larger clade that encompasses stem taxa, Salientia. Their earliest fossil record is restricted to two Early Triassic salientians from high latitudes in Pangea: Madagascar in the south (*Triadobatrachus massinoti*; [1,10,11]), and Poland in the north (*Czatkobatrachus*; [12,13]). The next oldest record, *Prosalirus bitis*, from

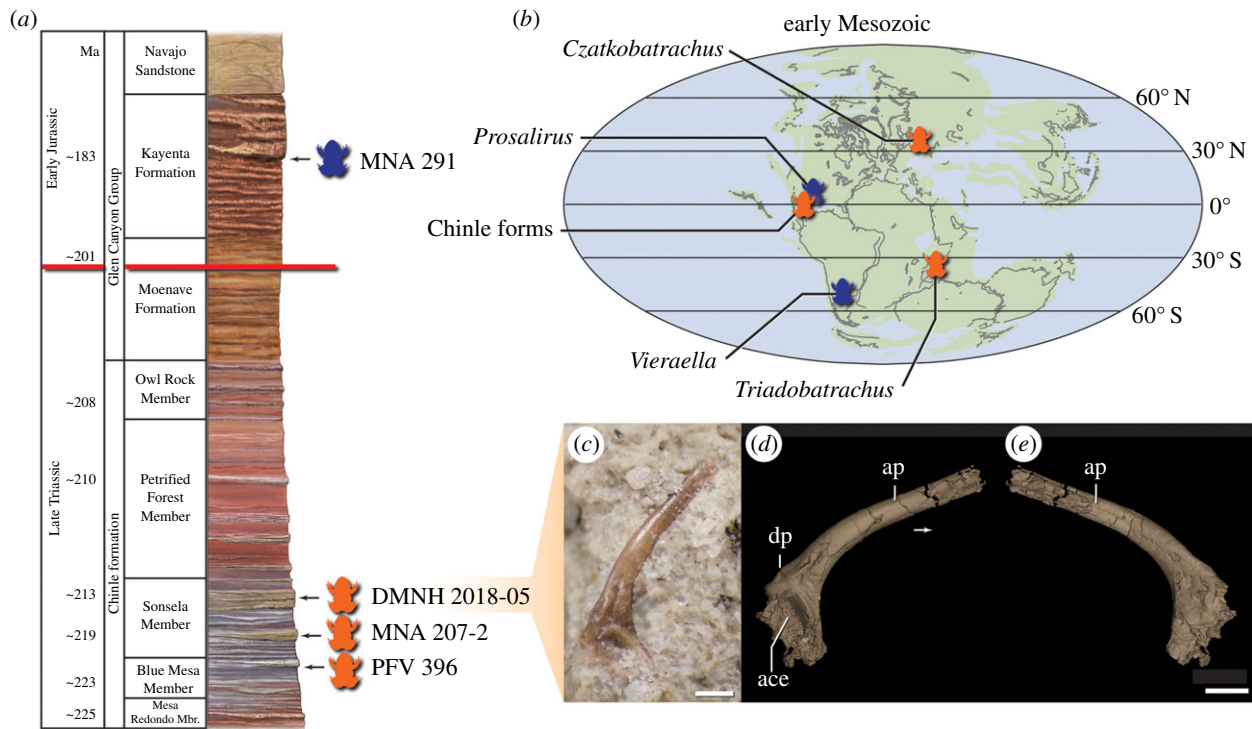


Figure 1. Time-calibrated stratigraphic and biogeographic distribution of Triassic Period and Jurassic Period anuran specimens. (a) Time-calibrated stratigraphic column for the Chinle Formation (Upper Triassic) and overlying Glen Canyon Group of the southwestern USA. Frog icons mark the stratigraphic position at which each specimen was collected; orange indicates a Triassic locality, whereas blue indicates the locality of the Jurassic *Prosalirus bitis*. (b) Palaeogeographic distribution of early Mesozoic salientian fossils. Orange icons indicate Triassic forms (*Czatkobatrachus*, *Triadobatrachus*, and the Chinle forms), whereas blue indicates Jurassic forms (*Prosalirus*, *Vieraella*). The Chinle exemplar, the right ilium DMNH 2018-05-0002, is shown in lateral view in photograph (c) and in lateral (d) and medial (e) CT surface images. Abbreviations: ace: acetabulum; ap: anterior process; dp: dorsal process. Small arrow in (d) indicates anterior direction. Scale bar equals 1.0 mm. (Online version in colour.)

the Early Jurassic Kayenta Formation of the Navajo Nation in the southwestern United States, ends an approximately 60 Myr gap in the frog fossil record. Furthermore, *Prosalirus* is hypothesized to represent the earliest bauplan associated with hopping locomotion in salientians [14,15] and shows that much of the transition from a plesiomorphic locomotor strategy to hopping remains unrecorded in the fossil record. Moreover, most time-calibrated molecular phylogenies suggest that crown-group anurans originated in the Late Triassic [16], but no fossils correspond to this important interval for anuran evolution.

Here, we partially fill this chronologic gap by describing the earliest salientian material from the equatorial regions of Pangea from the Upper Triassic (Chinle Formation, Arizona). Lithostratigraphic correlation of the primary specimen to dated horizons suggests a maximum depositional age between approximately 217 Ma and approximately 213 Ma [17,18], bridging previous Early Triassic and Early Jurassic records. This new material represents exceptionally small individuals (snout–vent length [SVL] of 20 mm or less), filling a chronological and geographical gap near the origin of crown-group anurans.

2. Systematic palaeontology

Lissamphibia Haeckel 1866

Batrachia Latreille 1800

Salientia Laurenti 1768

(a) Specimens

DMNH (Perot Museum of Nature and Science, Dallas, TX) 2018-05-0002: nearly complete right ilium (see electronic supplementary material, table S1 and [19] for data)

PEFO (Petrified Forest National Park) 41743: left ilium
MNA (Museum of Northern Arizona) V12365: left ilium
MNA V12366: left ilium
MNA V12369: partial maxilla

(b) Locality and age

Specimens were collected from three localities within the Chinle Formation: (1) a green conglomeratic lens (DMNH 2018-05) within the lower part of the Jim Camp Wash beds (Sonsela Member) south of PEFO dated to between ~ 217.7 Ma and 213.870 ± 0.078 Ma [20]; (2) a carbonate nodule-rich mudstone layer within the lower-middle portion of the Sonsela Member near St. Johns, Arizona, (*Placerias* Quarry, MNA 207-2) dated to 219.39 ± 0.16 Ma [20]; (3) a coprolitic horizon near Billing's Gap at PEFO ('Coprolite Layer', Petrified Forest Vertebrate locality (PFV) 396; see [9,21]) in the uppermost Blue Mesa Member (Chinle Formation) dated between 223.036 ± 0.059 and 220.123 ± 0.068 Ma [18]. See electronic supplementary material for collection method details.

(c) Description

In crown-group anurans, each ilium has an elongated shaft that extends roughly parallel to the urostyle and joins the sacral vertebra at its anteriormost end in a unique mobile joint in which the diapophysis of the sacrum overlies the ilium dorsally [22]. Furthermore, among tetrapods, anurans are unique in having an acetabulum located far posterior to the sacrum [23,24]. The material from the Chinle Formation, exemplified by DMNH 2018-05-0002, bears a combination of

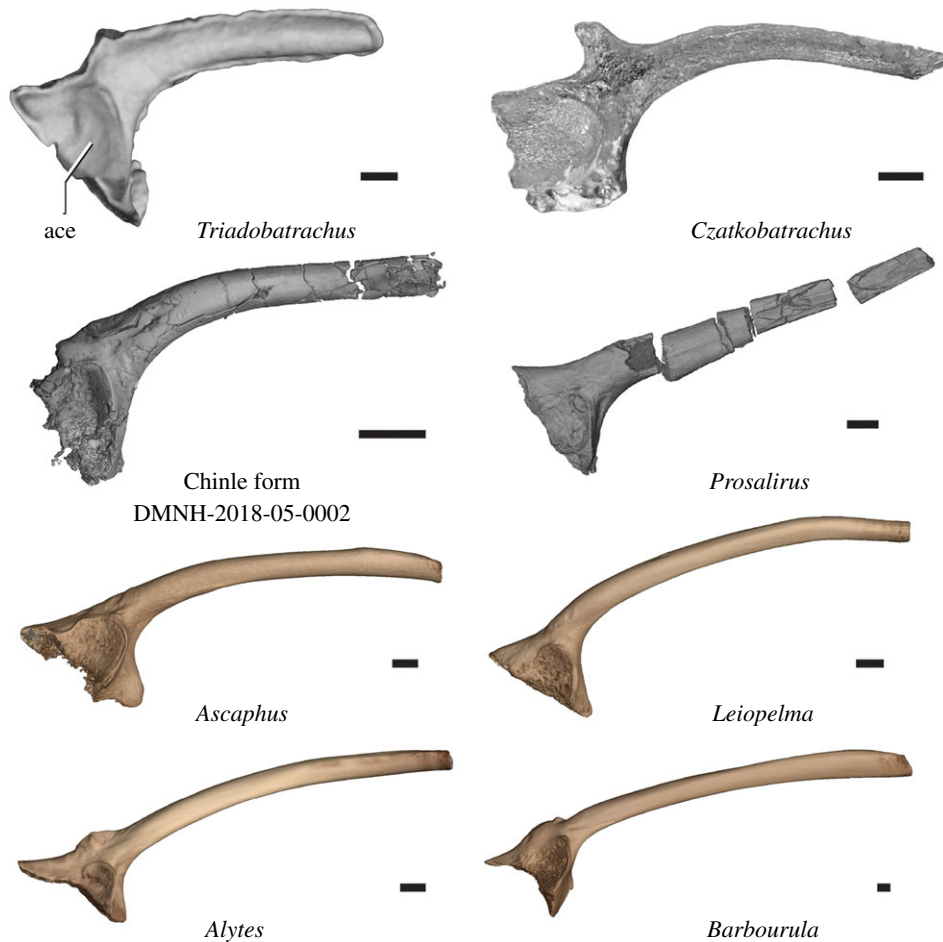


Figure 2. Comparisons of the primary Late Triassic specimen from the Chinle Formation (DMNH-2018-05-2002) to the ilia of stem anurans, including *Triadobatrachus* (MNHN-F-MAE126), *Czatkobatrachus* (ZPAL Ab IV/114; surface file shared by T. Sulej), *Prosalirus* (MCZ-VP-9324A) and extant anurans from the earliest diverging crown lineages, including *Ascaphus truei* (UF-Herp-80664), *Leiopelma hamiltoni* (CAS-Herp-53931), *Alytes obstetricans* (CAS-SU-21691) and *Barbourula busuangensis* (KU 309278). All figured in right lateral view with anterior to the right. Abbreviations: ace: acetabulum. Scale bar equals 1.0 mm. (Online version in colour.)

these characters that are unique to anurans, including an elongate and distally hollow iliac shaft that is directed anteriorly (figure 1), though this is also found in some stem-anuran salientian taxa such as *Czatkobatrachus*. Both extant and stem salamanders (Caudata) have compact ilia with short shafts and an acetabulum largely ventral to the shaft, and extant caecilians (Gymnophiona) lack both limbs and girdles [25]; no comparisons can be made with putative stem caecilians because they have no clearly identified pelvic material [26,27]. We rule out that these specimens belong to metoposaurids—a common Late Triassic clade found in the same deposits—because they possess distally hollow, and not solid, iliac blades, the acetabulum is offset rather than centered, in lateral view, the anteroventral edge of the iliac blade is concave rather than sigmoidal, and there is a tuber on the posterodorsal aspect of the acetabulum (the dorsal prominence) rather than a smooth surface (electronic supplementary material).

The ilia from the Chinle Formation have an elongate and distally hollow shaft that would have accommodated a cartilaginous tip in life and a posteriorly placed acetabulum. These ilia are distinctive in their small size (approx. 6.2 mm ilium length). If representing an adult individual, these would be similar in size to extant anurans typically considered miniature (less than 25 mm SVL; [28]). For instance, the miniature *Brachycephalus ephippium* [29] has a SVL of 17.1 mm and an ilium length of 7.2 mm (MCZ A-108655) and *Paedophryne amauensis*—perhaps the smallest extant frog [30]—has a

SVL of 7.9 mm and an ilium length of 3.6 mm (LSUMZ 95004). Though the posteroventral edge of the ilium posterior to the acetabulum is broken and missing, most of the acetabular region appears complete. The anterior margin of the acetabulum is well defined, similar to *Triadobatrachus*. The acetabulum does not appear to share the demarcated roughened area observed in *Notobatrachus* and *Triadobatrachus* [31]. The acetabulum in DMNH 2018-05-0002 thus is more similar to that of *Prosalirus* and extant anurans (figure 2). There is no ventral acetabular expansion as in some extant anurans (e.g. *Ascaphus*; figure 2). The anterodorsal tip of the iliac blade is slightly crushed but is assumed to be complete because it terminated within the matrix with no additional fragments. The elongated and anterodorsally curved iliac shaft lacks a dorsal crest and is squared-off at its anterior extent, similar to *Czatkobatrachus* [13]. Similar to *Prosalirus* and extant anurans, the shaft of the ilium in DMNH 2018-05-0002 is substantially longer than the anteroposterior length of the acetabular region, whereas it is approximately only three times longer in *Triadobatrachus* and *Czatkobatrachus* (figure 2; [23]). The dorsal prominence is barely discernable and located just anterodorsal to the acetabulum. It is much less prominent than that in either *Triadobatrachus* or *Czatkobatrachus*, and more similar to early-diverging crown-group anurans that generally lack this feature (figure 2; [23]).

The unique hopping locomotion of extant anurans is facilitated by elongate iliac shafts and a mobile sacroiliac joint, and

the palaeontological record indicates that these characteristics were present at least by the Early Jurassic [22]. The elongate iliac shaft of the Chinle frogs (figure 1) indicates at least that the acetabulum was displaced more posteriorly than in *Triadobatrachus* and *Czatkobatrachus* and revises the possibility of an origin of the mobile sacroiliac joint to the Late Triassic. The sacroiliac joint of *Triadobatrachus* is characterized by a posteriorly expanded sacral diapophysis that likely abutted the medial surface of the ilium [32]. This morphology defies categorization with respect to the crown-group anurans [1], though the joint seems unlikely to have been mobile. Similarly, the sacral diapophysis of *Czatkobatrachus* likely abutted the medial surface of the anterior iliac shaft [13]. By contrast, *Prosalirus* from the Early Jurassic likely had a mobile sacroiliac joint owing to the combination of an elongate iliac shaft and rod-like sacral diapophyses [14]. By the Middle Jurassic, stem anurans such as *Notobatrachus* certainly had a mobile sacroiliac joint as in extant anurans [31].

Additional possible salientian material from the Chinle Formation includes the posterior portion of a maxilla (MNA V12369) from the same locality as MNA V12365 and V12366. The maxilla fragment (electronic supplementary material, figure S1) appears to bear an undulating dorsal margin representing the ventral edge of the orbit [25] and the attachment sites and broken proximal portions of pedicellate teeth (see electronic supplementary material), a dentition unique to lissamphibians [25].

This earliest equatorial occurrence of salientians demonstrates that this group had a Pangean distribution during the early stages of their evolution in the Triassic. This equatorial record from the Chinle Formation (deposited between palaeolatitudes 5°S and 15°N; [33]) records a shifting palaeoclimate between a warm and humid megamonsoonal climate and an arid post-monsoonal climate [34] further affected by orbital eccentricities in the Early Jurassic [35]. That salientians are known from the overlying Kayenta Formation (*Prosalirus*; [14]) suggests they survived the aridification of this region in

the early Mesozoic. More broadly, frogs are traditionally viewed as members of the current ecosystem [36], not becoming diverse and widespread until the Jurassic as a consequence of the end-Triassic extinction [36]. The presence of these possible crown-group anurans in the Chinle Formation adds further to the Triassic origin of the living fauna, as predicted by molecular data [16], which then become more well-sampled later in the Mesozoic.

Data accessibility. CT scan data are available through www.morpho-source.org. See electronic supplementary material, table S1 for specifics and DOIs.

Authors' contributions. M.R.S., S.J.N. and W.G.P. conceived of the field study; M.R.S., S.J.N., B.T.K., A.D.M. and W.G.P. carried out the field and laboratory work, participated in data analysis, designed the study and drafted the manuscript; D.J.P. and D.C.B. collected CT data, participated in data analysis and drafted the manuscript. All authors gave final approval for publication and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Competing interests. The authors declare no competing interests.

Funding. David B. Jones Fund provided funding to M.R.S., S.J.N., B.T.K., A.D.M. and W.G.P. for fieldwork support. M.R.S., S.J.N. and B.T.K. were additionally funded by the Virginia Tech Department of Geosciences. B.T.K. was supported by the Petrified Forest Museum Association and the Friends of Petrified Forest National Park. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138 and DGE-1842473 to D.J.P. Digital comparative collections of anurans were made possible by NSF DBI-1701714 to D.C.B.

Acknowledgements. We thank our reviewers and the journal editorial board, Traegen Knight and family and Hunt Oil for land access, and the Perot Museum for curation support. We thank D. Germain (Muséum national d'Histoire naturelle, Paris) for making CT scans available of *Prosalirus* and T. Sulej (Institute of Paleobiology, Polish Academy of Sciences) for sharing a three-dimensional surface file of *Czatkobatrachus*. This is Petrified Forest National Park Paleontological Contribution #62. Views expressed herein are those of the authors and do not represent the views of the United States Government.

References

1. Ascarrunz E, Rage JC, Legreneur P, Laurin M. 2016 *Triadobatrachus massinoti*, the earliest known lissamphibian (Vertebrata: Tetrapoda) re-examined by μ CT scan, and the evolution of trunk length in batrachians. *Contrib. Zool.* **85**, 201–234.
2. Fraser NC, Sues H-D. (eds). 1994 *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge, UK: Cambridge University Press.
3. Langer MC, Ezcurra MD, Bittencourt JS, Novas FE. 2010 The origin and early evolution of dinosaurs. *Biol. Rev.* **85**, 55–110. (doi:10.1111/j.1469-185X.2009.00094.x)
4. Simões TR et al. 2018 The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature* **557**, 706–709. (doi:10.1038/s41586-018-0093-3)
5. Borsuk-Białynicka M, Cook E, Evans SE, Maryańska T. 1999 A microvertebrate assemblage from the Early Triassic of Poland. *Acta Palaeontol. Pol.* **44**, 167–188.
6. Schoch RR, Seegis D. 2016 A Middle Triassic palaeontological gold mine: the vertebrate deposits of Vellberg (Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **459**, 249–267. (doi:10.1016/j.palaeo.2016.07.002)
7. Sues H-D, Olsen PE, Kroehler PA. 1994 Small tetrapods from the Upper Triassic of the Richmond Basin (Newark Supergroup), Virginia. In *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods* (eds NC Fraser, H-D Sues), pp. 161–170. Cambridge, UK: Cambridge University Press.
8. Heckert AB. 2004 *Late Triassic microvertebrates from the lower Chinle Group (Otschalkian-Adamanian: Carnian), southwestern USA*. New Mexico Museum of Natural History and Science Bulletin 27.
9. Kligman BT, Marsh AD, Parker WG. 2018 First records of diapsid *Palacrodon* from the Norian, Late Triassic Chinle Formation of Arizona, and their biogeographic implications. *Acta Palaeontol. Pol.* **63**, 117–127. (doi:10.4202/app.00426.2017)
10. Piveteau J. 1936 Une forme ancestrale des Amphibiens Anoures dans le Trias inférieur de Madagascar. *Comptes Rendus de l'Académie des Sciences* **102**, 1607–1608.
11. Rage J-C, Roček Z. 1989 Redescription of *Triadobatrachus massinoti* (Piveteau, 1936) an anuran amphibian from the Early Triassic. *Palaeontogr. A* **206**, 1–16.
12. Evans SE, Borsuk-Białynicka M. 1998 A stem-group frog from the Early Triassic of Poland. *Acta Palaeontol. Pol.* **43**, 573–580.
13. Evans SE, Borsuk-Białynicka M. 2009 The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontol. Pol.* **65**, 79–105.
14. Jenkins FA, Shubin NH. 1998 *Prosalirus bitis* and the anuran caudopelvic mechanism. *J. Vertebr. Paleontol.* **18**, 495–510. (doi:10.1080/02724634.1998.10011077)
15. Reilly SM, Jorgensen ME. 2011 The evolution of jumping in frogs: morphological evidence for the basal anuran locomotor condition and the radiation of locomotor systems in crown group anurans. *J. Morphol.* **272**, 149–168. (doi:10.1002/jmor.10902)

16. Feng Y-J *et al.* 2017 Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. *Proc. Natl Acad. Sci. USA* **114**, E5864–E5870. (doi:10.1073/pnas.1704632114)
17. Parker WG, Martz JW. 2010 The Late Triassic (Norian) Adamanian–Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona. *Earth Environ. Sci. Trans. R. Soc. Edinburgh* **101**, 231–260. (doi:10.1017/S1755691011020020)
18. Ramezani J *et al.* 2011 High-precision U–Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. *Geol. Soc. Am. Bull.* **123**, 2142–2159. (doi:10.1130/B30433.1)
19. Stocker MR *et al.* 2019 Data from: the earliest equatorial record of frogs from the Late Triassic of Arizona. *Morphosource*. (doi:10.17602/M2/M55545)
20. Ramezani J, Fastovsky DE, Bowring SA. 2014 Revised chronostratigraphy of the lower Chinle Formation strata in Arizona and New Mexico (USA): high-precision U–Pb geochronological constraints on the Late Triassic evolution of dinosaurs. *Am. J. Sci.* **314**, 981–1008. (doi:10.2475/06.2014.01)
21. Kligman BT, Parker WG, Marsh AD. 2017 First record of *Saurichthys* (Actinopterygii) from the Upper Triassic (Chinle Formation, Norian) of western North America. *J. Vertebr. Paleontol.* **37**, e1367304. (doi:10.1080/02724634.2017.1367304)
22. Shubin NH, Jenkins Jr FA. 1995 An Early Jurassic jumping frog. *Nature* **377**, 49–52. (doi:10.1038/377049a0)
23. Gómez RO, Turazzini GF. 2016 An overview of the ilium of anurans (Lissamphibia, Salientia), with a critical appraisal of the terminology and primary homology of main ilial features. *J. Vertebr. Paleontol.* **36**, e1030023. (doi:10.1080/02724634.2015.1030023)
24. Ročková H, Roček Z. 2005 Development of the pelvis and posterior part of the vertebral column in the Anura. *J. Anat.* **206**, 17–35. (doi:10.1111/j.0021-8782.2005.00366.x)
25. Carroll RL. 2009 *The rise of amphibians: 365 million years of evolution*, p. 360. Baltimore, MD: The Johns Hopkins University Press.
26. Jenkins FAJ, Walsh DM, Carroll RL. 2007 Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic. *Bull. Mus. Comp. Zool.* **158**, 285–365. (doi:10.3099/0027-4100(2007)158[285:AOEMAL]2.0.CO;2)
27. Pardo JD, Small BJ, Huttenlocker AK. 2017 Stem caecilian from the Triassic of Colorado sheds light on the origins of Lissamphibia. *Proc. Natl Acad. Sci. USA* **114**, E5389–E5395. (doi:10.1073/pnas.1706752114)
28. Yeh J. 2002 The effect of miniaturized body size on skeletal morphology in frogs. *Evolution* **56**, 628–641. (doi:10.1111/j.0014-3820.2002.tb01372.x)
29. Truab L, Alberch P. 1985 Miniaturization and the anuran skull: a case study of heterochrony. *Vertebr. Morphol.* **30**, 113–121.
30. Rittmeyer EN, Allison A, Gründler MC, Thompson DK, Austin CC. 2012 Ecological guild evolution and the discovery of the world's smallest vertebrate. *PLoS ONE* **7**, e29797. (doi:10.1371/journal.pone.0029797)
31. Báez AM, Nicoli L. 2004 A new look at an old frog: the Jurassic *Notobatrachus* Reig from Patagonia. *Ameghiniana* **41**, 257–270.
32. Roček Z, Rage J-C. 2000 Proanuran stages (*Triadobatrachus*, *Czatkobatrachus*). In *Amphibian biology* **4** (eds H Heatwole, RL Carroll), pp. 1283–1294. Surrey, UK: Beatty & Sons.
33. Zeigler KE, Geissman JW. 2011 Magnetostratigraphy of the Upper Triassic Chinle Group of New Mexico: implications for regional and global correlations among Upper Triassic sequences. *Geosphere* **7**, 802–829. (doi:10.1130/GES00628.1)
34. Nordt LC, Atchley SC, Dworkin SI. 2015 Collapse of the Late Triassic megamonsoon in western equatorial Pangea, present-day American Southwest. *Geol. Soc. Am. Bull.* **127**, 1798–1815. (doi:10.1130/B31186.1)
35. Kent DV *et al.* 2018 Empirical evidence for stability of the 405-kiloyear Jupiter–Venus eccentricity cycle over hundreds of millions of years. *Proc. Natl Acad. Sci. USA* **115**, 6153–6158. (doi:10.1073/pnas.1800891115)
36. Evans SE, Milner AR. 1994 Middle Jurassic microvertebrate assemblages from the British Isles. In *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods* (eds NC Fraser, H-D Sues), pp. 303–321. Cambridge, UK: Cambridge University Press.