

1 First record of the amphibamiform *Micropholis stowi* from the lower Fremouw Formation
2 (Lower Triassic) of Antarctica

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11 RH: GEE AND SIDOR—*MICROPHOLIS* FROM ANTARCTICA

ABSTRACT—The fossil record of temnospondyl amphibians in the immediate wake of the Permo-Triassic mass extinction captures extensive taxic and ecological diversity, with most records known from high paleolatitudinal settings. In southern Pangea, the most substantial records come from South Africa and Australia, with a total of over 20 taxa presently recognized. Temnospondyls have also been known from correlated horizons in the lower Fremouw Formation of Antarctica since the late 1960s, but these records are mostly fragmentary, thereby limiting taxonomic resolution to the family level and subsequent biostratigraphic correlations and comparisons between high-latitude basins. Here we report substantial new material of the amphibamiform *Micropholis stowi*, a relic dissorophoid previously known only from the Katberg Formation (*Lystrosaurus declivis* Assemblage Zone) of South Africa, from the lower Fremouw Formation. The exceptional preservation of the recently recovered material permits not only confident taxonomic referral but also tentative association of several individuals to the broad-headed morph of the taxon. The recognition of *M. stowi* in Antarctica represents only the fourth geographic occurrence of a dissorophoid from southern Pangea and supports the hypothesis that high-latitude environments served as refugia for temnospondyls during the mass extinction. In the case of *M. stowi*, such refugia permitted the persistence of a predominantly Permo-Carboniferous clade, and the Antarctic records discussed here further hint at a poorly sampled cryptic distribution, both of amphibamiforms in southern Pangea and of small-bodied temnospondyls in early Mesozoic deposits.

INTRODUCTION

Temnospondyls are a diverse clade of non-amniote tetrapods ('amphibians') that are often hypothesized to be linked to the origin of lissamphibians (e.g., Schoch and Milner, 2004; Ruta and Coates, 2007; Anderson, 2008; Anderson et al., 2008; Pardo et al., 2017; Schoch, 2018). The clade has a lengthy geologic history stretching from the late Carboniferous to the Early Cretaceous and thus survived two of the five mass extinctions (Schoch, 2013). As with other tetrapod clades, temnospondyls suffered major losses in the Permo-Triassic mass extinction, including the loss of nearly all non-stereospondylomorph clades. Intriguingly however, deposits from the immediate recovery interval, primarily at high paleolatitudes, record high taxic and ecological diversity (e.g., Cosgriff, 1984; Sennikov, 1996; Shiskin et al., 2000; Warren et al., 2001; Damiani, 2004; Tarailo, 2018). The Early Triassic temnospondyl radiation includes the earliest known representatives of many of the major stereospondyl clades (e.g., brachyopoids [inclusive of plagiosaurids], capitosauroids, trematosauroids), establishing the foundation for a renewed habitation of non-marine environments for the group during the Mesozoic. One important attribute of the post-extinction radiation is the documentation of numerous small-bodied taxa (e.g., skull length ~ 2 to 4 cm) distributed among several distantly related clades; small-bodied forms are otherwise exceedingly rare in Mesozoic deposits, especially after the Early Triassic.

Small-bodied temnospondyls also played a pivotal role in the history of vertebrate paleontology in Antarctica, as they were among the first tetrapod fossils to be recovered from the continent, specifically from Lower Triassic exposures of the Fremouw Formation (Barrett et al., 1968; Kitching et al., 1972; Colbert and Cosgriff, 1974; Cosgriff and Hammer, 1984).

Subsequent Antarctic fieldwork led to the recovery of large-bodied temnospondyl material from the overlying upper Fremouw Formation (Hammer, 1988, 1990; Sidor et al., 2007, 2008, 2014), which is likely either Middle or Late Triassic in age (Peacock et al., 2019). However, in contrast to the temnospondyl taxa from the upper Fremouw, the taxa from the lower Fremouw are represented by fragmentary or poorly preserved material. Both the putative brachyopoid *Austrobrachyops jenkensi* and the putative lydekkerinid *Cryobatrachus kitchingi* have been designated as *nomina dubia* by recent workers (Schoch and Milner, 2000, 2014; Warren and Marsicano, 2000). Consequently, the lower Fremouw temnospondyl assemblage, which represents an important non-amniote perspective on the recovery from the Permo-Triassic extinction, remains poorly understood. Characterization of the Antarctic assemblage is crucial for improved understanding of this recovery and for examining regional-scale patterns by comparison with the better-known coeval assemblages of South Africa (e.g., Damiani, 2004) and Australia (e.g., Warren et al., 2001).

From very early on, the tetrapod assemblage of the lower Fremouw Formation has been studied in comparison to the Lower Triassic *Lystrosaurus* biozone of South Africa's Karoo Basin (Kitching et al., 1972). Among the small-bodied clades documented in the *Lystrosaurus* biozone is Amphibamiformes, a diverse clade of diminutive dissorophoid temnospondyls and one of the few Paleozoic temnospondyl clades to survive the mass extinction. Amphibamiforms (encompassing Branchiosauridae and what was historically termed 'Amphibamidae'; Schoch, 2018) have long been of interest for both their body size (e.g., Fröbisch and Schoch, 2009a; Pérez-Ben et al., 2018) and for their proposed relationship to crown Lissamphibia in the ongoing debate on lissamphibian origins from the paleontological perspective (e.g., Anderson et al., 2008; Pardo et al., 2017; Marjanović and Laurin, 2019; Schoch, 2018; Schoch et al., 2020).

Dissorophoids were exceptionally diverse, with over 75 recognized species, but nearly all of them occur in either the late Carboniferous or the early Permian. A handful of dissorophid taxa are documented in Guadalupian deposits of eastern Eurasia (Gubin, 1980; Li and Cheng, 1999; Liu, 2018). The branchiosaurid *Tungussogyrinus bergi* from Siberia is of uncertain late Permian or Early Triassic age (Shishkin, 1998; Werneburg, 2009; Schoch and Milner, 2014). Thus, the only definitive Mesozoic dissorophoid is the micropholid amphibamiform *Micropholis stowi*. This taxon has long been known from several localities in the *Lystrosaurus declivis* Assemblage Zone (LAZ; revised terminology follows Botha and Smith, 2020) in the Karoo Basin and has been well studied by previous workers (Huxley, 1859; Watson, 1913; Broili and Schröder, 1937; Boy, 1985; Schoch and Rubidge, 2005).

In addition to its unique temporal occurrence, *Micropholis stowi* is also notable for its geographic occurrence. The only other dissorophoid records from southern Pangea are an indeterminate middle Permian branchiosaurid from Turkey, the paleolatitude of which remains tenuous (Fortuny et al., 2015), and the micromelerpetid *Branchierpeton saberi* from the late Carboniferous of Morocco (Werneburg et al., 2019). *Micropholis stowi* is known from several widely separated localities within the Karoo Basin (Schoch and Rubidge, 2005). This taxon's temporal and geographic isolation, together with phylogenetic analyses that recover *M. stowi* as an early diverging amphibamiform, have led previous workers to interpret *M. stowi* as a relic taxon. The marked spatiotemporal separation from other dissorophoid occurrences suggests a largely unrecorded history of global dispersal and southern Pangean biodiversity that remains to be discovered through collection efforts outside of classic localities and regions in western Europe and North America (Werneburg et al., 2019). The persistence of amphibamiforms into the Triassic of South Africa and perhaps Siberia also suggests that the high paleolatitudes may

have provided some modicum of a refugium for temnospondyls across the Permo-Triassic extinction, as originally proposed by Yates and Warren (2000). Romano et al. (2020) similarly proposed that the water-dependent temnospondyls would have been largely relegated to more temperate climates at high paleolatitudes in the post-extinction interval.

In the austral summer of 2017–18, fieldwork conducted in the Shackleton Glacier region of Antarctica led to recovery of substantial amounts of well-preserved temnospondyl material. Here we report the first occurrence of *Micropholis stowi* from Antarctica based on a block preserving four individuals from the lower Fremouw Formation at Halfmoon Bluff. This documentation expands the geographic range of the taxon and fleshes-out the polar tetrapod community, particularly by making the first species-level connection to the South African Karoo Basin.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **BP**, Evolutionary Studies Institute, University of the Witswatersrand, Johannesburg (formerly Bernard Price Institute); **UWBM**, University of Washington Burke Museum, Seattle.

MATERIALS and METHODS

The slab that preserves UWBM VP 118681 was surface collected in four pieces. The broken pieces were cleaned of loose matrix and then Paleobond Penetrant Stabilizer was used for reassembly. Preparation, which substantially reduced the size of the initial block, was performed by R. Masek under high magnification using a PaleoTools ME9100 aircscribe for rough matrix removal, followed by a PaleoTools MicroJack 3 with a sharp pointed stylus, running at low air

122 pressure. The prepared specimens were photographed with a Nikon D7100 camera and 105mm
123 macro lens and a Canon EOS 5DS camera with a 100mm macro lens.

124

125 SYSTEMATIC PALEONTOLOGY

126

127 DISSOROPHOIDEA Bolt, 1969

128 AMPHIBAMIFORMES Schoch, 2018

129 MICROPHOLIDAE Watson, 1919 sensu Schoch, 2018

130 *MICROPHOLIS* Huxley, 1859

131 *MICROPHOLIS STOWI* Huxley, 1859

132 (Figs. 1–6)

133 *Micropholis stowii* Huxley, 1859:649.

134 *Micropholis stowi* Owen, 1876:67.

135 *Petrophryne granulata* Owen, 1876:68.

136 *Micropholis stowi* Zittel, 1890:397, fig. 387.

137 *Micropholis stowei* Lydekker, 1890:174.

138 *Micropholis stowi* Watson, 1913:340, figs. 1–4.

139 *Micropholis stowi* Abel, 1919:281.

140 *Micropholis stowi* Broili and Schröder, 1937:37, figs 1–7, pls. 1–3.

141 *Micropholis stowi* Romer, 1947:147, figs. 12, 13, 27.

142 *Micropholis stowi* Bolt, 1974:438.

143 *Micropholis stowi* Boy, 1985:30, figs. 1–5.

144 *Micropholis stowi* Schoch and Rubidge, 2005:503, figs. 1–7.

145 *Micropholis stowi* Schoch and Milner, 2014:60, figs. 29D, 31B.

146 **Revised Diagnosis**—Amphibamiform characterized by the following autapomorphies:
147 dermal ornamentation consisting of minute pustules; prominently elevated ridge on ventral
148 surface of the cultriform process bearing teeth throughout its length (contrasted with the non-
149 elevated dentulous process of *Amphibamus* and the edentulous processes of other
150 amphibamiforms); proportionately elongate transverse processes of the vertebrae; and median
151 intervomerine fontanelle at the anterior margin of the intervomerine fossa.

152 **Remarks**—The diagnosis is modified from that of Schoch and Rubidge (2005), which
153 lists five autapomorphies, and Schoch and Milner (2014), which lists 10 features in the
154 diagnosis. The latter includes several features that partially contribute to a unique combination of
155 characters but that are not autapomorphic among amphibamiforms, such as a narrow palatine and
156 ectopterygoid (an amphibamiform synapomorphy; Schoch, 2018) or accessory vomerine ‘fangs’
157 (a micropholid synapomorphy; Schoch, 2018). Similarly, the two listed plesiomorphies, a long
158 skull table and a postparietal much longer than the tabular, are only useful as part of a unique
159 combination of characters. A short basiptyergoid ramus of the pterygoid is common to small-
160 bodied dissorophoids. Prominent posterolateral projections of the basal plate of the parasphenoid
161 are only developed in the long-headed morph of *Micropholis stowi* and are also found in
162 *Amphibamus grandiceps* (Schoch and Milner, 2014). Two other features, hyobranchial skeleton
163 well-ossified and tail short are excluded here because these regions of the skeleton are too
164 infrequently preserved in other non-branchiosaurid amphibamiforms to be certain of their
165 diagnostic value. Note that the cultriform process of *Pasawioops mayi* is covered in denticles
166 (Fröbisch and Reisz, 2008), but the denticles are born by three distinct plates that are separated
167 from the process itself. It is unclear whether the plates might have fused with the process to form

the condition of *M. stowi*, as those authors suggested, or whether they remained separate and were simply part of the larger covering of the interpterygoid vacuities by small, irregular denticulate plates.

Referred Material—UWBM VP 118681, a block containing portions of four individuals.

Locality and Horizon—Collected from the middle portion of the lower Fremouw Formation at Halfmoon Bluff, UWBM locality C2931 at 85° 13.279' S, 175° 25.898' W, Antarctica. Note that evidence of excavation was found at this site in 2017, but it is unclear how C2931 relates to previous reports of fossils collected at Halfmoon Bluff in the literature (e.g., Colbert, 1987).

Comment—UWBM VP 118681 is a block preserving portions of the skeleton of four individuals, all of which are represented by partial to complete skulls with associated mandibles. One is preserved in ventral view, and three are preserved in dorsal view. For ease of reference in this paper, letter sub-designations have been created and are indicated in Figure 1; note that these are not indicated on the physical specimen. “Specimen” refers to the entire block and “individual” to any of the singular four skeletons preserved on the block. As seen in Figure 1, the skull on the right side of the block that has lost most of the roofing elements is termed 118681A. The skull exposed in ventral view with the mandibles in articulation is termed 118681D. A complete skull, exposed dorsally and with part of the vertebral column and the limbs in articulation, is termed 118681B. The slightly larger dorsally exposed skull is termed 118681C.

DESCRIPTION

The osteology of *Micropholis stowi* has been well-characterized by previous workers (e.g., Boy, 1985; Schoch and Rubidge, 2005). Our description focuses on characterizing the specimen in relation to the Karoo Basin material and on providing details that would allow a composite OTU to be formed for the Fremouw Formation material in future phylogenetic analyses. Although we are confident in our referral of all four individual to *Micropholis stowi*, each individual preserves a varying suite of apomorphic features and skeletal overlap with other individuals. We recognize that taxonomic identifications are hypotheses that can and should be re-tested by future workers, and because other small-bodied temnospondyls (e.g., lapillopsids, lydekkerinids) are common in Lower Triassic deposits, future work on these clades could reduce the validity or distinctiveness of the presently utilized apomorphies. As such, each individual is described separately (though without redundancies in subsequent sections) such that the description can be parsed out by future workers in case the identity of at least one individual is questioned. The individuals are described in order of completeness and quality of preservation.

UWBM VP 118681C

This individual consists of a nearly complete skull lacking only the right suborbital region and the tip of the snout and with most of the sutures clearly defined; it forms the basis for most of the cranial osteology that we describe (Fig. 2). The skull measures 32.5 mm in midline length as preserved and was likely no more than 34 mm when complete. A portion of the left dentary is articulated ventral to the orbit but is mostly unexposed. The skull is only deformed in the post-orbital region where it is slightly depressed. The skull is modestly broad, expanding gradually posterior to the temporal region and being widest just anterior to the level of the otic notch. In dorsal view (Fig. 2A–C), the margins of the skull form a continuous curve except along

the occipital margin, where there is a biconcave outline formed by a slight posterior bulge at the midline from the postparietals. Although the postparietals are slightly distorted, the distortion appears to have minimized this expansion rather than to have exaggerated it. Most specimens from the Karoo Basin have continuously curved occipital margins, but Schoch and Rubidge (2005:fig. 5B) illustrate at least one relatively larger specimen with a biconcave margin. The orbits are large ovals with the long axis aligned sharply anteromedially. The dominant ornamentation pattern consists of small pustules, an apomorphic condition among dissorophoids, with shallow ridges and small pits on the lateral elements (maxilla, jugal) and at the tip of the snout (anteriormost nasal, premaxilla). In some areas, the pustules are aligned in radiating rows extending from an element's center (e.g., nasal, frontal, supratemporal), mirroring the radiating pit-and-groove system found in many temnospondyls. Lateral line grooves are definitively absent, suggesting a terrestrial lifestyle (e.g., Moodie, 1915).

The premaxilla is a triangular element in dorsal view, with a posterolateral process below the naris, meeting the maxilla, and a dorsal alary process projecting into the nasal and nearly to the level of the posterior narial margin (Fig. 2A–C). Tooth count is difficult to estimate because the premaxillary teeth have mostly been lost, and the sockets are not identifiable in the exposed profile. At least seven positions are conservatively identified; Schoch and Rubidge (2005) suggested *Micropholis* had 8–10 positions. The septomaxilla is a smooth, flat bone flooring the naris that curves dorsolaterally to abut the inner surface of the premaxilla and the maxilla (Fig. 2).

The maxilla is a long and slender element that extends posterior to the orbit and that is tallest just anterior to the orbit. We note that it is only very narrowly excluded from the orbit (Fig. 2D–E), more similar in this regard to Boy's (1985) reconstruction than to that of Schoch

and Rubidge (2005). It is unclear at what position the tooth row ends. At least 19 positions are identified over a length about 60% of the entire maxilla. This observation suggests a tooth count closer to the broad-headed morph (31 positions) than to the slender-headed morph (42 positions) per Schoch and Rubidge (2005). The teeth are conical and recurved, without external expression of plicidentine. We could not confidently identify any teeth with crowns distinctly offset from the base as reported by Schoch and Rubidge (2005), but many of the teeth are damaged or not fully exposed.

The nasal is a broad rectangular element that frames the naris posteromedially (Fig. 2A–C). One deviation of note when compared to specimens described from South Africa is the partial separation along the midline at the anterior region by the premaxillae (specifically the right premaxilla) in UWBM VP 118681C (Fig. 2A–B); the premaxilla-nasal suture is transversely straight in South African specimens (Schoch and Rubidge, 2005).

The lacrimal is slender and rectangular, bridging the naris and the orbit dorsal to the maxilla (Fig. 2). There is no clear foramen for the nasolacrimal duct, but a groove is present on the inner surface of the left lacrimal.

The lacrimal is separated from the jugal along the ventral orbital margin by a lateral exposure of the palatine (LEP), which is triangular and tapers posteriorly (Fig. 2). The exposure is shallowly depressed such that it medially frames a more starkly defined ridge along the orbital margin than in other circumorbital regions.

The prefrontal is a crescentic element at the anteromedial margin of the orbit (Fig. 2A–C). It can be seen on the smooth inner rim of the orbital margin in the form of a ventrally descending process (the ventral palatine / palatal / prefrontal process; VPP) that is typical of xerodromes (non-micromelerpetid dissorophoids; Schoch and Milner, 2014).

The rectangular frontal enters the orbit and has anterior and posterior margins that are more or less in line with those of the orbit (Fig. 2A–C). The midline suture has a prominent interdigitation from the left frontal into the right frontal. The parietal is a broad rectangular element with a large pineal foramen located in the anterior third of the midline suture (Fig. 2A–C). The foramen is always in the anterior third of the parietals but often becomes increasingly anteriorly situated throughout ontogeny (Schoch and Rubidge, 2005:fig. 3). Its relative position here suggests that this individual was not mature. Like other amphibamiforms, the parietals are constricted anteriorly by the posteromedial expansion of the postfrontal. In UWBM VP 116861C, the parietals are widest just posterior to this constriction, forming a more pentagonal outline. The lateral expansion in this region prominently subdivides the postfrontal from the supratemporal. This subdivision is found in both morphs of *Micropholis stowi* according to Schoch and Rubidge (2005), but the expansion is only a narrow process in the slender-headed morph; the condition of UWBM VP 116861C is more like that observed in the broad-headed morph regardless of ontogenetic stage.

The postparietals are rectangular and wider than they are long (Fig. 2A–C). There is no transverse ridge (nuchal ridge) along the occipital margin. The occipital flange is either not preserved or is too vertically oriented to be exposed due to the adjacent skull of UWBM VP 116861B.

The tabular is a small sub-triangular element with a discrete horn that projects posterolaterally to a distinct rounded terminus that is very slightly downturned (Fig. 2). The development of the tabular horn with respect to length and nature of the terminus (blunt or sharply tapered is variable throughout ontogeny and both within and between morphs (Schoch and Rubidge, 2005:fig. 3).

The postfrontal is a highly variable element with respect to shape (Schoch and Rubidge, 2005:fig. 3); here it is a crescentic element that frames the posteromedial margin of the orbit (Fig. 2A–C). It ends bluntly on both ends and has a curved medial contact with the parietal.

The postorbital is a rectangular element forming most of the posterior orbital margin (Fig. 2A–C). It has a slender medial process that partially separates the postfrontal from the orbit and is squared-off posteriorly, rather than terminating in a tapering tip.

The jugal is a long and slender element that forms the posterolateral margin of the orbit (Fig. 2). It meets the LEP to exclude the maxilla from the orbit and extends posteriorly toward the otic notch where it sutures with the quadratojugal posteroventrally.

The quadratojugal is normally a large element in amphibamiforms and is present in some form on the left side but is largely obscured by matrix due to the narrow separation from UWBM VP 116861B, and the right quadratojugal appears to be lost (Fig. 2). The left quadratojugal is probably incomplete posteriorly as there is no evidence of the quadrate.

The squamosal is a large element dorsal to the jugal and the quadratojugal (Fig. 2). The ornamented portion has an anteriorly directed process that partially divides the postorbital and the jugal. A broad unornamented sheet of bone forming the otic notch extends posteroventrally at about a 45-degree angle towards the inferred position of the quadrate.

The squamosal sutures with the supratemporal, a rectangular element exposed on the dorsal surface (Fig. 2A–C). Their suture is about 75% of the length of the supratemporal. The right supratemporal is excluded from the otic notch by the squamosal and the tabular; the same condition can be inferred for the left side based on the lateral margin being almost entirely traceable and without any lateral projection to enter the notch. It is not possible to assess the presence of a ventral projection of the supratemporal into the otic notch (semilunar flange), but

one would not be predicted given our interpreted squamosal-tabular contact. We also cannot assess whether there was a semilunar curvature of the supratympanic flange (Fig. 2D–E).

A cluster of slightly ornamented plates is found along the dorsal margin of the left orbit (Fig. 2). These are identified as palpebral ossifications like those known from other amphibamiforms (e.g., Bourget and Anderson, 2011; Maddin et al., 2013) and previously reported in *Micropholis stowi* (Schoch and Rubidge, 2005), being distinguished from sclerotic plates by their shape, orientation, and ornamentation.

Limited exposures of the palatine, the ectopterygoid, and the pterygoid are visible through the left orbit. They contribute little information beyond the observation that the palatine and the ectopterygoid are relatively narrow and that the palatine-pterygoid contact is formed by a head-on contact rather than by partial medial overlap of the palatine by the pterygoid's anterior termination (Fig. 2A–C). The palatine-pterygoid contact is like that found in the broad-headed morph (Schoch and Rubidge, 2005). A portion of the dentary is articulated with the maxilla below the orbit, but it preserves no informative features, and teeth are not exposed. No aspects of the braincase are identified.

UWBM VP 118681A

This individual is preserved in dorsal view, although the skull was compressed and partially disarticulated (Fig. 3). Most of the cranial elements have been lost, possibly because this individual was partially exposed at the time of discovery, in contrast to the remaining three, which were uncovered in the course of preparation. The skull is distinctly larger than the other three skulls, measuring around 39 mm in preserved midline length (based on dimensions of the left lower jaw), and would have exceeded 40 mm when complete (the largest specimen reported

by Schoch and Rubidge, 2005 is 43.5 mm). Ornamentation is like that of UWBM VP 118681C, consisting mostly of pustules and without evidence of lateral line grooves.

Preserved portions of the skull roof include part of the snout, including the elements framing the right naris and the left maxilla, the left frontal and the left postfrontal (tentatively identified by the partial orbital margins) and a large fragment with faint ornamentation and no discernible landmarks that probably represents most of the left cheek (i.e., postorbital, jugal, squamosal, quadratojugal). Sutures are not identifiable on most parts of the skull. The left maxilla preserves 30 tooth positions with the most posteriorly preserved tooth being markedly smaller than the others, indicating the termination of the tooth row well before the termination of the maxilla. Thus, the estimated tooth count is close to that of the broad-headed morph and of that inferred for UWBM VP 118681C. This individual has the most clearly exposed marginal dentition, and the teeth do not differ from that of UWBM VP 118681C. For example, there is no constriction at the crown in the teeth of either individual. If it is assumed that the element was simply flattened in place, the relative position to the naris indicates that the left maxilla is essentially complete.

Some aspects of the right palatal elements are exposed in dorsal view. A large plate-like fragment with two large partial teeth has been flipped upside-down and displaced next to the left frontal. Based on the large gap between these teeth, one of which is distinctly larger than the other and both of which are larger than the marginal dentition, and on the size of the fragment, this is probably a fragmentary vomer. Under this interpretation, the larger tooth is one of the large vomerine ‘fangs’ found anterior to the choana, and the smaller tooth is a slightly enlarged palatal tooth bordering the intervomerine fossa (not preserved). The anteriormost extent of the cultriform process is exposed and reveals a trough for the sphenethmoid along its dorsal surface.

Portions of the right pterygoid are exposed in dorsal view adjacent to the partial right dentary and at the posterior skull where the quadrate ramus overlaps a large mass of damaged bone that is inferred to be the base of the quadrate. The base of the ascending lamina is preserved next to the basiptyergoid ramus. The thin bones medial to the dentary are too wide to be coronoids, but no sutures of palatal elements are clearly identified; probably these represent the ectopterygoid and pterygoid and perhaps part of the palatine as well. A curved element lying medial to the quadrate ramus of the pterygoid is interpreted to be the right stapes. The proximal end is partially subdivided, as reported by Schoch and Rubidge (2005) and probably bore a stapelial foramen although its posterior surface is damaged. There is a slight dorsal curvature towards the tapering distal end. A similarly shaped bone lacking other distinctive features that lies near the left jaw articulation may be the left stapes.

The left lower jaw is nearly complete though exposed mostly dorsally and slightly labially and without clear sutures in most areas. The right lower jaw consists only of an anterior portion of the dentary exposed in dorsal profile. The left lower jaw preserves 27 tooth positions, with the posterior termination of the tooth row just anterior to the flattened coronoid process. Based on the preserved curvature of the dentary, probably no more than a dozen additional tooth positions would have been present. The tooth morphology is like that of the maxillary dentition, although several positions have the crowns broken by a horizontal crack, all at about the same height. The absence of this feature in all of the teeth suggests that this is not evidence for pedicely. Ornamentation on the labial surface of the lower jaw consists of faint ridges; in well-preserved South African material, the ridges are formed by rows of pustules (Schoch and Rubidge, 2005), but discrete pustules are not discerned here. The angular is identified largely by the presence of more pronounced pustules. The coronoid process has been flattened over the

adductor chamber, but its relative length (shared with other dissorophoids) and modest height are apparent. The relative contribution of different elements to the coronoid process is unclear. The surangular is present by virtue of the completeness of the lower jaw labially, but its margins cannot be demarcated. The articular has a transversely broad articulation surface with a developed retroarticular process that is slightly upturned at the posterior end.

Posterior to the large cranial fragments and on the same bedding plane are dorsally projecting remnants of what may represent at least two neural arches; they are identified largely on the basis of relative position and cannot be identified to a specific position (Fig. 3). Additional fragments in this region may be vertebral in nature. Slightly more posterior and to the right is an articulated forelimb consisting of the humerus, the radius, and the ulna (Fig. 1, 4C). This material is tentatively associated with this individual with the caveat that the association is made more on the basis of relative position than on distinctive features of the elements. The ends of the humerus are damaged, precluding any substantial characterization beyond noting expansion at both ends. Of the two zeugopodial elements, the longer is interpreted as being the ulna, with markedly expanded ends set at an angle to each other and a straight shaft. An olecranon process is not distinct, as with the South African material (Schoch and Rubidge, 2005), although the proximal end is relatively squared off in comparison to the rounded distal end. The radius has a flatter shaft, less expansion of the ends, and a distinct curvature. The ends of both the radius and the ulna appear to have been poorly ossified at the time of death. Despite the degree of articulation otherwise present in the forelimb, the manus is absent.

There are also four elements positioned beside the individual that merit brief mention, although an association with this individual, and in turn with *Micropholis stowi*, is less certain (Fig. 1). There is at least one dorsally unfused set of neural arches that bears prominent

398 transverse processes and that resembles the arches of UWBM VP 118681B. There is also a
399 partial femur, preserved distally that is similarly adjacent to the left jaw. Its anatomy generally
400 conforms to that described by Schoch and Rubidge (2005), with remnants of a prominent
401 adductor crest extending straight down the shaft and a squared-off, expanded distal end.
402 However, it is already longer than the complete humerus of this individual (Schoch and Rubidge
403 state that both are about the same length in articulated specimens) and clearly incomplete,
404 without the predicted defining features of the proximal end preserved. An adjacent element
405 appears to have the general morphology of a tetrapod tibia (expanded proximal end, narrow
406 distal end, slight curvature of the shaft), but it is much smaller than the partial femur. A flat
407 element lying on top of the partial femur has a broad rectangular process that is somewhat
408 reminiscent of the ischium of *M. stowi* (as figured by Schoch and Rubidge, 2005:fig. 6G), but
409 skeletal interpretation is predicated on the assumption that the femur belongs to this taxon.

410

411 **UWBM VP 118681D**

412 This individual is preserved in ventral view with the posterior region of the palate and the
413 mandibles preserved (Fig. 5). Conceivably, most of the skull could be present, but only the
414 posteroventral portions (maxilla, quadratojugal) can be exposed on either side. The left lower
415 jaw measures 30 mm along the long axis, and the specimen was therefore likely close to the size
416 of UWBM VP 118681C when complete. The exposed cranial elements confer little new
417 information beyond indicating that the quadratojugal is ornamented like the other cranial
418 elements, has a convex ventral margin, and dips below the level of the other marginal elements
419 to partially overlap the posterior portion of the lower jaw, as in the South African material

(Schoch and Rubidge, 2005). An ornamented fragment positioned dorsal to the posterior end of the left quadratojugal appears too large to be any part of the quadrate.

This individual preserves the most information regarding the palatal anatomy of *Micropholis stowi* from Antarctica. The parasphenoid consists of the broad basal plate and the anteriorly projecting cultriform process. The margins of the basal plate are not well-preserved, but the plate is wider than it was long, largely flat, and lacking denticles. On the right side, there appear to be two discrete posterolateral processes, as seen in the slender-headed morph, but taphonomic damage cannot be excluded. As in the South African material (Schoch and Rubidge, 2005), no foramina or grooves for the carotid arteries are identified, but insufficient preservation should also be considered as an explanator. The cultriform process is slender and forms a tooth-bearing ridge, a feature listed by Schoch and Rubidge (2005) as apomorphic and that we included in our revised diagnosis. Bony fragments extending dorsally from the right side of the cultriform process might represent the sphenethmoid. No braincase elements are otherwise identified. The basiptyergoid joint is formed by a socket joint, which is infilled with matrix on the left side and which appears to not have been tightly sutured. Participation by an element on the dorsal surface of the joint (most likely the epiptyergoid) is not apparent.

The pterygoid is the typical triradiate morphology of dissorophoids. The tooth-bearing surfaces are ventrally offset from the basiptyergoid ramus. Denticles are represented only by their broken exposed bases. The palatine ramus is covered in denticles over most of its surface, except in a marked depression that is framed by a dentulous ridge along the interptyergoid vacuity margin. The ramus expands posterolaterally into a transverse flange that descends nearly to the ventral margin of the lower jaw. The quadrate ramus forms a narrow blade-like posterolateral projection. Overlap of the quadrate is absent on the right side (no quadrate) and is

unclear on the left side. The anterior terminus of the pterygoid is not exposed, and the ectopterygoids and the palatines are of uncertain presence since they would be predicted to be narrow and thus obscured by the mandibles. The vomers are more definitively lost.

The mandibles are complete posteriorly, but as with UWBM VP 118681A, the identification of different elements is based on a combination of ornamentation patterns and general position along the lower jaw's length. The angular is again identified by its more pronounced ornamentation, with a clear radiating pattern extending from the mid-length of the ventral margin. The retroarticular process, formed partially by the surangular and the articular in the South African material (Schoch and Rubidge, 2005), is present on the right lower jaw, but sutures are not distinct. The lingual surface is mostly obscured by matrix —no Mecklelian foramen is exposed— and the posterolabial surface is covered by the quadratojugals. The angular's contact with the postsplenial is tentatively identified on the left lower jaw. No teeth or their presumed tooth-bearing elements are discretely identified. The anterior end of the right lower jaw ends with what appears to be a clean, post-fossilization break.

Paired clavicles are positioned directly posterior to the parasphenoid. The ventral blade is exposed, revealing faint transverse striations. Although damaged, there appears to be a dorsoventral offset of the posterior half on the right clavicle. The dorsal stems are not exposed.

UWBM VP 118681B

This individual is a partial skeleton with a skull of slightly smaller size than the adjacent UWBM VP 118681C (measuring 28 mm) but is of poorer preservation, lacking much of the left antorbital region and with most of the sutures being indiscernible except on the posterior skull table where they can be identified on at least one side (Fig. 6). The otic notches have been

466 variably damaged. The morphology and proportions of the defined elements do not differ from
467 that of UWBM VP 118681C. A large LEP like that of UWBM VP 118681C on the left side of
468 the skull evidences its dissorophoid identity (Fig. 6). As in UWBM VP 118681C, the occipital
469 margin is biconcave (Figs. 2, 6). Ornamentation consists of small pustules like in other
470 individuals. Teeth are not preserved or are not exposed save for the broken cross-sections of two
471 teeth in the left orbit that probably belong to the lower jaw based on their vertical orientation.
472 Elements of the lower jaw are not identifiable, but a few fragments below the level of the skull
473 also hint at the partial preservation of the mandibles. The palatal exposures are only through the
474 orbit and are too damaged to be informative. Nondescript flat fragments in the snout region at
475 about the level of the palate (beyond those labeled in the figure) might be the vomers.

476 The most informative aspect of this individual is its articulated postcrania, comprising
477 part of the vertebral column and limbs (Fig. 6). Eight neural arches are preserved in a string from
478 the occiput extending posteriorly (Fig. 4A). Two isolated arches, exposed in either anterior or
479 posterior view, are adjacent to the left humerus. The arches were either all damaged dorsally
480 such that the spines were all sheared off or were not completely ossified at the time of death. We
481 consider the latter to be more likely, as one of the isolated neural arches also lacks the spine and
482 given the relatively small size of the skull. Broken cross-sections or weakly ossified surfaces are
483 not identified. Similarly, morphological differentiation of the positions is minimal beyond a
484 slightly greater width anteriorly. We infer that the first two identified positions are the atlas and
485 axis based on their position relative to the skull, but distinguishing features of those positions are
486 not identified, nor is any portion of the occiput exposed in articulation with the first vertebral
487 position. As noted by Schoch and Rubidge (2005), the transverse processes are relatively long in
488 the presacral region and more specifically in the region preserved in this individual.

We can identify only a single rib as a long and relatively undifferentiated rod-like structure posterior to the articulated string of neural arches. An additional three ribs may be present more peripherally near the putative right hindlimb, but their association is more tentative (Fig. 1). In the same region is a small flat bone with a similar morphology to the putative ischium found near UWBM VP 118681A (Fig. 1).

No elements of the pectoral or the pelvic girdle are confidently identified. A flat oval exposure posterior to the right humerus could be the ventral portion of the clavicle, but distinguishing features are lacking. Other crushed or obscured fragments lie between the humeri and the vertebral column and could represent other pectoral elements.

Both humeri are preserved and are largely complete, although the distal end of the right humerus is damaged, and that of the left is partially obscured by one of the isolated neural arches (Fig. 4A). The proximal end is greatly expanded and is joined by a short and slender shaft to the slightly less expanded distal end, with the ends offset by a sharp angle. In the absence of a full exposure, the 90-degree angle approximated by Schoch and Rubidge (2005) seems reasonable in this individual. Both humeri are interpreted to be exposed primarily in anterior view based on the shallow depression on the proximal end and the absence of any other landmark features. Supinator processes and entepicondylar foramina are absent as far as can be determined. The boss at the end of the deltopectoral crest noted in some South African specimens by Schoch and Rubidge (2005) is not present here.

Hindlimb material is questionably identified. Posterior to the remainder of the skeleton are variably preserved paired elements on each side (Fig. 4B). These elements are in the predicted position for articulation and of the right size to belong to this individual. The perception of their representation as hindlimbs is in part exaggerated by the preparation, which

pedestaled these elements around their contour. However, these elements lie in a distinctly higher plane than the rest of the skeleton, which partially accounts for their pedestaled position. Furthermore, the more proximal of the two elements on the right side is smaller than the more distal one with which it articulates. This observation disagrees with the previously reported anatomy (and dissorophoid hindlimb morphology in general) in which the femur is distinctly longer (not present here) and in which the tibia tapers sharply distally (also not present here). In fact, it appears as though the inverse could be true – that the more distal element could be a femur (the preserved end appears to have two distinct facets) and that the more proximal element could be a tibia (disparity in the width of each end is pronounced). The elements of the left side are too fragmentary for comparison or identification. A putative fibula is not identifiable on either side. It would be unexpected for the hindlimb to have been detached and flipped 180-degrees into a position that still resembled an articulated hindlimb. The total absence of more near-sacral vertebral positions and the entire sacrum also casts some doubts on the association of these elements as the hindlimb of this individual. The right pair of elements are questionably referred here with a note that they contribute no definitive phylogenetically informative information.

DISCUSSION

Taxonomic Identification

We refer all four individuals of UWBM VP 118681 to *Micropholis stowi* but note that each preserves varying degrees of taxonomically informative anatomy. Not all individuals are generically referable under an apomorphy-based system or require a certain inference of higher

taxonomic affinities (e.g., Dissorophoidea) in order to identify apomorphies. For example, pustulated ornamentation is apomorphic for *M. stowi* among dissorophoids (found in all four individuals described here), but this type of ornamentation is also found in at least part of the skull in the enigmatic *Peltobatrachus pustulatus* (Panchen, 1959), the small-bodied lapillopsids (e.g., Yates, 1999), and in some stereospondyls, including plagiosaurids (e.g., Dias-da-Silva and Milner, 2010; Schoch and Witzmann, 2012), rhytidosteids (e.g., Dias-da-Silva and Marsicano, 2011), and laidleriids (e.g., Warren, 1998a; Piñeiro et al., 2007). *Micropholis* is the only unequivocal dissorophoid from the Triassic and is known from the geographically adjacent Karoo Basin, so our referral may appear intuitive. However, we emphasize the importance of avoiding the use of circumstantial evidence as the primary rationale to make taxonomic identifications in order to avoid circular logic (e.g., Bell et al., 2010). This section briefly discusses our rationale for taxonomic referral of each individual (in the order of their description).

UWBM VP 118681C preserves three of the features listed in the diagnosis of *Micropholis stowi* by Schoch and Milner (2014): dermal ornament consisting of small pustules (an apomorphy in our diagnosis); a narrow palatine and ectopterygoid (an amphibamiform feature); and a postparietal that is anteroposteriorly much longer than the tabular (a plesiomorphy). Of these, the dermal ornament is the most compelling. No features of the well-resolved cranial sutures differ from other specimens of *M. stowi*.

UWBM VP 118681A preserves two features, both shared with UWBM VP 118681C (ornamentation, narrowness of palatine and ectopterygoid). This individual does not preserve any of the characteristic features of dissorophoids, such as the lateral exposure of the palatine (LEP) found in UWBM VP 118681C. However, this individual can be differentiated from

stereospondyls by the slender palatine and ectopterygoid. The absence of lateral line grooves rules out most stereospondyls, including the similarly sized *Lapillopsis nana*, which has pustulated ornamentation in some regions of the skull (Yates, 1999). Based on the proposed amphibamiform affinities, the ornamentation then supports referral to *Micropholis stowi*.

UWBM VP 118681B preserves two of the diagnostic features of Schoch and Milner (2014), the ornamentation and the short basipterygoid process of the pterygoid (the latter a feature of small-bodied dissorophoids). It can be inferred that the ectopterygoid and parts of the palatine are preserved but obscured by the articulated mandibles due to the slenderness of the palatal elements. Furthermore, the prominently elevated (ventrally offset) denticle-bearing ridge on the cultriform process was listed as diagnostic by Schoch and Rubidge (2005); to the best of our knowledge, this feature remains unknown in other amphibamiforms, and we included it in our revised diagnosis. Extensive covering of the parasphenoid (and the palate in general) with denticles is a plesiomorphic trait that also differentiates this individual from stereospondyls, in addition to the distinct basicranial joint, which contrasts with a tight abutting contact in stereospondyls (e.g., Eltink et al., 2019). There is no clear evidence for an exit of the internal carotid artery in this individual (a second diagnostic feature listed by Schoch and Rubidge, 2005 but not by Schoch and Milner, 2014), but caution should be exercised in using this feature given the potential confounding by ontogeny and taphonomy.

UWBM VP 118681B preserves the same three diagnostic features as UWBM VP 118681C despite the poorer preservation of the skull, as well as a LEP that supports dissorophoid affinities. Additionally, it preserves one feature listed by Schoch and Rubidge (2005), laterally extensive transverse processes of the vertebrae, which is not listed by Schoch and Milner (2014) but which the former study listed as the most diagnostic feature of the taxon and which we

included in our revised diagnosis. Most terrestrial amphibamiforms lack sufficient vertebral material for comparison, including the closest inferred relatives (*Pasawioops*, *Tersomius*). To the best of our knowledge, the (re-)description of taxa with postcrania subsequent to Schoch and Rubidge's study (e.g., Huttenlocker et al., 2007; Clack and Milner, 2009; Sigurdson and Bolt, 2010) has not identified similarly extensive processes.

Ontogenetic Maturity and Morph Differentiation

Micropholis stowi is relatively rare among temnospondyls in being known from two morphotypes whose differences pertain largely to skull proportions; the source of such variation remains unknown given the challenges of testing hypotheses such as sexual dimorphism in most extinct tetrapods but is discussed in brief further below. Schoch and Rubidge (2005) noted that confident assignment of juveniles to one morph is difficult due to reduced morphological differentiation among juveniles. Asymmetry within individuals of any stage in qualitative aspects of shape and proportion of cranial elements further confounds definitive categorization. The most complete individuals described here have a midline skull length around 30 to 35 mm from the tip of the premaxilla to the posterior margin of the postparietals along the dorsal surface, but the more fragmentary UWBM VP 118681A would have exceeded 40 mm. The largest known specimens of *M. stowi* also exceed 40 mm, and there is no evidence for advanced ossification in the new Fremouw material that suggests maturation at a smaller body size.

There are five identified features that separate the slender- and broad-headed morphs, although differentiation is increasingly complicated with greater immaturity (Schoch and Rubidge, 2005). Three features of the palate (viz. choana proportions, degree of contact between the palatine and the vomer, and vomerine dentition) cannot be assessed in any of the Fremouw

604 individuals. The fourth feature, general skull proportions, is very much a qualitative assessment
605 that presumably lies along a gradient within the ontogeny of a single individual and perhaps
606 between the different morphs. UWBM VP 118681B and UWBM VP 118681D are within the
607 size range at which morphs are not clearly differentiated. UWBM VP 118681A and UWBM VP
608 118681C appear to have proportionately broad skulls, suggesting they belong to the broad-
609 headed morph, although the former is closer in size to the other two specimens than to the latter.
610 The fifth feature, maxillary tooth count, can be assessed in the largest individual, UWBM VP
611 118681A. The left maxilla is complete and preserves around at least 30 teeth and likely not many
612 more, a count in line with that of the broad-headed morph. Schoch and Rubidge (2005) urged
613 some caution in the use of this feature as a differentiator given the paucity of specimens in which
614 it can be assessed, but this observation provides a second line of evidence for identification as a
615 broad-headed morph. Estimation of the tooth count in UWBM VP 118681C also indicated a total
616 count closer to that of the broad-header morph.

617 Determination of the biological significance of two morphs in *Micropholis stowi* remains
618 elusive in the absence of recognized morphs in other temnospondyls. It is beyond the scope of
619 this study to further explore this phenomenon, but an alternative to sexual dimorphism that we
620 consider plausible here is developmental plasticity. Many extant lissamphibian taxa exhibit
621 morphs, which often derive from alternative developmental pathways (metamorphosing vs. non-
622 metamorphosing). This is often termed facultative neoteny or facultative paedomorphosis (e.g.,
623 Whiteman, 1994; Denoël et al., 2005; Laudet, 2011). The determination of an individual's
624 developmental trajectory is linked to abiotic (e.g., water quality) and biotic (e.g., population
625 density) factors and the specific advantages between terrestrial and aquatic environments. This
626 phenomenon often facilitates intraspecific niche differentiation between morphs (e.g., Lejeune et

al., 2018, 2020). Developmental plasticity was not well-known or characterized in many temnospondyls prior to Schoch and Rubidge (2005) but has subsequently been explored in a number of taxa.

Facultative neoteny is observed in the small branchiosaurid amphibamiforms (e.g., Werneburg, 2002; Schoch and Fröbisch, 2006; Fröbisch and Schoch, 2009b) and micromelerpetids (e.g., Boy, 1995, 2003; Boy and Sues, 2000), but it does not occur within any single species or population, instead occurring between different congeners (*Apateon*, *Micromelerpeton*). Bone histology has been shown to capture the divergent developmental pathways of different species of *Apateon* living in different lacustrine environments (Sanchez et al., 2010a, 2010b). Gee et al. (2020) identified developmental plasticity in the terrestrial amphibamiform *Doleserpeton annectens*, but this taxon does not have morphs, and the observed plasticity was primarily related to a poor correlation of size with inferred age; distinctly divergent trajectories are not apparent from the data. The sample is also time-averaged and thus definitively non-equivalent to modern populations (see discussion of this frequent problem of non-equivalence of “populations” across time by Schoch, 2009, 2010, for the stereospondylomorph *Sclerocephalus*). The histology of *Micropholis stowi* has only been analyzed from a single specimen (McHugh, 2015), so much remains unknown of the taxon’s histology and development. However, most specimens of *M. stowi* are singletons from localities across the Karoo Basin (see specimen list of Schoch and Rubidge, 2005:502–503) that range across most of the stratigraphic extent of the LAZ, and the best representatives of the two morphs do not co-occur. Therefore, further exploration of the mechanism behind morph differentiation in this taxon might await the discovery of new material with spatial overlap of both morphs (if this occurred). While the documentation of facultative neoteny in the closely

related branchiosaurids and micromelerpetids is compelling for extending the inference to *M. stowi*, those taxa lived in drastically different environments, which may have exerted more influence than phylogenetic relatedness.

Implications for Lower Fremouw Formation Tetrapod Assemblages

Despite the longstanding recognition that the tetrapod assemblage of the lower Fremouw Formation generally mirrors that of the *Lystrosaurus* biozone of South Africa (Kitching et al., 1972; Colbert, 1982), its temnospondyl subcomponent has defied a correspondingly simple characterization for at least three reasons. First, the temnospondyls best known from the Lower Triassic of South Africa (viz. *Lydekkerina* and *Micropholis*) were unknown from Antarctica. It should be noted that Botha and Smith (2020) listed nine temnospondyl genera from the *Lystrosaurus declivis* AZ, but most are either based on singleton specimens (e.g., *Thabanchuia oomie*; Warren, 1998b) and/or of dubious taxonomic validity (e.g., '*Broomulus dutoiti*'; Jeannot et al., 2006). Second, the temnospondyls that have been described from Antarctica have a checkered taxonomic history and most can be identified only to the family level (Colbert and Cosgriff, 1974; Cosgriff and Hammer, 1984), owing in large part to their more fragmentary nature. For example, *Austrobrachyops jenseni* (the first temnospondyl named from the lower Fremouw Formation) and *Cryobatrachus kitchingi* (the second such species), were considered as *nomina dubia* by recent workers (Warren and Marsicano, 2000; Schoch and Milner, 2000, respectively). Third, the lower Fremouw Formation includes temnospondyl material referable to clades that do not appear in the fossil record of South Africa until the overlying *Cynognathus* AZ (e.g., Brachyopoidea; Chernin, 1977; Damiani and Jeannot, 2002; Damiani and Kitching, 2003).

The recognition of *Micropholis stowi* from Antarctica increases the taxonomic correspondence of the lower Fremouw assemblage with that of the *Lystrosaurus declivis* AZ, but several outstanding faunal questions remain. In particular, the taxonomic identity of *Cryobatrachus kitchingi* should be ascertainable. Its holotype, AMNH FARB 9503, is a nearly complete skull roof preserved in internal view (Cosgriff and Hammer, 1984). Previous workers have suggested lydekkerinid or capitosaurian affinities (Schoch and Milner, 2000; Sidor et al., 2008), but advanced visualization techniques, better comparative material, and increased resolution of ontogenetic transformations are now available to help resolve the issue. A second line of inquiry is the relationship of the lower Fremouw assemblage to contemporaneous assemblages in Australia. Besides the report of a single specimen of *Lydekkerina huxleyi* from the Rewan Formation (Warren et al., 2006), the bulk of Lower Triassic temnospondyl diversity in Australia is endemic and thus lacks representation elsewhere in southern Pangea (Warren et al., 2001, 2006). The Beacon Basin of Antarctica was interposed between the basins in Australia and South Africa (Catuneanu, 2004), and so some degree of biogeographic connectedness might be expected, given sufficient sampling.

Presently, family- to superfamily-level comparisons of the temnospondyl assemblages in southern Gondwana indicate that the lower Fremouw Formation assemblage remains undersampled compared to coeval deposits in South Africa, Australia, India, and Madagascar (Fig. 7). Presently, only amphibamiforms and brachyopoids can be confidently stated to have existed in the lower Fremouw. Cosgriff and Hammer (1984) reported fragmentary rhytidosteid material from the lower Fremouw but justified their referral only on the basis of apparently similar ornamentation; rhytidosteids would be expected given their rich record in Australia (Watson, 1956; Cosgriff, 1965, 1974; Howie, 1972; Warren and Black, 1985; Warren and

Hutchinson, 1987; Yates, 2000) and the LAZ (Cosgriff and Zawiskie, 1979). Peacock et al. (2019) noted the presence of lapilopsids in the lower Fremouw based on a single specimen referenced in a conference abstract (Beightol et al., 2013). This specimen is currently under study by the authors, and we note that some recent studies indicate that *Lapillopsis* (and therein Lapillopsidae) is nested within Lydekkerinidae (e.g., Eltink et al., 2019). If true, the recognition of a more inclusive Lydekkerinidae would account both for the present relative paucity of lydekkerinids to lapilopsids in Australia and the inverse pattern (with total absence of lapilopsids) in the LAZ. However, Lapillopsidae remains relatively poorly known, with only three described species from Australia and India (Warren and Hutchinson, 1990; Yates, 1999; Yates and Sengupta, 2002). Lastly, despite the continued uncertainty regarding *Cryobatrachus kitchingi*, lydekkerinids (as presently defined to the exclusion of *Lapillopsis*) are known from all adjacent geographic regions. Lydekkerinids had already been reported from South Africa, Madagascar, and India at the time of the description of *C. kitchingi*, and it is possible that these records influenced the interpretation of the holotype. Records of *Lydekkerina huxleyi* in the Karoo Basin to the northwest and the Gailee Basin to the northeast suggest that this particular lydekkerinid species likely existed somewhere in Antarctica, though perhaps not where rocks of the lower Fremouw are currently accessible.

Several other clades may have been more sporadically distributed across southern Pangea (i.e. their known occurrences are a more accurate representation of their Early Triassic range). Both dinosaurs and rhinesuchids are predominantly Paleozoic clades. The former is represented only by *Thabanchuia oomie* from South Africa and rare tupilakosaurid material from India (Warren, 1998b:145–146, and references therein), and the latter is represented solely by *Broomistega putterilli* from the LAZ in the Mesozoic (Shishkin and Rubidge, 2000; Fernandez et

al., 2013). Plagiosaurids, the sister group to brachyopids, are an entirely Mesozoic clade, but they are mostly known from the northern hemisphere throughout their temporal range (e.g., Schoch and Milner, 2014), and the Australian *Plagiobatrachus* is known from very limited material (Warren, 1985). Both trematosauroids and capitosauroids achieved widespread distributions by the Middle Triassic, but within the Karoo Basin, both clades appear only in the uppermost horizons of the LAZ and did not overlap with either *Micropholis stowi* or with the lydekkerinids. Thus, their absence in the lower Fremouw Formation could simply be an indication that the correlates of the uppermost LAZ are either not preserved or are not fossiliferous. It is however curious that there is no record of trematosauroids throughout the Fremouw Formation, as capitosauroids are well-represented in the upper Fremouw (Sidor et al., 2007, 2008, 2014). This discrepancy might relate to the marine lifestyle inferred for at least some trematosauroids (e.g., Hammer, 1987).

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 1026 YYYY

FIGURE LEGENDS

FIGURE 1. Block with multiple fossilized individuals of *Micropholis stowi* (UWBM VP 118681) collected from the lower Fremouw Formation. **A**, photograph and **B**, interpretative drawing showing the identification of elements assigned to the four preserved individuals (demarcated by colors) described in the text. Unassigned elements are shown in gray.

Abbreviations: **cl**, clavicle; **f**, femur; **h**, humerus; **is**, ischium; **r**, rib; **ra**, radius; **ti**, tibia; **u**, ulna; **v**, vertebra. Scale bar equals 10 millimeters. [Intended for page width]

FIGURE 2. Skull of *Micropholis stowi* (UWBM VP 118681C) in dorsal (**A**, **B**, **C**) and oblique left lateral (**D**, **E**) views. Fine dashed lines represent topographic surfaces; coarse dashed lines represent inferred sutures. Abbreviations: **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **lep**, lateral exposure of the palatine; **m**, maxilla; **n**, nasal; **pb**, palpebral; **pf**, prefrontal; **pmx**, premaxilla; **p**, parietal; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **pt**, pterygoid; **qj**, quadratojugal; **smx**, septomaxilla; **sq**, squamosal; **st**, supratemporal; **t**, tabular. Scale bar equals 5 millimeters. [Intended for page width]

FIGURE 3. Skull of *Micropholis stowi* (UWBM VP 118681A) in dorsal view. **A**, photograph; **B**, interpretive line drawing. Fine dashed lines represent topographic surfaces. Abbreviations: **an**, angular; **ar**, articular; **c3**, third coronoid; **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pa**, prearticular; **po**, postorbital; **pof**, postfrontal; **psp**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **sa**, surangular; **sq**, squamosal; **stp**, stapes; **v**, vertebra. Scale bar equals 5 millimeters. [Intended for page width]

1050

1051 FIGURE 4. Representative postcranial elements of *Micropholis stowi*. **A**, photograph of anterior
1052 vertebral column of UWBM VP 118681B. **B**, interpretive line drawing; note only identifiable
1053 elements associated with this individual are figured. **C**, possible hindlimbs of UWBM VP
1054 118681B. **D**, right forelimb of UWBM VP118681A. Abbreviations: **f**, femur; **h**, humerus; **ra**,
1055 radius; **t**, tibia; **u**, ulna; **v**, vertebra. Scale bars equal 5 millimeters. [Intended for page width]

1056

1057 FIGURE 5. Skull of *Micropholis stowi* (UWBM VP 118681D) in ventral view. **A**, photograph;
1058 **B**, interpretive line drawing. Fine dashed lines represent topographic surfaces. Abbreviations: **an**,
1059 angular; **ar**, articular; **cl**, clavicle; **d**, dentary; **m**, maxilla; **psp**, parasphenoid; **pt**, pterygoid; **qj**,
1060 quadratojugal; **sa**, surangular; **sph**, sphenethmoid. Scale bar equals 5 millimeters. [Intended for
1061 page width]

1062

1063 FIGURE 6. Skull of *Micropholis stowi* (UWBM VP 118681B) in dorsal view. **A**, photograph; **B**,
1064 interpretive line drawing. Fine dashed lines represent topographic surfaces; coarse dashed lines
1065 represent inferred sutures. Abbreviations: **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **lep**, lateral
1066 exposure of the palatine; **m**, maxilla; **n**, nasal; **p**, parietal; **pf**, prefrontal; **pmx**, premaxilla; **pp**,
1067 postparietal; **po**, postorbital; **pof**, postfrontal; **psp**, parasphenoid; **pt**, pterygoid; **qj**,
1068 quadratojugal; **st**, supratemporal; **sq**, squamosal; **t**, tabular; **v**, vomer. Scale bar equals 5
1069 millimeters. [Intended for page width]

1070

1071 FIGURE 7. Schematic showing the taxonomic composition (left) and geographic position (right)
1072 of five major Early Triassic temnospondyl assemblages from southern Pangea. Stars on the map

1073 denote the: *Lystrosaurus declivis* Assemblage Zone (South Africa), Sakamena Formation
1074 (Madagascar), Panchet Formation (India), Arcadia Formation (Australia), and lower Fremouw
1075 Formation (Antarctica). Black boxes represent presence, white boxes represent absence, and gray
1076 boxes represent disputed or equivocal presence. Questionable presence of lydekkerinids in
1077 Madagascar relates to the unresolved affinities of *Deltacephalus whitei* (e.g., Jeannot et al.,
1078 2006); see main text for discussion of tentative documentation of clades in Antarctica. The
1079 phylogenetic topology shown is intended only as a conceptual guide (derived primarily from
1080 Schoch, 2013; Eltink et al., 2019) and not as a novel hypothesis of relationships; the position of
1081 Lapillopsidae in particular remains poorly resolved. Map reconstruction based on data from
1082 Lawver et al. (2009) and modified from Sidor et al. (2013). [Intended for page width]