A new lapillopsid from Antarctica and a re-appraisal of the phylogenetic relationships of early diverging stereospondyls.

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Running Header: Gee et al.—Lapillopsid from the Triassic of Antarctica

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ABSTRACT—Stereospondyls underwent a global radiation in the Early Triassic, including an abundance of small-bodied taxa, which are otherwise rare throughout the Mesozoic. Lapillopsidae is one such clade and is presently known only from Australia and India. This clade's phylogenetic position, initially interpreted as micropholid dissorophoids and later as early diverging stereospondyls, remains uncertain. Although the latter interpretation is now widely accepted, lapillopsids' specific relationship to other Early Triassic clades remains unresolved; in particular, recent work suggested that Lapillopsidae nests within Lydekkerinidae. Here we describe *Rhigerpeton isbelli*, gen. et sp. nov., based on a partial skull from the lower Fremouw Formation of Antarctica that is diagnosed by a combination of features shared with at least some lapillopsids, such as a longitudinal ridge on the dorsal surface of the tabular, and features not found in lapillopsids but shared with some lydekkerinids, such as the retention of pterygoid denticles and a parachoanal tooth row (as in *Lydekkerina*, for example). A series of phylogenetic analyses confirm the lapillopsid affinities of *R. isbelli* but provide conflicting results regarding the polyphyly and/or paraphyly of Lydekkerinidae with respect to lapillopsids. The position of Lapillopsidae within Temnospondyli is highly sensitive to taxon sampling of other predominantly Early Triassic temnospondyls. The occurrence of a lapillopsid in Antarctica brings the documented temnospondyl diversity more in line with historically well-sampled portions of southern Pangea but robust biogeographic comparisons remain hindered by the inability to resolve many historic Antarctic temnospondyl records to the finer taxonomic scales needed for robust biostratigraphy.

INTRODUCTION

Temnospondyls were a diverse clade of non-amniote ('amphibian') tetrapods spanning the Carboniferous to the Cretaceous, with a global fossil record over much of that temporal range. Temnospondyls exhibited a high degree of morphological and ecological variation, with major shifts often coinciding with global-scale events (Stayton and Ruta, 2006; Angielczyk and Ruta, 2012; Fortuny et al. 2011, 2016; Carter et al., 2021). The Early Triassic is a particularly noteworthy interval for temnospondyl evolution—like other survivors of the Permo-Triassic mass extinction, temnospondyls underwent pronounced diversification in the post-extinction interval (e.g., Yates and Warren, 2000; Ruta and Benton, 2008; Tarailo, 2018). The Early Triassic records the first appearance of most major clades of stereospondyls, a subclade which includes nearly all Mesozoic temnospondyls, as well as the last occurrence of relict species of predominantly late Paleozoic clades. While post-Early Triassic stereospondyls were predominantly medium- to large-bodied, the Early Triassic is notable for the presence of numerous small-bodied taxa (skull length < 10 cm; Fig. 1). Such diminutive taxa belong to a variety of clades, including lapillopsids (Warren and Hutchinson, 1990; Yates, 1999; Yates and Sengupta, 2002); lydekkerinids (e.g., Hewison, 1996, 2007; Jeannot et al., 2006), rhinesuchids (e.g., Shishkin and Rubidge, 2000), rhytidosteids (e.g., Yates, 2000), and late surviving non-stereospondyls (e.g., Warren, 1998a; Schoch and Rubidge, 2005; Gee and Sidor, 2021).

Despite the appreciable taxic diversity of small-bodied temnospondyls during the Early Triassic, such forms are overall relatively cryptic in the Mesozoic, often being represented by singleton specimens or a handful of specimens from one local geographic region (e.g., Hewison, 1996; Yates, 1999, 2000; Shishkin and Rubidge, 2000; Yates and Sengupta, 2002). Taken at face value, this record suggests that small-bodied taxa were part of an initial post-extinction radiation of temnospondyls largely confined to southern Pangea (e.g., Australia, South Africa; Yates, 1999, 2000; Fig. 1) but were ultimately unsuccessful insofar as these clades disappeared after the Early Triassic. However, other possible narratives can be hypothesized, such as taphonomic and collection bias against small-bodied tetrapods or habitat occupancy away from preserved depositional environments, among other hypotheses. Such hypotheses are substantiated by the growing documentation of a diverse assemblage of small-bodied temnospondyls in the Late Triassic of North America (e.g., Wilson, 1948; Bolt and Chatterjee, 2000; Pardo et al., 2017; So et al., 2018) and the long-cryptic record of crown lissamphibians, which were all small-bodied, spanning the entire Triassic (e.g., Rage and Roček, 1989; Evans and Borsuk-Bialynicka, 1998; Stocker et al., 2019). They are also substantiated by the general paucity of small-bodied juveniles of taxa that are known to have reached large body size throughout the Mesozoic. These gaps and the uncertainty they introduce into interpretations of the evolution of temnospondyls place a premium on both the description of new small-bodied specimens and the reassessment of historic material.

The record of small-bodied Early Triassic temnospondyls is largely confined to high paleolatitudes in the southern hemisphere (e.g., India, Madagascar, South Africa, Australia). Despite a temnospondyl jaw being the first tetrapod fossil collected from the Fremouw Formation within the Transantarctic Mountains (Barrett et al., 1968), fossils of small-bodied temnospondyls have been relatively uncommon, especially well-preserved cranial materials (Colbert and Cosgriff, 1974; Cosgriff and Hammer, 1984). As a result, the taxonomic validity and relationships of even the most complete material has frequently been questioned by contemporary workers (e.g., Schoch and Milner, 2000; Warren and Marsicano, 2000; Jeannot et al., 2006; Hewison, 2007; Gee et al., 2021). Recent collecting in the Fremouw Formation of Antarctica in the 2017/18 austral summer led to the recovery of substantial, more diagnostic remains of small-bodied temnospondyls from the informally recognized lower member (Collinson and Elliot, 1986; Sidor et al., 2019). As part of our study of this new material, we identified the first occurrence of the relict amphibamiform *Micropholis stowi* (Gee and Sidor, 2021) as well as more confident documentation of the small-bodied Lydekkerinidae and the large-bodied Capitosauria (Gee et al., 2021). Here we document the presence of a distinct taxon that does not exhibit clear affinities to one of these previously recorded clades but that instead exhibits many similarities to another small-bodied clade, the enigmatic Lapillopsidae, previously known from three species in Australia and India (Yates, 1999; Yates and Sengupta, 2002). The specimen described here has been mentioned previously in the literature (Beightol et al., 2013; Peecook et al., 2019), but without formal naming or analysis.

Institutional Abbreviations—QM, Queensland Museum, South Brisbane, Queensland, Australia; **UWBM**, University of Washington Burke Museum, Seattle, Washington, U.S.A.

MATERIALS AND METHODS

UWBM VP 95522 (field number F21) was collected on December 30, 2010. It was subsequently prepared by R. Masek, who used air scribes and pin vises to expose the skull roof, palate, and other small bones in the block. Since CVB completed stipple drawings of the specimen, damage to the temporal region of the skull has occurred, resulting in the small hole seen in the photographs (compare Figs. 2 and 3).

Terminology—Several groups of temnospondyls relevant to the current study have not been defined phylogenetically, or vary markedly in their composition based on the results of a particular cladistic analysis. For this reason, we operationally define several terms here for purposes of this study:

1) Lydekkerinidae sensu lato (nominal lydekkerinids): This includes all presently valid taxa previously suggested to belong to the family (viz. *Lydekkerina huxleyi*, Schoch and Milner, 2000; Jeannot et al., 2006; Hewison, 2007) and therefore includes *L. huxleyi* (and junior synonyms '*Broomulus dutoiti*' and '*Limnoiketes paludinatans*' following Jeannot et al., 2006, contra Hewison, 2007); *Eolydekkerina magna*; *Deltacephalus whitei*; *Chomatobatrachus halei*; *Luzocephalus blomi*; and *Luzocephalus kochi* (contra the '*Aquiloniferus*' of Bjerring, 1999, and inclusive of junior synonyms '*Lu. johanssoni*' and '*Lu. rapax*').
2) Lydekkerinidae sensu stricto: This includes only those taxa that fall within the definition of the family provided by McHugh (2012) and Eltink et al. (2019): the most inclusive clade containing *Lydekkerina huxleyi,* but not *Mastodonsaurus giganteus*. There has never been a formally published analysis of all nominal lydekkerinids (see Dias-da-Silva and Hewison, 2013, for a conference abstract on such a study), but previous analyses have often recovered whatever nominal lydekkerinids were included as polyphyletic or as a paraphyletic grade that, given aforementioned phylogenetic definition, would potentially encompass many more taxa (e.g., Ruta et al., 2007; Schoch, 2013; Maganuco et al., 2014), including *Lapillopsis* (Eltink et al., 2019).

3) Lapillopsidae sensu lato (nominal lapillopsids): This family was erected by Yates (1999) for *Lapillopsis nana* and *Rotaurisaurus contundo* and subsequently expanded to include *Manubrantlia khaki* by Yates and Sengupta (2002); however, neither of these studies defined Lapillopsidae. This three-taxon concept is employed here as 'Lapillopsidae sensu lato.'
4) Lapillopsidae sensu stricto: McHugh (2012) provided the first definition of this clade as the least inclusive clade including the most recent common ancestor of *Lapillopsis nana* and *Rotaurisaurus contundo*. This definition has not been modified by subsequent workers, likely because *L. nana* has been typically sampled as the sole representative of the clade in large-scale analyses (e.g., Schoch, 2013, and derivates; Eltink et al., 2019). We adopt this definition herein.

SYSTEMATIC PALEONTOLOGY

Temnospondyli Zittel, 1887-1890

Stereospondyli Zittel, 1887-1890

Lapillopsidae Yates, 1999

Definition—The least inclusive clade including the most recent common ancestor of *Lapillopsis nana* and *Rotaurisaurus contundo* (from McHugh, 2012).

RHIGERPETON ISBELLI, gen. et sp. nov.

(Figs. 2, 3, 8A)

Holotype—UWBM VP 95522, a partial skull with articulated palate.

Locality and Horizon—Collected approximately 35 meters above the base of the Fremouw Formation, near the middle of the informally recognized lower member, at Graphite Peak, UWBM locality C1585 (85° 3.145'S, 172° 22.910'E), Antarctica. See Peecook et al. (2019:fig. 2) for additional stratigraphic context.

Etymology—*Rhigo*, Greek for frost or cold; *herpeton*, Greek for creeping animal; *isbelli*, in honor of John Isbell for his important contributions to understanding the depositional history and paleoenvironment of the Beacon Group of Antarctica.

Diagnosis—Stereospondyl diagnosed by the following unique combination of characters: presence of dorsal ridge on tabular horn; broad, shallow groove on the temporal region (temporal trough); pterygoid retracted such that the ectopterygoid enters the interpterygoid vacuity; pterygoid with denticles; parachoanal tooth row present along elongate choana with parallel sides.

PHYLOGENETIC METHODS

Originally described as micropholid dissorophoids (Warren and Hutchinson, 1990), lapillopsids are accepted by contemporary workers to be stereospondyls, but there is no consensus on their position within Stereospondyli. Phylogenetic analyses have produced discordant results (e.g., Yates, 1999; Schoch and Milner, 2000; Yates and Warren, 2000; Ruta et al., 2007; Maganuco et al., 2009, 2014; McHugh, 2012; Dias-da-Silva and Hewison, 2013; Schoch, 2013; Dilkes, 2015; Marsicano et al., 2017; Eltink et al., 2019), some of which fail to recover this clade (viz. *Lapillopsis nana*) within Stereospondyli (including the widely propagated and widely cited temnospondyl matrix of Schoch, 2013). Some of this disparity likely stems from the stereospondyls-only focus of several studies, which underscores the importance of testing the position of lapillopsids within a matrix encompassing a broad array of temnospondyls. Finally, nearly all previous analyses have only included *L. nana*, and none has sampled all three of the nominal lapillopsids.

Source Matrices—In order to test the position of *Rhigerpeton* and Lapillopsidae, we employed two matrices: a derivation from the family of matrices originating with Schoch (2013) and a derivation of the matrix of Eltink et al. (2019). The first matrix represents a combination of derivates of Schoch (2013), which comprehensively samples Temnospondyli. We opted for this family of matrices to test the position of lapillopsids (viz. *Lapillopsis nana*) without introducing any preconceptions about its position relative to Stereospondyli. This matrix was modified by Pardo et al. (2017), who added new taxa (*Chinlestegophis jenkinsi*, *Rileymillerus cosgriffi*, and numerous extinct and extant lissamphibians) and over a hundred new characters. This was then independently modified by Daza et al. (2020) and Schoch et al. (2020). Daza et al. added one OTU (the albanerpetontid *Yaksha peretti*) to the matrix, whereas Schoch et al. added several OTUs (the lissamphibian *Triassurus sixtelae* and the lepospondyls *Batropetes fritschi*, '*Brachydectes elongatus*,' and *Rhynchonkos stovalli*) but removed 18 temnospondyls. Schoch et al. (2020) also added 15 new characters, whereas Daza et al. did not add any. The most expansive temnospondyl sampling is that of Pardo et al. (2017), mirrored in Daza et al. (2020), and includes 63 temnospondyls. Because we wanted to maximize the temnospondyl sample but are not addressing lissamphibian origins, which lapillopsids have never been implicated in, we selected the Pardo et al. (2017) matrix as the source matrix and then removed all lissamphibians. Many of the retained taxa were scored for the 15 characters added by Schoch et al. (2020) in that matrix, and those scores were added to the matrix of Pardo et al. (2017). These characters (346–360) were then newly scored for the eighteen taxa sampled by Pardo et al. that were omitted by Schoch et al. The matrix therefore samples two outgroups (*Proterogyrinus scheelei*, *Greererpeton burkemorani*), 63 temnospondyls, and 360 characters. Although constructed using Pardo et al. (2017) as the base matrix, the resultant matrix could also be viewed as the matrix of Schoch et al. (2020), with lepospondyls and lissamphibians excluded and with the re-addition of omitted taxa that had been previously scored for characters 1–345 by Schoch (2013) and Pardo et al. (2017). The set of matrices and their MPTs that are associated with these analyses are available in the Electronic Supplement as well as on MorphoBank (project 4591; http://morphobank.org/permalink/?P4591).

The second matrix is the recently published stereospondylomorph matrix of Eltink et al. (2019), which is selected following the results of analyzing the previous matrix. This matrix densely samples non-stereospondyl stereospondylomorphs and early diverging stereospondyls (37 taxa for 221 characters), including *Lapillopsis nana*, and is therefore well-suited to test the relationships of the latter. We added additional lapillopsid and lydekkerinid taxa to the matrix, which previously sampled only *Eolydekkerina magna*, *Lapillopsis nana*, and *Lydekkerina huxleyi*. Newly added taxa (with literature sources in parentheses) are the nominal lapillopsids *Manubrantlia khaki* (Yates and Sengupta, 2002) and *Rotaurisaurus contundo* (Yates, 1999) and the nominal lydekkerinids *Chomatobatrachus halei* (Cosgriff, 1974; Warren et al., 2006); *Deltacephalus whitei* (Hewison, 1996); *Luzocephalus blomi* (Shishkin, 1980), and *Luzocephalus kochi* (Säve-Söderbergh, 1935). Following the suggestion of Eltink et al. (2019) for testing whether lapillopsids nest within Lydekkerinidae, we also added seven rhytidosteids, focusing on the more completely known taxa and seeking to capture the range of variation across

Rhytidosteidae: *Deltasaurus kimberleyensis* (Cosgriff, 1965); *Derwentia warreni* (Cosgriff, 1974); *Laidleria gracilis* (Warren, 1998b); *Mahavisaurus dentatus* (Lehman, 1966; Maganuco et al., 2014); *Nanolania anatopretia* (Yates, 2000); *Sangaia lavina* (Dias-da-Silva et al., 2006); and *Trucheosaurus major* (Marsicano and Warren, 1998). It should be noted that the monophyly of Rhytidosteidae remains an open question (e.g., Dias-da-Silva and Marsicano, 2011; Schoch, 2013), but this study does not seek to test this question. This matrix and the set of MPTs associated with its analysis are available in the Electronic Supplement.

Baseline Analysis—The combination of characters and taxa captured in the expanded matrix of Pardo et al. (2017) has never been analyzed; therefore, a baseline topology needed to be established for comparison. Both PAUP* and TNT have been used to analyze Schoch's (2013) matrix and its derivates. The difference is largely one of personal preference, but because Silva and Wilkinson (2021) identified the presence of multiple tree islands in their repeated PAUP* analysis of Pardo et al.'s (2017) matrix, we also employed PAUP* version 4.0a169 (Swofford, 2021). This sacrifices the computational speed of TNT in exchange for the ability to identify such islands and to compute consensus trees for them, which is only doable in PAUP*. We ran a heuristic search with 10,000 random-addition sequence replicates and TBR, holding 10 trees per step; these are similar to the parameters used by Pardo et al. (though they did not specify how many trees were held per step; default in PAUP* is 1 tree). PAUP* allows for the use of multiple operational outgroups, so we used both *Proterogyrinus* and *Greererpeton*, compared to only the former in previous studies. Characters were left unordered and equally weighted, which follows Schoch (2013), Pardo et al. (2017), and Schoch et al. (2020). Although we personally prefer to order characters that can be reasonably inferred to occur along a morphocline, the decision not to order any in this baseline analysis was made to maximize the analytical similarity with previous derivates. Character ordering is employed in a later analysis. Details of the bootstrapping procedure used by Pardo et al. (2017) were not specified, so here we performed bootstrapping with 100,000 fast stepwise addition replicates. It is worth noting that conducting even 1,000 bootstrap replicates with a full heuristic search of the same parameters as the initial search would have been prohibitively time consuming.

Analysis 1—Because of the conflict between the phylogenetic position of *Lapillopsis nana* and its phenetic placement within Stereospondyli, we wanted to explore possible explanators for these results. We first began by examining the most proximal primary data: character scores for *Lapillopsis nana*. A total of 54 cells were changed for *L. nana* (15.6% of the 345 characters for which it has been previously assessed); while one of us (CAS) has personally observed material of this taxon, all scoring changes can be justified from the literature alone. Twelve of these changes were corrections (a previously scored cell was changed to another character state); 18 were updates (a previously unscored cell was scored); 14 were “unscored” (a previously scored cell was changed to unknown); six were designated as inapplicable (from a previously scored cell); two were expanded (a previously scored single-state cell was scored as polymorphic); and two were partially expanded (a previously scored single-state cell was scored as partial uncertainty). This survey led to a few wholesale scoring changes for certain characters that could only be scored if a feature was present but that had been scored for state 0 even when the feature was absent. For example, character 209 relates to the presence or absence of osteoderms. When osteoderms are absent (as in most temnospondyls, including *Lapillopsis*; 209–0), characters 210 and 211 (osteoderm width and osteoderm series) should be scored as inapplicable because these characters require osteoderms to be present. However, most temnospondyls were scored for state 0 for both characters 210 and 211 (‘simple set of osteoderms arranged in one layer if present' and 'narrow,' respectively), including both taxa scored for 209–0 and those that were left as unknown for character 209. When these characters had to be rescored for *L. nana* on the basis of a logical dependency or other philosophical grounds that applied to the entire character, they were rescored for all taxa to avoid introducing scoring asymmetry within a given character. All scoring changes are listed and justified in Appendix S1. Two characters were omitted as they were parsimony-uninformative characters intended to characterize lissamphibians or lepospondyls that were sampled in previous versions of these matrices but not in our matrices. We used the same program and parameters as the baseline analysis.

Analysis 2—The recognition of numerous unsubstantiated or missing scores for *Lapillopsis nana* implicitly raises questions about whether a broader pattern of errors exists within the matrix. As part of another study (Kligman et al., 2023), the matrix of Schoch et al. (2020), a derivate of Pardo et al. (2017), was systematically examined for such errors, leading to the identification of similarly pervasive issues, such as scoring of postcranial characters for taxa for which postcrania are entirely unknown. Note that this also led to additional changes to the scoring of *L. nana* when characters were modified in part or in full to properly reflect and account for the range of anatomy in the sampled taxa. These changes are detailed in Gee (2022) and are implemented here, with additional changes noted in Appendix S2, and the associated NEXUS file is included as electronic supplemental material. Scores for the 18 temnospondyls that were originally sampled by Schoch (2013) and propagated by Pardo et al. (2017) but omitted by Schoch et al. (2020) and thus omitted by Kligman et al. (2023) were also systematically checked. The resultant matrix only retained 346 characters of the original 360, and 44 of the retained characters were ordered. This matrix was then analyzed with and without UWBM VP

95522 to test the position of this specimen. In the iteration with UWBM VP 95522, we also added *Rotaurisaurus contundo*, previously scored into this family of matrices by Gee et al. (2021) and modified slightly here in line with other modifications. We used the same program and parameters as the baseline analysis with the exception of character ordering; any character that could be inferred to occur along a morphocline was ordered here and is scripted into the NEXUS file as such. This decision is motivated by empirical and simulated evidence that character ordering improves accuracy and by the conceptual notion that unordering is not a "neutral decision" and could therefore be considered erroneous when character states seem likely to occur along a morphocline (e.g., Fröbisch and Schoch, 2009; Grand et al., 2013; Rineau et al., 2018).

Analysis 3—Given the extensive corrections made as part of Analyses 1 and 2, we also surveyed the matrix of Eltink et al. (2019), which originally sampled 37 taxa for 221 characters. We first began by examining scores of the focal taxa, in this case *Lapillopsis nana, Lydekkerina huxleyi*, and *Eolydekkerina magna*, as well as those of the operational outgroup, "*Dendrerpeton acadianum*" (which is actually a composite Dendrerpetidae OTU; see Appendix 4). Only Dendrerpetidae had more than five scoring changes, and this taxon was below a 5% total error rate. We subsequently examined *Trimerorhachis insignis* to see whether the non-stereospondylomorph outgroups might have a higher error rate than the stereospondylomorphs (Eltink et al. indicate no personal observations were made for Dendrepetidae and *T. insignis*), but this was not found to be the case. We next examined certain blocks of characters (e.g., all vertebral characters) for non-random errors that would be easy to visually detect, such as the scoring of postcranial characters for taxa without postcrania. We also did not detect systemic issues with the matrix in this regard (e.g., taxa without postcrania were not scored for any postcranial characters). Finally, we compared cells (same taxa, same character) shared with the matrix derived from the family of matrices originating with Schoch (2013). Many equivalent cells were scored differently between matrices, suggesting that they were either newly scored or were previously examined by Eltink et al. (2016, 2019). We therefore did not conduct a systematic review of all scores as in Analysis 2. Changes to scores and characters and their justifications are listed in Appendix S3; the revised character list is Appendix S4; and the associated NEXUS file is provided as electronic supplementary material. One character (a joint carpus-tarsus character) was split into two, producing 222 characters, but 13 of these were omitted from this analysis (as indicated in Appendix S4). This revised matrix was analyzed both with and without *Rhigerpeton* (listed as UWBM VP 95522 in the matrix). As with Analysis 2, we treated certain multistate characters as ordered, which also follows the original analysis by Eltink et al. (2019).

The analysis was run using the same parameters as Eltink et al. (2019): a 'traditional search' in TNT version 1.5 (Goloboff and Catalano, 2016) using 10,000 random-addition sequence replicates and TBR, holding 20 trees per replicate, and designating the composite Dendrerpetidae OTU as the operational outgroup. The same search was run on the MPTs saved to RAM from the initial search for a second round of TBR.

DESCRIPTION

Skull roof

The holotype of *Rhigerpeton isbelli* is a partial skull representing much of the right half of the skull (Figs. 2, 3). As preserved, it measures about 30 mm longitudinally and can be reasonably estimated to correspond to a total skull length less than 40 mm. This estimate is based on our inference of a semi-parabolic skull, which is supported by the proportions and positions of the interpterygoid vacuity and the choana (contrasted with longirostrine taxa like archegosaurids or longochorhynchine trematosaurs; e.g., Witzmann, 2005; Eltink et al., 2016). This places its complete length closest to that of *Rotaurisaurus contundo* among the nominal lapillopsids (Yates, 1999; Yates and Sengupta, 2002). Some sutures are indiscernible, while others are difficultly observed under a microscope when examining much of the skull roof. Additionally, some sutures have been lost between the initial illustration of the dorsal skull roof and the present study, between which some damage occurred to the temporal region. In the preorbital region, the contours of the prefrontal are largely resolved, showing a straight lateral margin that sutures to the lacrimal and the jugal (Fig. 2). The anterior terminus is a rounded point. The posteromedial contacts are unresolved. The lacrimal is only defined posteriorly, with the posteriormost extent of the lateral and posterior margins being visible. The jugal definitively extends past the level of the anterior orbital margin, but its total extent is unclear. The lateral margin of the jugal is entirely undefined, although this is formed almost entirely by the maxilla in all temnospondyls. There is no evidence for a lateral exposure of the palatine (LEP) or the ectopterygoid (LEE). Posteriorly, the jugal typically meets the quadratojugal, but because of the lack of a preserved jugal-maxilla suture, whether a short transverse suture is the posterior end of the jugal or of the maxilla is unclear. The maxilla is clearly incomplete posteriorly as well, further precluding confident determination.

Most sutures can be identified in the temporal region (Fig. 2). The lateralmost extent of the supratemporal is exposed. As preserved, it is very narrowly excluded from the otic notch by the squamosal and the tabular, but the region at which these elements meet is damaged, so the visible sutural contact is internal. We infer here that the contact was consistent through to the skull roof, but it remains possible that the dorsal exposure and contacts differed from the internal exposure. Anterior to this, the lateral half of the postorbital is preserved; it does not have the prominent lateral expansion seen in many lydekkerinids and rhinesuchids (e.g., Shishkin et al., 1996; Jeannot et al., 2006; Marsicano et al., 2017; also convergent in capitosaurs; e.g., Schoch and Milner, 2000; Damiani, 2001). Whether it had a posteriorly projecting terminus or was squared-off is unknown, but the preserved suture with the supratemporal is nearly straight transversely. Lateral to the postorbital, the squamosal is mostly defined. It also sutures to the supratemporal, the tabular, the jugal, and the quadratojugal. It forms most of the otic notch, a large, laterally facing embayment. The skull roof projects slightly laterally over the otic notch to form a supratympanic shelf like that observed in many terrestrial dissorophoids (e.g., Bolt, 1974). Ventral to the anteriormost portion of this shelf is a thin unornamented flange. This flange is oriented vertically and longitudinally in its dorsal portion. It then curves ventrolaterally such that it partially faces dorsally (more horizontal and posterolateral orientation) and is entirely exposed in dorsal view. It also broadens towards the region of the quadrate and the quadratojugal (Fig. 2A). This flange does not extend along the dorsal margin of the otic notch (ventral to the tabular, supratemporal, and squamosal); instead, there is only a short unornamented rim in the anterior half. For this reason, the flange is not considered homologous with the 'supratympanic flange' (sensu Bolt, 1974) that is found in in certain large dissorophoids (predominantly olsoniforms, in which this feature was originally defined by Bolt) and is instead more comparable to the less extensive flange of small dissorophoids. The posteriormost contact between the squamosal and the quadratojugal is visible at about the mid-length of the ventral border of the otic notch, but the remainder of the suture is largely indiscernible. It probably occurred in the marked temporal groove (see next paragraph) and may therefore be obscured by remaining matrix or have been partially obliterated by remodeling or weathering in this region. The quadratojugal forms the posterolateral corner of the skull and is unremarkable in shape when viewing the skull roof. The tabular is incomplete and is dorsal to the otic notch. It has a distinct posteriorly projecting horn with a broad rounded terminus. The occipital aspects (e.g., the ventral tabular crest) are obscured by matrix (if they are preserved at all, for which there is no evidence; e.g., the exoccipitals have clearly been lost).

Dermal ornamentation is progressively weathered anteriorly from the suborbital region to the snout (Fig. 2). As preserved, the specimen exhibits no clear deformation. The skull was therefore relatively tall, with the cheek region, including the otic notch, being more vertical than horizontal and the orbits facing at least as much laterally as they did dorsally (Fig. 2B). The posterior orbital rim is slightly elevated from the skull roof, but there is no indication of an elevated ventral/lateral or anterior orbital rim. Although the snout is not well preserved, there appears to be a shallow depression between the orbit and the predicted region of the naris, based on the remaining rostral bone fragments and internal mold preservation. The ornamentation consists of small, circular pits with one nutrient foramen in each. The intersections between pits form small pustules. Pits are sometimes slightly oval in shape, but there are no elongate grooves or any pattern (e.g., radiating outward from the ossification center). Ventral to the otic notch (presumably on the quadratojugal but possibly on part of the squamosal as well) is a longitudinal ridge, formed by more laterally protruding ornamentation. A second ridge formed by ornamentation is also found along the posteroventral margin of the skull (presumably on the quadratojugal and jugal). There is no evidence for lateral line grooves, but the two ridges frame a broad and shallow trough; this is differentiated from a lateral line groove in being floored by the same ornamentation as the rest of the skull and is here termed the temporal trough in *Lapillopsis* *nana* (following Yates, 1999). A similar trough may have been present in *Rotaurisaurus contundo* as well, as there is a prominent longitudinal ridge within the weathered quadratojugal that could demarcate the ventral border of the trough.

Palate

The lateral elements of the palate and their sutures are preserved (Fig. 3). At least the quadrate, the pterygoid, the ectopterygoid, the palatine, and the vomer are represented. A small, triangular ventral exposure of the jugal is also identified at the anterior margin of the subtemporal vacuity. The parasphenoid is entirely absent. The pterygoid is incomplete, with only the palatine and the quadrate rami preserved; whether there was a distinct slender basipterygoid ramus (as in *Lapillopsis nana* and *Rotaurisaurus contundo*; Yates, 1999) or merely a broad corpus that abutted the parasphenoid (as in higher stereospondyls) is unclear. The palatine ramus of the pterygoid extends anteriorly along the medial edge of the ectopterygoid but fails to contact either the palatine or the vomer; the ectopterygoid therefore enters the interpterygoid vacuity. A transverse flange extends posteroventrolaterally from the lateral edge of the palatine ramus with its terminus oriented nearly vertically. Such an angling is highly atypical among stereospondyls but reminiscent of some terrestrial dissorophoids in which the flange is below the plane of the rest of the palate (e.g., Dilkes, 1990; Liu, 2018; Gee et al., 2019). The quadrate ramus of the pterygoid extends posterolaterally to frame the quadrate medially. It is more vertically than horizontally aligned and relatively flat. A flange lies dorsal to the quadrate ramus when the skull is viewed from below, but whether it is exclusively the ascending lamina or also includes a descending flange from the overlying roofing elements is unclear. This flange is exposed dorsally through the incomplete skull roof and appears to have at least closely approached the skull roof. Definitive contact between the pterygoid and the squamosal (thereby precluding a palatoquadrate fissure) cannot be determined. The remaining body (corpus) of the pterygoid is flat. The broken medial edge shows no evidence for constriction into a rod-like process to form part of the basicranial articulation like in *Lapillopsis*, but the amount that has been lost is difficult to discern. No ornamentation is identified on the palatine ramus, but an extensive covering of denticle sockets is present across the pterygoid. These are identified as such based on their dense distribution, uniform shape, and slight raised edges with frequent mineral infilling that is darker in coloration than the matrix and that is inferred to be from the pulp cavity. By contrast, in taxa with pterygoid ornamentation, there is frequently a radiating pattern, with more elongate grooves concentrated on the posteromedial half of the palatine ramus (e.g., Yates, 1999; Jeannot et al., 2006; Hewison, 2007).

The quadrate is represented only by a poorly ossified mass with a subtriangular ventral profile (Fig. 3). A faint and shallow groove may divide the two condyles. The quadrate's lateral suture with the quadratojugal is not identified. The dorsal surface could not be fully prepared, but no dorsal process of the quadrate like in dissorophoids is identified.

The ectopterygoid is a slender rectangular element in ventral view (Fig. 3). It was probably excluded from the subtemporal vacuity by the ventral exposure of the jugal. Only one complete tooth is present, but bases of at least two or three more are identified. None appears substantially larger than another or than the marginal dentition. Denticles are entirely absent from the ectopterygoid.

As seen in Figure 3, the palatine is largely obscured by an overlying bone of uncertain association with the skull (if associated, it would represent an indeterminate limb bone). A narrow posterior flange of the palatine extends along the medial edge of the ectopterygoid, but the remainder of the ectopterygoid-palatine suture is obscured. Based on the near sagittal orientation of the anteriormost extent, we infer that the suture was not straight but rather stepped, with a more posteriorly extensive posteromedial process, as occurs in many early diverging stereospondyls. The main body of the palatine is then covered anteriorly by the unidentified bone such that the palatine-vomer suture is not confidently identified. We presume that the palatine contributed to at least the posteriormost margin of the choana. The dentition of the palatine is therefore entirely unknown; one tooth medial to the posteriormost extent of the choana could belong to the palatine. A broken cross-section below the unidentified bone appears too large to be a tooth, although it is in the position predicted for a palatal 'tusk' and could be dislodged and broken in a fashion that make it harder to identify as such.

The vomer presumably jointly frames the oval choana with the palatine and the maxilla, but only the suture with the latter is preserved at the anterolateral corner. The choana is essentially of uniform width throughout, with the lateral and medial margins being straight rather than outwardly convex. A row of eight parachoanal teeth extends posteriorly along the anteromedial margin of the choana; it is unclear how many are exclusively on the vomer. The teeth are of a subequal size to the one preserved on the ectopterygoid. Part of one vomerine tusk is preserved anteromedial to the anteriormost region of the choana; this tooth is larger than those along the choana and the marginal dentition. The remainder of the vomer is flat, but it is incomplete medially and anteriorly such that it is not possible to determine whether any fossa or fenestra was present along the midline, and a second indeterminate bone overlies the medialmost preserved portion. Denticles are absent from the vomer. There is no evidence for a transvomerine tooth row.

The ventral surface of the maxilla is defined by its dentition and relation to the other palatal elements (Fig. 3). It is incomplete posteriorly, but the tooth row extends past the anterior margin of the subtemporal fenestra. Other gaps preclude a confident tooth estimate, but at least 19 positions are confidently identified, appearing to represent no more than half of the possible tooth-bearing surface. Teeth are monocuspid, non-pedicellate, straight, and decrease in size posteriorly. The maxilla definitively contributes to the lateral margin of the choana, but this margin is obscured posteriorly such that the relative contribution and the contact with the palatine are unknown.

PHYLOGENETIC RESULTS

Baseline Analysis—The baseline analysis in PAUP* recovered 90 MPTs with a length of 1,212 steps (CI = 0.306; RI = 0.685; Fig. 4). All MPTs belong to one tree island. The strict consensus is largely resolved, more so than that of Pardo et al. (2017), and is largely consistent with previous derivates of this matrix. *Lapillopsis nana* was recovered as the sister taxon to Dissorophoidea, which is also consistent with previous derivates of this family of matrices. The main area of topological disparity from previous derivates is within higher stereospondyls (post-lydekkerinid stereospondyls). *Laidleria gracilis* was recovered as the sister taxon to Brachyopoidea, which includes Brachyopidae + Plagiosauridae, Chigutisauridae, and *Chinlestegophis* + *Rileymillerus* in a polytomy; previously, *L. gracilis* was recovered as the sister taxon to Plagiosauridae, nested within Brachyopoidea, and *Chinlestegophis* + *Rileymillerus* was recovered as the sister taxon to Brachyopoidea (e.g., Schoch, 2013; Pardo et al., 2017). The early diverging capitosaur *Edingerella madagascariensis* and the early diverging trematosaur *Benthosuchus sushkini* were single branches in a polytomy of all other capitosaurs and a clade of trematosaurs, brachyopoids, *L. gracilis*, and the rhytidosteid *Sangaia lavina*. *Peltobatrachus* *pustulatus* was also recovered as the sister taxon to Dissorophoidea + Eryopiformes; previously it was in a polytomy with these clades (Schoch, 2013; Pardo et al., 2017). Statistical support for most nodes is weak (Bremer < 2; bootstrap < 50%), including *Lapillopsis* + Dissorophoidea (Bremer = 2; bootstrap = 20%).

Analysis 1—This analysis in PAUP* (modifications only to *Lapillopsis*) recovered 384 MPTs with a length of 1,222 steps (CI = 0.304; RI = 0.682; Figs. 5, 6). MPTs were divided between five disparately sized islands (1–6; 7–234; 235–246; 247–294; 295–384; Fig. 6). The strict consensus of all MPTs is markedly unresolved (Fig. 5A) and consists of two major polytomies, a basal one comprising *Capetus*, Dendrerpetidae, Dvinosauria, Edopoidea, and *Iberospondylus*, and a higher nested one comprising all remaining temnospondyls. Dissorophoidea is not recovered, and *Lapillopsis* is a single branch in the higher nested polytomy. The disparate position of *Lapillopsis* across the five tree islands is a major contributor to the lack of resolution in the strict consensus. Comparison of the strict consensus of the five tree islands reveals three different positions. The first position, found in island 5 (295–384) is the closest to the previous studies that utilized this matrix; here *Lapillopsis* nests within Dissorophoidea as the sister taxon to *Apateon*, which in turn is the sister taxon to Micromelerpetidae (Fig. 6C). The second position, found in island 1 (1–6) and island 4 (247–294), nests *Lapillopsis* securely within Stereospondyli (Fig. 6A). Here, it clusters with two of the three rhytidosteids (*Laidleria* and *Sangaia*, excluding *Peltostega*), brachyopoids, *Gerrothorax*, *Chinlestegophis*, and *Rileymillerus*, forming the earliest diverging taxon in this clade. The third position, found in island 2 (7–234) and island 3 (235–246), recovered *Lapillopsis* in a clade with the same taxon, but instead it was recovered as the sister taxon to *Chinlestegophis* + *Rileymillerus*, forming an early diverging clade at the base of the larger clade (Fig. 6B).

Predictably, statistical support remains weak for the few nodes that were recovered in the strict consensus of all MPTs, as in the baseline analysis.

Analysis 2—This analysis (substantial modifications for all taxa) recovered 210 MPTs with a length of 1,681 steps (CI = 0.310; RI = 0.766; Fig. 7A). All MPTs belong to a single tree island. The increase in the length of MPTs compared to Analysis 1 (an additional 253 steps) underscores the substantial scoring changes made to this matrix, particularly the new scoring of polymorphisms and the removal of many unsubstantiated scores, which collectively resulted in decreased resolving power. Despite this, the strict consensus is relatively resolved and similar in topology to the baseline analysis (Fig. 4), except for poor resolution among the higher stereospondyls and minor loss of resolution within Dissorophoidea. *Peltobatrachus pustulatus* and *Iberospondylus schultzei* have also shifted in position to be successive sister taxa of Zatracheidae + Dissorophoidea. *Lapillopsis nana* is recovered within Stereospondyli in a large polytomy that includes brachyopoids, plagiosaurids, the rhytidosteid *Laidleria gracilis*, and the other diminutive taxa *Chinlestegophis jenkinsi* and *Rileymillerus cosgriffi*. Statistical support remains weak for most nodes.

When *Rotaurisaurus contundo* and *Rhigerpeton isbelli* were included in the analysis, the search recovered 126 MPTs with a length of 1,691 steps (CI = 0.309; RI = 0.624; Fig. 7B). All MPTs belong to a single tree island, and the intrarelationships of most taxa are the same as in the iteration without these taxa. Interestingly, the addition of these taxa has led to increased resolution among higher stereospondyls (e.g., within Trematosauria), although all newly recovered nodes are poorly supported. *Rhigerpeton isbelli* and *Ro. contundo* were recovered as the sister taxa to *Lapillopsis nana*, and this trichotomy was recovered in the same position as *L. nana* alone in the previous iteration. *Lapillopsis nana* and *Rh. isbelli* were recovered as exclusive sister taxa within Lapillopsidae in 71% of the MPTs. Statistical support for Lapillopsidae is relatively robust compared to other nodes, with both strong Bremer and bootstrap support.

Analysis 3—The analysis in TNT that did not include *Rhigerpeton isbelli* but that did expand the sample of early diverging stereospondyls recovered 10 MPTs with a length of 842 steps (CI = 0.300; RI = 0.577; Fig. 8A). The topology of non-stereospondyls is nearly identical to the original of Eltink et al. (2019) with one exception: a previously recovered polytomy of *Archegosaurus decheni*, *Collidosuchus tchudinovi*, and Platyoposauridae is now resolved, with *C. tchudinovi* diverging first, followed by *A. decheni*. Within Stereospondyli, the relationships of non-focal groups also remained the same: the composition and topology of Rhinesuchidae and the two respective subfamilies; the early diverging positions of *Peltobatrachus pustulatus* and *Arachana nigra*; and the clade formed by *Benthosuchus sushkini*, *Mastodonsaurus giganteus*, and *Trematolestes hagdorni* (Neostereospondyli sensu Eltink et al., 2019).

As with the original analysis of Eltink et al. (2019), nominal lydekkerinids did not form a clade. *Eolydekkerina magna* and *Lydekkerina huxleyi* were recovered as the earliest diverging lydekkerinids as individual branches in a trichotomy. The third branch of this polytomy is a clade of all remaining nominal lydekkerinids, all lapillopsids, and all rhytidosteids. Within this clade, the three lapillopsids form a basal polytomy. *Deltacephalus whitei* is the next taxon to diverge and is the sister taxon to a highly nested clade of all rhytidosteids, *Chomatobatrachus halei*, and both species of *Luzocephalus*. All rhytidosteids form a single polytomy. This clade is the sister taxon to *C. halei* + *Luzocephalus* spp. Based on these results, the definition of Lydekkerinidae proposed by McHugh (2012) and adopted by Eltink et al. (2019) would result in a far more inclusive clade than previously conceived, as it would include not only all nominal lydekkerinids and all nominal lapillopsids but also all sampled rhytidosteids.

When *Rhigerpeton isbelli* was included, the analysis recovered 27 MPTs with a length of 845 steps (CI = 0.299; RI = 0.575; Fig. 8B). The topology was largely unchanged from the previous iteration, but *Eolydekkerina magna* was recovered as the earliest diverging lydekkerinid, followed by *Lydekkerina huxleyi*. The next node is a trichotomy of *Deltacephalus*, the three lapillopsids + *R. isbelli*, and all remaining lydekkerinids + rhytidosteids. Rhytidosteidae no longer forms a clade, with each nominal rhytidosteid forming a single branch of a large polytomy with one branch for *Chomatobatrachus halei* + *Luzocephalus* spp. While *R. isbelli* clusters with lapillopsids, there is no further resolution within Lapillopsidae in the strict consensus. Four different configurations were identified by examining the individual MPTs (Fig. 8C–F). In all of these, *R. isbelli* would not be considered a lapillopsid sensu stricto (*Lapillopsis nana*, *Rotaurisaurus contundo*, and their most recent common ancestor), and in some, *Manubrantlia khaki* would also not be considered a lapillopsid under that definition.

DISCUSSION

Systematic Position of *Rhigerpeton isbelli*

Despite the paucity of apomorphic cranial sutures, numerous qualitative aspects of the skull and preserved details of the palate proved to be highly informative for resolving the position of the holotype of *Rhigerpeton isbelli* (Figs. 7, 8). Features such as the ventral exposure of the jugal and the retracted pterygoid that results in the ectopterygoid entering the interpterygoid vacuity (typical stereospondyl features; Fig. 3); a tall cheek with a large, laterally facing otic notch (an atypical stereospondyl feature, usually associated with terrestriality, like in dissorophoids; Fig. 2B); and the steeply angled, posteroventrolaterally directed transverse flange of the pterygoid (an atypical stereospondyl feature that is also found in at least *Lapillopsis nana* among lapillopsids; Warren and Hutchinson, 1990; Yates, 1999; Fig. 3) quickly refined its placement. Dental features also proved informative, such as the presence of at least an ectopterygoid tooth row (a stereospondylomorph feature); presence of denticles on the pterygoid (a plesiomorphic feature lost in most stereospondyls); and a parachoanal tooth row (a feature only common in 'higher stereospondyls'). Finally, the presence of a ridge along the dorsal margin of the tabular horn and the presence of a well-developed temporal trough are specifically features shared with *L. nana* (Yates, 1999). As noted in the description, a temporal trough may also have been found in *Rotaurisaurus contundo* based on the presence of a longitudinal ridge on the quadratojugal (Yates, 1999) and could thus this trough could represent a synapomorphy of Lapillopsidae. Collectively, these qualitative comparisons indicate close affinities of *R. isbelli* with small-bodied early diverging stereospondyls (predominantly Lapillopsidae and Lydekkerinidae).

Our phylogenetic analyses also provide support for this position within Stereospondyli and specifically provides support for a close relationship of *Rhigerpeton isbelli* to, or inclusion in, Lapillopsidae (Figs. 7, 8). The primary question is whether *R. isbelli* is closer to Lapillopsidae or to Lydekkerinidae (either sensu stricto or sensu lato), a question complicated by the paraphyly / polyphyly of nominal lydekkerinids in both the original analysis of Eltink et al. (2019) and our analysis of a modified derivate. If a phenetic comparison is restricted to the eponymous taxon of each clade, features shared with *La. nana* (Yates, 1999) but not with *Ly. huxleyi* (Jeannot et al., 2006; Hewison, 2007) include: (1) vertically oriented cheek with laterally facing otic notch; (2) presence of temporal trough; (3) absence of lateral line groove on the temporal region; (4) presence of dorsal ridge along tabular horn; (5) absence of vomerine denticles; (6) more elongate, narrow choana with parallel sides (compared to the more rounded, circular choana of *Ly. huxleyi*); and (7) marginal dentition extends past the level of the anterior margin of the subtemporal fenestra. The possible absence of a transvomerine tooth row in *R. isbelli* is a feature found in *La. nana* but not in *Ly. huxleyi.* Features shared with *Ly. huxleyi* but not with *La. nana* include: (1) presence of pterygoid denticles; and (2) presence of a parachoanal tooth row. Both of these features are also absent in *Rotaurisaurus contundo* but present in *Eolydekkerina magna*. The possible presence of a continuous palatine-ectopterygoid tooth row and a possible long parasphenoid-pterygoid suture formed by an abutting contact are two features found in *Ly. huxleyi* and *E. magna* but not *La. nana* or *Ro. contundo* (Shishkin et al., 1996; Yates, 1999).

The phenetic comparisons therefore align with the phylogenetic results and support a closer relationship with Lapillopsidae because features like the dorsal ridge on the tabular and the temporal trough are exceedingly rare compared to features such as the absence of vomerine denticles (i.e., dentition appears more labile in temnospondyl evolution); neither feature is captured as a phylogenetic character in either matrix that we used but would undoubtedly further strengthen the relationship between *Rhigerpeton isbelli* and *Lapillopsis nana* (but possibly weaken Lapillopsidae inclusive of *Rotaurisaurus contundo*). The primary obstacle to phenetic inclusion of *Rh. isbelli* within Lapillopsidae is that the absence of pterygoid ornamentation, instead replaced by pterygoid denticles, and the presence of the parachoanal row in *Rh. isbelli* are contrary to the diagnosis of Yates (1999), though neither feature was included in the diagnosis of Schoch and Milner (2000). In this scenario, *Rh. isbelli* would be ‘lapillopsid-like’ rather than a ‘lapillopsid proper’ as the probable sister taxon to a more exclusive Lapillopsidae. Having compared *Rh. isbelli* closely with *L. nana* (Fig. 9), we can at least be confident that the ornamentation in the latter is not misidentified denticle sockets (Warren and Hutchinson, 1990, identified both denticles and ornamentation on the pterygoid). In specimens of *L. nana*, the pits become elongate grooves anterolaterally, which are absent in *Rh. isbelli*. Interestingly, in *Eolydekkerina magna*, most of the pterygoid is ornamented, but this grades anterolaterally into a denticle field near the pterygoid-ectopterygoid contact and might relate to the peculiar asymmetry of dentition in the holotype of this taxon (Shishkin et al., 1996). One possibility is that weathered or overprepared denticles would not be distinguishable if they are intermingled with ornamentation in historic specimens, especially small ones. It is also possible that accessory palatal dentition was fairly labile in early stereospondyls, as there is also variation in other dental features, such as the presence/absence of vomerine denticles (only present in *Lydekkerina huxleyi* among nominal lydekkerinids; Jeannot et al., 2006). As another line of evidence in support of this hypothesis, rhytidosteids have notable variation in the presence/absence of palatal tooth rows and palatal denticles (e.g., Cosgriff, 1965; Warren and Black, 1985; Warren, 1998b; Maganuco et al., 2014).

A final consideration is whether UWBM VP 95522 might represent a particularly large and mature individual of *Lapillopsis nana*. The specimen is distinctly larger than all previously reported specimens of *L. nana*, and Yates (1999) expressed uncertainty about the maturity of even the largest specimens of this species. At present, there is no evidence that the features separating *Rhigerpeton isbelli* from *L. nana* (pterygoid denticles instead of ornamentation, parachoanal tooth row, possible ectopterygoid tooth row) are ontogenetically influenced features. They do not change in the partially known ontogeny of *L. nana*, nor are they present in the holotype of *Rotaurisaurus contundo*, which is of similar size to UWBM VP 95522. The holotype of *Rh. isbelli* is closest in size to *Ro. contundo* among lapillopsids, but it does not display any autapomorphies of this taxon as prescribed by Yates (1999) and shares features with *L. nana* that differentiate both from *Ro. contundo* (e.g., the tabular horn is mostly posteriorly directed, as in *L. nana* and most temnospondyls, not mostly laterally, as in *R. contundo*). Separation from *Ro. contundo* is therefore also well-justified. Finally, it is not possible to evaluate whether this could be a juvenile of *Manubrantlia khaki*, which is only known from a lower jaw that produces skull length estimates of about four times as large as *L. nana*. In the same vein, it is also not possible to disprove the hypothesis that *M. khaki* is a large individual of one of the other named lapillopsids, although this cannot be tested at present and is only mentioned here to indicate that is a gap in knowledge across all nominal lapillopsids.

Relationships of Early Diverging Stereospondyls

Early diverging stereospondyls include at least Lapillopsidae, Lydekkerinidae, Rhinesuchidae, Rhytidosteidae, and various nominal taxa without definitive placement such as *Arachana nigra*, *Uruyiella limnea*, and *Peltobatrachus pustulatus*. Elucidating the relationships between these clades is greatly complicated by a lack of consensus on the composition of most of these clades other than Lapillopsidae (only three species beyond *Rhigerpeton isbelli*; Yates, 1999; Yates and Sengupta, 2002) and Rhinesuchidae (well-established as the earliest diverging and earliest appearing clade; e.g., Ruta et al., 2007; Schoch, 2013; Cisneros et al., 2015; Marsicano et al., 2017). The lack of agreement regarding the definition (and therefore the composition) of Lydekkerinidae and Rhytidosteidae inherently influences whether these clades are recovered as monophyletic or not, and these implications are discussed in the context of our own analyses.

The composition of Rhytidosteidae has long been disputed (e.g., Cosgriff, 1965; Cosgriff and Zawiskie, 1979; Warren and Black, 1985; Shishkin, 1994; Warren, 1998b; Marsicano and

Warren, 1998; Schoch and Milner, 2000; Dias-da-Silva and Marsicano, 2011; Schoch, 2013). Furthermore, the lack of monophyly among nominal rhytidosteids sampled in large-scale temnospondyl analyses (e.g., Yates and Warren, 2000; Ruta et al., 2007; McHugh, 2012; Schoch, 2013; Maganuco et al., 2014) questions whether this family is monophyletic. The lack of a consensus stems from the high degree of variation among all the species previously ascribed to Rhytidosteidae compared to the interspecific variation in other family-level clades; some taxa have parabolic skulls and otic notches (e.g., *Arcadia myriadens, Derwentia warreni*), whereas others have triangular skulls with no otic notches (e.g., *Laidleria gracilis*, *Trucheosaurus major*). Certain features, such as the absence of a lacrimal in most nominal rhytidosteids, are probably homoplastic with other stereospondyls (brachyopids, chigutisaurids, and a few trematosaurs in this case). Size disparity is also stark. These attributes in turn confound phylogenetic analyses, which for temnospondyls largely utilize equal-weights parsimony and therefore are susceptible to homoplasy. Qualitative features in particular (e.g., skull shape) can be inadvertently overweighted for many rhytidosteids because most taxa are only known from cranial material and therefore have a high proportion of missing data in large-scale matrices that sample characters from across the entire skeleton. The most recent revision of rhytidosteids by Dias-da-Silva and Marsicano (2011) recovered conflicting results depending on the character sampling and weighting scheme employed. In particular, the diminutive *Nanolania anatopretia*, the fragmentary *Rhytidosteus capensis* and *T. major*, and *L. gracilis* sometimes clustered with other clades. Only through the use of implied weighting were they able to largely restore rhytidosteid monophyly, and this still excluded the eponymous *R. capensis*. Underscoring the aforementioned point about missing postcranial data, their matrix comprised 75 cranial/palatal characters and 12 mandibular characters but did not contain any postcranial characters.

Similar variation among nominal lydekkerinids has also proven problematic for this clade. In the most expansive concept of the clade (e.g., Schoch and Milner, 2000), Lydekkerinidae included *Chomatobatrachus halei*, *Deltacephalus whitei*, *Eolydekkerina magna*, *Luzocephalus blomi*, *Luzocephalus kochi*, and *Lydekkerina huxleyi* (and its junior synonyms like '*Broomulus dutoiti*' and '*Limnoiketes paludinatans*'). However, most other workers excluded at least one of these taxa from Lydekkerinidae (e.g., Shishkin, 1980; Milner, 1990; Shishkin et al., 1996; Jeannot et al., 2006; Hewison, 2007), and previous phylogenetic analyses of all scales and focuses rarely recovered their respective subsets of nominal lydekkerinids in a clade (e.g., Yates and Warren, 2000; Damiani and Yates, 2003; Maganuco et al., 2009, 2014; Dias-da-Silva and Marsicano, 2011; Schoch, 2013; Pardo et al., 2017; Eltink et al., 2019; but see Ruta and Bolt, 2008; McHugh, 2012, for counterexamples). In particular, the long-snouted *Luzocephalus* from Russia has alternatively been positioned close to trematosaurs, and the relatively large *C. halei* and the diminutive *D. whitei* are also contentious (e.g., Cosgriff, 1974, 1984; Shishkin, 1980; Shishkin et al., 1996; Bjerring, 1999; Damiani, 2001; Hewison, 2007). There are then questions about the possible synonymy of the various South African lydekkerinids. The holotype and only specimen of *E. magna* is an uncontroversial lydekkerinid (e.g., Shishkin et al., 1996; Hewison, 2007), but there are some doubts about whether it might merely be an atypically large individual of *Ly. huxleyi* (Jeannot et al., 2006). The histological findings of Canoville and Chinsamy (2015), which suggested that typically sized individuals of *Ly. huxleyi*—much smaller than the type of *E. magna*—are not adults, reinforces such questions. So too does the paraphyletic Lydekkerinidae recovered by Eltink et al. (2019) in which *E. magna* diverges first, as it may be drawn towards large members of Neostereospondyli with more derived features that only appear in mature lydekkerinids, whereas the smaller *Ly. huxleyi* clusters with the more similarly sized

Lapillopsis nana, the latter also probably not represented by 'adults' (Yates, 1999). Both '*B. dutoiti*' and '*Li. paludinatans*' are historical junior synonyms of *Ly. huxleyi* (e.g., Jeannot et al., 2006; Warren et al., 2006), but at least one if not both have been considered valid by some workers (e.g., Shishkin et al., 1996; Schoch and Milner, 2000; Hewison, 2007). Finally, there is the recent question posed by Eltink et al. (2019) of whether lapillopsids (viz. *Lapillopsis nana* in their analysis) are a subclade of Lydekkerinidae.

Our analyses confer further support for the general consensus that not all nominal lydekkerinids properly belong in Lydekkerinidae. In the broad temnospondyl samples of Analyses 1 and 2, *Lydekkerina huxleyi* and *Chomatobatrachus halei* were successively diverging taxa (i.e., paraphyletic; Figs. 5–7). In Analysis 3, which featured a more restricted taxonomic sample, *Eolydekkerina magna*, *L. huxleyi*, and *Deltacephalus whitei* form a grade between Rhinesuchidae and a clade including all lapillopsids, all other nominal lydekkerinids, and all nominal rhytidosteids (Fig. 8). *Chomatobatrachus halei* and *Luzocephalus* spp. formed a clade as part of a rhytidosteid polytomy; a close relationship between *Luzocephalus* and rhytidosteids has been previously recovered by some analyses (e.g., Damiani and Yates, 2003; but see Dias-da-Silva and Marsicano, 2011; Maganuco et al., 2014, for differing positions separated from *Ly. huxleyi*). A phenetic similarity between *Chomatobatrachus* and *Luzocephalus* has also been cited by some workers as evidence for the placement of the latter in Lydekkerinidae (e.g., Warren and Black, 1985; but see Hewison, 2007, for dissent). Also notable is that with the expanded taxon sampling, Lapillopsidae does not nest within Lydekkerinidae unless Lydekkerinidae is much more inclusive than previously recognized. The paraphyly of Lydekkerinidae has been previously suggested by other workers (e.g., Milner, 1990; Yates and Warren, 2000).

Implications for the lower Fremouw Temnospondyl Assemblage

The comparatively limited fieldwork opportunities in Antarctica make it a foregone conclusion that the tetrapod assemblage of the lower Fremouw Formation is undersampled relative to that of the *Lystrosaurus declivis* Assemblage Zone (LAZ) of South Africa. Despite this uneven sampling, recent attention to Antarctic temnospondyls has made substantial progress in refining and adding to their occurrence data. For example, Gee and Sidor (2021) recently reported the first record of *Micropholis stowi* from Antarctica, which is an amphibamiform otherwise only known from the LAZ of South Africa. In addition, Gee et al. (2021) reidentified the holotype of *Cryobatrachus kitchingi* as likely representing a juvenile capitosaur, and provisionally referred another specimen to Lydekkerinidae. The recognition of *Rhigerpeton isbelli* as a probable lapillopsid (sensu lato) means that at least five family or supra-family level temnospondyl clades are now represented in the lower Fremouw Formation, which compares favorably to historically better sampled areas like the LAZ or the Arcadia Formation of Australia. However, despite recent progress in documenting temnospondyl diversity in the lower Fremouw Formation, there is still a dearth of genus-level identifications (e.g., Brachyopidae, Capitosauria, Lydekkerinidae, and possibly Rhytidosteidae), which limits the biostratigraphic and biogeographic comparisons that can be made. At present, the current data—summarized in Figure 10—show that some temnospondyl clades were broadly distributed across southern Pangea (e.g., Lapillopsidae, Lydekkerinidae), whereas some others seem to show more regionality (e.g., Chigutisauridae, Brachyopidae, Plagiosauridae).

Our phylogenetic analyses also provide further insights into the biogeography of Early Triassic temnospondyls. For example, Lydekkerinidae is globally distributed in its most expansive composition, but the paraphyly recovered here (especially with respect to the separation of *Luzocephalus* from most other nominal taxa) may be interpreted as support for a more restricted concept of Lydekkerinidae in which the clade is found only in the southern hemisphere. Strictly southern Pangean ranges are documented for chigutisaurids, lapillopsids (sensu lato), and rhinesuchids throughout their respective Triassic ranges. The only definitive occurrence of brachyopids in the northern hemisphere is the near-equatorial records from the Moenkopi Formation, *Hadrokkosaurus* and *Vigilius* (Welles and Cosgriff, 1969; Warren and Marsicano, 2000); *Batrachosuchoides* from Russia and Poland (Shishkin, 1967; Shishkin and Sulej, 2009) has been suggested to instead be a dvinosaur by some workers (e.g., Warren and Marsicano, 2000; Schoch and Milner, 2014). *Luzocephalus* is the only nominal lydekkerinid from the northern hemisphere and occurs at high paleolatitudes of Russia and Greenland which would have required a rapid and widespread radiation to achieve this global distribution by the end of the Early Triassic. By contrast, most workers favor a hypothesis of stereospondyl origins in southern Pangea (e.g., Milner, 1990; Schoch and Milner, 2000; Yates and Warren, 2000; Warren et al., 2001; Eltink et al., 2019), where their fossils are most abundant. As a result, dispersal into the northern hemisphere would require that these lydekkerinids traversed the equatorial regions, from which they are entirely unknown (e.g., western North America, central Europe) and from which temnospondyls tend to be proportionately scarce compared to amniotes, even in well-sampled regions (as recently summarized by Romano et al., 2020). Low-latitude temnospondyl occurrences are restricted to larger, more aquatic taxa like capitosaurs and trematosaurs in the Early Triassic (e.g., Schoch, 2011), and the overall paucity of temnospondyls may reflect a genuine climatic and/or geographic barrier (e.g., Sun et al., 2012; Bernardi et al., 2018; Romano et al., 2020), such that only the fully aquatic clades like capitosaurs and trematosaurs could have crossed the equatorial regions during the Early Triassic. If *Luzocephalus* is in fact more closely related to capitosaurs (in the contemporary context) or to trematosaurs (e.g., Bjerring, 1999; Yates and Warren, 2000; Steyer, 2002), then lydekkerinids would be restricted to the southern hemisphere, and *Luzocephalus* would instead represent one of many occurrences of either capitosaurs or trematosaurs in the northern hemisphere. Similar considerations are warranted for rhytidosteids, of which only a small subset occur in the northern hemisphere, also only at high paleolatitudes (*Boreopelta vavilovi*, *Peltostega erici*, *Rhytidosteus uralensis*). *Peltostega erici* has been sampled in the large-scale matrix of Schoch (2013, and derivates) and consistently clusters with trematosaurs rather than with the other two sampled nominal rhytidosteids, *Laidleria gracilis* and *Sangaia lavina*. This discussion demonstrates how shifts to the taxonomic framework inherently alter interpretations of biogeography, among other broad paleobiological narratives, and this connectivity underscores the continued import of taxonomic and phylogenetic work.

Finally, these open questions around phylogeny and biogeography are likely intertwined with the inferred lifestyle of Lower Triassic temnospondyls. Unequivocally terrestrial taxa (lapillopsids, *Micropholis*) occur only at relatively high southern paleolatitudes. Several other early diverging stereospondyl clades are more uncertainly inferred or may have had variation in lifestyle within the clade, such as the rhinesuchids (aquatic to semi-aquatic; e.g., Shishkin and Rubidge, 2000; Dias and Schultz, 2003; Pawley and Warren, 2004; Fernandez et al., 2013; McHugh, 2014; Rey et al., 2020) and lydekkerinids (semi-aquatic to terrestrial; e.g., Pawley and Warren, 2005; Jeannot et al., 2006; Hewison, 2007; Canoville and Chinsamy, 2015; McHugh, 2015). Unequivocal members of these clades are also restricted to the southern hemisphere. Rhinesuchids are of interest given their appearance in the early Permian of South America (Cisneros et al., 2015) as they never reached the northern hemisphere despite a dispersal of various stereospondylomorphs in the opposite direction during the middle to late Permian (from northern hemisphere to southern hemisphere; Eltink et al., 2019).

In contrast to the southern restriction of these clades with at least a degree of inferred terrestrial capability, other stereospondyls of more unequivocal aquatic lifestyles in Lower Triassic environments (e.g., brachyopoids, capitosaurs, trematosaurs) and the relict tupilakosaurid dvinosaurs were globally distributed by the end of the Early Triassic. These disparities hint at a barrier extending from the Permian to the Early Triassic that partially obstructed the movement of non-obligately aquatic temnospondyls, which may not have been able to utilize the same aquatic corridors as obligately aquatic taxa. This hypothesis can be augmented by the record of olsoniform dissorophoids (terrestrial) and eryopoids (semi-terrestrial). These clades are well-documented in the Permian of North America, Europe, and China but are without occurrences in the southern hemisphere despite a hypothesized faunal connection between North and South American paleoecosystems during the Cisuralian based on similar tetrapod assemblages that include the shared presence of dvinosaurs (Cisneros et al., 2015, 2020; Marsicano et al., 2021). Such a scenario would be compatible with a post-extinction radiation from a high southern paleolatitudinal refugium, with the more terrestrially capable taxa like lapillopsids and lydekkerinids being restricted to largely or entirely southern distributions.

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FIGURE LEGENDS

FIGURE 1. Comparative skull size chart for Early Triassic temnospondyls. Shaded region corresponds to small-bodied forms with a skull length of less than 100 mm. Taxa are sorted by geographic occurrence (hemispheres), then by clade, and finally by species in alphabetical order. Measurements were sourced from the literature (refer to Table S1) and should not be considered comprehensive as a result; they are only intended to give a general characterization of the range of sizes among Early Triassic taxa and the relative paucity of even partial ontogenetic series for most taxa. [Intended for page width]

FIGURE 2. Holotype of *Rhigerpeton isbelli*, gen. et sp. nov. (UWBM VP 95522). Partial skull in **A**, dorsal view, and **B**, right lateral view. Abbreviations: j, jugal; l, lacrimal; m, maxilla; n, nasal; qj, quadratojugal; pf, prefrontal; po, postorbital; pt, pterygoid; sq, squamosal; st, supratemporal; t, tabular. Scale bars equal 5 mm.

FIGURE 3. Holotype of *Rhigerpeton isbelli*, gen. et sp. nov. (UWBM VP 95522). Partial skull shown in ventral view. Abbreviations: ec, ectopterygoid; j, jugal; m, maxilla; pal, palatine; pt, pterygoid, q, quadrate; qj, quadratojugal; v, vomer. Scale bars equal 5 mm.

FIGURE 4. Strict consensus topology recovered from the new baseline analysis with no scoring modifications or taxon additions. **A**, broader relationships of Temnospondyli; **B**, specific relationships of Dvinosauria; **C**, specific relationships of Edopoidea; **D**, specific relationships of Dissorophoidea; **E**, specific relationships of early diverging stereospondyls; **F**, specific relationships of Capitosauria. The following clades only comprise two taxa and are therefore visually condensed: Dendrerpetidae (*Balanerpeton* + *Dendrerpeton*); Zatracheidae

(*Acanthostomatops* + *Zatrachys*); Eryopoidea (*Eryops* + *Onchiodon*); and Plagiosauridae (*Gerrothorax* + *Plagiosuchus*). Taxa marked with single quotation marks were recovered as paraphyletic in this analysis but reflect historical and/or previously recovered clades. Only nominal stereospondyls are color-coded; colors match those for clades in Figure 1. *Lapillopsis* is bolded as the focal taxon of this particular analysis. The five major nodes depicted in filled circles follow the nomenclature and definitions given by Schoch (2013) and Eltink et al. (2019). Bremer decay index values are given above the lines, and bootstrap support values are given below the lines. Gray values are below the thresholds traditionally considered for strong support (Bremer < 3; bootstrap < 50%). [Intended for page width]

FIGURE 5. Strict consensus topology of all MPTs recovered from Analysis 1 (new baseline analysis with scoring modifications to *Lapillopsis nana*). **A**, broader relationships of Temnospondyli; **B**, specific relationships of Dvinosauria; **C**, specific relationships of Edopoidea; **D**, specific relationships of the polyphyetic 'Amphibamiformes' (excludes the branchiosaurid *Apateon* here); **E**, specific relationships of Rhinesuchidae (to the exclusion of *Australerpeton*); **F**, specific relationships of Capitosauria. The following clades only comprise two taxa and are therefore visually condensed: Dendrerpetidae (*Balanerpeton* + *Dendrerpeton*); Zatracheidae (*Acanthostomatops* + *Zatrachys*); Micromelerpetidae (*Limnogyrinus* + *Micromelerpeton*); Eryopoidea (*Eryops* + *Onchiodon*); and Plagiosauridae (*Gerrothorax* + *Plagiosuchus*). Only nominal stereospondyls are color-coded; colors match those for clades in Figure 4. *Lapillopsis* is bolded as the focal taxon of this particular analysis. Bremer decay index values are given above the lines, and bootstrap support values are given below the lines. Gray values are below the

thresholds traditionally considered for strong support (Bremer < 3; bootstrap < 50%). [Intended for 2/3-page width]

FIGURE 6. Strict consensus topologies of different tree islands recovered from Analysis 1 ((new baseline analysis with scoring modifications to *Lapillopsis nana*). **A**, condensed strict consensus from tree islands 1 and 4; **B**, condensed strict consensus from tree islands 2 and 3; **C**, condensed strict consensus from tree island 5. Note that trees are condensed to the focal *L. nana* and only as many other clades as are necessary to demonstrate its position; therefore, some tree islands have the same 'condensed' strict topology but not the same 'full' strict topology. Only nominal stereospondyls are color-coded; colors match those for clades in Figure 5. [Intended for column-width]

FIGURE 7. Strict consensus topology recovered from Analysis 2 (new baseline analysis with scoring modifications to all taxa). **A**, relationships of Temnospondyli without *Rhigerpeton* and *Rotaurisaurus*; **B**, specific relationships of higher stereospondyls with *Rhigerpeton* and *Rotaurisaurus*. Lines and text are grayed out for non-stereospondyls, whose intrarelationships are not shown here as they are not the focus of this study. The following clades only comprise two taxa and are therefore visually condensed: Dendrerpetidae (*Balanerpeton* + *Dendrerpeton*); Zatracheidae (*Acanthostomatops* + *Zatrachys*); Micromelerpetidae (*Limnogyrinus* + *Micromelerpeton*); Eryopoidea (*Eryops* + *Onchiodon*); and Plagiosauridae (*Gerrothorax* + *Plagiosuchus*). The following clades comprise more than two taxa but have the same composition (though not necessarily the same relationships) as depicted in Figure 4: Amphibamiformes' (exclusive of *Apateon* here); and Olsoniformes. Only nominal

stereospondyls are color-coded; colors match those for clades in Figure 4. *Lapillopsis* is bolded in part A as the focal taxon of this particular analysis, and *Rhigerpeton* is bolded in part B. Bremer decay index values are given above the lines, and bootstrap support values are given below the lines. Gray values are below the thresholds traditionally considered for strong support (Bremer < 3; bootstrap < 50%). [Intended for page width]

FIGURE 8. Strict consensus topology recovered from Analysis 3 (modified derivate from Eltink et al., 2019). **A**, relationships of Temnospondyli without *Rhigerpeton*; **B**, specific relationships of higher stereospondyls with *Rhigerpeton* and *Rotaurisaurus*; **C**-**F**, different topologies of Lapillopsidae, with the corresponding number of MPTs in which each topology was recovered shown on the bottom left. Lines and text are grayed out for non-stereospondyls, whose intrarelationships are not shown here as they are not the focus of this study. Only nominal stereospondyls are color-coded; colors match those for clades in Figure 7. *Rhigerpeton* is bolded in part B as the focal taxon of this particular analysis. Bremer decay index values are given above the lines, and bootstrap support values are given below the lines. Gray values are below the thresholds traditionally considered for strong support (Bremer < 3; bootstrap < 50%). [Intended for page width]

FIGURE 9. Comparison of pterygoid morphology in ventral view. **A**, right pterygoid of *Rhigerpeton isbelli,* gen et sp. nov. (UWBM VP 95522); **B**, left pterygoid of QM F35386 (referred specimen of *Lapillopsis nana*); **C**, basicranium with articulated pterygoids of QM F14501 (referred specimen of *L. nana*). Scale bars equal to 5 mm. [Intended for page width]

FIGURE 10. Schematic showing the taxonomic composition (left) and geographic position (right) of six major Early Triassic temnospondyl assemblages from southern Pangea. Stars on the map denote the Sanga do Cabral Formation (Brazil), *Lystrosaurus declivis* Assemblage Zone (South Africa), Sakamena Formation (Madagascar), Panchet Formation (India), Arcadia Formation (Australia), and lower Fremouw Formation (Antarctica). Columns are ordered from longitudinal position (west-east), with the Fremouw column on the far right. Black boxes represent presence, white boxes represent absence, and gray boxes represent disputed or equivocal presence. For Lapillopsidae and Lydekkerinidae, the most expansive concepts of the clades are utilized. The phylogenetic topology shown is intended only as a conceptual guide (derived primarily from Schoch, 2013; Eltink et al., 2019) and not as a novel hypothesis of relationships; the position of Lapillopsidae in particular remains poorly resolved. Map reconstruction based on data from Lawver et al. (2009) and modified from Sidor et al. (2013). This schematic represents an updated version from that published by Gee and Sidor (2021). [Intended for page width]