

BIOCHRONOLOGY OF LATE TRIASSIC METOPOSAURIDAE (AMPHIBIA, TEMNOSPONDYLI) AND THE CARNIAN PLUVIAL EPISODE

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Abstract: During the Late Triassic, metoposaurids were one of the last significant families of temnospondyl amphibians, and they have long been used in the correlation of Late Triassic tetrapod assemblages. Their fossil record extends across much of Late Triassic Pangea, including important metoposaurid fossils from the USA, Canada, Portugal, Germany, Poland, Morocco, India and Madagascar. Six genera of metoposaurids are recognized: 1) Adamanian-Apachean *Apachesaurus*, endemic to the western USA, 2) Otischalkian *Arganasaurus* and *Dutuitosaurus*, endemic to Morocco, 3) Otischalkian-Revueltian *Koskinonodon*, endemic to the western USA, 4) *Panthesaurus* from the Otischalkian of India, and 5) Otischalkian-Adamanian *Metoposaurus*, known from the western USA, eastern Canada, Portugal, Italy, Germany, and Poland. Of the metoposaurid genera, only *Metoposaurus* has a broad enough palaeogeographic distribution and relatively restricted temporal range to be of biochronological value; its biochron identifies the Otischalkian–Adamanian (middle–late Carnian). The oldest metoposaurids are of middle Carnian age, the age of the Carnian pluvial episode of global climate. The middle Carnian broad palaeogeographic distribution, diversity and cosmopolitanism of the metoposaurids, followed by reduced diversity and relative endemism, likely indicates that climate changes were an important factor in their evolution.

Key words: Land-vertebrate faunachron, Krasiejów level, Otischalkian, Adamanian, Revueltian, Apachean, Carnian wet episode.

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INTRODUCTION

The temnospondyls are a diverse group of Palaeozoic–Mesozoic amphibians with a fossil record that begins in the Mississippian and extends through the Early Cretaceous (e.g., Schoch and Milner, 2000; Schoch, 2014). The youngest time interval of substantial temnospondyl diversity was the Late Triassic (Lucas, 2018). As part of this Late Triassic diversity, metoposaurids were a significant temnospondyl family with a fossil record known from across much of Late Triassic Pangea (Fig. 1). This record has long been applied to the correlation of Late Triassic tetrapod assemblages. The present account reviews the geographic, stratigraphic and temporal distribution of metoposaurids to evaluate their utility in Late Triassic tetrapod biochronology. The author concludes by discussing the relationship of metoposaurid distribution to the Carnian pluvial episode, a relationship that indicates that climate was a significant factor in metoposaurid evolution.

LATE TRIASSIC TIMESCALE

Lucas (1998, 2010; also see Lucas and Hunt, 1993; Lucas and Huber, 2003; Lucas *et al.*, 2007b; Lucas, 2018) presented a comprehensive global Triassic tetrapod biochronology (Fig. 2). This biochronological timescale divides the Triassic into eight time intervals (land-vertebrate faunachrons, LVFs), based on biochronological datums that represent tetrapod evolutionary events. This model has been tested and refined for nearly two decades and was last reviewed for the Late Triassic by Lucas (2018). Correlations presented here are within the framework of this tetrapod biochronology, with the genus as the operational taxonomic unit for biochronology. It should be noted that the Carnian–Norian boundary here is placed at ~220 Ma, so that the “long Norian” concept is rejected on the basis of the arguments of Lucas *et al.* (2012).

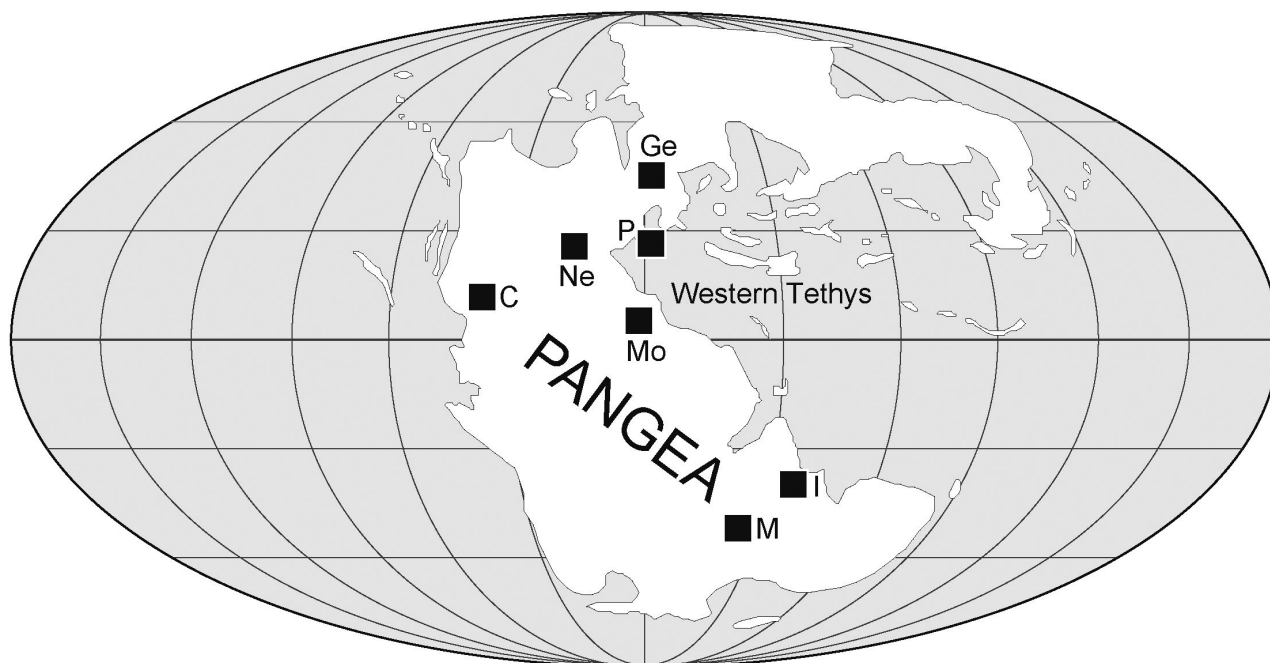


Fig. 1. Map of Late Triassic Pangea showing major areas where metoposaurid fossils are found. C – Chinle Group basin, western USA, GE – Germanic basin, Germany and Poland, I – India, M – Madagascar, Mo – Morocco, Ne – Newark Supergroup basins, eastern USA and Canada, P – Portugal.

Use of a tetrapod biochronology that assigns ages and correlates on the basis of the tetrapods, themselves, frees vertebrate biostratigraphers from attempting to correlate tetrapods directly to the standard global chronostratigraphic scale (SGCS), the “marine timescale” (Lucas, 2015). The correlation to the SGCS is a separate cross-correlation between vertebrate biochronology and marine biochronology that usually relies on other data (palynostratigraphy, magnetostratigraphy, radioisotopic ages) to be completed. Sometimes, a Triassic terrestrial/freshwater fossil vertebrate is found displaced in marine deposits, which allows some direct cross-correlation of vertebrate taxa to the SGCS (Lucas and Heckert, 2000), but typically that cross-correlation relies wholly on non-vertebrate-fossil data.

TAXONOMY

Metoposaurids were 2–5-m-long, aquatic predators that can simply be described as looking like giant salamanders with very large and flattened, shovel-shaped skulls (Fig. 3). Their extensive fossil record owes much to mass death assemblages in Portugal, Poland, Morocco and the western USA that provide relatively large samples of metoposaurid crania and postcrania, which can be used to interpret morphological variation to an extent rare among Triassic tetrapods (Dutuit, 1976; Sulej, 2002, 2007; Lucas *et al.*, 2010, 2016; Brusatte *et al.*, 2015).

Metoposauridae are a very distinctive and clearly monophyletic family of temnospondyls. They are characterized by many features, including a very short preorbital region, small and laterally located orbits, large and closely spaced

external nares that open anteriorly, and a broad and flat cultriform process of the parasphenoid (Schoch and Milner, 2000).

Colbert and Imbrie (1956) and Hunt (1993) provided comprehensive revisions of metoposaurid taxonomy. Schoch and Milner’s (2000) review employed the taxonomy of Hunt (1993). The purpose of the present author is not to revise taxonomy here, but there is a need to comment briefly on some taxonomic decisions made since the revision of Hunt (1993), pending a more complete treatment of metoposaurid taxonomy underway by L. F. Rinehart and the present author. These comments are:

1. Gee and Parker (2017, 2018) and Gee *et al.* (2017) suggested that *Apachesaurus* may be a juvenile *Koskinonodon*, though they retained *Apachesaurus* as a valid genus. However, Rinehart and Lucas (2018) described a juvenile skull and definitively associated partial postcranium of *Apachesaurus* that establishes that *Apachesaurus* is not a juvenile of a larger taxon. Thus, *Apachesaurus* has its own growth trajectory, different from that of the larger metoposaurids. The present author thus recognizes *Apachesaurus* as a valid genus. It should be noted also that Buffa *et al.* (2019) recovered *Apachesaurus* as a distinct genus in their phylogenetic analysis of metoposaurids.
2. Gee *et al.* (2019) redescribed the holotype skull of *Anaschisma browni* from the Otischalkian of Wyoming, claiming it has diagnostic morphology (contra Hunt, 1993 and Schoch and Milner, 2000, who considered *A. browni* a nomen dubium), and concluding that *Koskinonodon* is a junior subjective synonym of *Anaschisma*. However, the present author also has studied the type skull of

A. browni firsthand, which is damaged and partly restored in plaster, and cannot verify the bone map of that skull published by Gee *et al.* (2019), particularly the configuration of the lacrimal. Therefore, the present author regards *Anaschisma* as a nomen dubium and uses the name *Koskinonodon* for the large Chinle Group metoposaurid, long called by the preoccupied name *Buettneria*.

- Chakravatari and Sengupta (2019) proposed the new generic name *Panthisaurus* for the Indian species, originally known as *Metoposaurus maleriensis* (see Roychowdhury, 1965). Their diagnosis indicates that this species shares many features with *Metoposaurus*, and to the present author their claims of distinctiveness are better dealt with at the species than the genus level. However, the present author identifies the Indian metoposaurid as *Panthisaurus* here, pending more detailed study.

GEOGRAPHIC, STRATIGRAPHIC AND TEMPORAL DISTRIBUTION

Europe

In Europe, metoposaurid fossils that can be assigned to genus- and species-level taxa have been documented from Portugal, Italy, Germany and Poland. Fragmentary specimens from France and Switzerland can only be assigned to Metoposauridae.

Portugal

Earlier reports of fragmentary material of metoposaurids from southern Portugal (e.g., Witzmann and Gassner, 2008) were followed by Brusatte *et al.* (2015), who described more complete metoposaurid fossils from a bonebed (their “Penina Bonebed”) in the Grés de Silves Formation. They assigned these fossils to *Metoposaurus* as a new species, *M. alarvensis*.

The Penina bonebed also contains fragmentary, indeterminate phytosaur fossils. Mateus *et al.* (2014) described these fossils and assigned the bonebed a late Carnian–early Norian age, because they considered that to be the temporal range of *Metoposaurus*. However, the genus has a middle–late Carnian temporal range (see below), so that is the most precise age that can now be assigned to the Penina Bonebed.

Germany

Metoposaurid fossils were first described from Germany, by Meyer (1842), when he coined the name *Metopias diagnosticus*. Subsequent German records have been documented by various workers (e.g., Fraas, 1889, 1896, 1913; Kuhn, 1932, 1936; Werneburg, 1990). These fossils are all assigned to *Metoposaurus diagnosticus* and come from the Schilfsandstein (Stuttgart Formation) and overlying Lehrberg Schichten (Steigerwald Formation), with the highest stratigraphic occurrences in the Kieselsandstein (Hassberg Formation) (e.g., Lucas, 1999; Schoch and Wild, 1999). These are records of Otischalkian-Adamanian age (Kozur and Weems, 2005, 2007, 2010; Lucas, 2010, 2018).

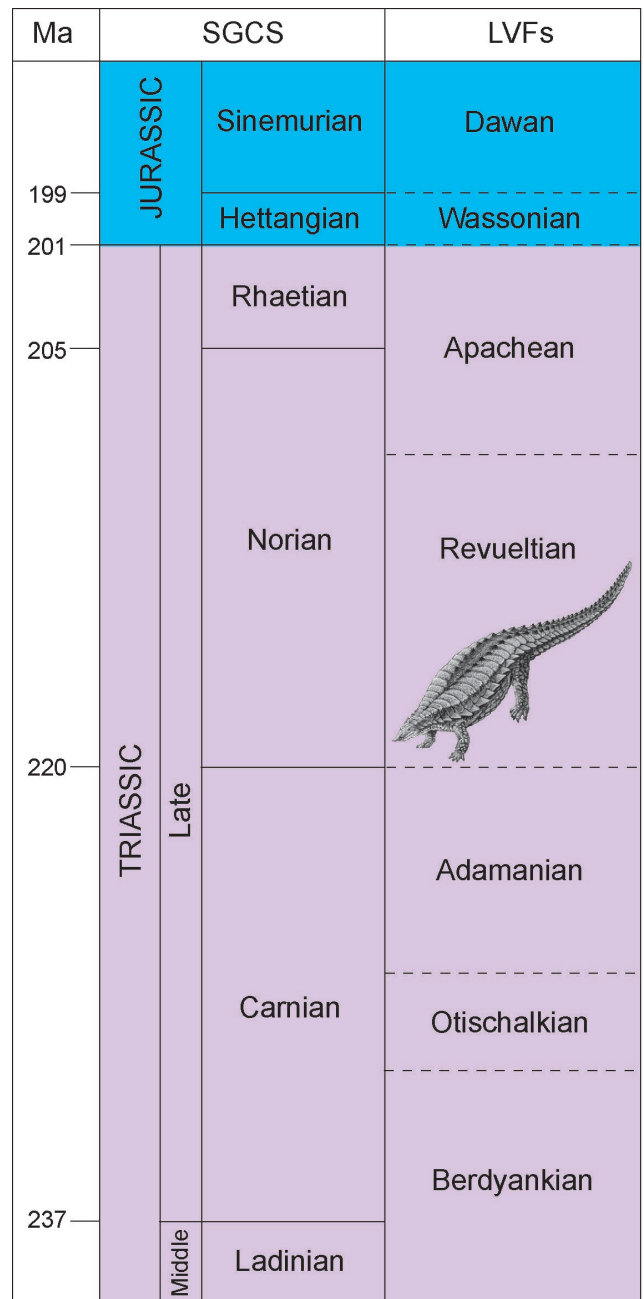


Fig. 2. The Triassic timescale based on tetrapod biostratigraphy and biochronology (after Lucas, 2018). Restoration of *Typothorax* by Matt Celeskey.

Milner and Schoch (2004) claimed the presence of *Metoposaurus* in the Revueltian Stubensandstein of Germany. However, that claim met a detailed refutation from Lucas *et al.* (2007b) and Lucas (2015). Thus, the present author considers the youngest records of *Metoposaurus* in Germany to be Adamanian.

Poland

The Krasiejów bonebed in Silesia, Poland, has yielded an extensive assemblage of metoposaurid fossils assigned to *Metoposaurus* that has been the subject of diverse

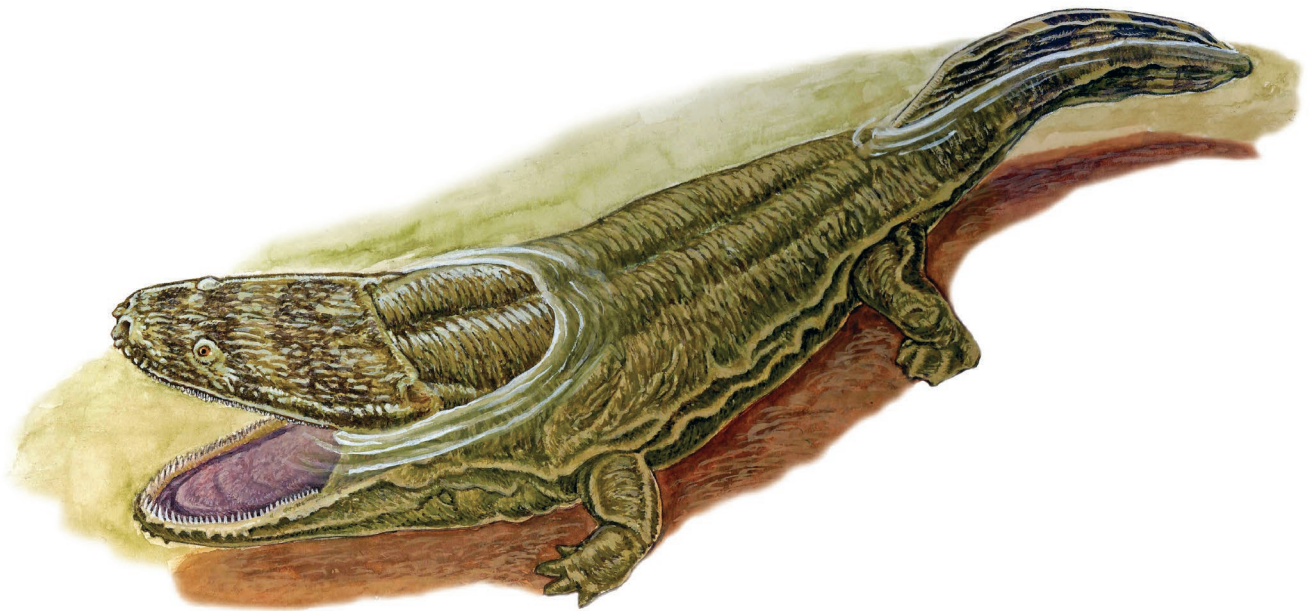


Fig. 3. Restoration of *Metoposaurus* by Matt Celeskey.

publications (e.g., Sulej, 2002, 2007; Dzik and Sulej, 2007; Konietzko-Meier *et al.*, 2013, 2018; Gruntmejer *et al.*, 2016; Antczak and Bodzioch, 2018;). The Krasiejów tetrapod assemblage includes the amphibians *Cyclotosaurus* and *Metoposaurus*, the phytosaur *Parasuchus*, the aetosaur *Stagonolepis*, the rauisuchian *Teratosaurus* and the dinosauriform *Silesaurus* (Lucas, 2015). This assemblage is from strata ~ 80 m above the Reed Sandstone (a Schilfsandstein equivalent) that are homotaxial to the German Lehrberg Schichten and is of Adamanian age (Lucas, 2015).

Some published direct correlations to the GSCS have assigned the Krasiejów level to the Carnian (e.g., Dzik and Sulej, 2007) and Sulej (2007) correlated Krasiejów to the German Lehrberg Schichten. However, Szulc *et al.* (2015a, b; also see Szulc, 2005), largely on the basis of palynostratigraphy, assigned it to the Norian, an age assignment contradicted by the vertebrate biostratigraphy (Lucas *et al.*, 2007a; Lucas, 2015).

Other European localities

Fragmentary metoposaurid fossils have been reported from France and Switzerland and a diagnostic skull is known from Italy. Corroy (1928) reported but did not illustrate fragmentary specimens he identified as metoposaur from the lower Keuper at Gemmalaincourt in the Vosges Mountains of France. Cuny and Ramboer (1991) illustrated a fragment of a right clavicle and mentioned other fragmentary metoposaurid fossils from the Rhaetian Saint-Nicholas-de-Port locality in France (see Debuyschere *et al.*, 2015) that they assigned to *Metoposaurus*. However, the clavicle fragment they illustrate (Cuny and Ramboer, 1991, fig. 1h) is more likely cyclotosaur than metoposaur: note the very thin and widely spaced ridges characteristic of cyclotosaurs (see Sulej and Majer, 2005, text-fig. 6), unlike the thicker

and more closely spaced ridges of *Metoposaurus* (compare Sulej, 2007, figs 43–44). Therefore, the present author rejects the identification of *Metoposaurus* at Saint-Nicholas-de-Port and refer to the specimens Cuny and Ramboer (1991) recorded as Metoposauridae.

Leonardi (1952) reported fragmentary metoposaurid specimens from the Raibl Beds in Switzerland. Koken (1913) described a skull he named *Metoposaurus santacrucis* from the Raibl Beds in northern Italy. The shallow-marine/deltaic Raibl Beds are of middle Carnian age, correlative to the German Schilfsandstein (e.g., Hornung *et al.*, 2007).

North America

In North America, metoposaurid fossils come from the Chinle Group in the western USA and the Newark Supergroup of the eastern USA and Canada. Long and Murry (1995) reviewed in some detail the Chinle Group metoposaurid record, which comes from the states of Wyoming, Colorado, Utah, Arizona, New Mexico, Oklahoma and Texas. It includes three mass death assemblages of metoposaurids – Lamy in New Mexico (Lucas *et al.*, 2010) and Rotten Hill and Elkins, both in Texas (Case, 1932; Lucas *et al.*, 2016). Records in Wyoming, Arizona, New Mexico and Texas have been the source of specimens that became the bases of new taxa (e.g., Lucas, 1904; Branson, 1905; Case, 1922, 1932; Branson and Mehl, 1929; Sawin, 1945; Hunt, 1993; Long and Murry, 1995; Spielmann and Lucas, 2012). Three genera are recognized: Otischalkian *Metoposaurus*, Otischalkian-Revueltian *Koskinonodon* and Adamanian-Apachean *Apachesaurus*. The large metoposaur *Koskinonodon* is more common than *Apachesaurus* in Adamanian strata, whereas *Apachesaurus* is more common in Revueltian strata (Hunt, 1993; Hunt and Lucas, 1993).

The Newark Supergroup in eastern North America has produced generally fragmentary metoposaurid material that has received taxonomic names now regarded as *nomen dubia* (e.g., Leidy, 1856; Cope, 1868; Huene, 1921; Baird, 1987; Huber *et al.*, 1993; Hunt, 1993; Schoch and Milner, 2000; Sues and Olsen, 2015). The metoposaurid fossils come from various localities, ranging geographically from North Carolina to Nova Scotia. An important record is a skull roof from the Evangeline Formation in Nova Scotia (cf. Weems *et al.*, 2016) that has been assigned to *Metoposaurus bakeri*, a species known elsewhere only from the Otischalkian of Texas (Sues and Olsen, 2015). Huber *et al.* (1993) showed the total range of metoposaurids in the Newark Supergroup as Adamanian–Apachean (Sanfordian–Cliftonian). They considered the Evangeline Formation record to be Adamanian, but it is more likely Otischalkian (Lucas, 2018).

India

Metoposaurid fossils have long been known from the Maleri Formation in the Pranhita-Godavari Valley (Lydekker, 1882, 1885; Huene, 1940; Roychowdhury, 1965; Sengupta, 1992, 2002) and are also known in the correlative Tiki Formation of the Son-Mahandari Valley (Sengupta, 1992). These specimens were originally assigned to *Metoposaurus maleriensis* Roychowdhury, 1965, but have also been assigned to *Buettneria* (Sengupta, 2002) and *Panthesaurus* (Chakravarti and Sengupta, 2019), and the latter assignment is tentatively followed here. The Maleri and Tiki vertebrate faunas are of Otischalkian age (Lucas, 2010, 2018)

Africa

Morocco

Dutuit (1976) published a monograph on the extensive metoposaur assemblages from the t5 interval of the Timesgadouine Formation in the Argana basin of Morocco. Hunt (1993) revised the taxonomy of these metoposaurids to recognize three genera, *Metoposaurus*, *Arganasaurus* and *Dutuitosaurus* (the latter two named by Hunt). Buffa *et al.* (2019) have reassigned the Moroccan *Metoposaurus* specimens to *Arganasaurus* as a distinct species, *A. ouazzii*, different from *A. lyazidi*, the type species of *Arganasaurus*. The t5 interval of the Timesgadouine Formation is of Otischalkian age (Lucas, 2010, 2018).

Algeria

Lehman (1971, pl. 5f) documented what may be fragmentary metoposaurid fossils from the Zarzaitine Series in Algeria. This is likely an Adamanian-age record (Jalil *et al.*, 1995).

Madagascar

Dutuit (1978) documented fragmentary metoposaurid specimens from the Isalo Group in Madagascar, for which he proposed the name *Metoposaurus hoffmani*. Fortuny *et al.* (2019) recently reviewed this taxon and concluded that *M.*

hoffmani is a *nomen dubium*. They stated that the type material of that taxon as well as undescribed fragmentary metoposaurid specimens they documented are from either the Isalo II or Isalo III stratigraphic intervals of the Isalo Group, and that the provenance of the fossils is too vague to determine which. However, in so doing, they erroneously stated that the vertebrate-fossil assemblage from the Poamay site in Madagascar documented by Burmeister *et al.* (2006) is from the Isalo III interval. But, according to Burmeister *et al.* (2006), that assemblage, which they regarded as tentatively of Norian age, is from the upper part of the Isalo II interval. Furthermore, even though that assemblage includes fragmentary remains of phytosaurs and aetosaurs, it lacks metoposaurs, an absence, to which Burmeister *et al.* (2006) drew attention.

This suggests to the present author that the Isalo metoposaurid fossils are likely from the lower part of the Isalo II interval, which produces a vertebrate fossil assemblage that includes the rhynchosaur *Hyperodapedon* and thus is of Otischalkian or Adamanian age (Lucas and Heckert, 2002; Lucas, 2010, 2018). Thus, it seems likely, though not certain, that the Malagasy metoposaurid fossils, which are generically indeterminate, are of Otischalkian or Adamanian age.

BIOCHRONOLOGY

Metoposaurids are a strictly Late Triassic taxonomic group, known from Otischalkian–Apachean strata (Hunt, 1993; Schoch and Milner, 2000; Lucas, 2018). There are no Middle Triassic, nor are there any Early Jurassic metoposaurids (Hunt, 1993; Schoch and Milner, 2000). Various workers have previously delineated the biostratigraphic distribution of the metoposaurids (e.g., Roychowdhury, 1965; Hunt, 1993; Sengupta, 2002; Chakravarti and Sengupta, 2019).

The metoposaurid record as just reviewed can be placed into the framework of Late Triassic correlations (Fig. 4) presented most recently by Lucas (2018; for a very different correlation, based largely on the “long Norian” concept, see Buffa *et al.*, 2019, fig. 9). This framework is based on vertebrate biostratigraphy, largely using phytosaurs and aetosaurs as index taxa, as well as other data, including palynostratigraphy, conchostracan biostratigraphy, a few radioisotopic ages, magnetostratigraphy and sequence stratigraphy.

Placed into that framework, the metoposaurid genera fall into three groups: (1) relatively endemic genera, limited to North America (*Apachesaurus*, *Koskinonodon*), India (*Panthesaurus*) and Morocco (*Arganasaurus*, *Dutuitosaurus*); (2) temporally long-ranging genera, *Apachesaurus* and *Koskinonodon*; and (3) a temporally more restricted genus (*Metoposaurus*), with a broad geographic distribution. Thus, the most biochronologically significant metoposaur is *Metoposaurus*, which has a biochron equivalent to Otischalkian–Adamanian (middle–late Carnian) time and is widely distributed across Late Triassic Pangea. The other metoposaurid taxa have limited biochronological significance because of their endemism and/or long temporal ranges.

| stage | LVF | western North America | eastern North America | Portugal | Italy | Germany | Poland | India | Morocco | Madagascar | metoposaurid temporal ranges | |
|-------------|--------------|--|---|--------------------------|-------|---------------------------------------|---------------------------------------|-------------------------|---------------------------------------|--------------------------------------|---|--|
| Rhaetian | Apachean | Rock Point sequence Redonda Fm, NM, characteristic Apachean assemblage | Cliftonian LVF | | | | | | | | | |
| | | | | | | | | | | | | |
| Norian | Revuelitian | Moss Back-Owl Rock sequence | Neshanician LVF | | | | | | | | Apachesaurus | |
| | | Bull Canyon Fm, NM, characteristic Revuelitian assemblage | | | | | | | | | | |
| Carnian | Adamanian | Blue Mesa Member, Petr Forest Fm, Arizona, characteristic Adamanian assemblage | Conewagian LVF | Grés de Silves Formation | | Mainhardt Formation (Ob Bunte Mergel) | Grabowa Formation | upper Maleri Formation? | | Isalo II tetrapod assemblage (lower) | | |
| | | | | | | Hassberge Formation (Blasensandstein) | | | | | | |
| | Otischalkian | Chinle Group | Shinarump-Blue Mesa sequence | Sanfordian LVF | | Raibl Beds | Stuttgart Formation (Schiffsandstein) | Reed Sandstone | basal Maleri Formation/Tiki Formation | Timesgadiouine Formation | Irohalene Member (T-5) | |
| | | | Colorado City Fm, Texas, characteristic Otischalkian assemblage | | | | | | | | | |
| Berdyankian | | | | | | Erfurt Formation (Lettenkohle) | | | | | Parifasaurus Arganasaurus Duitifosaurus Metoposaurus | |

Fig. 4. Correlation of metoposaurid-fossil-bearing units across Late Triassic Pangea and metoposaurid biochronology.

METOPOSAURS AND THE CARNIAN PLUVIAL EPISODE

Identification of a “pluvial episode,” an interval of unusually high humidity/rainfall during the Carnian, has gained broad support as a Pangaea-wide interval of humid climate (e.g., Ruffell *et al.*, 2016; Dal Corso *et al.*, 2020). The age of the Carnian pluvial episode (CPE) is well established in marine sections in Western Europe as late early Carnian (late Julian) to early late Carnian (early Tuvanian), sometimes referred to as “middle Carnian” (e.g., Hornung *et al.*, 2007; Rigo *et al.*, 2007; Kozur and Bachmann, 2010; Dal Corso *et al.*, 2015)

The beginning of the Otischalkian essentially corresponds to or overlaps the onset of the CPE (e.g., Kozur and Bachman, 2010; Lucas, 2018; Lucas and Tanner, 2018). Two groups of dominantly amphibious/aquatic tetrapods are abundant at this time, the metoposaurs and the phytosaurs. This may be a real acme as a response to wetter climates, but that conclusion may, in part, be confounded by taphonomy – preferential preservation of aquatic tetrapods by widespread river systems of the Carnian “pluvial.” That caveat aside, metoposaurs and phytosaurs are among the dominant components of almost all Otischalkian and younger Late Triassic tetrapod assemblages.

Metoposaurids first appeared during the CPE (Lucas, 2018; Buffa *et al.*, 2019; Fortuny *et al.*, 2019). Dal Corso *et al.* (2020) reviewed the many biotic events associated

with the CPE but neglected to mention the metoposaurids. During the CPE metoposaurids were widespread, relatively diverse (their highest generic diversity: Fig. 4) and cosmopolitan. After the CPE, metoposaurid diversity declined and they became more endemic in their distribution. Furthermore, the relatively terrestrially adapted metoposaurid *Apachesaurus* (Rinehart and Lucas, 2018) did not appear until after the CPE.

As aquatic predators, metoposaurids would no doubt have been favored by the wet environments of the CPE. After, the CPE, climates across Pangaea are thought to have been (seasonally) drier, and this climate change may explain the diminishment of metoposaurid diversity and cosmopolitanism, particularly during the Norian. Indeed, recent palaeohistological studies demonstrate that metoposaurs were climate sensitive in terms of their ontogeny (Konietzko-Meier and Klein, 2013; Teschner *et al.*, 2018, 2020). There thus seems to be a direct correlation between major climate events of the Late Triassic and major aspects of metoposaurid evolution. This correlation indicates that climate was an important factor that drove metoposaurid evolution during the CPE and its aftermath.

CONCLUSIONS

This article supports the following conclusions:

1. The fossil record of metoposaurid amphibians is found across much of Late Triassic Pangaea, including important

- records from the USA, Canada, Portugal, Germany, Poland, Morocco, India and Madagascar.
- There are six metoposaurid genera: Adamanian–Apachean *Apachesaurus*, endemic to the western USA; Otischalkian *Arganasaurus* and *Dutuitosaurus*, endemic to Morocco; Otischalkian–Apachean *Koskinodon*, endemic to the western USA; Otischalkian–Adamanian *Metoposaurus*, known from the western USA, eastern Canada, Portugal, Italy, Germany and Poland; Otischalkian *Panthsaurus* from India.
 - Only *Metoposaurus* has a broad enough palaeogeographic distribution and relatively restricted temporal range to be of biochronological value, with a biochron that identifies the Otischalkian–Adamanian (middle–late Carnian).
 - Metoposaurids appeared during the Carnian pluvial episode of global climate, during which they achieved their highest diversity, broadest palaeogeographic distribution and highest degree of cosmopolitanism. After the CPE, metoposaurids experienced reduced diversity and relative endemism.
 - The correlation between the CPE and metoposaurid diversity, distribution and cosmopolitanism indicates that climate changes were an important factor in their evolution.

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