

# First occurrence of a frog-like batrachian (Amphibia) in the Late Triassic Fleming Fjord Group, central East Greenland

VALERIAN J.P. JÉBUS, OCTÁVIO MATEUS, JESPER MILÀN & LARS B. CLEMMENSEN



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During the Triassic, Batrachia diverged into ancestors of frogs (Salientia) and salamanders (Caudata). Fossils of Triassic batrachians are rare and found only in a few outcrops, such as the Middle Sakamena Formation of Madagascar (Induan). Only three Triassic taxa have been described, the two early frogs *Triadobatrachus* and *Czatkobatrachus* and the early salamander *Triassurus*. Here we describe a right ilium, collected in 1991, attributed to the first batrachian from the Late Triassic Carlsberg Fjord Member (Ørsted Dal Formation, Fleming Fjord Group) in the Jameson Land Basin, located in central East Greenland. The fossil specimen only displays the proximal part of a right ilium, missing its shaft. After a thorough comparison with several clades (lizards, temnospondyls, salamanders and frogs), we consider the specimen as a lissamphibian sharing feature with salientians and anurans: squarish acetabular region, deeply concave acetabular surface, laterally projecting acetabular rim, flat mesial surface. It is the youngest Triassic specimen of Batrachia to date and one of the northernmost of the Late Triassic.

Supplementary file: Features potentially used for differentiating ilia of anurans and urodeles with updated nomenclature and specimen NHMD-154502, *Triadobatrachus*, *Czatkobatrachus*, *Triassurus* and *Kokartus*. <https://doi.org/10.37570/bgsd-2022-70-08s1>

**Keywords:** Lissamphibia, frogs, salamanders, ilium, Late Triassic, Fleming Fjord Group.

Valerian J. P. Jébus [[valerian.jesus@mail.com](mailto:valerian.jesus@mail.com)], Museu da Lourinhã 2530-158 Lourinhã, Portugal. Octávio Mateus [[omateus@fct.unl.pt](mailto:omateus@fct.unl.pt)], GEOBIOTEC, Departamento de Ciências da Terra, FCT-UNL Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Portugal & Museu da Lourinhã, Portugal. Jesper Milàn [[jesperm@oesm.dk](mailto:jesperm@oesm.dk)], Geomuseum Faxe, Østsjælland Museum, Rådhusvej 2, DK-4640 Faxe, Denmark. Lars B. Clemmensen [[larsc@ign.ku.dk](mailto:larsc@ign.ku.dk)], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

Late Triassic lake and fluvial deposits from the Jameson Land Basin of central East Greenland have provided many vertebrates (e.g. Jenkins *et al.* 1994; Clemmensen *et al.* 2016; Agnolin *et al.* 2018; Marzola *et al.* 2018; Sulej *et al.* 2020; Beccari *et al.* 2021). In addition, trackways of archosaurs, including dinosaurs, are known from the same deposits (Jenkins *et al.* 1994; Klein *et al.* 2016; Lallensack *et al.* 2017), as well as coprolites (Hansen *et al.* 2016; Milàn *et al.* 2021) and abundant invertebrate trace fossils (Bromley & Asgaard 1979).

There have been several expeditions to study the Late Triassic deposits of the Jameson Land Basin in East Greenland since the 19th century (Marzola *et al.* 2018). Many expeditions focused on Mesozoic strata in Jameson Land during the late 1960s and early 1970s, leading to the discovery of rare vertebrate fossils from Triassic deposits, most of them being temnospondyl remains (Clemmensen 1980b). From 1988 to 2001, the Late Triassic of the Jameson Land Basin was the subject of successive vertebrate palaeontological expeditions to sample fossil tetrapods by Harvard University

(HU), Massachusetts, USA, in collaboration with the University of Copenhagen (UC), Denmark and the Natural History Museum of Denmark (NHMD). The team from the 1991 expedition recovered a large number of vertebrate fossils. Among them, we identify and describe an amphibian ilium in this paper.

The Triassic period witnessed the development and appearance of most tetrapod groups that constitute modern vertebrate fauna, such as mammaliaforms, squamates, crocodylomorphs and lissamphibians (Jenkins *et al.* 1997; Irmis *et al.* 2013; Ascarrunz *et al.* 2016; Simões *et al.* 2018; Sulej *et al.* 2020).

However, Batrachia Latreille, 1800 is rarely preserved in the fossil record from the first half of the Mesozoic. The cladogenesis of Anura Duméril, 1805 (frogs) and Urodela Duméril, 1806 (salamanders) is obscure, and their divergence is still debated but often estimated as Early Permian (Pyron 2011; Marjanović & Laurin 2014, 2019). The earliest batrachians have been recovered in the Olenekian of Madagascar, with the sub-complete specimen *Triadobatrachus massinoti* (Piveteau, 1936) and Poland, with disarticulated remains of *Czatkobatrachus polonicus* Evans & Borsuk-Białynicka, 1998. Both are members of the clade Salientia Laurenti, 1768, also known as proto-frogs (Piveteau 1936; Evans & Borsuk-Białynicka 1998, 2009a; Rage & Roček 1989; Ascarrunz *et al.* 2016). In Kyrgyzstan, the earliest Caudata Scopoli, 1777 (proto-salamanders) is *Triassurus sixtelae* Ivakhnenko, 1978, known from Middle to Upper Triassic (Ladinian/Carnian), with two reasonably complete specimens (Ivakhnenko 1978; Schoch *et al.* 2020). Recently, some new specimens of Salientia have been reported from the lower part of the Tiki Formation of India (possible Carnian in age), an incomplete jaw of an indeterminate *Eodiscoglossus* sp. (Kumar & Sharma 2019) and from the Chinle Formation of the United States, in Arizona, consisting of several ilia and a partial maxilla from the Late Triassic (Carnian/Norian; Stocker *et al.* 2021). The indeterminate *Eodiscoglossus* sp. identification remains dubious based on the resemblance of the material to one of Grigorescu *et al.* (1999), which had been later reassigned to *Paralatonia transylvanica* Venczel & Csiki, 2003 (see Venczel *et al.* 2016).

Here, we describe the first batrachian remains from the Carlsberg Fjord Member (Ørsted Dal Formation) in the Late Triassic Fleming Fjord Group in the Jameson Land Basin in central East Greenland (Clemmensen *et al.* 2020). This find adds new knowledge to the palaeogeographical distribution of the clade and adds to the diversity of the Late Triassic Greenland vertebrate fauna.

## Taxonomic definition

Batrachia includes Salientia (frogs and proto-frogs) and Caudata (salamanders and proto-salamanders).

Salientia includes Anura (extant frogs) and every taxon closer to Anura than Urodela (Milner 1988).

Caudata includes Urodela (extant salamanders) and every taxon closer to Urodela than Anura (Milner 1988).

## Geological setting

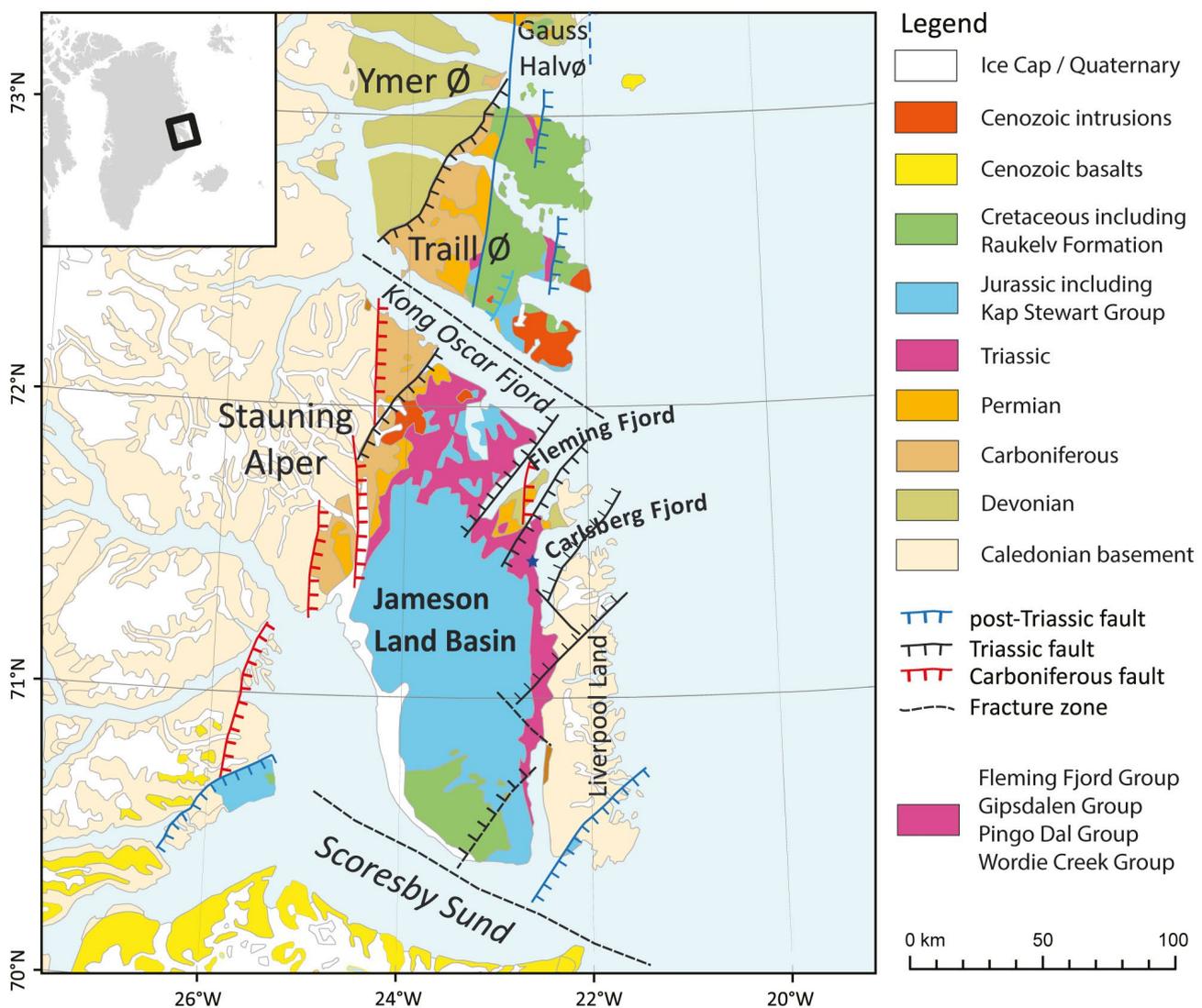
The Jameson Land Basin is situated in Jameson Land and Scoresby Land in central East Greenland, around 71° N (Clemmensen *et al.* 2020; Fig. 1). Its boundaries are the Stauning Alper in the west, the Liverpool Land area in the east, the fracture zones in the Kong Oscar Fjord region in the north and the Scoresby Sund in the south (Guarnieri *et al.* 2017; Clemmensen *et al.* 2020). During the Late Triassic period, East Greenland was located at 41° N on the northern rim of the supercontinent Pangaea, bordered by the Boreal Sea to the North (Clemmensen 1980a, b; Clemmensen *et al.* 1998; Kent & Tauxe 2005; Nøttvedt *et al.* 2008; Kent *et al.* 2014; Andrews & Decou 2018). The Jameson Land Basin was situated at the southern end of the East Greenland rift system, which formed part of a larger rift complex separating Greenland from Norway before the Atlantic opened (Ziegler 1988; Nøttvedt *et al.* 2008; Guarnieri *et al.* 2017). Since the Late Triassic, the basin has rotated 45° clockwise and translated 30° northward relative to present-day meridians (Kent & Tauxe 2005).

The Jameson Land Basin contains a relatively thick succession (~1.0 to 1.7 km) of Lower Triassic to Lower Jurassic continental sediments, including alluvial fan, braided river, aeolian dune, flood plain, saline playa lake and freshwater lake deposits (Clemmensen 1980a; Dam & Surlyk 1993; Clemmensen *et al.* 1998; Nøttvedt *et al.* 2008; Clemmensen *et al.* 2020). In the uppermost part of the Triassic succession (the Fleming Fjord Group), freshwater lake deposits are particularly well exposed on steep cliff sides facing the Carlsberg Fjord (Clemmensen *et al.* 2016, 2020). The Fleming Fjord Group, which has a thickness of about 350 m, consists of the basal Edderfugledal Formation, the middle Malmros Klint Formation and the uppermost Ørsted Dal Formation, including the Carlsberg Fjord Member (Clemmensen *et al.* 2020). Vertebrate fossils have primarily been found in lake and mudflat deposits from the two uppermost formations (Jenkins *et al.* 1994; Marzola *et al.* 2017; Clemmensen *et al.* 2020).

## Material and Methods

**Institutional Abbreviations:** BSM: Bavarian State Collection for Palaeontology and Geology (Bayerische Staatssammlung für Paläontologie und historische Geologie), Munich, Germany; DMNH: Dallas Museum of Natural History (Perot Museum of Nature and Science), Dallas, Texas, United States; FMNH: Field Museum of Natural History, Chicago, Illinois, United States; GIN: Geological Institute of the Russian Academy of Sciences (Geologicheskii Institut Ran), Moscow, Russia; JAM: Józef Attila City Library and Museum Collection (Józef Attila Városi Könyvtár és Muzeális Gyűjtemény), Komló, Hungary; HU: Harvard University, Cambridge, Massachusetts, United States; MMP: Municipal Museum of Natural Sciences 'Lorenzo Scaglia' (Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia'), Mar del Plata,

Argentina; MNHN: National Museum of Natural History (Muséum National d'Histoire Naturelle), Paris, France; NOVA: NOVA University Lisbon (Universidade NOVA de Lisboa), Lisbon, Portugal; NHMD: National History Museum of Denmark (Statens Naturhistoriske Museum), Copenhagen, Denmark; PEFO: Petrified Forest National Park; PIN: Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; TMP: Royal Tyrell Museum of Palaeontology, Drumheller, Alberta, Canada; UC: University of Copenhagen (Københavns Universitet), Copenhagen, Denmark; UMNH: Utah Museum of Natural History, Salt Lake City, Utah, United States; ZPAL: Institute of Palaeobiology, Polish Academy of Sciences (Instytut Palaeobiologii, Polskiej Akademii Nauk), Warsaw, Poland; ZIN PH: Palaeoherpetological Collection, Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.



**Fig. 1.** Geological map of central East Greenland with the Jameson Land Basin. The blue star indicates the location of Tait Bjerg (from Clemmensen *et al.* 2020, modified).

The material presented here (NHMD-154502) was collected in 1991 during an expedition involving collaborations between the NHMD, the UC and HU (Jenkins *et al.* 1994). The specimen described here was sampled at Tait Bjerg from a thin bone bed 50 m above the base of the Carlsberg Fjord Member (Jenkins *et al.* 1994; site 62/91/G). The thin bone bed is situated within chron E15 (Kent & Clemmensen 2021), dating the specimen to approximately 212.5 Ma. The Carlsberg Fjord Member has recently been dated by magnetostratigraphy and covers a period between 214 and 211 Ma within the Norian (Kent & Clemmensen 2021; Mau *et al.* 2022).

The material was photographed with a digital microscope (Dinolite pro AM4111T (R4)) and with an autonomous camera (FLEXACAM C1) fixed to a stereomicroscope (Leica M165 C) by stacking multiple pictures (~50) with the software Leica Application Suite X (LAS X) at the NOVA.

**Terminology:** We follow herein the terminology of Gómez & Turazzini (2016), slightly modified to adapt the comparison with non-salientian taxa. We decided to use ‘acetabular surface’ instead of ‘acetabular fossa’ since it can be flat and add three new terms: ‘lateral oblique groove’, ‘posterior margin’ and ‘anterior margin’. The specimen has been compared with multiple materials representing various taxa.

## Systematic palaeontology

Amphibia Linnaeus, 1758

Lissamphibia Haeckel, 1866

Batrachia Latreille, 1800

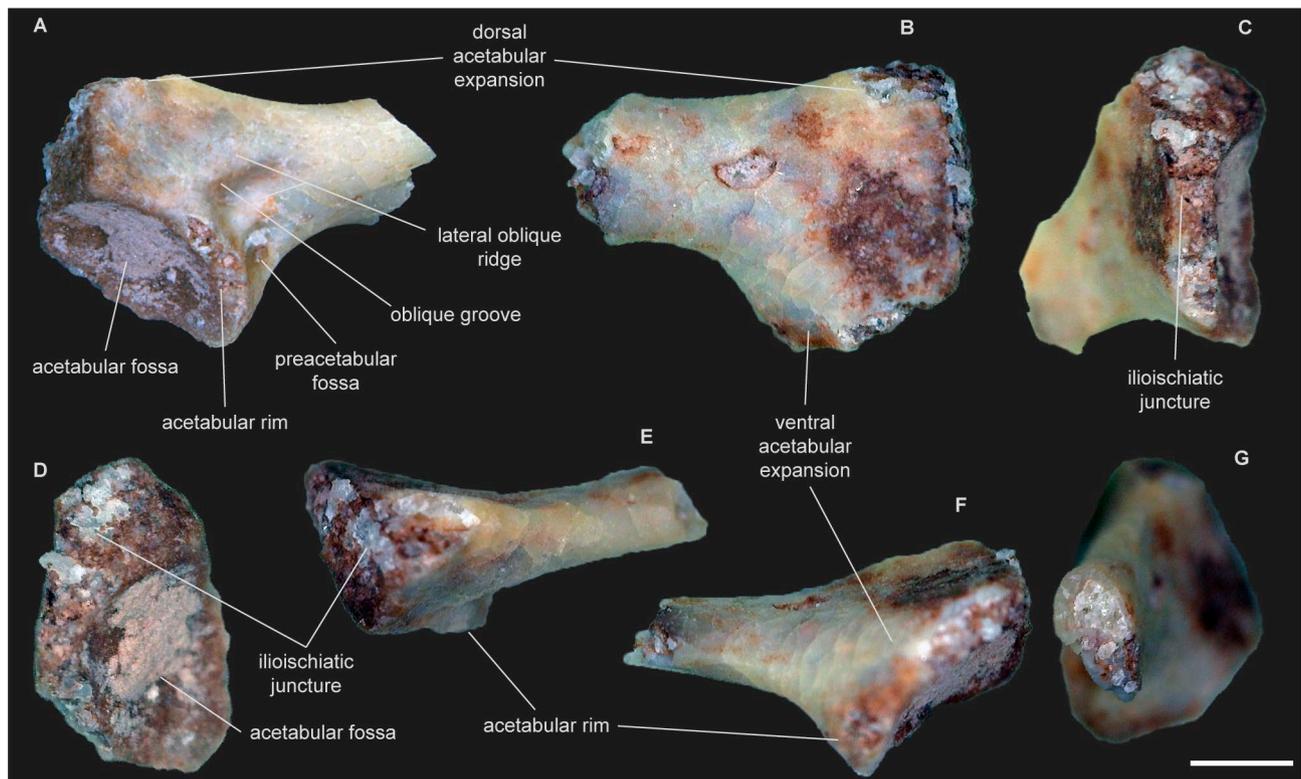
?Salientia Laurenti, 1768 (*sensu* Milner 1988) (aff.)

*Specimen referred.* Proximal part of a right ilium, NHMD-154502.

*Locality.* The specimen was collected during the 1991 American-Danish expedition to the eastern margin of the Jameson Land Basin, along the west slope of Tait Bjerg (71°28′34″ North 22°40′43″ West).

*Horizon.* A thin bone bed over- and underlain by purple, massive lake mudstone (Jenkins *et al.* 1994). Carlsberg Fjord Member of the Ørsted Dal Formation in the Fleming Fjord Group, Late Norian 212.5 Ma.

*Description.* The specimen (NHMD-154502) is a right ilium with a broken shaft. The acetabular surface



**Fig. 2.** Right ilium of the Greenland ?Salientia NHMD-154502. **A:** lateral view. **B:** medial view. **C:** proximal view. **D:** proximo-lateral view. **E:** ventral view. **F:** dorsal view. **G:** distal view.

forms a 1 mm wide (from the posteroventral edge to the acetabular rim) and 2 mm long (from posterior to ventral extremity) semi-circular deep concavity in the lateral view, sunk into the bone. It is bordered dorsally, anteriorly and ventrally by a convex acetabular rim strongly projected laterally, easily discernible anteriorly and ventrally (Figs 2A, E–F). Unfortunately, the posterior part of the dorsal acetabular expansion is not preserved, preventing us from fully understanding the actual shape of the ilial body. The dorsal acetabular expansion is well developed and triangular, while the ventral acetabular expansion is absent. The preacetabular zone is visible anterior to the acetabular surface. It is a circular fossa 0.5 mm broad and 0.1 mm deep (Fig. 2A). The medial surface is flat and slightly concave, with no interiliac tubercle (Figs 2B–C, E–F). In a proximal view, the ilioischiatric juncture is asymmetrical, its thickness varying mediolaterally, with the most dorsal part being 1 mm wide and the most ventral part 0.5 mm wide (Figs 2C–D). This difference in wideness is due to the dorsal acetabular expansion and acetabular rim participation and the absence of a ventral acetabular expansion in the shape of the ilioischiatric juncture. Its lateral half part is triangular with a roughened surface with its lateral tip joined by the acetabular rim. The rest of the ilioischiatric juncture surface has been damaged, not allowing us to understand how the ilium was attached to the ischium. The dorsal margin of the body between the shaft and the dorsal acetabular expansion is straight, lacking any dorsal prominence or dorsal tubercle (Figs 2A, F). The lateral surface exhibits two anterodorsally to posteroventrally inclined ridges, oblique to the shaft direction, anterior to the acetabular rim and dorsal to the preacetabular surface on the lateral surface (Fig. 2A). The most ventral ridge borders the preacetabular zone dorsally. It may be difficult to distinguish the dorsal lateral ridge from surface bone as it lacks any discernible process. The most notable features are its height and its flattened shape. The two short ridges are separated by a rectangular groove of 1 mm in length, 0.5 mm in width and as deep as the preacetabular zone (0.1 mm deep). The shaft cross-section is oval, with a height of 1.3 mm and a width of 0.7 mm; its ventral margin is mediolaterally compressed (Fig. 2G).

## Discussion

The attribution to Lissamphibia was based on comparisons with several vertebrates known from the Late Triassic of the Jameson Land Basin and nearby

localities (see Marzola *et al.* 2018). Despite differences in dimensions, it shares an overall similarity (ilial body and shaft) with several groups of Temnospondyli von Zittel, 1887 and Lepidosauromorpha Benton, 1983.

## Comparison to Lepidosauromorpha

The shaft represents less than 50% of the body width in lateral view (Fig. 2A), being thinner than in lepidosauromorphs (Borsuk-Białynicka 2007, fig. 3; Evans & Borsuk-Białynicka 2009b, figs 11A, 11C1; Paparella *et al.* 2019, figs 1A–1C, 1G). Squamates display three distinct processes: the posterior process (or posterior iliac-blade), the preacetabular process and the anterior supracetabular process, lacking in some lepidosauromorphs, like *Sophineta cracoviensis* Evans & Borsuk-Białynicka 2009a, from the Early Triassic of Poland (Paparella *et al.* 2019). None of these features appears in the Greenland specimen, which has a deeper acetabular surface.

## Comparison to Temnospondyls

### Comparison to large Triassic Temnospondyls

Many temnospondyl specimens have been found in the Jameson Land Basin, lacking an ilium for comparison (see Marzola *et al.* 2018). The material was compared to specimens from other crops in the Early Mesozoic, mostly from Capitosauria Yates & Warren, 2000 and Trematosauria Yates & Warren, 2000, the two main groups that lived during the Late Triassic (Warden & Snell 1991; Yates & Warren 2000; Maisch *et al.* 2004). Since within temnospondyls, the shape of the ilium is highly variable between each clade (Schoch 1999), the specimen was compared to both groups individually (Figs 3A–C).

For Capitosauria, three species have been selected: *Paracyclotosaurus davidi* Watson, 1958, *Stanocephalosaurus pronus* (Howie, 1970) and *Mastodontosaurus giganteus* Jaeger, 1828. Their ilium is a short and stout piece of the pelvic girdle, comprising two parts expanded anteroposteriorly, as in most capitosaurs (Watson 1958, fig. 12; Howie 1970, fig. 18; Schoch 1999, fig. 46). Watson (1958) did not describe the ilium of *Paracyclotosaurus*; it is very similar to *Stanocephalosaurus*, which is described as a dorsoventrally short bone with an elongated, flattened shaft that expands distally (Howie 1970). The shaft is longer in *Mastodontosaurus* (Schoch 1999; Fig. 3B). The cross-section of the shaft is oval to nearly round ventrally and flattens dorsally. The proximal region, bearing most of the acetabulum, is also well expanded anteroposteriorly, especially on the posterior side, with the acetabular surface almost entirely on the ilium and consisting

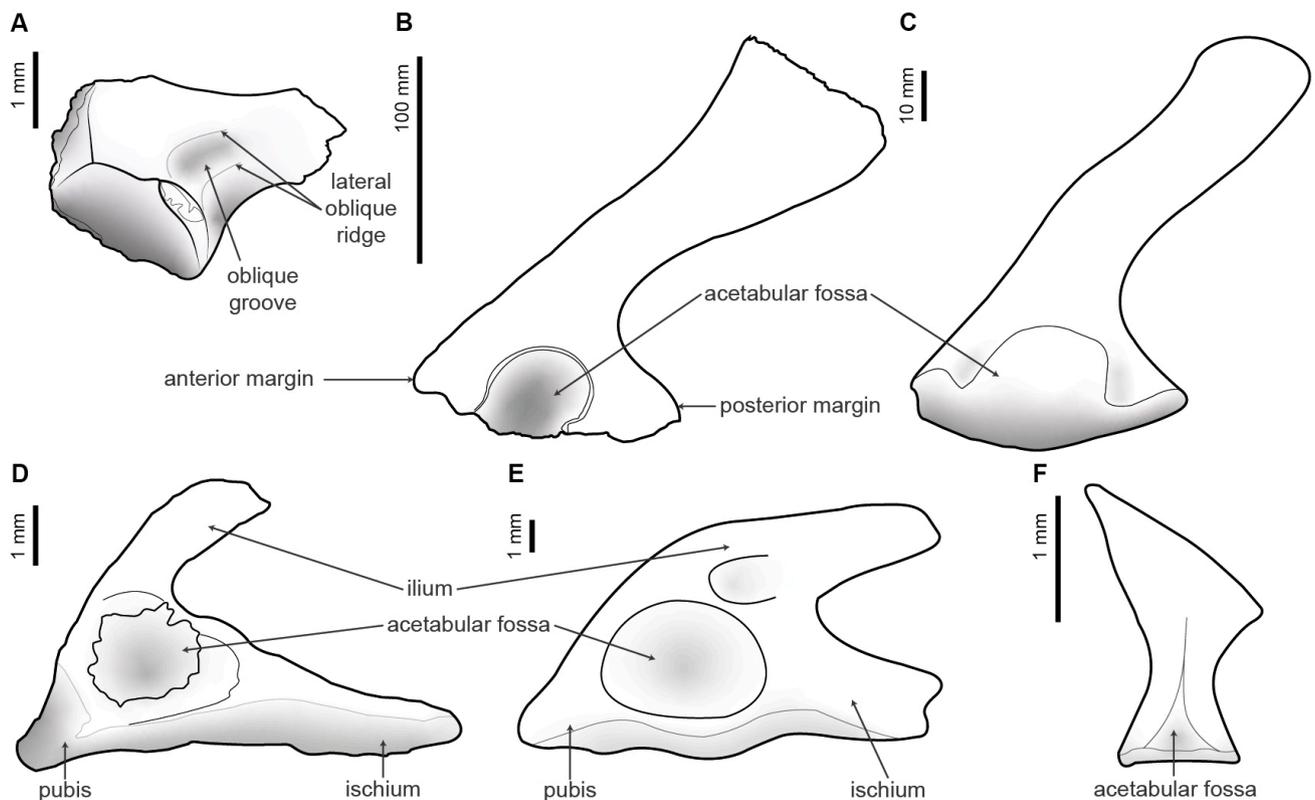
of a little round concavity (Watson 1958; Howie 1970; Schoch 1999).

Comparison with Trematosauria is based on ilia from two trematosauroids: an indeterminate trematosaurid from the Middle Jurassic (Maisch *et al.* 2004) and *Trematolestes hagdorni* Schoch, 2006, from the Middle Triassic. In addition, we compared NHMD-154502 with two brachyopoids from the Late Triassic, *Compsoceroops cosgriffi* Sengupta, 1935 and *Pelorocephalus mendozensis* Cabrera, 1944. Finally, two metoposauroids from the Late Triassic, *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002 and *Apachesaurus gregorii* Hunt, 1993 were also used for comparison. The ilium is very similar to what is seen in Lissamphibia, especially for metoposauroids, with a long shaft, barely expanded to unexpanded anteroposteriorly, corresponding to more than 60% of the total length of the ilium, whereas the ilial body is extended on either side of the acetabular surface (Sengupta 1935, fig. 14; Marsicano 1993, fig. 10; Maisch *et al.* 2004, fig. 2; Schoch 2006, fig. 6; Sulej 2007, figs 58, 59; Spielmann & Lucas 2012, figs 26, 27). *Metoposaurus* differs by having a sinu-

soidal shaft oval to round in cross-section (Sulej 2007; Fig. 3C). The trematosauroids possess a well-defined acetabulum, though smaller than in the Greenland specimen (Maisch *et al.* 2004, figs 1, 2A; Schoch 2006, fig. 6). *Pelorocephalus* does possess two ridges on its lateral surface running along the shaft and joining each other at mid-length, and only one is close to the acetabular surface, which is limited by a sizeable nail-shaped rim (Marsicano 1993, fig. 10). *Compsoceroops* has an acetabular surface that is more similar to our specimen. Its centre is under the edge of the base of the ilium; however, it is confined on both sides of its dorsal edge by two deep grooves (Sengupta 1935, fig. 14). The base of the ilium of metoposauroids has a right-angle shape, the lateral edge being the hypotenuse (Sulej 2007, fig. 59), a considerably different base compared to the Greenland specimen (Figs 2C, D).

### Comparison to Amphibamiformes

To help in the allocation of NHMD-154502 to a clade, we also compared it with three representative specimens of Amphibamiformes Schoch, 2019: *Doleserpeton*



**Fig. 3.** Compilation of ilia, NHMD-154502 and temnospondyls. **A:** Right ilium of Ørsted Dal Formation specimen (NHMD-154502), Norian. **B:** Left ilium (inversed) of *Mastodonsaurus giganteus*, Ladinian, after Schoch (1999). **C:** Right ilium of *Metoposaurus diagnosticus krasiejowensis*, (ZPAL AbIII/632), Norian, after Sulej (2007). **D:** Right pelvis (ilium, pubis and ischium) of *Doleserpeton annectens*, (FMNH UR1379), Lower Permian, after Sigurdson & Bolt (2010). **E:** Right pelvis (ilium, pubis and ischium) of *Micropholis stowi*, (BSM 1934 VIII 43C), Induan, after Schoch & Rubidge (2005). **F:** *Tungussogyrinus bergi*, (PIN 4262/4a), Late Permian to Early Triassic, after Wernerburg (2009).

*annectens* Bolt, 1969 (a Lower Permian amphibamid), *Micropholis stowi* Huxley, 1859 (a Lower Triassic micropholid) and *Tungussogyrinus bergi* Efremov, 1939 (a Late Permian – Early Triassic branchiosaurid); this clade, although mainly known in the Permian, is phylogenetically close to lissamphibians according to several analyses. We could not compare our specimen to *Gerobatrachus* due to a lack of details on the ilium of the specimen in the original publication.

The 4 mm long ilium of *Doleserpeton* is fused with pubis and ischium and has a dorsal blade oriented posterolaterally as large as two-thirds of the acetabular surface (Sigurdson & Bolt 2010; Fig. 3D). The authors have lightly described the ilium of *Doleserpeton* in itself; the drawing suggests that the concave acetabular surface occupies a large part of the body of the ilium, and the anterior margin is fine and straight, although the posterior margin is concave and skinny. It reminds NHMD-154502 if we consider the dorsal acetabular expansion as the posterior margin, the main difference being that *Doleserpeton* has a wider ilial shaft, corresponding to two-thirds of the width of the acetabular surface, and a thinner anterior margin. The shaft of NHMD-154502 only represents half of its acetabular surface, and its dorsal acetabular expansion is extremely large (Fig. 3A). According to the drawing and the authors, no lateral structure has been spotted.

Similarly, *Micropholis* has an ilium fused with the other pelvic belt bones (Schoch & Rubidge 2005; Fig. 3E). The body is vast, the acetabulum occupying about 55% with a skinny and angular posterior margin forming a slope with the dorsal margin of the blade and an extensive anterior margin. The dorsal blade, shorter, is more inclined horizontally and narrows ventrodorsally at the tip. The bone has an oval fossa positioned anterodorsally to the acetabulum on the lateral surface, but Schoch & Rubidge (2005) did not mention it.

*Tungussogyrinus* has an ilium shaped like an hourglass (Fig. 3F). It is shaped like an isosceles triangle and framed by anterior and posterior margins of the same width. The dorsal shaft extends in the anteroposterior axis, especially in the anterior direction (Werneburg 2009). The acetabulum occupies only a tiny proportion of the body.

NHMD-154502 differs from the typical ilia of Triassic temnospondyls. First, there is an essential variation in size between the multiple temnospondyl taxa and NHMD-154502. For example, the ilia of *Mastodontosaurus* are around 25 cm long (Fig. 3B), while the ilia of *Metoposaurus* vary from 6 cm to 10 cm long (Sulej 2007). NHMD-154502 is closer to amphibamiforms in size (e.g. *Doleserpeton*: 4 mm long). As seen before, temnospondyl ilia have an anteroposteriorly expanded dorsal blade and a massive anteroposteriorly

expanded ventral part bearing the dorsal part of the acetabular surface (Warden & Snell 1991). The acetabular surface is mainly centred in large temnospondyls (Schoch 1999, fig. 46; Maisch *et al.* 2004, fig. 1; Sulej 2007, figs 58, 59). On the other hand, this surface is offset in amphibamiforms and the Greenland specimen (Figs 3A, D–F), as in many salientians (Shubin & Jenkins 1995; Evans & Borsuk-Białynicka 1998; Ascarrunz *et al.* 2016; Stocker *et al.* 2019). Moreover, most temnospondyls lack any structure on the lateral surface of the ilium, as seen in the specimen presented here (Fig. 3A), refuting the possibility of attribution of the Greenland ilium to this group.

## Comparison to Caudata/Urodela

The ilium of salamander and frog are very alike. Thanks to a few papers, it is now easier to differentiate the two groups when only scattered fragments are present, such as, for example, the ilium. For salamanders, this element shares some similarities with ilia of non-lissamphibian temnospondyls (Fig. 4).

## Comparison to Caudata

Unfortunately, among the few ilia of stem-Caudata preserved, they are generally flattened due to the preservation, making it difficult to appreciate their actual shapes. Among the caudate species known in the bibliography, only ilia of *Triassurus sextelae* and *Kokartus honorarius* Nesov, 1988 could have been observed, the other taxa missing this element (see Skutschas *et al.* 2018 for *Kulgeriherpeton*; Evans *et al.* 1988 for *Marmorerpeton*; Skutschas & Krasnolutskii 2011 for *Urupia*). The ilium of *Triassurus* is very similar to those of temnospondyl, looking like an hourglass in lateral view, with a triangular acetabular region (Schoch *et al.* 2020: figs 1C, 2B).

Seven ilium fragments have been identified for *Kokartus*, preserving only the acetabulum region and the base of the shaft (Averianov *et al.* 2008; Fig. 4B). According to the authors, the acetabular surface has the shape of a kidney and is bordered anteriorly and posteriorly by slit-like depressions. The ilioischial junction is asymmetrical and convex, thickened anteriorly in a similar way to NHMD-154502, although it is thickened dorsally for the latter (see Averianov *et al.* 2008: fig. 7O). The authors did not mention the form of the acetabular surface, but it seems shallowly concave. The presence of a protuberance projecting laterally at the dorsal margin of the acetabular surface distinguishes it from our specimen.

## Comparison to Urodela

The ilium of Urodela does not differ significantly from stem-Caudata: a triangular acetabular region in lateral

view, with posterior and anterior margins almost subequally developed, with a smooth medial surface, either flat or convex and a thin asymmetrically concave ilioischialic juncture with lateral edge excavated and grading into the acetabular surface (Gardner *et al.* 2010). The acetabular surface of Urodela varies highly in shape: generally, distally elongate, longer than larger (kidney-shape), subtriangular or semi-circular (Gardner *et al.* 2010; Figs 4C–E). The acetabular surface varies from shallowly concave or flat to flat saddle-shaped or sinuous (Gardner *et al.* 2010; Roček *et al.* 2012). *Kokartus* shows that the acetabular surface can be delimited by a low rim that does not extend laterally (Averianov *et al.* 2008). In some cases, the portion closest to the base of the shaft can project laterally in a ramp-like structure (Roček *et al.* 2012), as seen in *Andrias scheuchzeri* (Holl, 1831) and the indeterminate Urodela (Roček *et al.* 2012, fig. 2S; Szentesi *et al.* 2020; Figs 4D–E).

### Comparison to Salientia/Anura

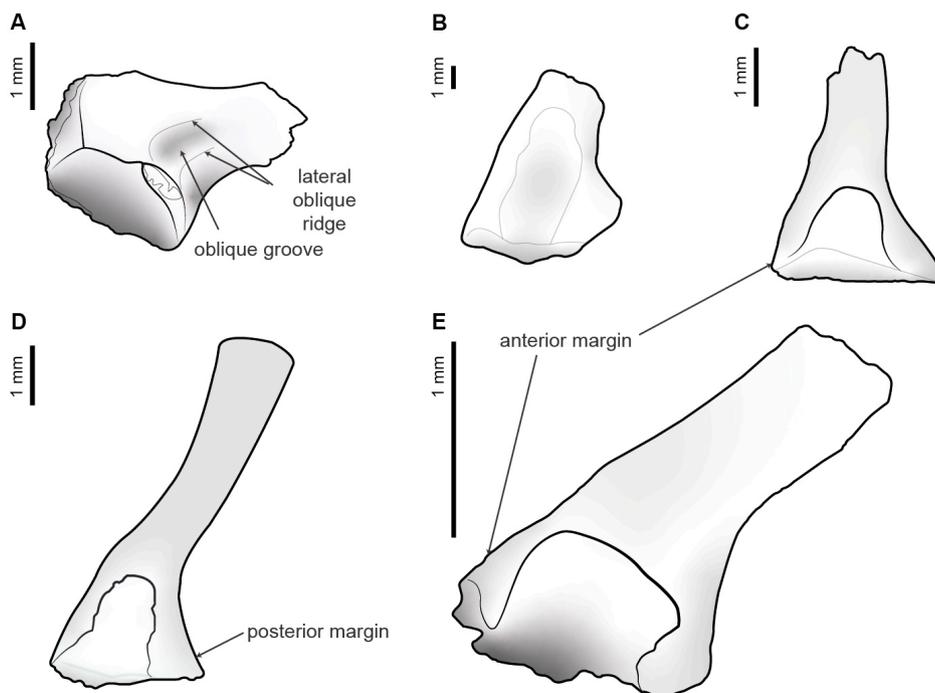
Contrary to salamanders, the pelvic girdle of frogs and their relatives had changed significantly from its ancestral state to allow the jumping locomotion specific to the group. Instead of projecting globally dorsally in salamanders, their elongated ilia display a shaft oriented anteriorly to anterodorsally (Milner 1988; Ford & Cannatella 1993) temnospondyls. This condition is present among the earliest salientians, *Triadobatrachus* and *Czatkobatrachus*, in the Chinle specimens and anurans (Gardner *et al.* 2010), although the shaft is shorter in the former. Due to this rotation, the

acetabular surface turns posterolaterally to laterally in extant frogs (Gardner *et al.* 2010; Roček *et al.* 2012). We note a similar condition in *Triadobatrachus*, where the acetabulum faces more laterally (Ascarrunz *et al.* 2016). Since the Greenland specimen is only an isolated ilium without its shaft, we can only suggest the putative direction of the acetabular surface being oriented posterolaterally and ventrally if considering the shaft is oriented laterally as in Salientia (Ford & Cannatella 1993).

### Comparison to Salientia

In contrast to Caudata, isolated ilia of Salientia have been found multiple times and described. The outline of their ilial body in lateral view, excluding the acetabulum fossa, is triangular as in *Triadobatrachus* and the Chinle specimens, or squarish as seen in *Czatkobatrachus*, with a dorsal acetabular expansion well developed and barely developed (or absent) ventral acetabular expansion for all three (Figs 5B–E). The acetabular surface on their ilia is semi-circular and concave (Rage & Roček 1989; Stocker *et al.* 2019), whereas in *Czatkobatrachus*, the whole surface is subtriangular and shallow (Evans & Borsuk-Białynicka 2009). The acetabular rim does not stand out in *Czatkobatrachus* while it is easily discernible anteriorly and ventrally for *Triadobatrachus* and the Chinle specimens (Stocker *et al.* 2019; Figs 5B, D–E).

The medial surface is smooth, flat (or slightly concave) and does not bear any trace of an interiliac tubercle in *Triadobatrachus* and *Czatkobatrachus*, while it is not visible in the Chinle specimens (Rage & Roček



**Fig. 4.** Compilation of ilia, NHMD-154502 and salamanders. **A:** Right ilium of Ørsted Dal Formation specimen (NHMD-154502), Norian. **B:** Left ilium of *Kokartus honorarius*, (ZIN PH 48/47), Bathonian, after Averianov *et al.* (2008). **C:** Left ilium of Urodela indet., (TMP 96.78.199), Campanian, after Roček *et al.* (2012). **D:** Left ilium of *Ambystoma mexicanum*, (TMP 2010.30.06), Recent, after Gardner *et al.* (2010). **E:** Left ilium of *Andrias scheuchzeri*, (JAM 2006.185.47), Miocene, after Szentesi *et al.* (2020).

1989; Evans & Borsuk-Białynicka 2009; Stocker *et al.* 2019: see supplementary file).

The ilioischial juncture has not been described or shown for *Triadobatrachus*, *Czatkobatrachus* or the Chinle specimens. For the first, ilia and ischia junctions are obscured because of overlapping in the fossil (Ascarrunz *et al.* 2016). In the case of *Czatkobatrachus*, the ilia are fused with the ischia, preventing any accurate description of the juncture (Evans & Borsuk-Białynicka 2009). Furthermore, for the Chinle specimens, this area is too damaged for accuracy (Stocker *et al.* 2019).

Both earliest salientians, *Triadobatrachus* and *Czatkobatrachus*, share a dorsal prominence positioned between the dorsal acetabular expansion and the ilial shaft (Rage & Roček 1989; Evans & Borsuk-Białynicka 2009), which differs them from NHMD-154502.

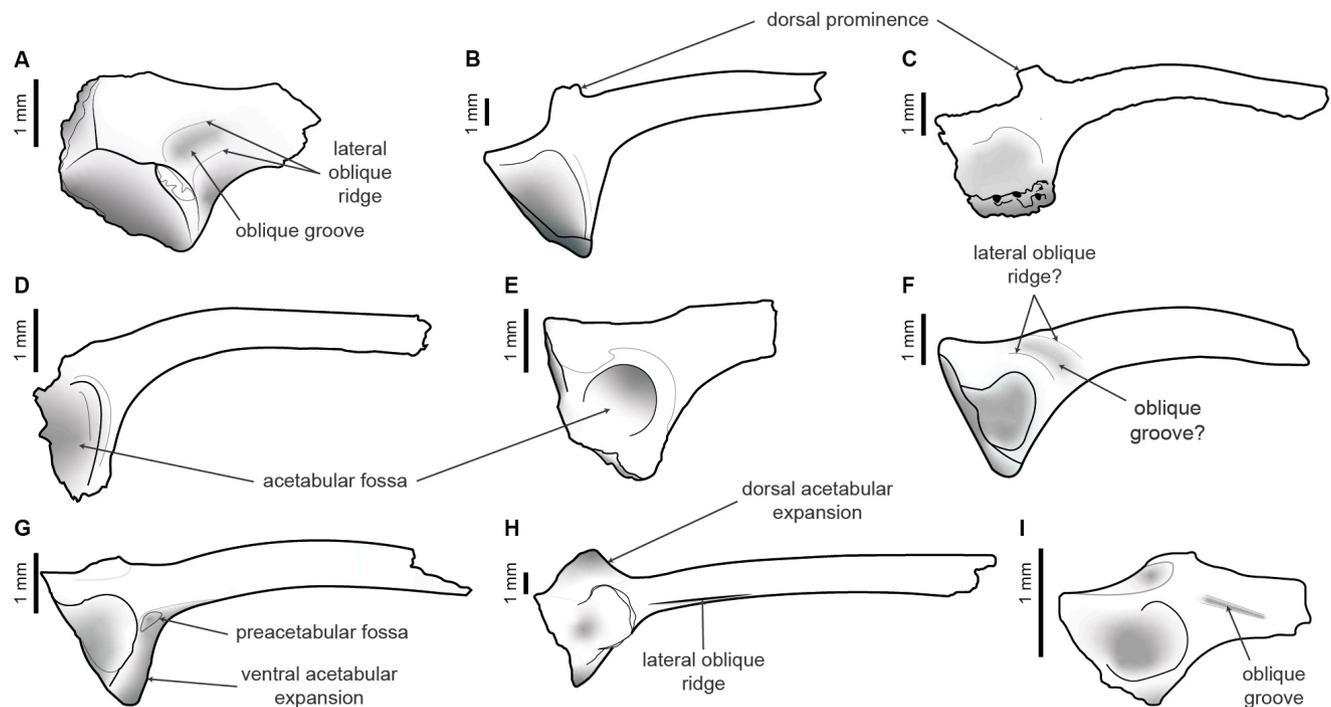
### Comparison to Anura

Frogs possess an ilium remarkably similar to stem-Salientia: a triangular to squarish ilial body in lateral view, with strongly divergent dorsal and ventral acetabular expansions; a small to a large semi-circular or subtriangular acetabular surface whose deepness varies from deeply concave to bowl-shaped and partially

sunk into the bone; the medial surface is smooth and flat to shallowly concave and may bear an interiliac tubercle; an ilioischial juncture flat or shallowly convex with a sharp posterolateral edge to distinct itself from the acetabular surface (Gardner *et al.* 2010).

Concerning the interiliac tubercle, anurans may bear a triangular one on the medial surface of the ilial body (Gardner *et al.* 2010; Roček *et al.* 2012), confirmed by Gómez & Turazzini (2016), who stated its absence in neobatrachians (except two genera), and that it is significantly developed only in aquatic taxa (e.g. pipids and palaeobatrachids). In extant frogs, the ilioischial juncture is thickened mediolaterally in most pipimorph and narrow in most other anurans (Gómez & Turazzini 2016), meaning that its thickness does not help in the differentiation between Anura and Urodela, as stated by Gardner *et al.* (2010) and Roček *et al.* (2012), even more, if we consider that both papers contradict them on that point.

As the description shows, NHMD-154502 displays various features on its lateral surface, like two ridges and a groove. A single lateral oblique ridge has been spotted in several pipimorphs (see Báez *et al.* 2012, figs 3B, 4A; Gómez & Turazzini 2016, fig. 3D; Fig. 5H). More



**Fig. 5.** Compilation of ilia, NHMD-154502 and frogs. **A:** Right ilium of Ørsted Dal Formation specimen (NHMD-154502), Norian. **B:** Right ilium of *Triadobatrachus massinoti*, (MNHN.F.MAE126), Induan, after Ascarrunz *et al.* (2016). **C:** Right ilium of *Czatkobatrachus polonicus*, (ZPAL AbIV/114), Induan, after Evans & Borsuk-Białynicka (2009a). **D–E:** Right ilia of Chinle Formation specimens (**D**, DMNH 2018-05-0002; **E**, PEFO 41743), Norian, after Stocker *et al.* (2019). **F:** Right ilium of *Prosalirus bitis*, (MCZ 9324A), Pliensbachian, after Jenkins & Shubin (1998). **G:** Left ilium (inversed) of *Bufo viridis*, (GIN-11142/120), early Middle Pleistocene, after Tesakov *et al.* (2019). **H:** Right ilium of a pipid from Daireaux (MMP M-5121), Upper Pleistocene, after Báez *et al.* (2012). **I:** Left ilium (reversed) of Dakota Formation specimen (UMNH 13158), late Cenomanian, after Roček *et al.* (2010).

interestingly, *Prosalirus bitis* Shubin & Jenkins, 1995, an early Jurassic anuran, possesses two lateral oblique ridges, although they are located more dorsally and are inclined in the opposite directions, perpendicular to the ilial shaft (Shubin & Jenkins 1995; Gardner *et al.* 2010; Fig. 5F). The groove separating the two lateral ridges is reminiscent of a similar wider and shorter structure described in anurans from the Late Cretaceous of Utah (Roček *et al.* 2010, figs 5J–K; Fig. 5I). NHMD-154502 shows both types of structures, ridges and a groove; thus, both structures could be present on other specimens, but their presence means nothing concerning the inclusion of NHMD-154502 in Anura since they have not been considered in numerous phylogenetic analyses, except Báez *et al.* (2012), and are typically absent in the majority of anuran (Gómez & Turazzini 2016).

### Summary of the comparison

The supplementary file (adapted from Gardner *et al.* 2010, Appendix 1) helps to differentiate the ilia of anurans, urodeles, NHMD-154502, two salientians (*Triadobatrachus* and *Czatkobatrachus*) and two caudates (*Triassurus* and *Kokartus*). The specimen shares more features with salientians and anurans than any other clade: squarish acetabular region, deeply concave acetabular surface, laterally projecting acetabular rim and flat mesial surface. Triassic caudates are incomplete

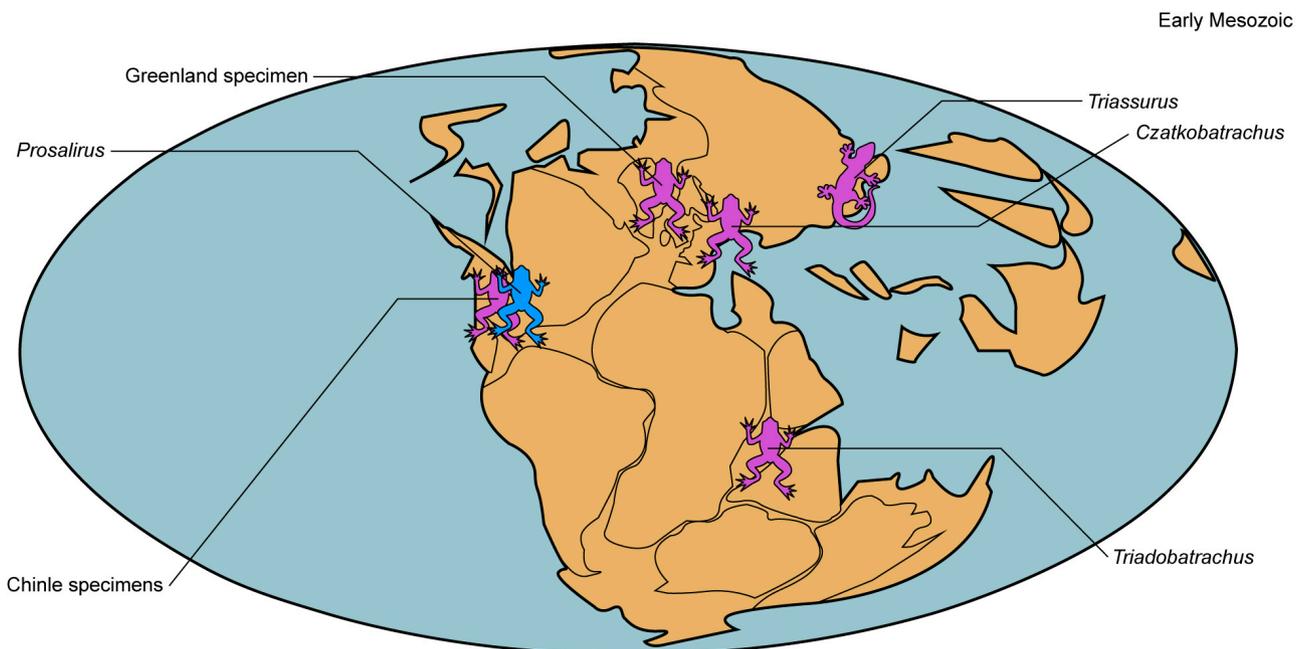
or not detailed enough, and the features concerning the shaft cannot be treated for NHMD-154502. Based on these statements, NHMD-154502 is considered as a batrachian closer to Salientia than to Caudata.

Triassic lissamphibians are poorly documented, with only three well-known genera: *Triadobatrachus*, *Czatkobatrachus* and *Triassurus* (Piveteau 1936; Ivakhnenko 1978; Evans & Borsuk-Białynicka 1998). The Greenland specimen is the first lissamphibian reported from the Jameson Land Basin in East Greenland. Therefore, it is one of the northernmost Triassic occurrences of Lissamphibia and most likely the youngest, dated to 212.5 Ma (Fig. 6). The earliest frogs (including at least a complete ilium) described from the Late Triassic are the Chinle specimens from Arizona, dated from 217 Ma to 213 Ma (Stocker *et al.* 2019).

### Conclusion

This study describes the first lissamphibian discovered from the Triassic of the Jameson Land Basin, Greenland, based on an incomplete right ilium from the Norian of the Carlsberg Fjord Member (Ørsted Dal Formation) in the Fleming Fjord Group.

The ilium has been compared to various taxa such as lepidosauromorphs, temnospondyls, salamanders and frogs. It is identified as a batrachian displaying



**Fig. 6.** Triassic palaeogeography, with localities of Triassic batrachian and the Greenland specimen. Frog and salamander icons mark the location of each specimen; purple for a Triassic locality and blue for an Early Jurassic locality (Paleobiology Database; Authorizers: M. Carrano, R. Butler, T. Cleary and J. Alroy).

several features suggesting an affinity with salientians: a squarish acetabular region, deeply concave acetabular fossa, laterally projecting acetabular rim, and flat mesial surface. This study reinforces the view that, during the Late Triassic, batrachians were more widespread than previously known and reached as far north as 41° palaeolatitude. It is also one of the northernmost occurrences of Batrachia from the Late Triassic.

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## References

- Agnolin, F.L., Mateus, O., Milàn, J., Marzola, M., Wings, O., Adolfssen, J.S. & Clemmensen, L.B. 2018: *Ceratodus tunuensis* sp. nov., a new lungfish (Sarcopterygii, Dipnoi) from the Late Triassic of central East Greenland. *Journal of Vertebrate Paleontology* 38, e1439834, 1–6. <https://doi.org/10.1080/02724634.2018.1439834>
- Andrews, S. & Decou, A. 2018: The Triassic of Traill Ø and Geographical Society Ø, East Greenland: Implications for North Atlantic palaeogeography. *Geological Journal* 54, 2124–2144. <https://doi.org/10.1002/gj.3287>
- Ascarrunz, E., Rage, J.-C., Legreneur, P. & Laurin, M. 2016: *Triadobatrachus massinoti*, the earliest known lissamphibian (Vertebrata: Tetrapoda) re-examined by  $\mu$ CT scan, and the evolution of trunk length in batrachians. *Contributions to Zoology* 85, 201–234. <https://doi.org/10.1163/18759866-08502004>
- Averianov, O.A., Martin, T., Skutschas, P.P., Rezvyi, A.S. & Bakirov, A.A. 2008: Amhíbians from the Middle Jurassic Balabansai Svita in the Fergana Depression, Kyrgystan (Central Asia). *Palaeontology* 51(2), 471–485. <https://doi.org/10.1111/j.1475-4983.2007.00748.x>
- Báez, A.M., Gómez, R.O. & Taglioretti, M.L. 2012: The archaic ilial morphology of an enigmatic pipid frog from the Upper Pleistocene of the South American Pampas. *Journal of Vertebrate Paleontology* 32, 304–314. <https://doi.org/10.1080/02724634.2012.637591>
- Beccari, V., Mateus, O., Wings, O., Milàn, J. & Clemmensen, L.B. 2021: *Issi saaneq* gen. et sp. nov. – A new sauropodomorph dinosaur from the Late Triassic (Norian) of Jameson Land, Central East Greenland. *Diversity* 13, 561. <https://doi.org/10.3390/d13110561>
- Benton, M.J. 1983: The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society, Series B* 302, 605–717. <https://doi.org/10.1098/rstb.1983.0079>
- Bolt, J.R. 1969: Lissamphibian Origins: Possible Protolissamphibian from the Lower Permian of Oklahoma. *Science* 166, 888–891. <https://doi.org/10.1126/science.166.3907.888>
- Borsuk-Białynicka, M. 2007: Evolution of the iliosacral joint in diapsid phylogeny. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen* 249, 297–311. <https://doi.org/10.1127/0077-7749/2008/0249-0297>
- Bromley, R.G., & Asgaard, U. 1979: Triassic freshwater ichnocoenosis from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28, 39–80. [https://doi.org/10.1016/0031-0182\(79\)90112-3](https://doi.org/10.1016/0031-0182(79)90112-3)
- Cabrera, A. 1944 : Sobre un estegocéfalo de la provincia de Mendoza. *Notas Museo Universidad Nacional de La Plata IX, Paleontología* 69, 421–429.
- Clemmensen, L.B. 1980a: Triassic lithostratigraphy of East Greenland between Scoresby Sund and Kejser Franz Josephs Fjord. *Grønlands Geologiske Undersøgelse Bulletin* 139, 56 pp. <https://doi.org/10.34194/bullggv.v139.6681>
- Clemmensen, L.B. 1980b: Triassic rift sedimentation and palaeogeography of central East Greenland. *Grønlands Geologiske Undersøgelse Bulletin* 136, 72 pp. <https://doi.org/10.34194/bullggv.v136.6678>
- Clemmensen, L.B., Kent, D.V. & Jenkins, F.A. Jr. 1998: A Late Triassic lake system in East Greenland: facies, depositional cycles and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 140, 135–159. [https://doi.org/10.1016/S0031-0182\(98\)00043-1](https://doi.org/10.1016/S0031-0182(98)00043-1)
- Clemmensen, L.B., Milàn, J., Adolfssen, J.S., Estrup, E.J., Frobøse, N., Klein, N., Mateus, O. & Wings, O. 2016: The vertebrate-bearing Late Triassic Fleming Fjord Formation of central East Greenland revisited: stratigraphy, palaeoclimate and new palaeontological data. In: Kear, B.P. *et al.* (eds): *Mesozoic Biotas of Scandinavia and its Arctic Territories*. Geological Society, London, Special Publications 434, 31–47. <https://doi.org/10.1144/SP434.3>
- Clemmensen, L.B., Kent, D.V., Mau, M., Mateus, O. & Milàn, J. 2020: Triassic lithostratigraphy of the Jameson Land Basin (central East Greenland), with emphasis on the new Fleming Fjord Group. *Bulletin of the Geological Society of Denmark* 68, 95–132. <https://doi.org/10.37570/bgds-2020-68-05>
- Dam, G. & Surlyk, F. 1993: Cyclic sedimentation in a large wave

- and storm-dominated anoxic lake; Kap Stewart Formation (Rhaetian–Sinemurian), Jameson Land, East Greenland. Special publication of the International Association of Sedimentologists 18, 419–448.
- Duméril, A.M.C. 1805: Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques, 344 pp. <https://doi.org/10.5962/bhl.title.44835>
- Efremov, J.A. 1939: First representative of Siberian early Tetrapoda. *Comptes-Rendus des Seances de l'Academie des Sciences de l'URSS* 23(1), 106–110.
- Evans, S. & Borsuk-Białynicka, M. 1998: A stem-group frog from the early Triassic of Poland. *Acta Palaeontologica Polonica* 43, 573–580.
- Evans, S. & Borsuk-Białynicka, M. 2009a: The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontologica Polonica* 65, 79–105.
- Evans S.E. & Borsuk-Białynicka, M. 2009b: A small lepidosauromorph reptile from the Early Triassic of Poland. *Paleontologica Polonica* 65, 179–202.
- Evans, S.E., Milner, A.R. & Mussett, F. 1988: The earliest known Salamanders (Amphibia, Caudata): A record from the Middle Jurassic of England. *Geobios* 21, 539–552. [https://doi.org/10.1016/s0016-6995\(88\)80069-x](https://doi.org/10.1016/s0016-6995(88)80069-x)
- Ford, L.S., & Cannatella, D.C. 1993: The major clades of frogs. *Herpetological Monographs* 7, 94–117. <https://doi.org/10.2307/1466954>
- Gardner, J.D., Roček, Z., Přikryl, T., Eaton, J.G., Blob, R.W. & Stankey, J.T. 2010: Comparative morphology of the ilium of anurans and urodeles (Lissamphibia) and a re-assessment of the anuran affinities of *Nezpercius dodsoni* Blob *et al.* 2001. *Journal of Vertebrate Paleontology* 30, 1684–1696. <https://doi.org/10.1080/02724634.2010.521605>
- Gómez, R.O. & Turazzini, G.F. 2016: An overview of the ilium of anurans (Lissamphibia, Salientia), with a critical appraisal of the terminology and primary homology of main ilial features. *Journal of Vertebrate Paleontology* 36, e1030023. <https://doi.org/10.1080/02724634.2015.1030023>
- Guarnieri, P., Brethes, A. & Rasmussen, T.M. 2017: Geometry and kinematics of the Triassic rift basin in Jameson Land (East Greenland). *Tectonics* 36, 602–614. <https://doi.org/10.1002/2016TC004419>
- Grigorescu, D., Venczel, M., Csiki-Sava, Z. & Limborea, R. 1999: New latest Cretaceous microvertebrate fossil assemblage from the Hațeg Basin (Romania). *Geologie en Mijnbouw* 78, 301–314. <https://doi.org/10.1023/A:1003890913328>
- Hansen, B.B., Milàn, J., Clemmensen, L.B., Adolfssen, J.S., Estrup, E.J., Klein, N., Mateus, O. & Wings, O. 2016: Coprolites from the Late Triassic Kap Stewart Formation, Jameson Land, East Greenland: Morphology, classification and prey inclusions. *Geological Society, London, Special Publications* 434, 46–49. <https://doi.org/10.1144/SP434.12>
- Hunt, A.P. 1993: Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from western North America. *Museum of Northern Arizona Bulletin* 59, 67–97.
- Huxley, T.H. 1859: On some amphibian and reptilian remains from South Africa and Australia. *Quarterly Journal of the Geological Society* 15, 642–649.
- Holl, F. 1831: *Handbuch der Petrefaktenkunde*. Dresden
- Howie, A.A. 1970: A new capitosaurid labyrinthodont from East Africa. *Palaeontology* 13, 210–253.
- Irmis, R.B., Nesbitt, S.J. & Sues, H.-D. 2013: Early Crocodylomorpha. In: S.J. Nesbitt, J.B. Desojo & R.B. Irmis (eds): *Anatomy, Phylogeny and Paleobiology of Early Archosaurs and their Kin*. Geological Society, London, Special Publications 379, 275–302. <https://doi.org/10.1144/SP379.24>
- Ivakhnenko, M.F. 1978: Tailed amphibians from the Triassic and Jurassic of Middle Asia. *Paleontological Journal* 3, 84–89.
- Jaeger, G.F. 1828: Über die fossile Reptilien, welche in Württemberg aufgefunden worden sind, 48 pp. Verlag der Metzler'schen Buchhandlung, Stuttgart.
- Jenkins, F.A., Jr., Shubin, N.H., Amaral, W.W., Gatesy, S.M., Schaff, C.R., Clemmensen, L.B., Downs, W.R., Davidson, A.R., Bonde, N. & Osbaeck, F. 1994: Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddelelser om Grønland, Geoscience* 32, 25 pp.
- Jenkins, F.A., Jr., Gatesy, S.M., Shubin, N.H. & Amaral, W.W. 1997: Haramiyids and Triassic mammalian evolution. *Nature* 385, 715–718. <https://doi.org/10.1038/385715a0>
- Kent, D.V. & Clemmensen, L.B. 2021: Northward dispersal of dinosaurs from Gondwana to Greenland at the mid-Norian (215–212 Ma, Late Triassic) dip in atmospheric pCO<sub>2</sub>. *Proceedings of the National Academy of Sciences* 118, e2020778118. <https://doi.org/10.1073/pnas.2020778118>
- Kent, D.V. & Tauxe, L. 2005: Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. *Science* 307, 240–244. <https://doi.org/10.1126/science.1105826>
- Kent, D.V., Malnis, P.S., Colombi, P.S., Alcober, O.A. & Martínez, R.N. 2014: Age constraints on the dispersal of dinosaurs in the Late Triassic from magnetostratigraphy of the Los Colorados Formation (Argentina). *Proceedings of the National Academy of Sciences* 111, 7958–7963. <https://dx.doi.org/10.1073/pnas.1402369111>
- Klein, H., Milàn, J., Clemmensen, L.B., Frobøse, N., Mateus, O., Klein, N., Adolfssen, J.S., Estrup, E. & Wings, O. 2016: Archosaur footprints (cf. *Brachychirotherium*) with unusual morphology from the Upper Triassic Fleming Fjord Formation (Norian–Rhaetian) of East Greenland. In: Kear, B.B. *et al.* (eds): *Mesozoic Biotas of Scandinavia and its Arctic Territories*. Geological Society, London, Special Publications 434, 71–85. <https://doi.org/10.1144/SP434.1>
- Kumar, J. & Sharma, M. 2019: Micro and mega-vertebrate fossils from the Late Triassic Tiki Formation, South Rewa Gondwana Basin, India: paleoenvironmental and palaeobiogeographic implications. *Journal of the Paleontological Society of India* 64, 151–168.
- Lallensack, J.N., Klein, H., Milàn, J., Wings, O., Mateus, O. & Clemmensen, L.B. 2017: Sauropodomorph dinosaur trackways

- from the Fleming Fjord Formation of East Greenland: Evidence for Late Triassic sauropods. *Acta Palaeontologica Polonica* 64(4), 833–843. <https://doi.org/10.4202/app.00374.2017>
- Laurenti, J.N. 1768: Specimen medicum, exhibens synopsis reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum [Medical ideas, showing an emended synopsis of the reptiles together with experiences in poisoning by and antidotes of Austrian reptiles]. Published and printed by Johann Thomas von Trattner, Vienna. <https://doi.org/10.5962/bhl.title.5108>
- Linnaeus C. 1758: *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Editio Decima 1, 824 pp. <https://doi.org/10.5962/bhl.title.156765>
- Maisch, M.W. & Matzke, A.T. 2004: A relict trematosauroid (Amphibia: Temnospondyli) from the Middle Jurassic of the Junggar Basin (NW China). *Naturwissenschaften* 91, 589–593. <https://doi.org/10.1007/s00114-004-0569-x>
- Marjanović, D. & Laurin, M. 2014: An updated paleontological timetree of lissamphibians, with comments on the anatomy of Jurassic crown-group salamanders (Urodela). *Historical Biology* 26, 535–550. <https://doi.org/10.1080/08912963.2013.797972>
- Marjanović, D. & Laurin, M. 2019: Phylogeny of Paleozoic limbed vertebrates reassessed through revision and expansion of the largest published relevant data matrix. *PeerJ* 6, e5565. <https://doi.org/10.7717/peerj.5565>
- Marsicano, C.A. 1993: Postcranial skeleton of a brachyopoid (Amphibia, Temnospondyli) from the triassic of Mendoza (Argentina). *Alcheringa: An Australasian Journal of Palaeontology* 17, 185–197. <https://doi.org/10.1080/03115519308619603>
- Marzola, M., Mateus, O., Milàn, J. & Clemmensen L.B. 2018: A review of Palaeozoic and Mesozoic tetrapods from Greenland. *Bulletin of the Geological Society of Denmark* 66, 21–46. <https://doi.org/10.37570/bgsgd-2018-66-02>
- Mau, M., Kent, D.V. & Clemmensen, L.B. 2022: Planetary chaos and inverted climate phasing in the Late Triassic of Greenland. *Proceedings of the National Academy of Sciences* 119, e2118696119. <https://doi.org/10.1073/pnas.2118696119>
- Milàn, J., Mateus, O., Mau, M., Rudra, A., Sanei, H. & Clemmensen, L.B. 2021: A possible phytosaurian (Archosauria, Pseudosuchia) coprolite from the Late Triassic Fleming Fjord Group of Jameson Land, central East Greenland. *Bulletin of the Geological Society of Denmark* 69, 71–80. <https://doi.org/10.37570/bgsgd-2021-69-05>
- Milner, A.R. 1988: The relationships and origin of living amphibians. In: Benton, M.J. (ed.): *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*. Systematics Association Special Volume 35A, 59–102. Clarendon Press, Oxford. <https://doi.org/10.1017/s0016756800006476>
- Nesov, L.A. 1988: Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta Zoologica Cracoviensis* 31, 475–486.
- Nøttvedt, A., Johannessen, E.P. & Surlyk, F. 2008: The Mesozoic of western Scandinavia and East Greenland. *Episodes* 31, 1–7.
- Paparella, I., LeBlanc, A.R.H., Doschak, M.R. & Caldwell, M.W. 2019: The iliosacral joint in lizards: an osteological and histological analysis. *Journal of Anatomy* 236, 668–687. <https://doi.org/10.1111/joa.13132>
- Piveteau, J. 1936: Origine et évolution morphologique des amphibiens anoures. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 103, 1084–1086. <https://doi.org/10.5962/bhl.part.5840>
- Pyron, R.A. 2011: Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Systematic Biology* 60, 466–481. <https://doi.org/10.1093/sysbio/syr047>
- Rage, J.-C. & Roček, Z. 1989: Redescription of *Triadobatrachus massinoti* (Piveteau, 1936) an anuran amphibian from the Early Triassic. *Palaeontographica Abteilung A206*, 1–16.
- Roček, Z., Eaton, J.G., Gardner, J. & Prikryl, T. 2010: Evolution of anuran assemblages in the Late Cretaceous of Utah, USA. *Palaeobiodiversity and Palaeoenvironments* 90, 341–393. <https://doi.org/10.1007/s12549-010-0040-2>
- Roček, Z., Gardner, J.D., Eaton, J.G. & Prikryl, T. 2012: Similarities and differences in the ilia of Late Cretaceous anurans and urodeles. *Bulletin de la Société Géologique de France* 183, 529–535. <https://doi.org/10.2113/gssgfbull.183.6.529>
- Schoch, R.R. 1999: Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) Germany (Baden-Württemberg, Bayern, Thüringen). *Stuttgarter Beiträge zur Naturkunde B278*, 175 pp.
- Schoch, R.R. 2006: A complete trematosauroid amphibian from the Middle Triassic of Germany. *Journal of Vertebrate Paleontology* 26, 29–43. [https://doi.org/10.1671/0272-4634\(2006\)26\[29:actaft\]2.0.co;2](https://doi.org/10.1671/0272-4634(2006)26[29:actaft]2.0.co;2)
- Schoch, R.R. 2019: The putative lissamphibian stem-group: Phylogeny and evolution of the dissorophoid temnospondyls. *Journal of Paleontology* 93, 137–156. <https://doi.org/10.1017/jpa.2018.67>
- Schoch, R.R. & Rubidge, B.S. 2005: The amphibamid *Micropholis* from the Lystrosaurus assemblage zone of South Africa. *Journal of Vertebrate Paleontology* 25, 502–522. [https://doi.org/10.1671/0272-4634\(2005\)025\[0502:tamftl\]2.0.co;2](https://doi.org/10.1671/0272-4634(2005)025[0502:tamftl]2.0.co;2)
- Schoch, R.R., Werneburg, R. & Voigt, S. 2020: A Triassic stem-salamander from Kyrgyzstan and the origin of salamanders. *Proceedings of the National Academy of Sciences* 117, 11584–11588. <https://doi.org/10.1073/pnas.2001424117>
- Scopoli, G.A. 1777: *Introductio ad Historiam Naturalem, Sistens Genera Lapidium, Planatarum, et Animalium Hactenus Detecta, Characteribus Essentialibus Donata, in Tribus Divisa, Subinde ad Leges Naturae*. Gerle, Prague. <https://doi.org/10.5962/bhl.title.10827>
- Sengupta, D.P. 1935: Chigutisaurid temnospondyls from the Late Triassic of India and a review of the family Chigutisauridae. *Palaeontology* 38, 313–339.
- Shubin, N.H. & Jenkins, F.A., Jr. 1995: An Early Jurassic jumping frog. *Nature* 377, 49–51. <https://doi.org/10.1038/377049a0>
- Sigurdson, T. & Bolt, J.R. 2010: The Lower Permian amphibamid *Doleserpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. *Journal of Vertebrate Paleontology* 30, 1360–1377. <https://doi.org/10.1080/02724634.2010.501445>

- Simões, T.R., Caldwell, M.W., Talanda, M., Bernardi, M., Palci, A., VERNYgora, O., Bernardini, F., Mancini, L. & Nydam, R.L. 2018: The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature* 557, 706–709. <https://doi.org/10.1038/s41586-018-0093-3>
- Skutschas, P.P., Kolchanov, V.V., Averianov, A.O., Martin, T., Schellhorn, R., Kolosov, P.N. & Vitenko, D.D. 2018: A new relict stem salamander from the Early Cretaceous of Yakutia, Siberian Russia. *Acta Palaeontologica Polonica* 63, 519–525. <https://doi.org/10.4202/app.00498.2018>
- Skutschas, P.P. & Krasnolutskii, S.A. 2011: A new genus and species of basal salamanders from the Middle Jurassic of western Siberia, Russia. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* 315, 167–175.
- Spielmann, J.A. & Lucas, S.G. 2012: Tetrapod fauna of the Upper Triassic Redonda Formation, East-central New Mexico: the characteristic assemblage of the Apachean Land-vertebrate Faunachron. *New Mexico Museum of Natural History and Science Bulletin* 55, 119 pp.
- Stocker, M.R., Nesbitt, S.J., Kligman, B.T., Paluh, D.J., Marsh, A.D., Blackburn, D.C. & Parker, W.G. 2019: The earliest equatorial record of frogs from the Late Triassic of Arizona. *Biology Letters* 15, 1–5. <https://doi.org/10.1098/rsbl.2018.0922>
- Sulej, T. 2002: Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus*. *Acta Palaeontologica Polonica* 47, 535–546.
- Sulej, T. 2007: Osteology, variability, and evolution of *Metoposaurus*, a temnospondyl from the Late Triassic of Poland. *Paleontologica Polonica* 64, 29–139.
- Sulej, T., Krzesiński, G., Tałanda, M., Wolniewicz, A.S., Błazejowski, B., Bonde, N., Gutowski, P., Sienkiewicz, M. & Niedźwiedski, G. 2020: The earliest-known mammaliaform fossil from Greenland sheds light on origin of mammals. *Proceedings of the National Academy of Sciences* 117, 26861–26867. <https://doi.org/10.1073/pnas.2012437117>
- Szentesi, Z., Sebe, K. & Szabó, M. 2020: Giant salamander from the Miocene of the Mecsek mountains (Pécs-Danitzupusztá, southwestern Hungary). *Paläontologische Zeitschrift*, 94, 353–366. <https://doi.org/10.1007/s12542-019-00499-2>
- Tesakov, A.S., Simakova, A.N., Frolov, P.D., Sytchevskaya, E.K., Syromyatnikova, E.V., Foronova, I.V., Shalaeva, E.A. & Trifonov, V.G. 2019: Early-Middle Pleistocene environmental and biotic transition in north-western Armenia, southern Caucasus. *Palaeontologia Electronica* 22, 1–39. <https://doi.org/10.26879/916>
- Venczel, M., Gardner, J.D., Codrea, V.A., Csiki-Sava, Z., Vasile, S. & Solomon, A.A. 2016: New insights into Europe's most diverse Late Cretaceous anuran assemblage from the Maastrichtian of western Romania. *Palaeobiodiversity and Palaeoenvironments* 96, 61–65. <https://doi.org/10.1007/s12549-015-0228-6>
- Venczel, M. & Csiki, Z. 2003: New frogs from the latest Cretaceous of Hațeg Basin, Romania. *Acta Palaeontologica Polonica* 48, 609–616.
- Warden A.A. & Snell, N. 1991: The postcranial skeleton of Mesozoic temnospondyl amphibians: a review. *Alcheringa: An Australasian Journal of Paleontology* 15, 43–64. <https://doi.org/10.1080/03115519108619009>
- Watson, D.M.S. 1958: A new labyrinthodont (*Paracyclotusaurus*) from the Upper Trias of New South Wales. *Bulletin of the British Museum of Natural History of Geology* 3, 233–263.
- Werneburg, R. 2009: The Permian branchiosaurid *Tungusosgyrinus* Efremov, 1939 (Temnospondyli, Dissorophoidea) from Siberia restudied. *Fossil Record* 12, 105–120. <https://doi.org/10.1002/mmng.200900001>
- Yates A.M. & Warren A.A. 2000: The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* 128, 77–121. <https://doi.org/10.1111/j.1096-3642.2000.tb00650.x>
- Ziegler, P.A. 1988: Evolution of the Arctic-North Atlantic and the Western Tethys. *American Association of Petroleum Geologists, Memoirs* 43, 164–196. <https://doi.org/10.1306/M43478>
- von Zittel, K.A. 1887: *Handbuch der Paläontologie. I. Abtheilung – Paläozoologie. III. Band – Vertebrata (Pisces, Amphibia, Reptilia, Aves)*, 900 p. R. Oldenburg, München.