

# A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders

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The origin of extant amphibians (Lissamphibia: frogs, salamanders and caecilians) is one of the most controversial questions in vertebrate evolution, owing to large morphological and temporal gaps in the fossil record<sup>1–3</sup>. Current discussions focus on three competing hypotheses: a monophyletic origin within either Temnospondyli<sup>4–7</sup> or Lepospondyli<sup>8–10</sup>, or a polyphyletic origin with frogs and salamanders arising among temnospondyls and caecilians among the lepospondyls<sup>11–16</sup>. Recent molecular analyses are also controversial, with estimations for the batrachian (frog–salamander) divergence significantly older than the palaeontological evidence supports<sup>17,18</sup>. Here we report the discovery of an amphibamid temnospondyl from the Early Permian of Texas that bridges the gap between other Palaeozoic amphibians and the earliest known salientians<sup>19,20</sup> and caudatans<sup>21</sup> from the Mesozoic. The presence of a mosaic of salientian and caudatan characters in this small fossil makes it a key taxon close to the batrachian (frog and salamander) divergence. Phylogenetic analysis suggests that the batrachian divergence occurred in the Middle Permian, rather than the late Carboniferous as recently estimated using molecular clocks<sup>18,22</sup>, but the divergence with caecilians corresponds to the deep split between temnospondyls and lepospondyls, which is congruent with the molecular estimates.

Tetrapoda Haworth, 1825

Temnospondyli Zittel, 1888

Amphibamidae Moodie, 1909

*Gerobatrachus hottoni* gen. et sp. nov.

## Holotype

United States National Museum of Natural History (Smithsonian Institute) (USNM) 489135. Discovered by P. Kroehler, a Museum Specialist at the USNM.

## Etymology

*Geros* (Greek), meaning aged or elder, and *batrachus* (Greek), meaning frog. Specific epithet is in honour of the late N. Hotton, vertebrate palaeontologist from the USNM.

## Locality and horizon

Locality number USNM 40971, 'Don's Dump Fish Quarry', Clear Fork Group, Baylor County, Texas, USGS Soap Creek 7.5' quad. More specific locality information is on file at the USNM.

## Age

Early Permian, Leonardian.

## Diagnosis

Amphibamid temnospondyl with 21 tiny pedicellate teeth on the premaxilla, and 17 presacral vertebrae; shares with crown group

salamanders a *basale commune* (combined distal tarsals 1 and 2) and tuberculum interglenoideum ('odontoid process') on atlas; shares with salientians and caudates an anteroposteriorly reduced vomer; shares with *Triadobatrachus* and crown group frogs a rod-like, laterally directed palatine; shares with *Karaurus*, *Triadobatrachus* and crown group frogs a broad skull, shortened presacral vertebral column; shares with most temnospondyls, frogs and basal salamanders a pedal phalangeal formula of ?-2-3-4-3; shares with frogs, *Amphibamus*, *Doleserpeton*, *Platyrhinops* and *Eoscopus* a large otic notch closely approaching the orbit; shares with frogs, salamanders, caecilians, *Amphibamus*, *Tersomius* and *Doleserpeton* pedicellate teeth; shares with *Amphibamus*, *Doleserpeton* and *Platyrhinops* a foreshortened supratemporal; shares with *Amphibamus*, *Doleserpeton*, frogs and salamanders a foreshortened parasphenoid basal plate with wide lateral processes.

The holotype and only known specimen of *Gerobatrachus hottoni* was found in a two foot thick lens of fine-grained red siltstone sitting on the top of a knob, which was subsequently entirely excavated. The 110-mm-long specimen (Fig. 1) is preserved fully articulated in ventral view, and is missing only the stylopods, zeugopods, and ventral portions of the skull and pectoral girdle.

Most strikingly, the broad skull shape, the greatly enlarged vacuities on the palate, and the shortened vertebral column and tail give the immediate impression of a Palaeozoic batrachian. The premaxilla bears at least 21 small, pedicellate, monocuspid teeth that are not labiolingually compressed (Figs 2, 3a), a remarkable number for such a small element, and similar to the condition in batrachians. The frontals flare laterally at their anterior margin, as in derived amphibamids, and formed the dorsal orbital margin. The presence of a large parietal foramen near the frontoparietal suture indicates that this skeleton belonged to a juvenile individual (Fig. 2). The postparietals are surprisingly long elements in *Gerobatrachus*, but this unusual condition can be attributed to their exposure in internal view in this skull. Tabulars are restricted to the posterolateral corners of the skull table, and bear a hook-like posterior process, or 'horn', that extends posterior to the presumed location of the occiput.

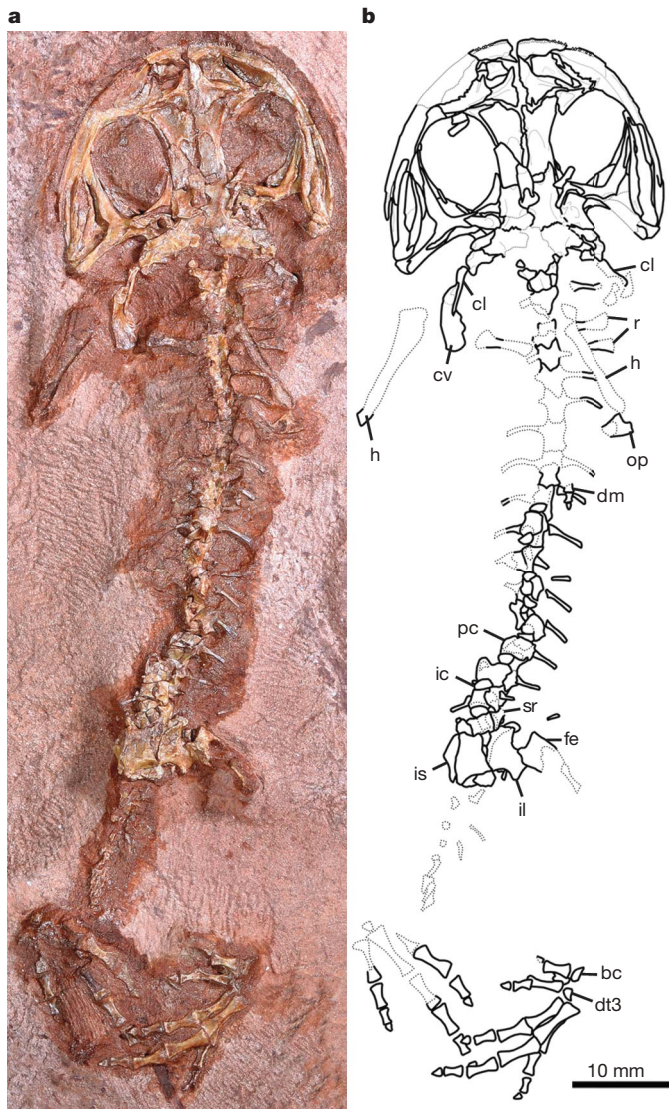
The palate and braincase are only partially preserved, but the exposed portions show several batrachian features. The vomer is anteroposteriorly narrow (not a broad plate as in other amphibamids), lacks palatal fangs, and has teeth restricted to a few rows on a raised patch along the medial margin of the choana. At its posterolateral extremity a portion of the rod-like, laterally directed palatine can be seen, a feature seen in *Triadobatrachus* and most crown group frogs<sup>20,23</sup>. Dorsal to the basicranial process of the salientian-like pterygoid, a small, rod-like, anterior projection is present, identical to epipterygoids described in the archaeobatrachian *Leipelma*<sup>24</sup>. The pterygoid is prevented from reaching the lateral margin of the palate

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(except, perhaps, by an overlapping dorsal process) by a medially projecting process of the ectopterygoid. The parabasisphenoid complex is fragmentary, preserving only portions of the basicranial articulation, and a portion of the cultriform process; however, the overall shape of the parasphenoid plate can be determined to have been much wider than long, as is common for amphibamids, branchiosaurids, frogs and salamanders.

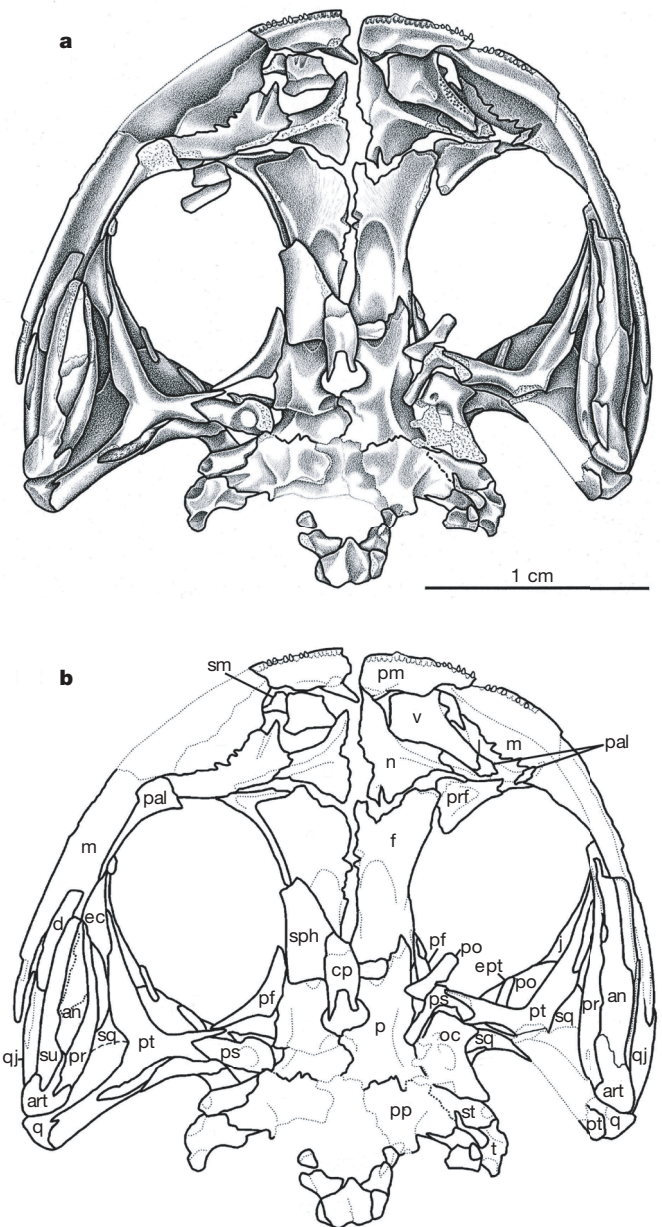
*Gerobatrachus* has 17 presacral vertebrae, which is transitional in number between other derived amphibamids (~21) and the salientian *Triadobatrachus* (14)<sup>20</sup> and caudatans *Karaurus* and *Chunerpeton* (14–15)<sup>21,25</sup>. As in salamanders, an anteriorly directed tuberculum interglenoideum of the atlas centrum is present, and at least the posterior vertebrae have narrow intercentra between holospondylous pleurocentra. Caudal vertebrae are very poorly ossified, similar to the condition seen in *Triadobatrachus* and some salamanders. The olecranon process of the ulna is surprisingly well-ossified for the inferred young ontogenetic stage of this specimen. The ilium lacks the posterior process common to temnospondyls but the presence of an anterior process, a salientian character, is obscured by an overlying fragment of the femur. An element identified as a sacral rib



**Figure 1** | *Gerobatrachus hottoni*, gen. et sp. nov., holotype specimen USNM 489135. Complete specimen in ventral view, photograph (left) and interpretive outline drawing (right). Abbreviations: bc, *basale commune*; cl, cleithrum; cv, clavicle; dm, digital elements of the manus; dt3, distal tarsal 3; fe, femur; h, humerus; ic, intercentrum; il, ilium; is, ischium; op, olecranon process of ulna; pc, pleurocentrum; r, radius; sr, sacral rib.

is located cranial to the ischial plate's anterior margin (Fig. 1), suggesting that a short anterior process might have been present. As in basal batrachians, the pubis is unossified.

Only two tarsal elements are present (Fig. 3b). A small, weakly ossified third distal tarsal is in articulation with the third metatarsal. At the base of the left first and second metatarsals is an elongate distal tarsal bone, broadly rounded distally but with a straighter margin proximally. Its position and large size is nearly identical with the combined distal tarsals 1 and 2, also called the *basale commune*, previously known exclusively in Caudata. While large enough to articulate with the proximal surfaces of metatarsals 1 and 2, it would



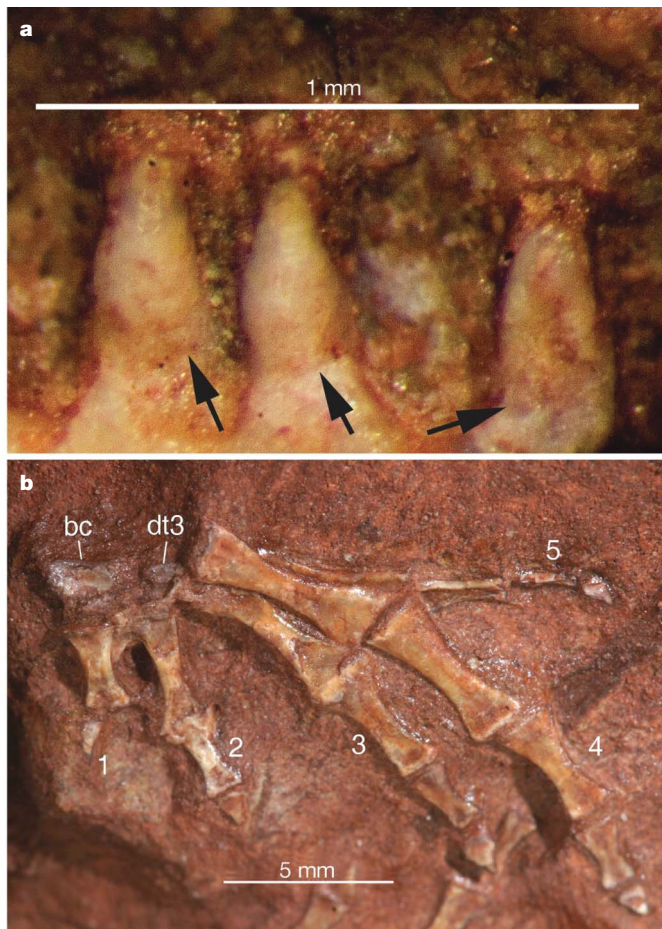
**Figure 2** | *Gerobatrachus hottoni*, gen. et sp. nov., holotype specimen USNM 489135. a, Close-up interpretive specimen, and b, outline drawing of skull in ventral view. Abbreviations are the same as for Fig. 1 and: an, angular; art, articular; cp, cultriform process of parasphenoid; d, dentary; ec, ectopterygoid; ept, epipterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; oc, portion of otic capsule; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; pr, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sm, septomaxilla; sph, sphenethmoid; sq, squamosal; st, supratemporal; su, surangular; t, tabular; v, vomer.



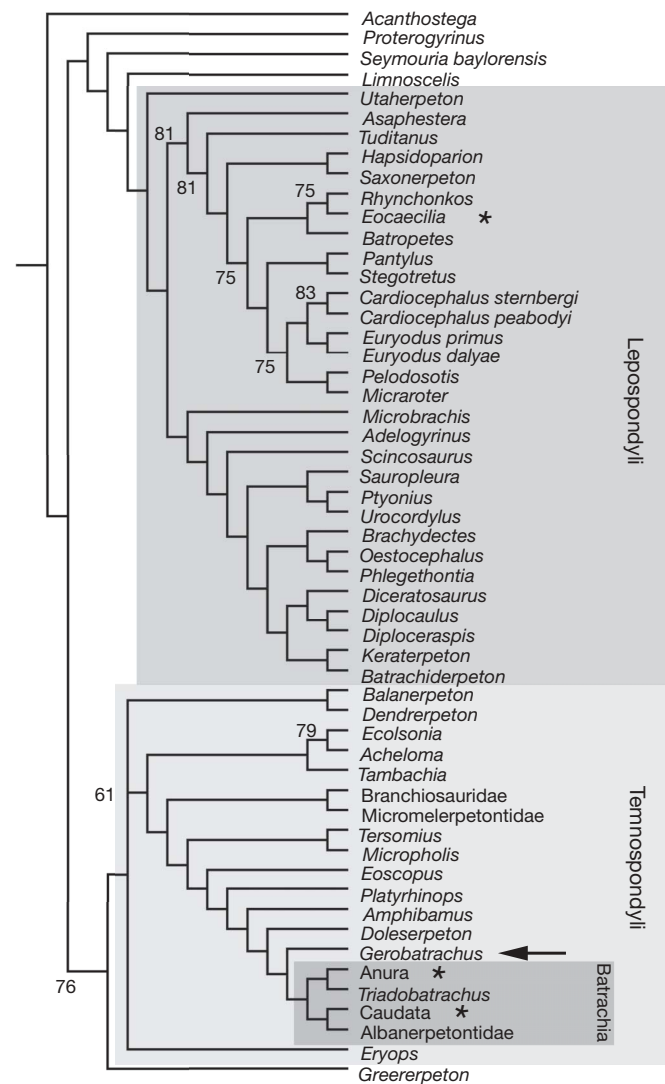
not do so completely, which is also the condition seen in salamanders. In extant salamanders the *basale commune* ossifies precociously<sup>26,27</sup>, a pattern that is consistent with this element being one of the only ossified tarsals in the juvenile skeleton of *Gerobatrachus*. Furthermore, the *basale commune* is the first mesopodial element to form during the initial mesenchymal condensation and chondrification and is a starting point for the establishment of the digital arch in a preaxial position, with subsequent condensations continuing post-axially<sup>27</sup>. This general directionality is mirrored by the subsequent ossification. Amniotes and frogs, on the contrary, ossify proximal mesopodial elements first, and then the distal postaxial elements, with the digital arch developing in a postaxial-to-preaxial direction. The presence of the *basale commune* and a more poorly ossified distal tarsal 3 as the only ossified mesopodial elements in *Gerobatrachus* suggests that it also may have had preaxial digital development. If our interpretations are correct, the preaxial pattern of digital development is either independently derived in *Gerobatrachus* and salamanders, or primitive in batrachians but reversed in frogs. Knowledge of development in fossil taxa is always inferential, especially when based on a single specimen, but our speculative hypothesis is testable with a more complete developmental series of either *Gerobatrachus* or another amphibamid. A preaxial pattern of digital development has recently been demonstrated in branchiosaurids<sup>28</sup>, which are thought to be closely related to, if not included within, Amphibamidae (Fig. 4), but branchiosaurids lack ossified carpals and tarsals and thus it remains unknown if they possessed a *basale*

*commune*. This observation, however, may support the possibility that preaxial development is primitive for batrachians (and more basal amphibamids), and will be the subject of future research.

We conducted a new phylogenetic analysis of basal tetrapod relationships to determine the placement of *Gerobatrachus* and test lissamphibian monophyly. A large matrix of lepospondyl relationships<sup>11</sup>, as recently modified<sup>12</sup>, was combined with a matrix of amphibamid relationships<sup>29</sup>. Duplicate characters were examined for inconsistencies in coding, which were rescored (based on direct observation of specimens whenever possible) if present, and then the duplicates were deleted. Redundant taxa were removed from the analysis. The number of taxa was further reduced to decrease computation time by eliminating highly fragmentary lepospondyl species. The final matrix (see Supplementary Information), containing 54 taxa and 219 characters, was subjected to parsimony analysis in PAUP\* 4.0b10. One hundred heuristic replicates (TBR branch swapping on shortest trees, random addition sequence) found 131 most parsimonious trees 1,125 steps long (consistency index 0.250, retention index 0.587; statistics calculated by PAUP\*).



**Figure 3 | *Gerobatrachus hottoni*, gen. et sp. nov., holotype specimen USNM 489135. a**, Close-up of left premaxillary teeth in lingual view, showing the presence of the dividing zone of poor ossification that separates the tooth cusp from the pedicel (indicated by arrows). **b**, Close-up photograph of the left pes, with the digital identification indicated by numbering. Abbreviations are the same as previous.



**Figure 4 | Majority rule consensus tree of 131 most parsimonious trees.** Numbers indicate the percentages of trees in which the given node appears, unnumbered nodes represent appearance in all trees. Lissamphibian taxa are indicated by \*, and *Gerobatrachus* is highlighted by an arrow. Recovery of lissamphibian monophyly within temnospondyls requires an additional 24–27 steps (Batrachia and Procera topologies, respectively), and recovery of lissamphibian monophyly within lepospondyls takes 30 additional steps.

Our analysis finds *Gerobatrachus* to be the immediate sister taxon to Batrachia (Fig. 4), with the amphibamids *Doleserpeton*, *Amphibamus* and *Platyrhinops* as successively more basal taxa. In addition, the oldest known caecilian *Eocaecilia* falls within recumbirostrine lepospondyls, sister group to *Rhynchonkos* and, one step further out, the brachystelechids. Thus, the available morphological evidence supports the hypothesis of a diphyletic origin of extant amphibians from Palaeozoic tetrapods, with a separate origin of the limbless, largely fossorial caecilians from within the lepospondyls, whereas Batrachia originates within Temnospondyli.

The discovery of a stem batrachian in the Early Permian places a new lower limit on the divergence between frogs and salamanders. *Gerobatrachus* is undeniably derived in comparison with other amphibamids, and therefore is most plausibly a recent addition to the Early Permian fauna, and not a relict form. The upper bound on the divergence is the occurrence of *Triadobatrachus* in the Triassic, so the divergence itself must have occurred between then and some point after the Early Permian, possibly the Middle Permian—(270–260) ± 0.7 Myr ago—considering the number of derived features *Gerobatrachus* shares with batrachians. Recent divergence estimates based on molecular clocks<sup>17,18</sup> are much older, placing this divergence in the late Carboniferous—308 ± 20 Myr ago<sup>18</sup>, and 357 ± 40 Myr ago<sup>17</sup>—although more recent unpublished estimates are much younger (D. San Mauro and D. Wake, personal communication). However, our finding of a diphyletic origin of lissamphibians places the divergence of batrachians and caecilians much earlier in tetrapod history, at the split between temnospondyls and lepospondyls. The minimum divergence of this event is 328–335 Myr ago, when the first temnospondyls and lepospondyls appear in the fossil record, which is much more consistent with the molecular estimates than implied by either of the monophyly hypotheses<sup>30</sup>.

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Supplementary Information is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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