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Palaeontology

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

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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

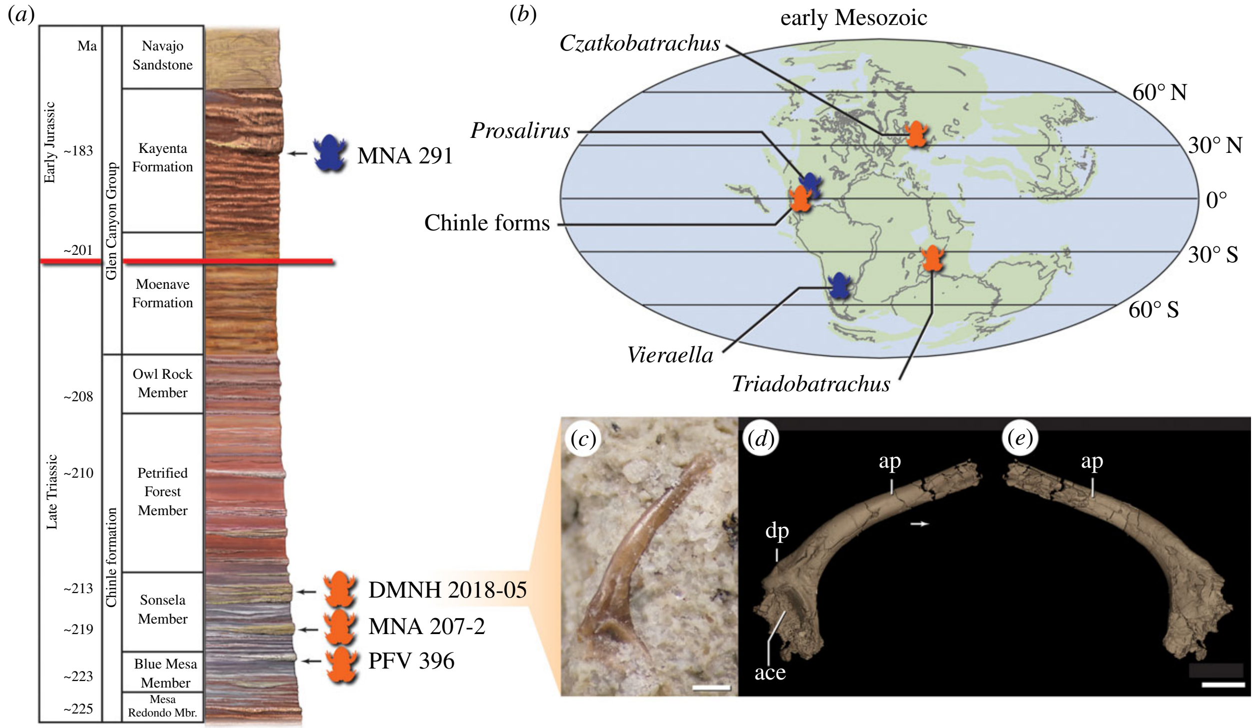

Figure 1. Time-calibrated stratigraphic and biogeographic distribution of Triassic Period and Jurassic Period anuran specimens. (*a*) Time-calibrated stratigraphic column for the Chinle Formation (Upper Triassic) and overlying Glen Canyon Group of the southwestern USA. Frog icons mark the stratigraphic 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

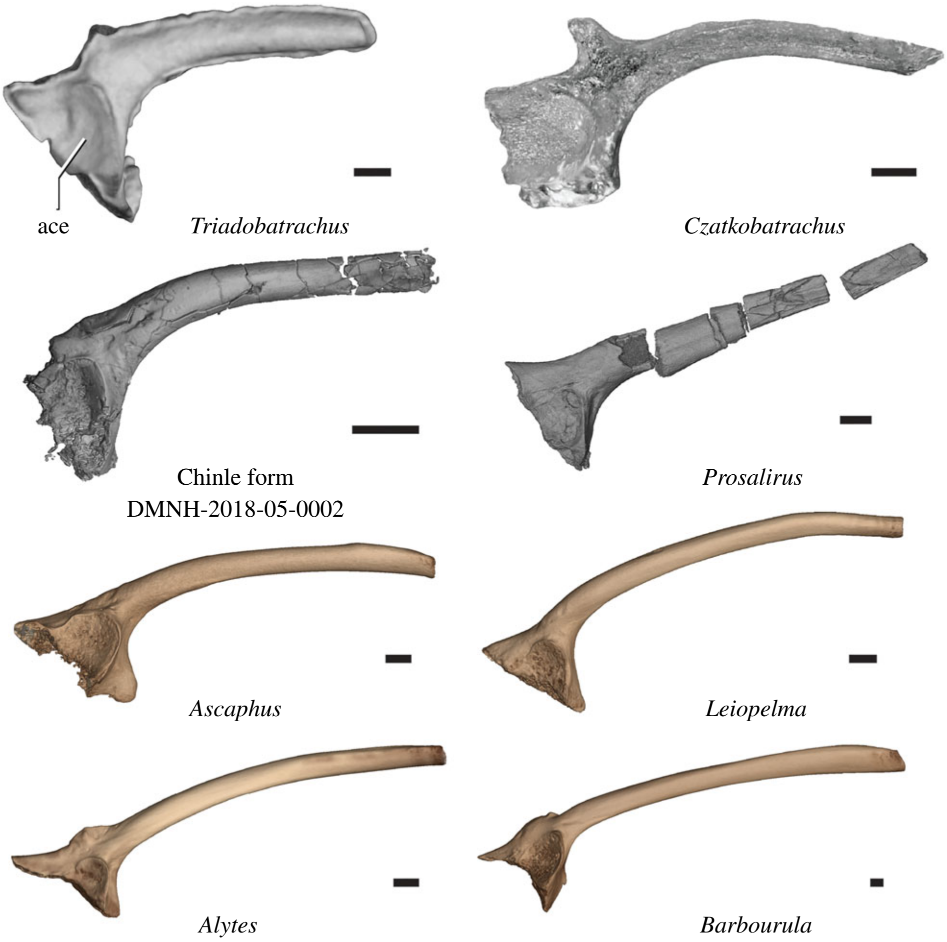

Figure 2. Comparisons of the primary Late Triassic specimen from the Chinle Formation (DMNH-2018-05-2002) to the ilia of stem anurans, including *Triadobatrachus* (MNHN-F-MAE126), *Czatkobatrachus* (ZPAL Ab IV/114; surface file shared by T. Sulej), *Prosalirus* (MCZ-VP-9324A) and extant anurans from the earliest diverging crown lineages, including *Ascaphus truei* (UF-Herp-80664), *Leiopelma hamiltoni* (CAS-Herp-53931), *Alytes obstetricans* (CAS-SU-21691) and *Barbourula busguangensis* (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.morphosource.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.

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