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Memorial Jean-Claude Rage – A life of paleo-herpetologist –

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New data on the Triassic temnospondyls from the Karoo rift basins of Tanzania and Zambia

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ABSTRACT

Temnospondyl specimens collected recently in the Middle-?Late Triassic of the Ruhuhu (Tanzania) and Luangwa (Zambia) rift basins are described and figured. They are attributed to cf. *Cherninia megarhina* (Chernin & Cosgriff, 1975), Mastodonsauroidea indet., Stereospondyli indet., and cf. Stereospondyli, as well as intercentra of small adult individual(s) which may belong to a new taxon. Although fragmentary, this new material allows taxonomic updates to the Triassic temnospondyl assemblages of Tanzania and Zambia and documents an interesting phylogenetic and ecological diversity. For example, among the Triassic mastodonsauroids of Zambia, *Cherninia megarhina* coexisted with *Stanocephalosaurus pronus* (Howie, 1970) in nonmarine environments. Similar to that of the South African Karoo Basin, these temnospondyl assemblages also illustrate the rapid recovery of the group after the Permian-Triassic mass extinction and contribute to a better understanding of the impact of this extinction on the tetrapod faunas of southern Pangea.

KEY WORDS
Amphibia,
Karoo system,
Permo-Triassic extinction,
extinction recovery.

RÉSUMÉ

Nouvelles données sur les temnospondyles triasiques des bassins du rift tanzanien et zambien.

Des restes de temnospondyles découverts récemment dans le Trias Moyen- ?Supérieur des bassins de Ruhuhu (Tanzanie) et Luangwa (Zambie) sont décrits et figurés ici. Ils sont attribués à cf. *Cherninia megarhina* (Chernin & Cosgriff, 1975), Stereospondyli indet., et cf. Stereospondyli, et regroupent notamment de petits intercentres d'individu(s) adulte(s) qui pourraient correspondre à un nouveau taxon. Ces découvertes, bien que fragmentaires, permettent de mettre à jour les assemblages des temnospondyles de Tanzanie et Zambie et montrent une intéressante diversité aussi bien phylogénétique qu'écologique : par exemple, concernant les mastodonsauroïdes du Trias de Zambie, *Cherninia megarhina* a co-existé avec *Stanocephalosaurus pronus* (Howie, 1970) dans les environnements non-marins. Comparable à celui du Bassin du Karoo d'Afrique du Sud, ces assemblages illustrent la reconquête du groupe après l'extinction en masse du Permien-Trias et permettent une meilleure compréhension de l'impact de cette crise sur les faunes de tétrapodes du sud de la Pangée.

MOTS CLÉS
Amphibia,
système Karoo,
extinction permo-triasique,
reconquête post-crise.

INTRODUCTION

The Karoo System consists of several Carboniferous-Triassic basins in southern and eastern Africa (Catuneanu *et al.* 2005), including the main Karoo foreland basin of South Africa, and the Ruhuhu and Luangwa rift basins of Tanzania and Zambia respectively (Fig. 1). The South African Karoo Basin has been the subject of intensive research for over 150 years (see historical reviews in Kitching 1977; Day 2013), and it now occupies a foundational position in our understanding of Permo-Triassic terrestrial paleontology and biostratigraphy. However, work on the Ruhuhu and Luangwa basins has been much more sporadic. Beginning in 2007, our research group has worked to expand the available data from Tanzania and Zambia with the goal of gaining an improved understanding of the impact of the Permo-Triassic mass extinction on tetrapod communities across southern Pangea (Sidor & Nesbitt 2018). During the course of our ongoing fieldwork in the east African rift basins we have discovered numerous Triassic tetrapods that provide key insights into the evolutionary history of specific clades (e.g., Nesbitt *et al.* 2010, 2017) as well as new information on how terrestrial ecosystems recovered from the Permo-Triassic extinction in this region (Sidor *et al.* 2013; Roopnarine *et al.* 2018). Among our newly-collected material are the remains of temnospondyl amphibians.

Historically, Molyneux (1908) described the first temnospondyl specimens from the region that now includes Tanzania and Zambia. Subsequent fieldwork in the 1930s, 1960s, and 1970s by various geologists and paleontologists resulted in the collection of additional material (e.g., Haughton 1932; Nowack 1937; Drysdall & Kitching 1963; Attridge *et al.* 1964; Kemp 1975). Three temnospondyl taxa have been described from the Triassic Lifua Member of the Manda Beds (Ruhuhu Basin) and the upper portion of the Ntawere Formation (Luangwa Basin) (Fig. 1): the mastodonsauroids *Cherninia megarhina* (Chernin & Cosgriff, 1975) Damiani, 2001 and *Stanocephalosaurus pronus* (Howie, 1970), and the brachyopid *Batrachosuchus concordi* Chernin, 1977. These Tanzanian and Zambian formations have been biostratigraphically correlated with the *Cynognathus* Assemblage Zone of the South African Karoo Basin, and may be of Anisian-Carnian age (Battail 1993; Hancox 2000; Kammerer *et al.* 2019; Nelsen *et al.* 2001; Peecook *et al.* 2018; Smith *et al.* 2018).

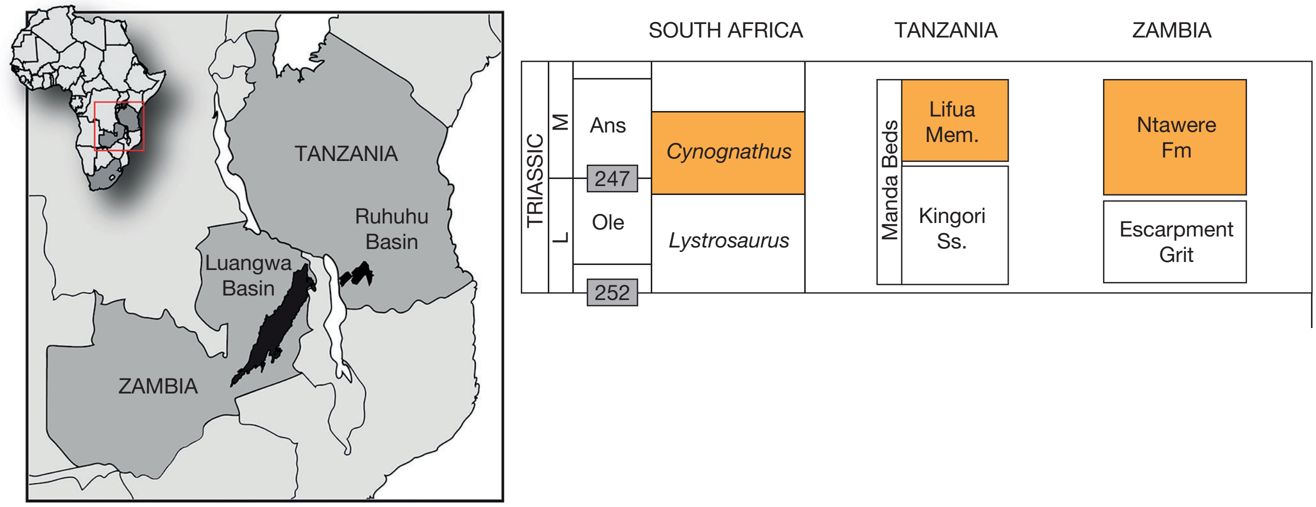

Fig. 1. — Geography and stratigraphy of the Luangwa (Zambia) and Ruhuhu (Tanzania) basins in Africa, which yielded Triassic temnospondyl material (modified from Sidor & Nesbitt 2018). The stratigraphical chart is based on Rubidge *et al.* (2013); the ages (in My) are from the 2019 International Chronostratigraphic Chart (see Cohen *et al.* 2013). The orange units containing temnospondyls are compared here. Abbreviations: **Ans**, Anisian; **Fm**, Formation; **L**, Lower; **Mem**, Member; **M**, Middle; **Ole**, Olenekian; **Ss**, Sandstones.

Here we describe, figure, and compare our newly-collected temnospondyl material from the Triassic of the Luangwa and Ruhuhu basins. We also update the composition of Triassic temnospondyl assemblages from Tanzania and Zambia, and compare them with that of the South African Karoo Basin in the context of the recovery from the Permo-Triassic mass extinction.

Institutional abbreviations

BP Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), Johannesburg, South Africa;
NHCC National Heritage Conservation Commission, Lusaka, Zambia;
NHMUK Natural History Museum, London;
NMT National Museum of Tanzania, Dar es Salam, Tanzania.

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1888
STEREOSPONDYLOMORPHA (Zittel, 1887) Yates & Warren, 2000
STEREOSPONDYLI Zittel, 1888

cf. Stereospondyli
(Figs 2; 3)

Referred material. — **Tanzania**. NMT RB464-468 (Fig. 2), five small thoracic intercentra (anteroposterior length of 3.6-5.7 mm) from Locality Z90, mid- to upper Lifua Member, Manda Beds, Middle-?Late Triassic (e.g., Nelsen *et al.* 2001; Smith *et al.* 2018) of the Ruhuhu Basin.
Zambia. NHCC LB 647, 679-687 (Fig. 3 and Peecook *et al.* 2018: fig. 4D-E), 10 small atlantal intercentra (L = 4.2 to 8.5 mm); NHCC LB688-689, two corresponding axes; and NHCC LB690-728, 39 small thoracic intercentra; all from Locality L82, upper horizon of the Ntawere Formation, Middle-?Late Triassic (e.g., Battail 1993; Hancox 2000; Peecook *et al.* 2018) of the Luangwa Basin (sensu Barbolini *et al.* 2016).

Description (see also Peecook *et al.* 2018)
All these vertebral elements are fully ossified.

The thoracic intercentra are well preserved, except NMT RB467, which looks anteriorly slightly compressed (Fig. 2). These intercentra are subcylindrical and closed dorsally into a stereospondylous condition. They are subcircular in anterior and posterior views, and subrectangular in lateral view (with a height/length ratio of around 1). Their external surfaces show small ridges and grooves. Anteriorly and posteriorly, notochordal pits are visible, but they do not pass through the whole vertebral bodies. Dorsally, facets for the attachment of the neural arch are also preserved.

The atlantal intercentra (Fig. 3 and Peecook *et al.* 2018: fig. 4) are relatively wide (l = 6.3 to 11.1 mm) and flat (h = 5 mm max). Their anterior side is biconcave to articulate with the exoccipital condyles, whereas their posterior side is concave. Their dorsal side presents a longitudinal groove for the neural canal.

Both the Tanzanian and Zambian intercentra were found associated with abundant silesaurid (*c.* thousands of elements in Tanzania) and rare cynodont remains.

Identification

Based on their strong degree of ossification the Tanzanian and Zambian intercentra belong to adult individuals (e.g., Steyer 2000). Their identification beyond Temnospondyli, possibly Stereospondyli, is difficult given that they were found as isolated elements and not associated with more diagnostic material (e.g., skull elements). Moreover, concerning the atlantes, these elements are rare in the temnospondyl fossil record and therefore difficult to assign. The stereospondylous condition of all these intercentra is also found among disparate clades of temnospondyls, including the tupilakosaurids (e.g., *Thabanchuia* Warren, 1998), metoposaurids, plagiosaurids, and mastodonsaurids

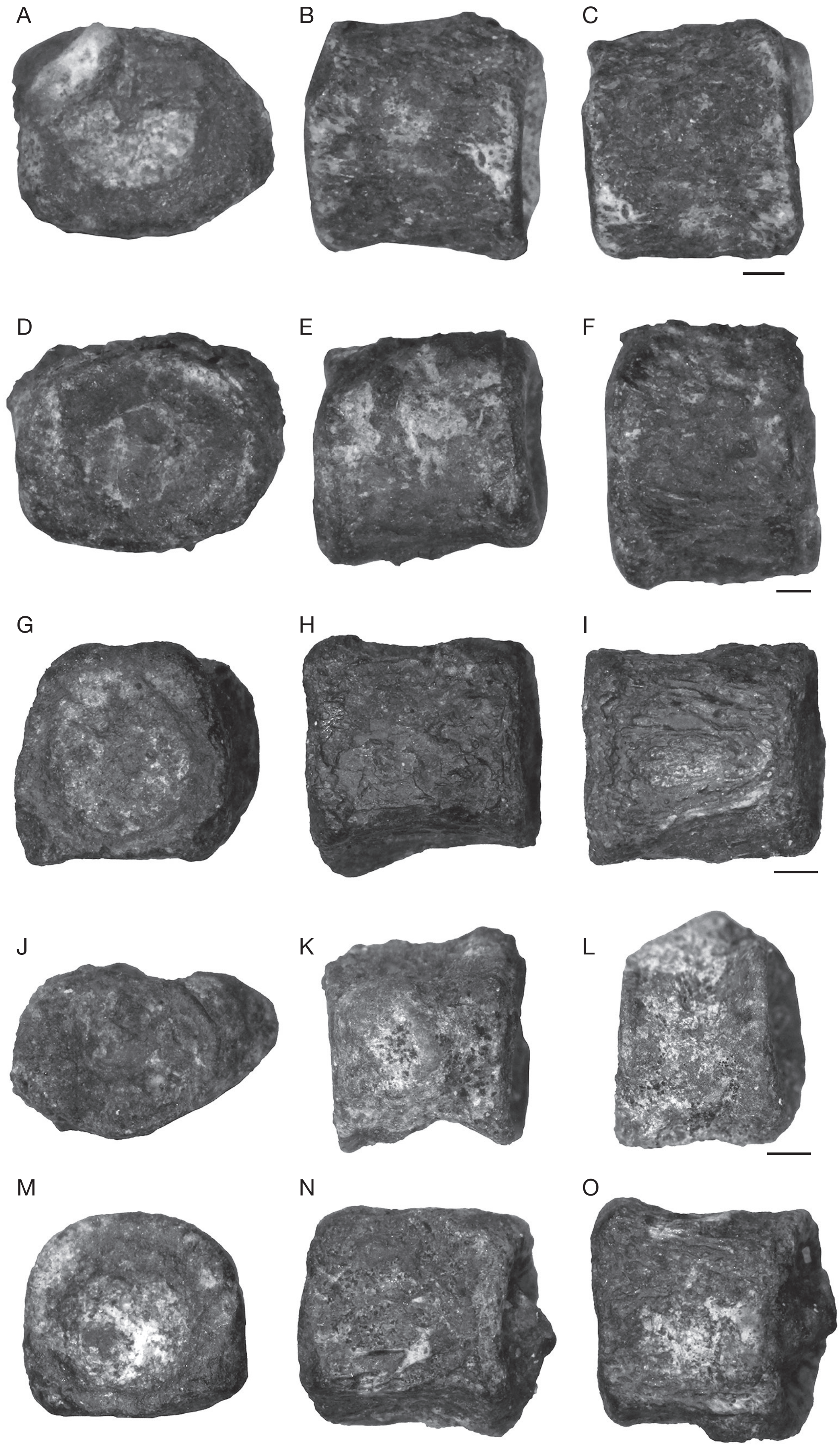

FIG. 2. — Five small intercentra (**A**-**C**, NMT RB464; **D**-**F**, NMT RB465; **G**-**I**, NMT RB466; **J**-**L**, NMT RB467; **M**-**O**, NMT RB468) of small cf. Stereospondyli from the Triassic (?Anisian) of Tanzania (Ruhuhu Basin) in anterior (**A**, **D**, **G**, **J**, **M**), lateral (**B**, **E**, **H**, **K**, **N**), and ventral (**C**, **F**, **I**, **L**, **O**) views. Scale bars: 1 mm.

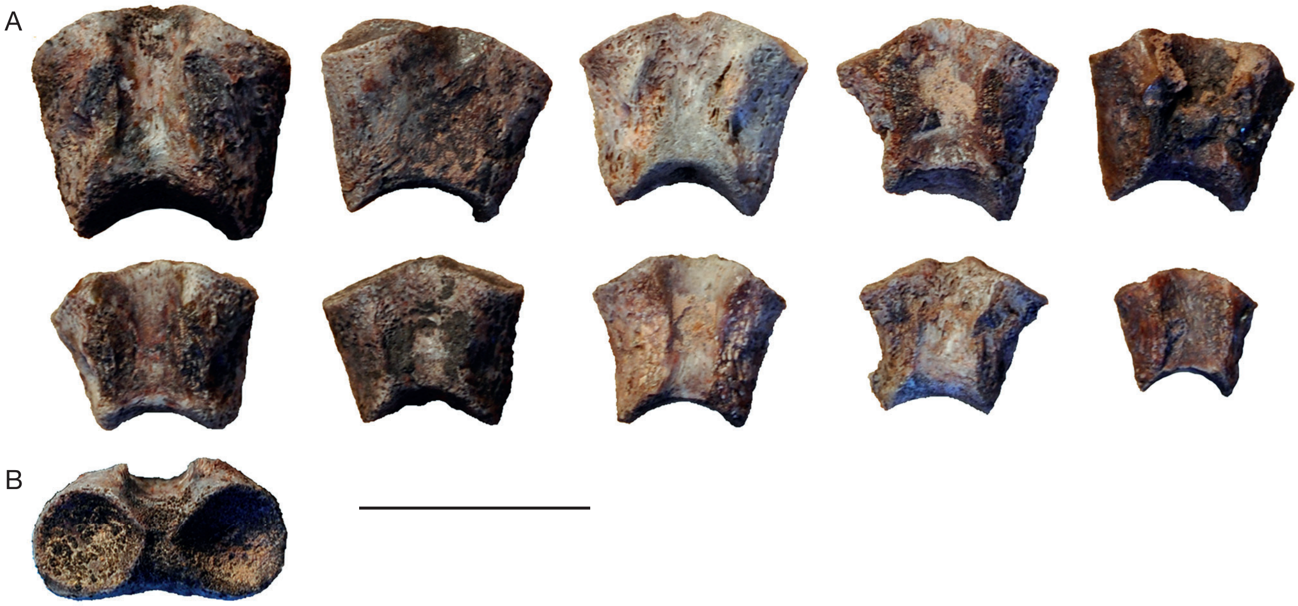

Fig. 3. — Ten atlantes (NHCC LB647, 679-687) of small adults of cf. Stereospondyli from the Triassic (?Anisian) of Zambia (Luangwa Basin) in dorsal (**A**) and anterior (**B**) views; **B**, NHCC LB647 is figured to show the two articular facets with the occipital condyles. Scale bar: 10 mm. Modified from Peecook *et al.* 2018.

(e.g., Yates & Warren 2000). The Tanzanian and Zambian intercentra are anteroposteriorly elongate, as is the case in metoposaurid stereospondyls (e.g., Hunt 1993; Gee *et al.* 2018; Buffa *et al.* 2019; Fortuny *et al.* 2019). However, this is only one character state, and the shape and proportions of the intercentra vary along a single vertebral column within temnospondyls. Therefore, we conservatively assign the specimens to "cf. Stereospondyli". Interestingly, these intercentra belong to small but adult individual(s) and clearly differ from the large, dorsally open intercentra of other temnospondyls from the same rock units (see below). They may correspond to a new small-bodied taxon but we prefer to leave this issue undecided, pending the discovery of additional material.

Stereospondyli indet.
(Fig. 4)

Referred material. — **Zambia.** NHCC LB678 (Fig. 4 and Peecook *et al.* 2018: fig. 4A-C), a partial right mandible of a small-sized, but adult, individual based on the well-developed ornamentation visible on its labial side (e.g., Steyer 2000) (Fig. 4A). The specimen was found by one of us (SJN) in 2014 together with small cylindrical vertebrae similar to NHCC LB690-728.

Locality and horizon. — Locality L290 near the village of Sitwe, upper horizon of the Ntawere Formation, Middle-?Late Triassic (e.g., Battail 1993; Hancox 2000; Peecook *et al.* 2018) of the Luangwa Basin (sensu Barbolini *et al.* 2016).

Description (see also Peecook *et al.* 2018)
This small mandibular portion (29 mm in length) preserves three partial bones; a dentary labially and dorsally (Fig. 4A, B[d]), and two coronoids lingually and dorsally (Fig. 4B, C[cor1 and cor2]). The partial dentary is well-ornamented, and its ornamentation pattern consists of interconnected pits of various sizes. It bears at least 12 marginal tooth sockets, which are slightly laterally compressed (a stereospondyl synapomorphy; e.g., Yates & Warren 2000). The socket Nr. 8 still preserves a partial tooth with its medullar cavity. The two partial coronoids are covered by dense and well-separated denticle patches (*c.* 3 teeth per mm^2). These denticles are conical, short (<1 mm), and taper to a sharp point. These denticle patches are separated by a depression in the posterior region of the specimen that is visible lingually. The anterior patch is complete and covers most of the length of the specimen. It is supported by the better-preserved coronoid (Fig. 4B, C[cor1]). The other denticle patch and its corresponding coronoid (Fig. 4B, C[cor2]) are partially preserved and only visible in the posterior extremity of the specimen. Due to the fragmentary nature of the specimen, it is not clear if these elements represent pre-, inter- or post-coronoids.

Identification
We identify this specimen as a stereospondyl based on the laterally compressed tooth sockets as well as the stereospondyl synapomorphy of a dentary that does not contribute substantially to the lingual side of the mandible (the dentary is clearly visible in lingual view in basal temnospondyls; e.g., Schoch & Milner 2000). It is difficult to assign a more precise identification because three stereospondyl clades have very dense denticle patches on at least two of their coronoids: the Rhinesuchidae, the Lydekkerinidae, and the Rhytidosteidae (e.g., *Mahavisaurus dentatus* Lehman, 1966, Maganuco *et al.* 2014: figs 8-9). Pending more discoveries, we therefore prefer to assign this fragmentary specimen to Stereospondyli.

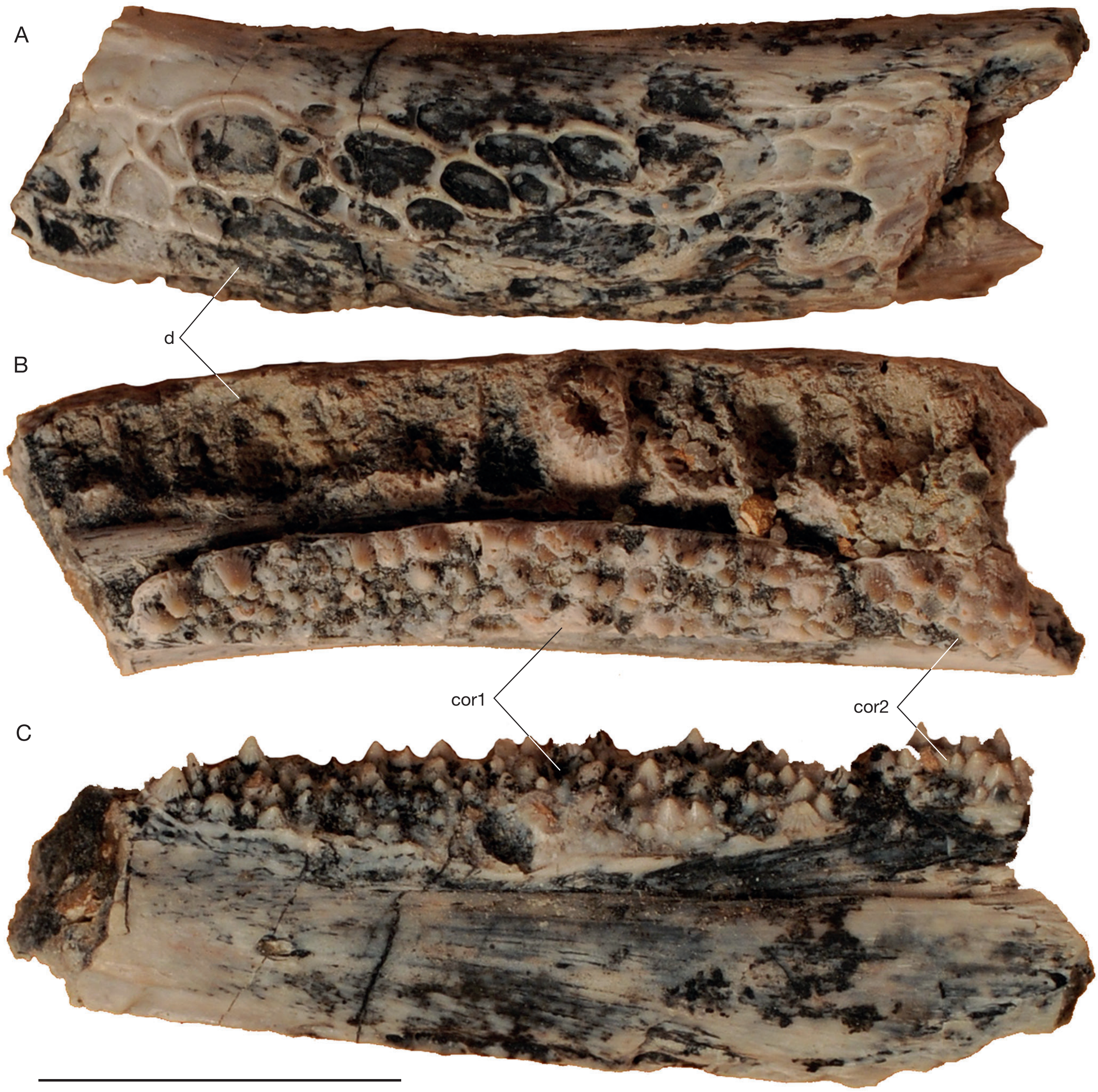

Fig. 4. — Partial mandible of Stereospondyli (NHCC LB678) from the Triassic (?Anisian) of Zambia (Luangwa Basin) in labial (**A**), dorsal (**B**) and lingual (**C**) views. Abbreviations: **cor1**, coronoid 1; **cor2**, coronoid 2; **d**, dentary. Scale bar: 10 mm. Modified from Peecook *et al.* 2018.

Mastodontosauroidea Lydekker, 1885 (*sensu* Damiani 2001b)

Mastodontosauroidea indet. (Figs 5; 6)

Referred Material. — **Zambia.** Large postcranial elements studied in 2015 by one of us (BRP) in the historical collections of the NHMUK, and labeled as 'cf. *Parotosuchus*' (Fig. 5): NHMUK R10271, a huge partial interclavicle of nearly ½ meter breadth (Fig. 5A); NHMUK R10272-R10273, two very large intercentra of 130 × 80 × 40 mm (Fig. 5B, C); NHMUK R10274, a partial right scapulocoracoid (Fig. 5D); and NHMUK R10275, a right complete ilium (Fig. 5E).

Tanzania. NMT RB537 (Fig. 6), a very large and robust intercentrum (132 × 88 × 43 mm) found isolated by one of us (SJN) in 2007 at the locality Z30, near the village of Gingama, in the grey siltstones of the Lifua Member, Manda Beds, Middle-?Late Triassic (e.g., Nelsen *et al.* 2001; Smith *et al.* 2018) of the Ruhuhu Basin.

Locality and horizon. — The Zambian specimens were collected in 1963 by a NHMUK and London University expedition which comprised Barry Cox, Alan Charig and colleagues (Attridge *et al.* 1964) at Locality 15 of Drysdall & Kitching (1963), about 6 km west of the village of Sitwe, upper horizon of the Ntawere Formation, Middle-?Late Triassic (Peecook *et al.* 2018) of the Luangwa Basin (sensu Barbolini *et al.* 2016).

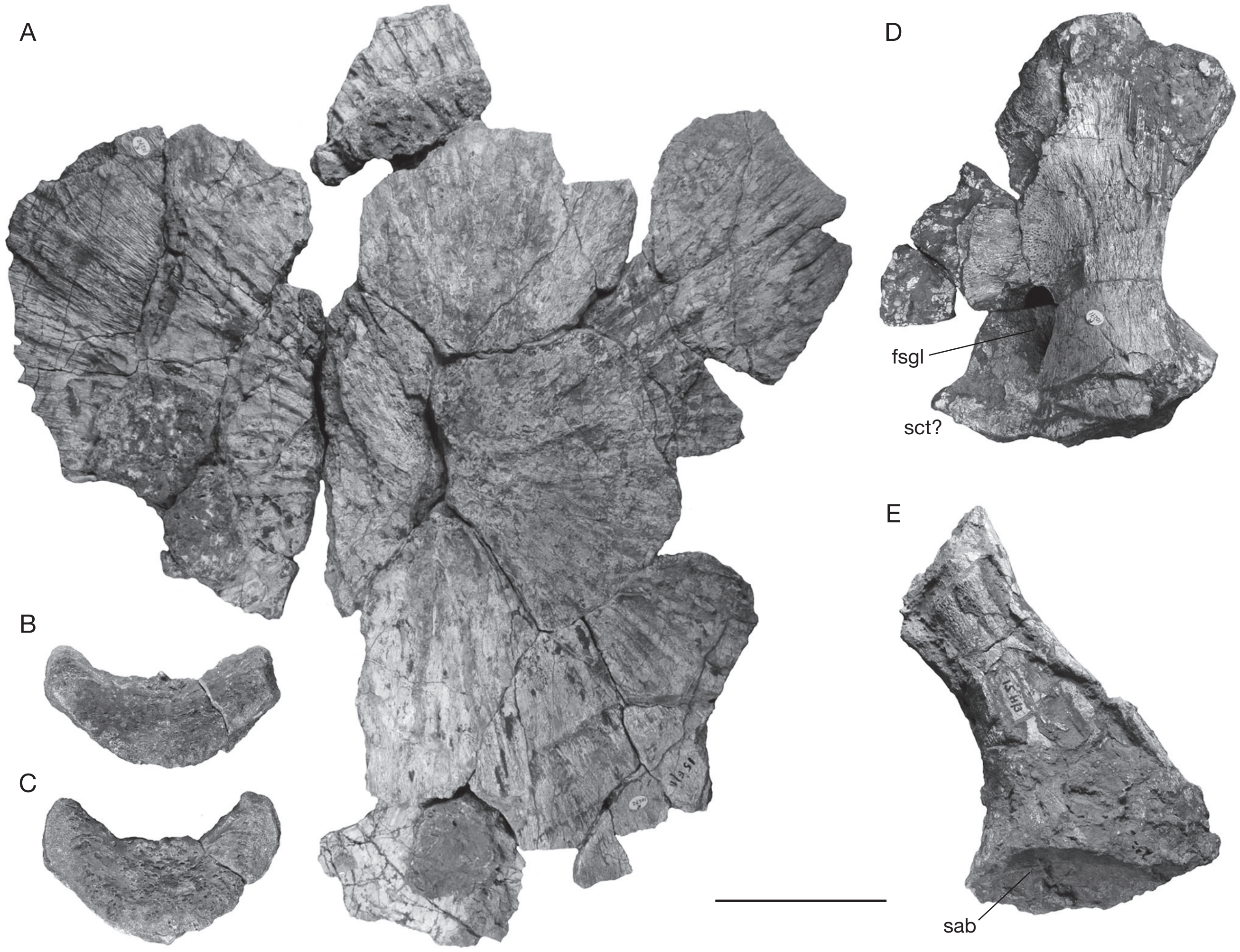

Fig. 5. — Postcranial specimens of Mastodonsauroidea collected in 1963 by A. Charig and colleagues in the Triassic (?Anisian) of Zambia (Luangwa Basin): **A**, partial interclavicle (NHMUK R10271) in ventral view; **B**, **C**, intercentra (NHMUK R10272-R10273) in anterior view; **D**, partial right scapulocoracoid (NHMUK R10274) in lateral view; **E**, right ilium (NHMUK R10275) in lateral view. Abbreviations: **fsgl**, supraglenoid fossa; **sab**, supracetabular buttress; **sct**, scapular tubercle. Scale bar: 10 cm.

Description

Zambian material

All the elements are fully ossified, robust and very large: they therefore belong to adult individual(s). The partial interclavicle NHMUK R10271 (Fig. 5A) bears radiating ridges and deep grooves on its ventral side. Most of the ridges are eroded, which suggests that this bone has been strongly weathered. Unfortunately, the margins of this interclavicle are not preserved, preventing a more precise assignment. The intercentra NHMUK R10272-R10273 (Fig. 5B, C) are crescentic, but with relatively low and short lateral flanks. The limited lateral flanks suggest a relatively reduced notochordal canal. The bone surfaces are relatively rugose, probably for contact with the cartilaginous intervertebral disks. The parapophyses are not well developed. The partial right scapulocoracoid NHMUK R10274 (Fig. 5D) is also massive and robust. Although only its central part is preserved, the typical fan shape is recognizable, with the supraglenoid fossa visible in lateral view. The supraglenoid fossa is oval in shape and very large compared with the width of the mid-shaft. It turns inside into the supraglenoid foramen. Lateral to the supraglenoid fossa, a small expansion of the bone could correspond to the scapular tubercle but its preservation is not sufficient to confirm this identification. The complete right ilium NHMUK R10275 (Fig. 5E) is well preserved. In lateral view, its dorsal iliac process is high and slightly widens dorsally. The supracetabular buttress is well pronounced ventrolaterally, even though its surface is relatively weathered.

Tanzanian material

NMT RB537 (Fig. 6A, B) is crescentic, with a reduced anteroposterior length (43 mm) compared to its height (88 mm). Its parapophyses are located posteriorly suggesting an attribution to a stereospondyl (e.g., Warren & Snell 1991; Witzmann & Schoch 2006). Compared with other stereospondyl taxa, this intercentrum is very robust, with large elevated flanks drawing dorsally the base of the central tube for the notochordal canal. This character is typical of the neorachitomous pattern (e.g., Watson

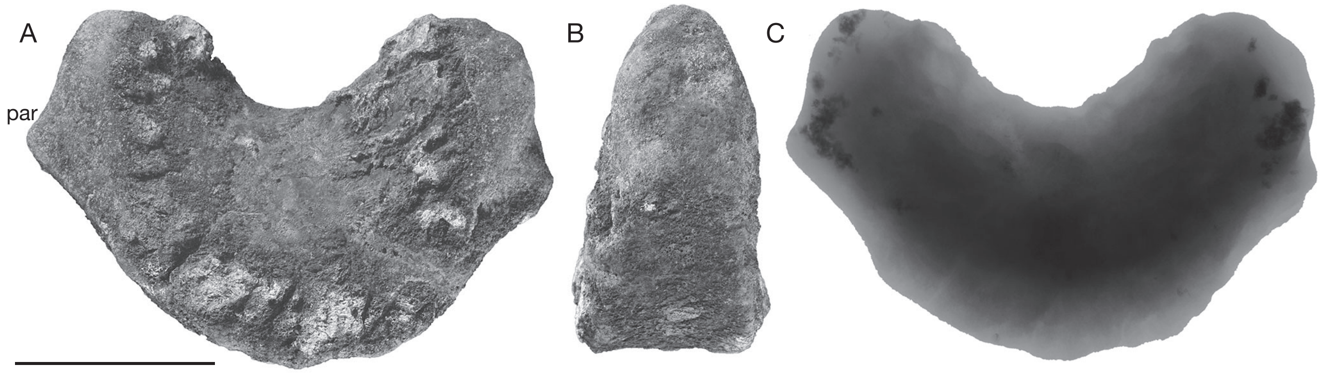

Fig. 6. — Intercentrum of Mastodonsauroidea (NMT RB537) from the Triassic (?Anisian) of Tanzania (Ruhuhu Basin) in posterior (**A**) and lateral (**B**) views; **C**, µCT-scan radiography. Abbreviations: **par**, parapophyses. Scale bars: 5 cm.

1919). The parapophyses are well separated from the rest of the vertebral element. Together with the strong degree of ossification of the intercentrum, this suggests that this element belongs to an adult individual (e.g., Steyer 2000). Its ventral, anterior, and posterior surfaces are very rugose. The latter two surfaces show a subcircular rugose zone for the contact with the cartilaginous intervertebral disks. The subcircular ventral side of the intercentrum, as well as the dorsal position and subtriangular shape of its parapophyses, suggests that this element was originally positioned between the middle and the posterior end of the presacral column. More precisely, the height of the parapophyses relative to the height of the intercentrum in lateral view suggests a rather posterior presacral element, by comparison with the vertebral columns of *Paracyclotosaurus davidi* Watson, 1958 and *Mastodonsaurus giganteus* (Jäeger, 1828) (respectively Watson 1958; Schoch 1999). The lateral expansions or "winglets" of the intercentrum suggest a relatively reduced notochordal canal. The ventral side of the intercentrum is wider than long. The parapophyses are entirely dorsally located on the corpus of the bone (not laterally and in between two intercentra).

One of us (TA) produced a µCT-scan of NMT RB537 at AST-RX (MNHN) (Fig. 6C). The radiographic image shows two inner zones: a large, dense and dark central zone transitioning relatively abruptly into a lighter peripheral zone. The abrupt transition between the two zones may correspond to a volume of decreasing or arrested growth (VAG, i.e., the 3D equivalent of an annulus or a line of arrested growth in 2D). The strong density of the central zone, if of biological origin, suggests osteosclerosis, a common phenomenon observed in giant temnospondyls (Schoch 2012). In this case, the central zone limited by the VAG corresponds to the juvenile shape of the intercentrum. If this strong density is of taphonomical origin, the central zone is therefore the medullar zone whose spongiose structure was infilled by dense minerals. In this interpretation, the peripheral zone is the cortical zone composed of endosteal bone. Reduced but localized black patches are also visible in the lateral regions of the intercentrum: they are interpreted as hypermineralized zones or inclusions.

Identification

Zambian material

These elements were labeled as 'cf. *Parotosuchus*' in the NHMUK historical collections, probably because they are very large and robust, and only *Parotosuchus* (Damiani, 2001) was known as a unique giant Triassic temnospondyl in the 1960s, when they were discovered. However, no diagnostic *Parotosuchus* characters have been observed on this postcranial material: we therefore prefer to broaden its assignment to Mastodonsauroidea.

Tanzanian material

The proportions of the bone and comparisons with other taxa in which intercentra are known (e.g., Howie 1970; Schoch 1999; Pawley 2006) suggest an individual of about 4 m in total body length. However, because of the lack of diagnostic characters visible on this intercentrum and the high variability of the shape of the intercentra along a single vertebral column (e.g., Schoch 1999), we prefer to broaden its assignment to Mastodonsauroidea.

Mastodontosauridae Lydekker, 1885
(*sensu* Damiani 2001b)

cf. ***Cherninia megarhina*** (Chernin & Cosgriff, 1975)
Damiani, 2001
(Fig. 7)

Referred Material. — **Zambia**. NHCC LB676, a partial but elongate left dentary of an adult individual based on its well-developed ornamentation (e.g., Steyer 2000). It was found by one of us (ST) in 2007, associated with many specimens of the bivalve *Unio karooensis* Cox, 1932.

Locality and horizon. — Locality L66 near the village of Sitwe, upper horizon of the Ntawere Formation, Middle-?Late Triassic (e.g., Battail 1993; Hancox 2000; Peecook *et al.* 2018) of the Luangwa Basin (sensu Barbolini *et al.* 2016).

Description

This partial dentary corresponds to the anterior half of the element. Its face is weathered with many broken teeth alongside

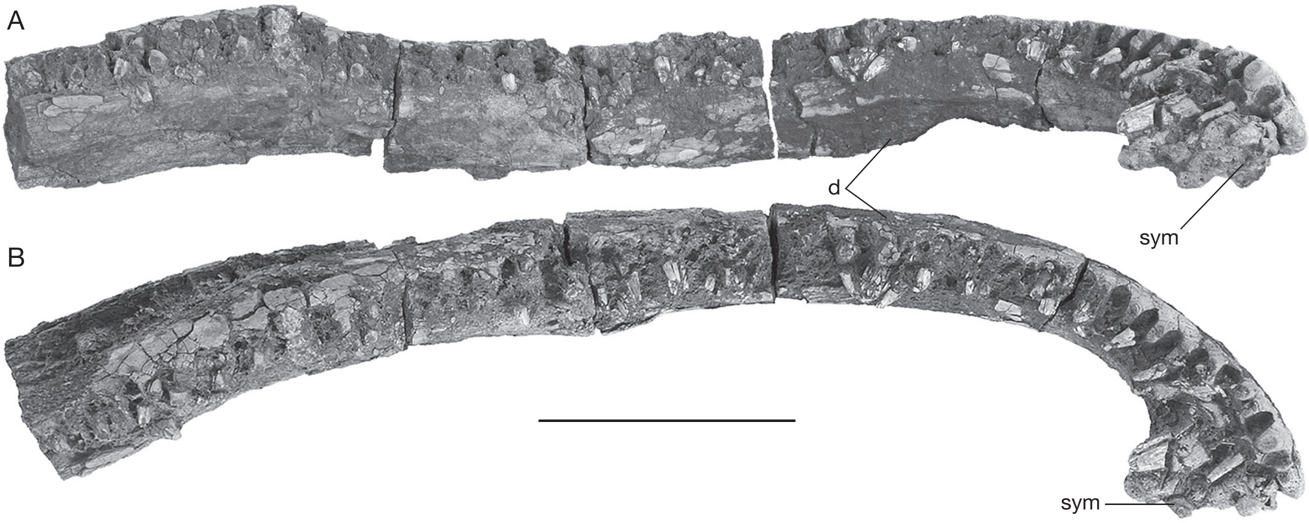

Fig. 7. — Partial left dentary of cf. *Cherninia megarhina* (Chernin & Cosgriff, 1975) (NHCC LB676) from the Triassic (?Anisian) of Zambia (Luangwa Basin) in lingual (**A**) and dorsal (**B**) views. Abbreviations: **d**, dentary; **sym**, symphyseal suture. Scale bar: 10 cm.

their sockets, but it is not deformed by compaction. Its bears at least 50 laterally compressed teeth or tooth sockets. In lingual view (Fig. 7A), the dentary is elongate (L = 380 mm) and naturally shallow (h = 61 mm max). In dorsal view (Fig. 7B), its anterior extremity is strongly curved and semi-circular, with a well-developed symphyseal region. The symphyseal region bears two large partial tusks and is expanded posteriorly, with an elongate symphyseal suture (59 mm).

Identification

Laterally compressed teeth are a stereospondyl synapomorphy (e.g., Yates & Warren 2000), whereas an elongate symphyseal suture is a common feature in Mastodonsauridae (e.g., Damiani 2001b). The semi-circular curvature of the dentary in dorsal view, together with its very large size, suggests a possible attribution of this specimen to *Cherninia megarhina*. This taxon is characterized by a very large skull and a semi-circular snout (Chernin 1974; Damiani 2001a), and the proportions and shape match those of NHCC LB676. Moreover, the type material of *C. megarhina* (BP/1/4223, a partial skull) was collected in the same region from time-equivalent strata (the type locality is "Locality 15" of Drysdall & Kitching 1963, also near the village of Sitwe). However, because the mandible of *C. megarhina* described by Chernin (1978) does not belong to the type material, we cautiously assign NHCC LB676 to "cf. *Cherninia megarhina*".

DISCUSSION

In addition to the newly referred material described above, the following temnospondyl taxa are known from the Triassic of Tanzania and Zambia. First, *Stanocephalosaurus pronus* is represented by several partial skulls from the Middle-?Late Triassic of both Tanzania (Lifua Member, Manda Beds, Ruhuhu Basin; Howie 1970) and Zambia (upper horizon of the Ntawere Formation; Chernin 1974). Second, the brachyopid *Batrachosuchus concordi* is represented by a partial skull (holotype BP/1/3728) from Locality 15 of Drysdall & Kitching 1963 (also the type locality of *Cherninia megarhina*, see above), near the village of Sitwe, upper horizon of the Ntawere Formation, Middle-?Late Triassic of the Luangwa Basin, Zambia (Chernin 1977).

The new material described here is fragmentary but the small unusual intercentra from the Tanzanian Z90 and Zambian L82 localities could belong to a new taxon or taxa (see above). This material allows the Triassic temnospondyl faunas of the Ruhuhu and Luangwa basins to be updated. Interestingly, *S. pronus* occurs in Zambia and Tanzania, whereas *C. megarhina* is only known in Zambia. Both *S. pronus* and *C. megarhina* therefore coexisted in Zambia but are not sister taxa (although relatively close; e.g., Schoch 2008; Eltink *et al.* 2016), suggesting phylogenetic diversity in the temnospondyl assemblage. Ecologically, *S. pronus* may have shared the same aquatic paleoenvironment with *C. megarhina*, yet probably not the same ecological niche as deduced by the morphology of the two species.

During *Cynognathus* Assemblage zone times, the South African Karoo Basin hosted a diverse temnospondyl assemblage: *Batrachosuchus*, *Vanastega* Damiani & Kitching, 2003, *Xenotosuchus* (Broom, 1909), *Paracyclotosaurus*, and *Microposaurus* Haughton, 1925 from the ?Anisian (*Cynognathus* Assemblage Zone, subzones *Trirachodon-Kannemeyeria* or *Cricodon-Ufudocyclops* sensu Hancox *et al.* 2020 = subzones B or C sensu Damiani & Rubidge 2003, respectively); and possibly *Laidleria* Kitching, 1957, *Rhytidosteus* Owen, 1884, *Bathignathus* (Haughton, 1925), *Jammerbergia* Damiani & Hancox, 2003, and *Parotosuchus* Broili & Schröder, 1937 from the ?Olenekian and/or ?Anisian (uncertain subzone of the *Cynognathus* Assemblage Zone; Damiani & Rubidge 2003). Consequently, *Batrachosuchus*, *Paracyclotosaurus* and their relatives occured across much of western Gondwana, and all these Karoo basins (South Africa, Tanzania and Zambia) hosted a mixture of endemic and cosmopolitan Triassic temnospondyls. A mixture of endemic and broadly distributed temnospondyls also characterizes the *Cynognathus* Assemblage Zone-equivalent rocks in Antarctica (Sidor *et al.* 2007; Sidor *et al.* 2008; Sidor *et al.* 2014). The reasons underlying the greater diversity of the South African assemblage are unclear. The difference may reflect the larger size and greater sampling intensity of the Karoo (e.g., see Roopnarine *et al.* 2018 for a discussion of sampling effects on Permian Luangwa and Ruhuhu Basin tetrapod assemblages). Likewise, recent radiometric dating of sediments that have been biostratigraphically correlated with the *Cynognathus* Assemblage Zone and new fossil discoveries have raised questions about the ages of these assemblages and whether they all were truly contemporary (e.g., Ottone *et al.* 2014; Liu *et al.* 2018; Marsicano *et al.* 2016; Peecook *et al.* 2018; Kammerer *et al.* 2019). Also recent radiometric dating of the Tashinga Formation of Zimbabwe gives a Late Triassic age for this Zimbabwean part of the Karoo Supergroup, in which temnospondyl and phytosaur remains have been found (Barrett *et al.* 2020). This raises the possibility that the South African, Tanzanian, and Zambian temnospondyl assemblages differ because they are not of the same age. If the observed differences are real and not a result of one of these potential biases, they would be further evidence for regional differences in the process of recovery from the Permo-Triassic mass extinction in southern Gondwana (Sidor *et al.* 2013; Steyer *et al.* 2015; Roopnarine *et al.* 2018; Tarailo 2018).

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