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PII: S1464-343X(21)00226-0

DOI: <https://doi.org/10.1016/j.jafrearsci.2021.104325>

Reference: AES 104325

To appear in: *Journal of African Earth Sciences*

Received Date: 18 December 2018

Revised Date: 3 July 2021

Accepted Date: 7 July 2021

Please cite this article as: Peacock, B.R., Bronson, A.W., Otoo, B.K.A., Sidor, C.A., Freshwater fish faunas from two Permian rift valleys of Zambia, novel additions to the ichthyofauna of southern Pangea, *Journal of African Earth Sciences* (2021), doi: <https://doi.org/10.1016/j.jafrearsci.2021.104325>.

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FRESHWATER FISH FAUNAS FROM TWO PERMIAN RIFT VALLEYS OF ZAMBIA,
NOVEL ADDITIONS TO THE ICHTHYOFAUNA OF SOUTHERN PANGAEA

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ABSTRACT

Toward the end of the Paleozoic, Earth's land masses formed the supercontinent Pangea. Despite the relative lack of large-scale physical dispersal barriers, patterns of endemism and regionalization existed, likely driven by climate. During the later Permian the fossiliferous southern region of Pangea has proven to be remarkably homogeneous in terms of terrestrial floras and faunas. However, these signals among vertebrates are best documented amongst tetrapods, and little attention has been paid to freshwater fish assemblages often occurring in the same rocks. Given the increasingly arid and landlocked conditions of the interior of Pangea, the study of freshwater vertebrate communities can help contribute to an understanding of biogeographic patterns across the supercontinent. Here we report two Permian fish assemblages from the Madumabisa Mudstone Formation of Zambia consisting of actinopterygians and large-bodied elasmobranchs: 1) a middle Permian assemblage from the Mid-Zambezi Basin; and 2) a late Permian assemblage from the Luangwa Basin. These assemblages are compared with other middle and late Permian freshwater ichthyofaunas from Australia, Brazil, Chile and South Africa and found to reinforce signals of faunal homogeneity for terrestrial assemblages found using the richer and more well-documented tetrapod fossil record.

Keywords:

Chondrichthyes

Actinopterygii

Permian

Madumabisa Mudstone Formation

Luangwa Basin

Mid-Zambezi Basin

1. Introduction

Today, less than 1% of the Earth's habitable aquatic environments are freshwater (>99% of the planet's available surface water is marine), but these freshwater environments are home to approximately 40% of fish species diversity (Tedesco et al. 2017). The diversification of freshwater fishes is often viewed from a modern teleost-focused perspective that emphasizes Mesozoic and Cenozoic evolutionary events (Friedman and Sallan 2012), and indeed the marine record generally receives more attention (Alfaro et al., 2018; Bazzi et al., 2018; Capobianco et al., 2020; Friedman, 2009). Though the Silurian and Devonian have been recognized as important times for the origin of most high-level gnathostome taxa, the Carboniferous and Permian have traditionally been considered an interval of evolutionary stasis in nonmarine fish evolution (Friedman & Sallan 2012; Giles et al. 2017; Romano et al. 2016; Sallan et al. 2011) following the end-Devonian mass extinction and the elimination of placoderms, ostracoderm stem-gnathostomes, and multiple sarcopterygian lineages (Sallan & Coates 2010). It is recognized that after the end-Devonian extinction, the modern freshwater (and marine) vertebrate assemblage of actinopterygians, chondrichthyans, and tetrapods was established.

However, this view of stasis is largely the result of phylogenetic uncertainty (particularly in the case of actinopterygians) and a lack of fossils (particularly in the case of early tetrapods); both of these are improving as part of a general increase in our knowledge of the Devonian-Carboniferous fossil record (Ahlberg and Clack, 2020; Anderson et al., 2015; Bronson et al., 2018; Challands et al., 2019; Chen et al., 2018; Clack et al., 2016, 2018, 2019; Figueroa et al., 2021; Goedert et al., 2018; Maissey et al., 2017a, b; Olive et al., 2016a, b; Pais de Rezende et al., 2021; Richards et al., 2018; Sallan and Coates, 2013; Smithson et al., 2012, 2016; Wilson et al., 2018). This is particularly significant as the initial crown group diversifications for

actinopterygians, chondrichthyans, and tetrapods have all been dated to between the Middle Devonian and Early Carboniferous (Coates et al., 2017, 2018; Giles et al., 2017; Pardo et al., 2020). Irrespective of phylogenetics, diverse nonmarine fish faunas are known from the Devonian onwards, though their taxonomic compositions vary (Carpenter et al., 2011, 2015, 2014; Cressler et al., 2010; Friedman and Sallan, 2012; Gess and Whitfield, 2020; Olive et al., 2016b, 2015; Otoo et al., 2018) and our knowledge of early and middle Early Carboniferous (Mississippian) faunas generally is still lacking. By the middle/late Permian (Guadalupian/Lopingian), a stereotyped freshwater fish assemblage had been established: xenacanthiform and hybodontiform stem-group elasmobranchs, stem-group lungfishes, and ‘palaeoniscoid’ actinopterygians (Cavin et al. 2007; Coates & Gess 2007; Friedman 2015; though xenacanthiforms may be stem-group chondrichthyans: Gillis & Donoghue 2007; Ginter 2004). However, these Permian ichthyofaunas are more infrequently preserved than contemporary tetrapod assemblages; thus, most Permian hypotheses of vertebrate biogeography make use of the tetrapod, rather than fish, record (Friedman & Sallan 2012; Sidor et al. 2013).

Middle and upper Permian tetrapod assemblages are distributed across Pangea, with the best records coming from the Karoo Basin in South Africa, the Ruhuhu Basin of Tanzania, and the Zambezi and Luangwa basins of Zambia in south central Pangea, and the Cis-Ural region of European Russia in north-central Pangea (Peacock 2016; Rubidge 2005; Sennikov & Golubev 2017; Smith et al. 2012). Mid-high latitude tetrapod assemblages of the middle-upper Permian, particularly those in southern Pangea, consistently show patterns of biogeographic homogeneity in terms of taxonomic and ecological diversity, ecosystem structure, and interconnectedness (Bernardi et al. 2017; Peacock 2016; Roopnarine et al. 2018; Sidor et al. 2013). However, biogeographic studies of middle-upper Permian terrestrial vertebrate assemblages have not

usually taken into account freshwater fish occurrences despite the existence of numerous Gondwanan freshwater fish localities: the Rangel Coal Measures in Australia, the Rio do Rasto Formation in Brazil, the Peine Formation of northern Chile, and the Karoo Basin sequence in South Africa. Here we provide a preliminary report on ichthyofaunas from the Mid-Zambezi and Luangwa basins of Zambia, a heretofore neglected part of the Permian vertebrate faunas of southern Pangea.

2. Gondwanan freshwater fishes from the middle and upper Permian

2.1 Rangel Coal Measures

Fossil fishes occur in shales that are interspersed with coal seams within the larger Rangel Coal Measures in the Bowen Basin, Queensland, Australia. Fish specimens are frequently associated with plant material, including *Glossopteris* leaves and upper Permian palynomorphs (Campbell & Duy Phuoc 1983). The depositional environment of the coals, shales, mudstones, and sandstones within the Rangel Coal Measures is interpreted as a floodplain with well-vegetated ephemeral lakes and laterally migrating river channels (Burgis 1975; Campbell & Duy Phuoc 1983; Ritchie & Edgecombe 2001). Several fish localities are mass mortality sites, producing numerous specimens (Leu 1989; Ritchie & Edgecombe 2001). The fish fauna of the Rangel Coal Measures is reported to be impressively rich: at least 12 genera of actinopterygians and two genera of elasmobranchs, though to date only two species have been formally named and described (McLoughlin 2017; Ritchie & Edgecombe 2001). The first, *Surcaudalus rostratus*, possesses prominent dorsal fin spines and a mix of traits seen in ctenacanth and different early elasmobranchs, leading Leu (1989) and Ivanov et al. (2018) to place *Surcaudalus* as an indeterminate euselachian (Ctenacanthiformes + Neoselachii). The

second, *Ebenaqua ritchiei*, is a deep-bodied actinopterygian with an advanced mobile maxilla, and has been allied with other deep-bodied forms like *Bobasatrania* since its description (Bender 2005; Campbell & Duy Phuoc 1983; Mickle & Bader 2009; Xu et al. 2014). In phylogenetic analyses *Ebenaqua* is found to be on the neopterygian stem (Argyriou et al. 2018; Giles et al. 2017; Hurley et al. 2007; Xu et al. 2014). Future work on Permian fishes must include the description of the outstanding Rangel Coal Measures taxa.

2.2 Passa Dois Group

In southeastern Brazil, the Permian Rio do Rasto Formation includes several localities spread over the Paraná Basin (Cisneros et al. 2005; Dias-da-Silva 2012; Langer 2000; Olroyd & Sidor 2017). Fishes in the Rio do Rasto Formation are often found as isolated elements in conglomerates and red mudstones representing lacustrine and channel deposits. Correlations between the localities are tentative and though there are few species-level shared taxa, most can reasonably be considered middle Permian in age based on the biostratigraphy of tetrapod taxa such as dinocephalian and anomodont therapsids, pareiasaurs, and temnospondyl amphibians (Boos et al. 2015; Cisneros et al. 2011, 2012; Olroyd & Sidor 2017). Chondrichthyans are represented by the sphenocanthid *Sphenacanthus riorastoensis* (Pauliv et al. 2012), hybodontiforms (50 mm dorsal fin spine), and xenacanthiforms (Dias 1996; Malabarba et al. 2003; Richter & Langer 1998), including the named taxa *Xenacanthus ragonhai* and *Triodus richterae* (Pauliv et al. 2014, 2017). Gnathorhizid lungfish and a coelacanth are evidenced by isolated toothplates and isolated scales, respectively, while scales, dermal fragments, and fin rays represent indeterminate ‘palaeonisciform’ actinopterygians (Cione et al. 2010; Dias 1996; Figueroa et al. 2017; Richter & Langer 1998; Toledo & Bertini 2005; see Vega-Dias et al. (2000) for figures of articulated

specimens of three as possibly novel species of actinopterygian). Two actinopterygian skeletons have been named: 1) *Rubidus pascoalensis* is an actinopterygian of dubious affinity, and 2) *Paranaichthys longianalis* is a deep-bodied form with a crushing dentition that has been allied to the platysomid stem-neopterygians (Dias 2012; Richter 2002).

The early middle Permian Teresina Formation underlies the Rio do Rasto Formation, and though salinity measurements vary throughout the formation, an isotopic analysis of fishes indicate that they at least inhabited continental (freshwater) systems, potentially representing allochthonous deposition (Richter 2005). Undescribed fish fragments and a partial scorpion, *Suraju itayma*, are known from the upper reaches of the Teresina Formation, which is considered to represent freshwater habitat (Martine et al. 2020). Additional fishes are known from lower in section: xenacanthiforms *Wurdigneria obliterated* and *Xenacanthus santosi*, a spine referred to *Ctenacanthus sp.*, and locally abundant actinopterygian teeth, as well as chondrichthyan teeth, fin spines, and scales (Richter 2005; Wüdig-Maciel 1975).

2.3 Peine Formation

The middle member (Miembro Medio) of the Peine Formation in Quebrada Sipico, near Salar de Atacama, in northern Chile consists of freshwater facies preserving low-energy environments of ephemeral lakes and floodplains with episodic input of eolian and coarse-grained alluvial-fan deposits (Richter and Breitzkreuz 1997). U/Pb radiometric dates in overlying ignimbrites and palynomorph analyses from industry reported by Flint et al. (1993) imply a late Permian age for the Miembro Medio of the Peine Formation.

Alongside conchostracans, the concretionary lacustrine deposits have produced a single named taxon of actinopterygian fish: *Arratiaichthys chilensis*. *Arratiaichthys*, is a contoured

fusiform fish with weakly ornamented scales that were found to be histologically “paleonsicoid” (Richter & Breitkreuz 1997).

2.4 Beaufort Group

The middle and upper Permian rocks of the Beaufort Group in the Karoo Basin are the global standard for terrestrial ecosystems during the latest Paleozoic (Rubidge 2005). An evolving scheme of tetrapod-defined vertebrate assemblages zones (AZs) in the Karoo has been used to correlate terrestrial Permian and Triassic rocks worldwide, and recently radiometric dates from within the Permian sequence have tied the scheme to the chronostratigraphic time scale (Rubidge 2013; Smith et al. 2020; Viglietti et al. 2016). The middle and upper Permian Beaufort sequence is famous for its preservation of numerous and abundant therapsid taxa, as well as early reptiles and amphibians, in fluvio-lacustrine deposits (Nicolas & Rubidge 2010; Rubidge 2005; Smith et al. 2012). To date, no Permian elasmobranchs or lungfishes have been described from the Karoo, but several actinopterygians are known: *Atherstonia scutata*, *A. minor*, *Blourugia seeleyi*, *Bethesdaichthys kitchingi*, and *Namaichthys digitata* range through middle and upper Permian AZs, while *Caruichthys ornatus*, *Elonichthys whaitsi*, *Pteronisculus meiringi*, and *Kompasia delaharpei* are restricted to the upper Permian *Cistecephalus* and *Daptocephalus* AZs (Bender 1998, 2001, 2002, 2005; Bender et al. 1991; Broom 1913; Jubb & Gardiner 1975; Murray 2000). Most original phylogenetic hypotheses and taxonomic classifications place these taxa as stem-actinopterygians (Bender 2001, 2002, 2005; Gardiner et al. 2005; Gardiner & Schaeffer 1989; Jubb & Gardiner 1975), but each would benefit from inclusion in more recent phylogenetic datasets (Argyriou et al. 2018; Giles et al. 2017). Importantly, Bender (1999) remarked that undescribed specimens from the Rangel Coal Measures share characters with the

deep-bodied taxon *Blourugia seeleyi*, thereby forming a potential biogeographic link between the Karoo and Bowen basins (Bender 2005).

2.5 *Zambian basins*

Here, we document additional Permian fossil fish occurrences from south central Pangea. Permo-Triassic fossils of terrestrial and aquatic vertebrates have been found in fluvio-lacustrine rocks within three rift basins in Zambia: the Luangwa, Luano, and Zambezi basins.

Paleontological fieldwork in Zambia's Luangwa Basin occurred sporadically throughout the early and middle twentieth century, and has been ongoing since 2009 (Figure 1; Angielczyk et al. 2014; Attridge et al. 1964; Dixey 1937; Drysdall and Kitching 1963; Kemp 1975; Kerr 1974; Sidor and Nesbitt 2018; Sidor et al. 2013). The fossil record of the Luangwa Basin is the richest in Zambia. The 1974 joint expedition between the Geological Survey of Zambia and Oxford University was the first to discover freshwater fish fossils from the upper Permian upper Madumabisa Mudstone Formation (Kemp 1975; Murray 2000), but they remained formally undescribed until now. In his initial publication Kemp (1975:415) described the upper Permian discoveries from the mid-luangwa Basin and listed: "... at one particular locality, numerous remains of fishes, including hybodont-like fin spines, palaeoniscid scales and the partial skull of an *Acrolepis*-like palaeoniscid." Peacock et al. (2018) described ptychoceratodontid lungfish toothplates and hybodontoid shark fin spines from the Middle-Upper Triassic Ntawere Formation, Luangwa Basin.

The Luano Basin is the smallest of the three Zambian basins discussed here and a single locality in the Madumabisa Shales along the Lunsempfwa River has produced several small actinopterygian fish skeletons. Haughton (1934) named *Ischnolepis bancrofti* for the most

abundant taxon present, referring a single small bodied specimen to ?*Pygopterus* and several larger-bodied specimens to cf. *Atherstonia*. Hutchinson (1973) redescribed *I. bancrofti* as a redfieldiiform, an assignment later confirmed by cladistic analysis (Schaeffer 1984). The age of the Maduambisa Shales in the Luano Basin is considered vaguely Early Triassic, but is poorly constrained (Schaeffer 1984).

Gair (1959) was the first to report Permian-aged vertebrate fossils from the Mid-Zambezi Basin in southern Zambia. Recent fieldwork there has confirmed the presence of a middle Permian vertebrate assemblage consisting of dinocephalian, biarmosuchian, gorgonopsian, and dicynodont therapsids, rhinesuchid temnospondyls, and the osteichthyan specimen described below (Olroyd & Sidor 2017; Peacock 2016; Sidor et al. 2014).

3. Methods

With the exception of NHCC LB597, all specimens in this manuscript were collected in 1974 as part of a joint expedition between the Geological Survey of Zambia and Oxford University and hail from a single locality (Kerr 1974; Locality 5 of Kemp 1975). A productive horizon of fish material encased in hematite nodules was fortuitously found on a hillside, and the productive layer excavated. This locality was relocated by our team in 2018 and we determined that it is near the middle of the section of Madumabisa Mudstone exposed in the Munyamadzi Game Management Area, suggesting a Wuchiapingian age. Large gorgonopsians and several dicynodonts (identified to Dicynodontoidea and ?*Diictodon* before preparation) were found in the immediate vicinity of the fish horizon, but the fossiliferous layer itself was no longer productive (Peacock 2016; Peacock et al. 2020). The 1974 collection was at the University of Oxford until 2018 when it was transferred to the Natural History Museum, London.

NHMUK PV P75419, P75420, P75421, P75422, and P75423 were studied and photographed using a Olympus SZX 16 dissecting microscope with an attached digital camera. We have not mechanically or chemically prepared the specimens, and are unaware of the precise chemical preparation conducted at Oxford: Kemp (1975) claimed the specimens are very suitable for acetic acid preparation.

NHCC LB597 was thin sectioned according to standard procedures outlined in Lamm (2013). The scale was embedded in Epothin Epoxy/Resin 2, sectioned to a thickness of approximately 2 mm on an Isomet 1000 saw and glued to glass slides using 2-ton epoxy. Slides were ground using a Metaserv 3000 lapidary plate until the specimen was approximately 80 µm thick or until optical clarity was reached. Thin sections were imaged using a Nikon Eclipse LV100POL microscope. Composite images were processed using Nikon NIS-ELEMENTS BR (version 4.3) imaging software.

Institutional Abbreviations. NHCC, National Heritage Conservation Commission, Lusaka, Zambia; NHMUK, Natural History Museum, London, United Kingdom.

4. Systematic Palaeontology

Chondrichthyes Huxley, 1880

Elasmobranchii Bonaparte, 1838

Referred Material. NHMUK PV P75421a (Figure 2)

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. Infraclass Euselachii (Bonaparte 1838) *incertae sedis*

Description. Fragment of the intramuscular portion of a dorsal fin spine of approximately 6cm in length. The ventralmost portion of the exposed ornamented surface, which shows a tuberculate ridge ornamentation, is visible dorsoanteriorly. The intramuscular portion is large and unornamented and tapers proximally towards the base of the dorsal fin (Fig. 2 I, J). The posterior concavity for articulation with the basal cartilage of the dorsal fin is filled by sediment but appears to extend through the whole length of the fragment.

Referred Material. NHMUK PV P75423 (Figures 2, 3)

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. *Euselachii incertae sedis*, may be within Order Synechodontiformes (Duffin and Ward 1993), based on the presence of denticles arranged in longitudinal ridges and the enameloid rib on the keel, as well as the slightly laterally compressed appearance.

Description. Spine fragment with denticles organized into longitudinal ridges and enameloid rib at its keel, slightly laterally compressed (Fig. 2 G, H; Fig. 3). Tubercles between 0.52 and 1.73 mm apart on lateral surfaces. Spine triangular to ovoid in cross section.

Referred Material. NHMUK PV P75420 (Figure 4)

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. *Elasmobranchii incertae sedis*, may be within Hybodontiformes (Maisey, 1978, 1989) based on strong concavity of the posterior surface (Fig. 4 A) and ornamentation in the form of rows of tubercles (Fig. 4 D) though much of this has been lost to taphonomy in this specimen, some denticles remain at the proximal end of the fragment), however no obvious sharp hook-denticles are apparent on the posterior surface of the spine.

Description. Fragment of dorsal fin spine approximately 3.3 cm in length, likely partially from within the intramuscular region of the spine, with sparse tubercles, overall cross-sectional shape rounded, approximately 1.1 cm wide, with strongly concave posterior surface (0.7 cm deep concavity within the approximately 1.4 cm anteroposterior length of the entire spine); tubular dentine visible in cross section and laterally where ornamentation is worn or broken away.

Referred Material. NHMUK PV P75422a/b (Figure 4)

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. *Euselachii incertae sedis*

Description. A 4 cm long fragment of a dorsal fin spine, with concave posterior face. No visible ornamentation. Proximally, the fragment is 3 cm long (anterior to posterior) and 2 cm wide, decreasing to 2.4 cm long 1.5 cm wide at the distal portion of the fragment. Both the pulp cavity and exposed components are preserved, visible in cross section (Fig. 4 B, C). The exposed component of the spine is strongly concave posteriorly, which could indicate ctenacanth or xenacanth affinity (Fig. 4 C).

Chondrichthyes Huxley, 1880

Elasmobranchii Bonaparte, 1838

Xenacanthida, Glikman 1964

Xenacanthidae, Fritsch 1889

Referred Material. NHMUK PV P75419, a dorsal fin spine (Figures 2, 5)

Horizon and Locality. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. Potentially within Order Xenacanthida, Family Xenacanthidae, based on the presence of large posterior tubercles along the edges of a concave, finely striated posterior wall, as well as the absence of anterolateral tubercles, presence of fine longitudinal costae on the anterolateral and posterior surfaces, and deep insertion of spine. However, this identification is putative due to preservation, pending detailed histological study of this specimen.

Description. Large spine, approximately 13.5 cm long, with many very small costae along the anterolateral and posterior surfaces, strongly concave posterior surface, and large denticles on posterolateral margins (Fig. 2 A-F and Fig. 5). Anterior edge of spine angular, and axis of spine is straight with a very slight curve nearing the apex; terminal apex of spine is broken off.

Osteichthyes Huxley, 1880

Actinopterygii Klein, 1885

Actinopterygii indet.

Referred Material. NHMUK PV75415, maxilla and cranial dermal bone (Figure 6A-F)

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. Apparent acrodin caps on the maxillary teeth allow for an actinopterygian identification. The maxilla is too damaged for its ornament (mostly or entirely lost) to be compared to the dermal bones, but their ornamentation is most consistent with that of actinopterygians. There are no diagnostic features preserved with which to provide a more precise identification but based on body size the Karoo taxa *Kompasia* (Bender 2002), *Blourgia* (Bender 2005), *Namaichthys* (Gardiner 1962) are all too small; *Bethesdaichthys* (Bender 2001) is

a possibility. NHMUK PV75415 is approximately half again as long as the maxilla of *Arratiaichthys* from the Peine Formation of Chile (Richter and Breitkreuz 1997).

Description and Comparison. Both of the dermal bones are contained in the same specimen, P75415A, on opposite surfaces. There are scales and other fossil material visible at different horizons within the specimen. The dermal bone retains only part of its original ornamented material (1.3 cm of ornamented bone, 3.4 cm total length). The ornamented portion is located at the slightly rounded end, which may be the anterior of the bone. The rest of the bone is represented by an elongate, posteriorly-incomplete impression with straight edges. The combination of size and shape suggest it might be a frontal or dermopterotic, but as there is no clear evidence of canals it could be any large dermal bone on the skull.

The maxilla (Fig. 6) is very worn and has lost its original ornament, as well as much of its original bone. There may be faint traces of striated ornament at the posterior end. It is also incomplete posteriorly and dorsally. However, partially due to an (incomplete) impression in the matrix extending posterodorsally, the postorbital expansion characteristic to actinopterygian maxillae is more readily seen. The anterior portion is elongated into the suborbital process, which has a finished edge and is gently convex. Additionally, at least three teeth are preserved, either by original material or impressions (Fig. 6). From what can be seen, the teeth are the simple conical shape typical of ‘palaeoniscid’ fishes, with a likely acrodin cap present on at least one (Fig. 6D). Overall, the maxilla as preserved is 7 cm long and 2.8 cm tall, including the impression. In terms of size, *Bethesdaichthys* is the closest match, with the caveat that size is a weak criterion for comparison, even with- or especially because of- the limitations of this material. However, the slope of the dorsal margin in this specimen is considerably gentler than in *Bethesdaichthys* (Bender 2001), even accounting for incompleteness. The ventral curve of the

jaw articulation (Fig. 6) appears to be genuine, as the bone in that region is not occluded by matrix and is reasonably complete; this feature also discounts a deep-bodied form such as *Blourgia*. While only additional, well-preserved specimens will determine whether the PR75415 maxilla represents *Bethesdaichthys* or a new taxon, it clearly implies a similarly large (body length ~30cm) fusiform fish.

Referred Material. NHMUK PV P75399, block with articulated fish body specimen

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. Based on the shape of the body outline as preserved, fusiform Karoo taxa such as *Kompasia* and *Namaichthys* are most likely.

Description and Comparison. P75399 is notable as it seems to preserve a partial body outline (Fig. 6G, H). Ridge scales are visible and taper towards one end, presumably the tail. At the end of this taper there is a rectangular ornamented scale. At the other end, the ridge scales grow smaller, and a patchy field of flank scales is visible. The flank scales are poorly preserved and presently provide no useful information. In the same specimen, there are approximately five ovoid scales preserved on-end (Fig. 6G, H). The surrounding area suggests a triangular shape reminiscent of a fin base, but the quality of the material prevents (and discourages) additional interpretation.

Referred Material. NHMUK PV P75415b/c, P75416a/b: hematite nodules filled with dermal bone, large/small scales articulated (Figure 7)

Horizon and Locality. Wuchiapingian, upper Permian. Locality 5 of Kemp (1975), upper Madumabisa Mudstone Formation, central Luangwa Basin.

Identification. see below

Description and Comparison. The rest of the material consists of scales that can only be treated as morphotypes for the time being. P75415b has a scale field on each side, each with a different morphology (Fig. 7A, C). Morphotype 1, on the numbered side of the specimen (Fig. 7A), is represented by five subcircular overlapping scales. Most of the enamel has been worn away. The ornament consists of ridges that curve in opposite directions away from the midline. Each is approximately 1 cm long by 1.5 cm broad. P75416b has a single scale of similar size with the same ornament pattern, though it appears to be less circular. On the opposite side, there is a scale field consisting of Morphotype 2. These scales are rhomboid in shape, 0.5–1 cm in length. The ornament consists of slightly curved subparallel ridges. Scales with this morphotype are also seen on both sides of P75415c (Fig. 7D). Morphotype 3 is present in P75416a, and consists of very small (0.1 cm) rectangular scales in rows. No ornament is visible. These scales are significantly smaller than those known from named South African Permian actinopterygians, and may in fact be fin rays and not scales at all. Morphotype 3 is visible in P75416c and is mostly represented by impressions. As far as can be determined as present, the scales are ~0.3 cm in length and have an elongate diamond shape. P75416d contains scales of Morphotype 4. These scales are small (~0.2 cm), diamond-shaped, and smooth. However, the lack of ornament could be due to wear; possible traces of ridges on several scales suggests that this is the case.

None of the morphotypes preserve diagnostic features and are not accompanied by material that allows for conclusive taxonomic assignments; improved identification would require histological study. However, some speculation is possible. The size of Morphotype 1 is comparable to those of *Bethesdaichthys* scales from ‘Area A’ (Bender 2001), but their different ornamentation and rounded shape imply a different identity, possibly coelacanth. *Namaichthys*

(Gardiner 1962) is a possibility for Morphotype 2, being too large for *Blourgia* and *Kompasia*. Alternatively, Morphotype 2 may represent ridge scales from *Bethesdaichthys*, based on their shape. Morphotype 4 is small enough in size and general enough in morphology that it is difficult to disqualify taxa or identify a body region (though *Bethesdaichthys* is less likely than smaller taxa), and must be relegated to Actinopterygii indet. In summary, the collection includes partial cranial bones, a partial body outline, and at least three, possibly four scale morphotypes. Fishes similar to *Bethesdaichthys* and *Namaichthys* are likely represented, though smaller taxa and a coelacanth may be present as well.

Referred Material. NHCC LB597, articulated and disarticulated scales as well as several fragmentary bones (Figure 8)

Horizon. Middle calcareous member of the Madumabisa Mudstone Formation, Lower Karoo Group, Mid-Zambezi Basin (Gair, 1959; Nyambe and Dixon, 2000; see Sidor et al. 2014 for review of stratigraphic nomenclature). The associated tetrapod assemblage indicates a Guadalupian age, likely correlating with either the *Eodicynodon* or *Tapinocephalus* assemblage zones of South Africa (Day et al. 2015).

Locality. Collected at locality L183, a locality within a relatively large outcrop that preserves fossils of burnetiamorph, dicynodont, and tapinocephalid therapsids, as well as temnospondyls (Sidor et al. 2014). Located approximately 18 km southwest of the village of Chamwe, Gwembe District, Southern Province, Zambia. Detailed coordinates are available to qualified researchers from the NHCC or by contacting BRP or CAS.

Identification. These rhomboid scales are referable to Actinopterygii based on the presence of peg-and-socket articulations in combination with stacked couplets of enamel and orthodentine superficial to a base of cellular bone.

Description. NHCC LB597 is the most complete actinopterygian material collected by our team from the lower Madumabisa Mudstone Formation (the only other material consists of small concentrations of jumbled ‘fish hash’). It consists of a large association of articulated and disarticulated scales, as well as some small, unidentified pieces of bone collected from a restricted area measuring less than 0.5-meters-squared. The specimen is notable in preserving a number of relatively large scales (over 2 cm in dorsoventral height) with a roughly parallelogram-shaped outline (Fig. 8A).

The external surface of the scales is mostly covered by a shiny capping tissue, except for a bony bar that is present along the anterior margin of the scale. The capping tissue bears fine, subparallel ridges that are oriented longitudinally and occasionally branch. On the internal surface, a trough-like depression extends from the ventral margin of the scale towards its midpoint, indicating the presence of a typical osteichthyan peg-and-socket mode of articulation. Small clusters of articulated scales are occasionally preserved (Fig. 8B) and show how the enamel-covered sections of the scales overlapped the non-enamel covered bars of adjacent scales.

We thin-sectioned a scale of NHCC LB597 to assess its internal organization (see Methods). The deepest tissue is a relatively thick layer of laminar cellular bone, which is overlain by couplets of orthodontine with a hypermineralized covering (Fig. 8C). We identify the latter as enamel based on its organization (Schultze 2016). Vascular spaces, visible as dark areas in Figure 8C, are concentrated near the junction of the bone and dentine layers. At higher magnification (Fig. 8D), the base of each unit of orthodontine has a vascular space present at its base, sometimes with a capping tissue still in place.

As with the rest of the osteichthyan/actinopterygian material described here, identifications are difficult to make and must be considered extremely preliminary. That said, the large size and ornamentation of the scales (particularly in Fig. 8A) are consistent with *Bethesdaichthys* (Bender 2001). Fig. 8A might be from 'Area A' posterior to the operculum (Bender 2001: Fig. 9) and the Fig. 8B scales might be ridge scales, though their orientation suggests otherwise.

5. Discussion

5.1 Chondrichthyan Fin Spines

Specimen NHMUK P 75419 is identified as a xenacanth based on the finely striated concave posterior face of the fin spine (as opposed to the generally convex posterior face of hybodont fin spines), as well as the presence of fine costae, absence of tubercles or large ridges over the anterolateral surfaces of the spine (which would be more consistent with a ctenacanth or hybodont affinity), and presence of denticulated ridges on the posterior face of the spine (Beck et al. 2016). Importantly, these traits must be considered altogether - ctenacanth fin spines can also have concave posterior faces, and severity of this concavity can vary depending on the level at which the spine is observed. Both ctenacanths and hybodonts are also known to have denticulated ridges on the posterior face of the spine, but the distribution and size of these denticles vary from the condition in xenacanths (for example, the typically downturned posterior denticles of hybodonts). Taken as a group of characteristics, this spine can be tentatively assigned to the xenacanth group, pending further study. Xenacanths were large, elongate predators bearing two anal fins and extremely characteristic teeth (Zangerl, 1981), specialized for grasping (Whitenack et al., 2011; Williams 2001). They were common throughout freshwater

Permian environments and likely represent a monophyletic group (Coates et al. 2018; Pradel et al. 2011).

Specimens NHMUK P25423 and 75421 cannot be identified definitively to the order level, but could represent ctenacanth selachians, based on the overall shape and posterior concavity of the fin spines. Ctenacanths are probably not a monophyletic group, and are more likely a paraphyletic group of stem-euselachians (Coates et al. 2018; Maissey et al. 2019; Pradel et al. 2011). Ctenacanths possess the cleaver-shaped palatoquadrate and cladodont dentition of many early euselachians, but are best known for their ornamented spines (Zangerl 1981), which can be differentiated on the basis of that ornamentation, including the distribution and shape of tubercles and costae, which are largely lost to taphonomy in the Zambian specimens described here. Ctenacanths have been described from North American and European localities spanning the Upper Devonian through the Triassic (Zangerl 1981), including freshwater deposits (*Bandringa*, Baird 1978), as well as from the lower Permian Irati Formation (Parána Basin) (Chahud et al. 2010) and the lower Permian Pedra de Fogo Formation (Figueroa & Gallo 2017; Figueroa & Machado 2018) of Brazil.

Lastly, it is possible that NHMUK PV P75420, P75422, and P75423 belong to the Order Hybodontiformes, which are characterized by dorsal fin spines that bear posterior marginal denticles and longitudinal ribbed costae, with a convex posterior surface and a deeply inserted base, as well as characteristic dentition and cephalic spines (Zangerl 1981). Hybodonts were particularly common from the Early Triassic through the Late Cretaceous (Cappetta 1987), but they originated by at least the Early Carboniferous (Coates et al. 2007, 2017) and may be as old as the Middle Devonian (Zangerl 1981). However, they are also known from the early Permian of North America, on the basis of isolated teeth and dorsal fin spines from freshwater deposits in

Texas (Johnson, 1979, 1981; Simpson 1974) and Oklahoma (May 2013), as well as from durophagous teeth from the middle Permian marine Kaibab Formation in the US southwest (Hodnett et al. 2013). Hybodonts are believed to be marine in origin, but representatives of several genera are known from freshwater or brackish deposits (Capetta 1987; Duffin 1985; Fischer 2008, Peacock et al. 2018). The Permian taxon *Wodnika* (Munster 1843), originally assigned to the Hybodontidae but now more likely a sphenacanthid (Maisey 1982), is known from skeletal remains, spines, and teeth. However, in general, hybodont remains from this period are more commonly teeth or spines, as is the case with *Arctacanthus* (Nielsen 1932), but generally freshwater Permian hybodonts were fairly small, as exemplified by the former waste-basket genus *Lissodus*. *Lissodus africanus* (Broom 1909) has been described from the Early-Middle Triassic *Cynognathus* AZ in the Karoo Basin, including skeletal material, though the specimen was initially described as *Hybodus africanus*, based on similarities of the dorsal fin spines with the genus *Hybodus* including characteristic ridging and posterior denticles. The denticle distribution on fin spine NHMUK PV 75423a appears somewhat similar to that of the genus *Asteracanthus*, but the denticles are not star-shaped in aspect (Capetta 1987); however, this could be due to taphonomic wear. Importantly, all of the specimens are broken or obscured by matrix where they would have inserted on the dorsum of the shark, so it is not possible to determine how the costae originate (whether they are bifurcations or additions from the posterolateral margins). However, the spine may also be similar to that of *Sphenacanthus*, which has similar ribbing between costae (Agassiz 1837), but lacks down curved posterior denticles (Maisey 1982). Sphenacanthids were also inhabitants of freshwater, and have been described from the Permian Rio do Rasto Formation (Pauliv et al. 2012).

5.2 Actinopterygian Material

The actinopterygian material is limited in both quantity and preservation. However, what is available indicates morphological similarity (if not taxonomic identity) with *Namaichthys* and *Bethesdaichthys* from the Karoo Basin, South Africa. *Namaichthys* and *Bethesdaichthys* were recovered as phylogenetically distinct in the analysis of Bender (2002), though the tree is generally poorly resolved. However, given the lack of resolution in ‘lower’ actinopterygian phylogeny (Giles et al. 2017) and the lack of inclusion of these taxa in more recent analyses, phylogenetic interpretations of both these taxa and this material are not practicable at this time. Further collecting and study will likely supersede the highly provisional identifications and interpretations made here.

6. Conclusions

6.1 Chondrichthyan Remains

The combination of chondrichthyan taxa reported here is interesting, not only for potential ecological inference but also because of the taxonomic diversity present. These represent the first xenacanth and putative ctenacanth fin spines (as well as potentially sphenacanthid or hybodont fin spines) recorded from the Madumabisa Mudstone Formation. As is often the case in chondrichthyan paleontology, without pristine preservation of spine ornamentation, and without associated dentition, these fossils cannot be placed below the family or superfamily level. Interestingly, xenacanths, ctenacanths, and hybodonts all persisted through the end-Permian extinction, and hybodonts survived well into the Cretaceous (Zangerl, 1981).

6.2 Osteichthyan Remains

Insofar as the actinopterygian material can be identified, it indicates a link to the ichthyofauna of the lower Beaufort Group, which agrees with the similarity previously noted for the corresponding tetrapod assemblages (Sidor et al. 2013; Peacock 2016; Bernardi et al. 2017; Roopnarine et al. 2018). However, there is as yet no evidence of *Blourgia* or a similar deep-bodied form in Zambia, which may suggest potential palaeoecological and palaeoenvironmental differences between the faunas. While the nature of the material limits severely limits comparisons, none of the unnamed species from the Rio do Rasto formation described by Vega-Diaz et al. (2000)- or similar fishes- appear to be present. This supports the hypothesis that there was biogeographic differentiation of nonmarine osteichthyan faunas by at least this point in the Permian. The Permian ichthyofauna of Chile (Richter and Breitkreuz 1997) is a possible further point of comparison if more material becomes available. The material does also raise the currently remote- possibility a coelacanth (P75415b, numbered side, see Fig. 7A) taxon is present, one comparable in size to the largest actinopterygian fishes present. If correct, it would represent the first coelacanth occurrence in the Madumabisa Mudstone Formation. However, the circumstantial nature of this evidence must be strongly emphasized.

6.3 Summary

Although the fragmentary nature of the Zambian material precludes detailed conclusions, the fossils described in this contribution allow for the following broad inferences to be made:

- 1) The taxonomic composition of the ichthyofaunas suggest entirely freshwater communities, in accordance with data on the development of these basins (Catuneanu et al. 2005).

- 2) The composition of the Madumabisa Mudstone ichthyofauna is consistent with freshwater ichthyofaunas globally in the middle and late Permian, at least to the level of taxonomic resolution available: xenacanth, and possibly hybodont and ctenacanth, chondrichthyans, at least two taxa of actinopterygians, and possibly a coelacanth. This observation parallels the better sampled tetrapod fossil record, which suggests a regionally homogenous fauna across southern Pangea during middle-late Permian times (Sidor et al. 2013).
- 3) More complete material will be needed to assess the ecology of the Permian fish of Zambia, although it is clear that some fossils represent large-bodied forms.
- 4) Freshwater ichthyofaunas are likely under-reported, especially during comparatively uneventful periods in fish or Earth history, but more work will be needed if the dynamics leading to modern freshwater biodiversity are to be understood. Yemane and Kelts (1990) noted that lacustrine systems were widespread and might have been the predominant deposition environment during the middle/late Permian in southern Africa, which is a promising avenue for future research.

7. Acknowledgments

Special thanks to T. Kemp for access to the specimens when they were still at Oxford in 2015, and to NHMUK curators M. Day and E. Bernard who facilitated loans of the material. Research on the Permian vertebrate fauna of Zambia has been supported by the National Geographic Society (grant 8571-08 to J. S. Steyer; 8962-11 to CAS; 158R-18 to BRP), The Grainger Foundation and Field Museum/IDP Foundation, Inc. African Partners Program (to K. D. Angielczyk), and the National Science Foundation (DDIG 1501097 to BRP; EAR-1337569 to CAS; EAR-1337291 to K. D. Angielczyk; EAR-1336986 to P. D. Roopnarine). We thank M. Whitney for assistance with thin-sectioning and C. Shin for illustrating the specimen in Figure 7A.

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Figure Legends

Fig 1. Map of Permo-Triassic basins in Zambia with the positions of the upper Permian (A) and middle Permian (B) fossil fish localities marked with circles, with the stratigraphic position of the Madumabisa Mudstone Formation below. Approximate ages of Madumabisa Mudstone fossil assemblages based on biostratigraphic correlation with Karoo Basin Assemblage Zones, with lighter shading denoting a more confident correlation. Black stars indicate radiometric dates for fossiliferous horizons in the Karoo Basin (Rubidge et al. 2013).

Fig 2. Upper Permian chondrichthyan fin spines from the upper Madumabisa Mudstone Formation (Luangwa Basin; Lopingian). NHMUK PV P75419, photographs of xenacanthiform fin spine in anterior (A), right lateral (B), posterior (C), and left lateral (D) views. Magnified photographs of lateral costae (E), and posterior surface with posterior denticles along the lateral margins (F). NHMUK PV P75423, photograph of ornamented elasmobranch dorsal fin spine in anterior (G) and right lateral (H) views. NHMUK PV P75421a, base of dorsal fin spine in left lateral (I) and right lateral (J) views.

Fig 3. Detailed images of the euselachian (possibly synechodontiform) fin spine NHMUK PV 75423, showing anterior (A) and lateral (B) views of ornamentation. Scale = 2 mm.

Fig 4. Cross sectional breaks through NHMUK PV 75420 (A), NHMUK 75422a (B) and 75422b (C) showing concave posterior surfaces and tubular dentine in NHMUK PV 75420. Detail of

1193 ornamentation of NHMUK PV 75420 (D). A, C, and D posterior to top, B anterior to top. Scale
1194 = 2 mm.

1195

1196 **Fig 5.** Detailed images of the probable xenacanthid fin spine NHMUK PV 75419, showing fine
1197 costae (A) in lateral view, and posterior tubercles (B) in posterior view. Scale = 2 mm.

1198

1199 **Fig 6.** Upper Permian Actinopterygii indet. fossils from the upper Madumabisa Mudstone
1200 Formation (Luangwa Basin; Lopingian). NHMUK PV P79415a, actinopterygian maxilla. (A)
1201 Specimen photograph with maxilla bone and natural mold in outline, and line drawing (B). (C)
1202 Photograph highlighting preserved tooth with its position on the maxilla noted and line drawing
1203 (D). NHMUK PV P79415a, actinopterygian dermal bones. (E) Specimen photograph with
1204 dermal cranial bone and natural mold in outline, and line drawing (F). NHMUK PV P75399,
1205 actinopterygian articulated scales, fin rays, and body outline. (G) Line drawing of articulated body
1206 section, and specimen photograph with outline (H).

1207

1208 **Fig 7.** Upper Permian actinopterygian scales showing different scale morphotypes from the
1209 upper Madumabisa Mudstone Formation (Luangwa Basin; Lopingian). (A) NHMUK PV
1210 P75415b and (B) NHMUK PV P75416b showing Morphotype 1. (C) NHMUK PV P75416b and
1211 (D) NHMUK PV P75415c showing Morphotype 2. (E) NHMUK PV P75416a showing
1212 Morphotype 3. (F) NHMUK PV P75416a opposite side showing Morphotype 4.

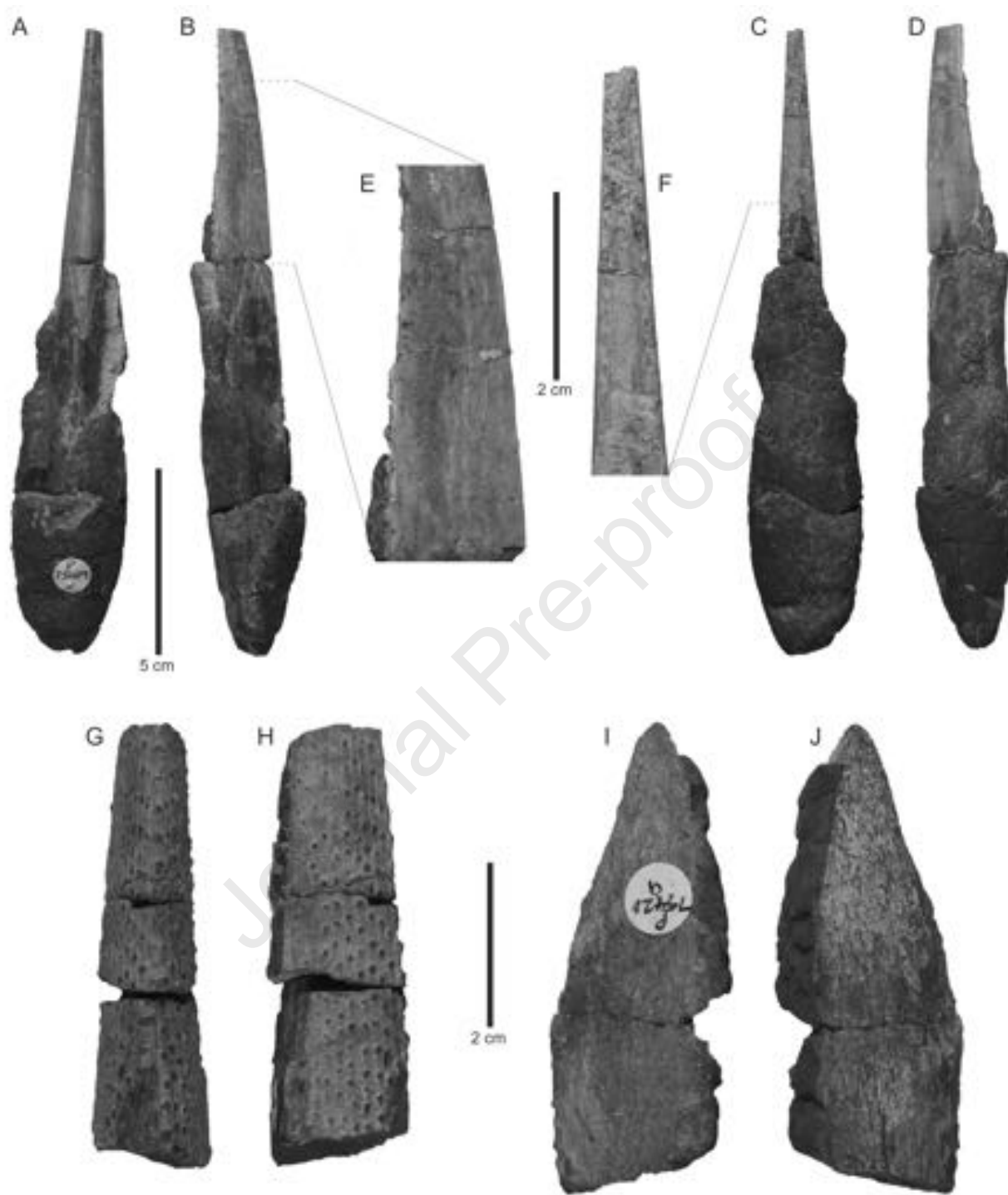
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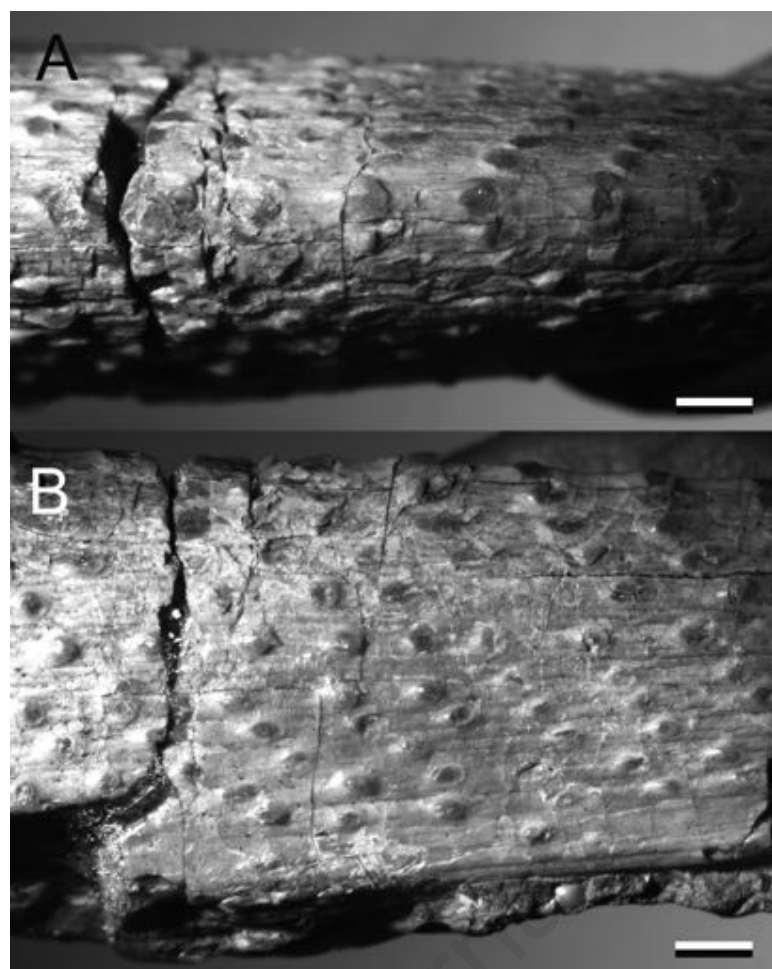
1214 **Fig 8.** Middle Permian Actinopterygii indet. (NHCC LB597) fossils from the lower
1215 Madumabisa Mudstone Formation (Mid-Zambezi Basin; Guadalupian). (A) Isolated scale and

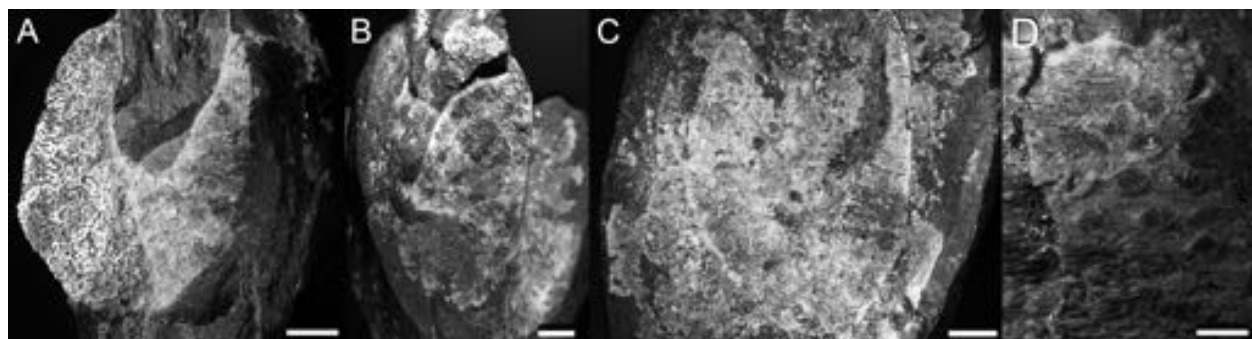
1216 interpretative drawing in external view. (B) Group of articulated scales in external view. (C)
1217 Thin section of entire scale under polarized light. (D) Higher magnification view of orthodentine
1218 and capping tissues, with cellular bone visible near the bottom of the image. **Anatomical**
1219 **abbreviations:** **b**, bone; **d**, dentine; **e**, enamel; **vc**, vascular canal. Scale bars represent 1 cm (A
1220 and B), 1 mm (C) and 100 μ m (D).

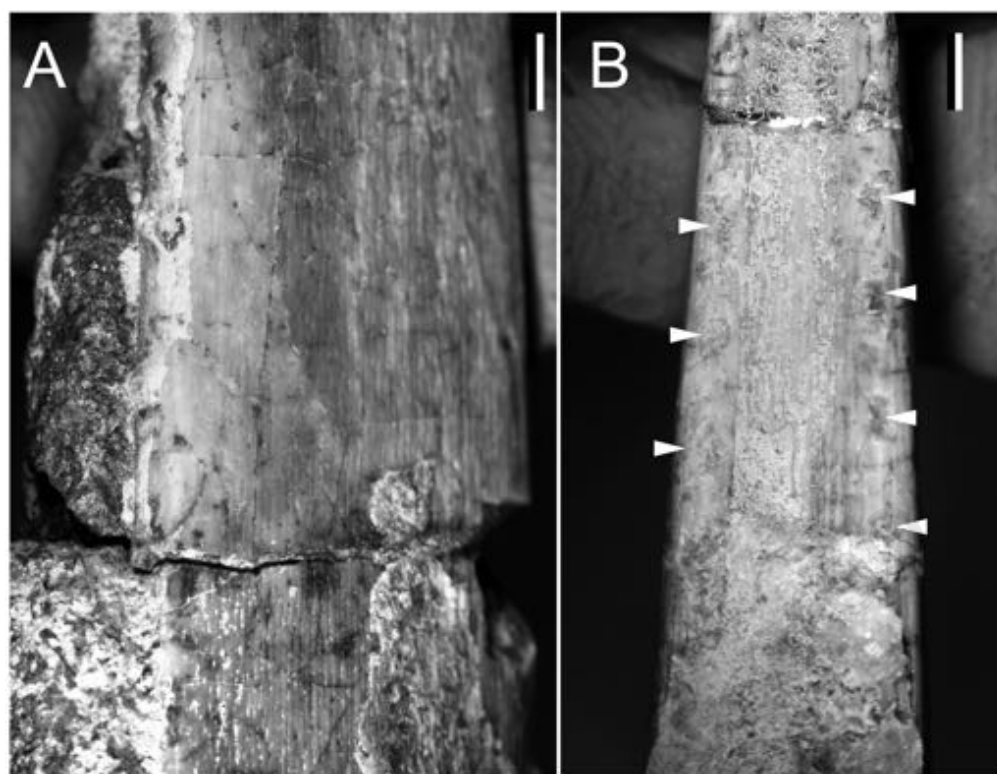


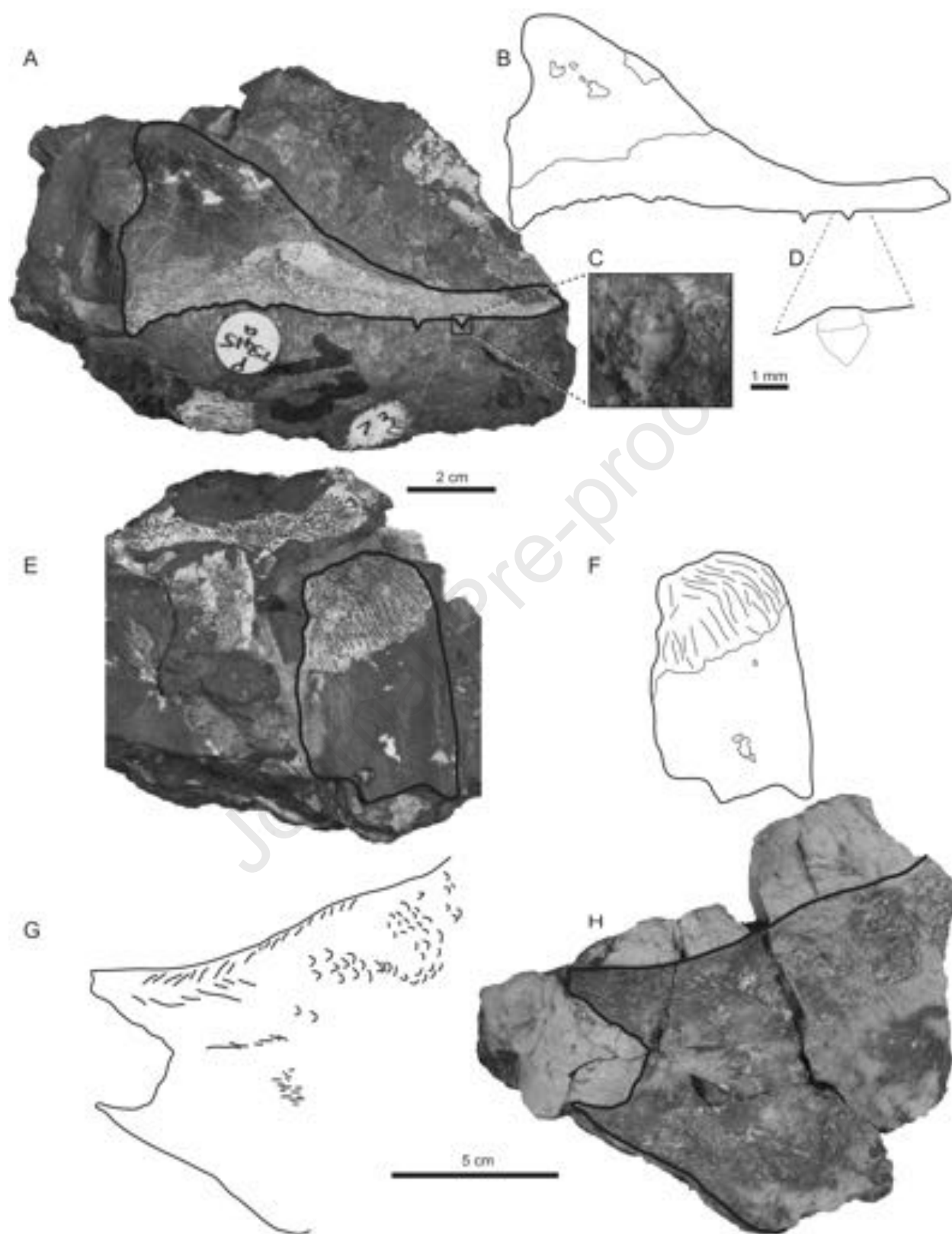
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|-------------|---------------|--------------------------|-------|---------------------------------|
| | 252.3 | upper | | |
| Lopingian | Changhsingian | <i>Daptocephalus</i> | lower | Upper Madumabisa Mudstone |
| | 254.1 | ★ <i>Cistecephalus</i> | | |
| | Wuchiapingian | ★ <i>Tropidostoma</i> | | |
| Guadalupian | 259.8 | ★ <i>Pristerognathus</i> | | |
| | Capitanian | <i>Tapinocephalus</i> | | Lower Madumabisa Mudstone |
| | | Assemblage Zone | | |
| | 265 | | | |

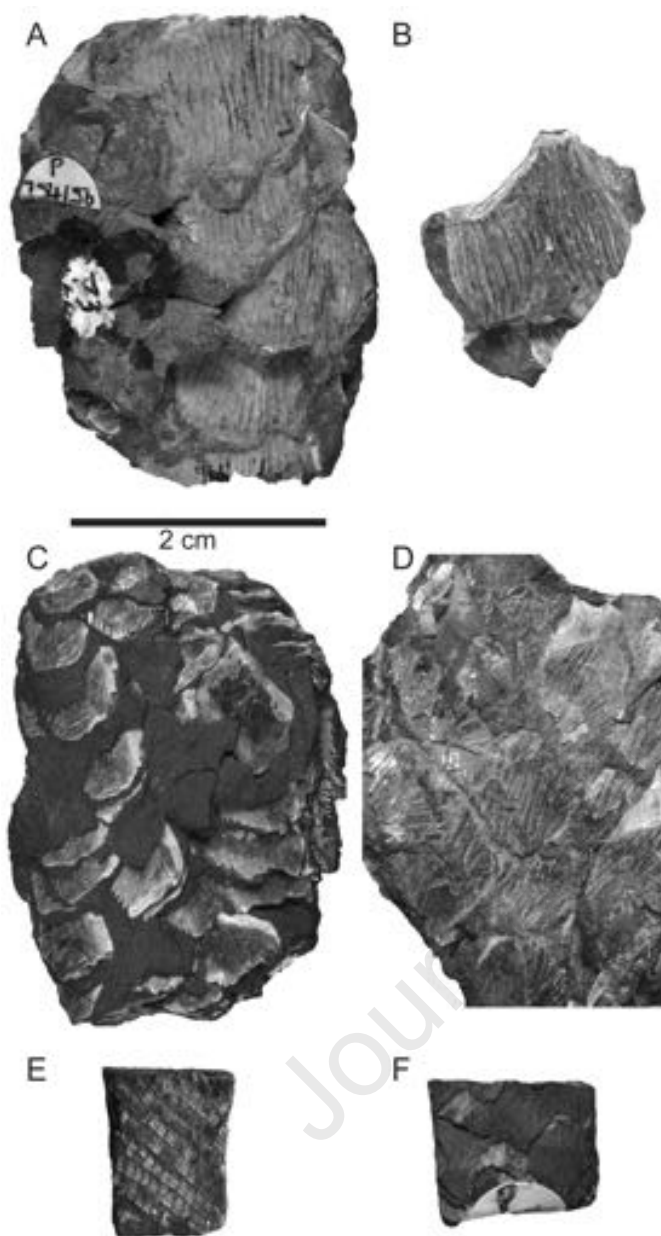


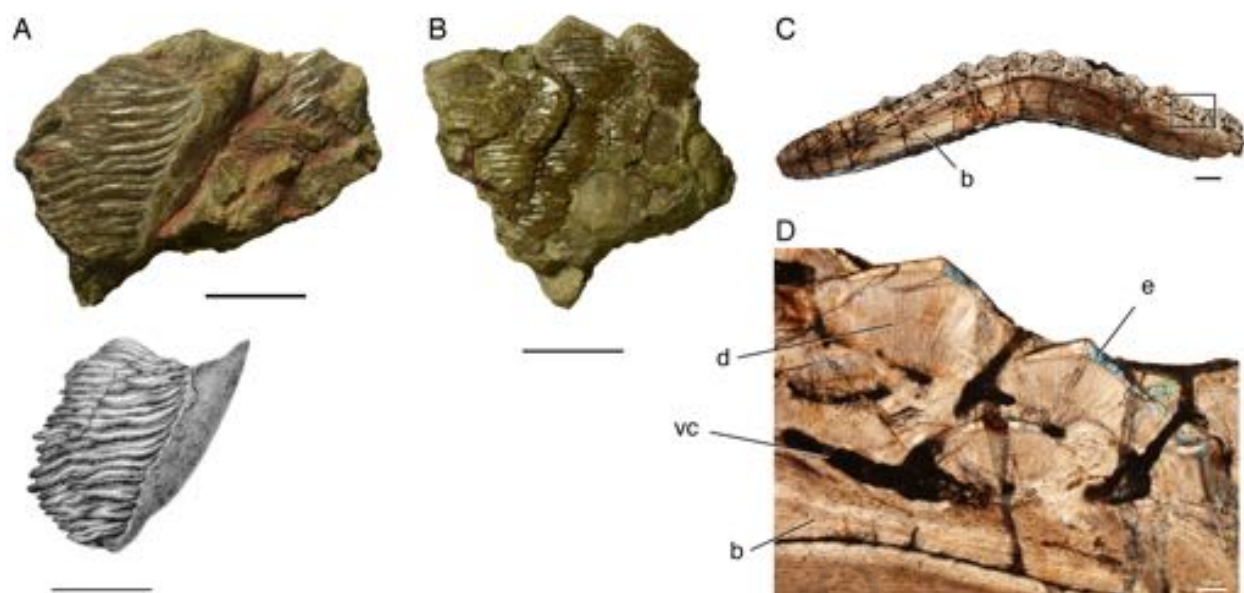












Highlights

FRESHWATER FISH FAUNAS FROM TWO PERMIAN RIFT VALLEYS OF ZAMBIA,
NOVEL ADDITIONS TO THE ICHTHYOFAUNA OF SOUTHERN PANGAEA

Peacock, Bronson, Otoo, & Sidor

- New freshwater vertebrate occurrences for the well-sampled Permian of Zambia
- Freshwater sharks (synechodontiform, xenacanth, hybodontiform) & ray-finned fishes
- Freshwater ichthyofaunas show patterns of faunal homogeneity across Permian Pangaea
- Zambian ichthyofaunas compared with Chile, Brazil, South Africa, & Australia

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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