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A new record of *Procynosuchus delaharpeae* (Therapsida: Cynodontia) from the Upper Permian Usili Formation, Tanzania

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Procynosuchus, the best-known Permian cynodont, has a remarkably broad geographic range, with records stretching from southern Africa to Europe. Fossils of *Procynosuchus* are most common in the Upper Permian *Dicynodon* Assemblage Zone of South Africa, but also occur in coeval East African rocks. Currently, there is one documented occurrence from the Madumabisa Mudstone Formation of Zambia, and two specimens from the Usili (=Kawinga) Formation of Tanzania. The Tanzanian specimens include a poorly preserved, incomplete skull and a partial cranium originally attributed to *Parathrinaxodon proops.* The latter is now considered a subjective junior synonym of *Procynosuchus delaharpeae.* Here we report on a new specimen collected in 2007 near the base of Kingori Mountain in Tanzania. It preserves the postorbital region of the skull and the posterior portions of both lower jaws, each containing several intact teeth. A well-preserved postcanine tooth exhibits the dental hallmarks of *Procynosuchus* and permits unambiguous referral to this taxon. Recent fieldwork corroborates previous suggestions that the Usili tetrapod fauna includes representatives of the *Tropidostoma, Cistecephalus* and *Dicynodon* assemblage zones of South Africa. Moreover, the presence of several endemic Usili taxa (e.g. *Katumbia, Kawingasaurus, Peltobatrachus*), suggests that a straightforward correlation between the Usili tetrapod fauna and a particular assemblage zone from the Beaufort Group may not be possible.

Keywords: *Procynosuchus,* Cynodontia, Permian, Tanzania, Usili Formation, Songea Group, Ruhuhu Basin.

INTRODUCTION

Cynodonts were the last major group of therapsids to diversify in the Permian, first appearing in the *Tropidostoma* Assemblage Zone of South Africa (Botha *et al.* 2007; Botha & Abdala 2008). They underwent a second radiation in the Triassic, diversifying into a wider range of body sizes and, presumably, ecological niches (Rubidge & Sidor 2001; Kemp 2005). With Mammalia as its extant subclade, Cynodontia is key for understanding the timing of the acquisition of numerous mammalian features, such as multicusped postcanines, a bony secondary palate, wide zygomatic arches, and a masseter muscle (Hopson & Barghusen 1986; Abdala & Damiani 2004; Sidor & Smith 2004).

Procynosuchus has been considered the first cynodont to attain a global distribution (Sues & Boy 1988; Abdala & Allinson 2005). The genus is well represented in the Beaufort Group of South Africa, especially in the *Dicynodon* Assemblage Zone, but less so elsewhere. In Germany, isolated postcanine teeth referred to *Procynosuchus* sp. have been recovered from the fissure-fill deposits within the lower Zechstein (Sues & Boy 1988; Sues & Munk 1996). Kemp (1979, 1980) described a nearly complete skeleton collected from the Madumabisa Mudstone Formation of Zambia. Finally, two specimens have been recorded from Tanzania: a fragmentary skull described by von Huene (1950) and a specimen that Parrington (1936) originally attributed to *Parathrinaxodon proops* (Gay & Cruickshank 1999; Abdala & Allinson 2005). Von Huene's specimen preserves the snout, but neither the braincase nor postorbital regions of the skull. Parrington's fossil is more complete, but lacks the zygomatic arches and the dorsal and posterior portions of the braincase. Neither Tanzanian specimen preserves the lower jaw.

Here we report on *Procynosuchus* material recently collected from the Upper Permian of Tanzania. Its identification lends further support to Abdala & Allinson's (2005) conclusion that *Procynosuchus* was widespread in southern Gondwana near the end of the Permian, and that only a single cynodont genus was present in the Usili (=Kawinga) Formation.

GEOLOGICAL SETTING

The main Karoo Basin of South Africa is a retro-arc foreland sag basin first formed in the Late Carboniferous in response to compressional thrusting and crustal loading along the subducting southern margin of Gondwana (Johnson *et al.* 1996). The basin was fairly continuously infilled with terrestrial sediments until the Early Jurassic, after which the tectonic regime switched to one of extension as eastern Gondwana began to break up. At the time of the infilling of the Karoo Basin, the crust to the north was subjected to several extensional phases punctuated by quiescence, forming a series of pull-apart rifts, grabens and half grabens filled with locally derived terrestrial sediments. Today, these small fault-bounded basins occur in a roughly NE/SW trending corridor extending from the coast of Kenya through Tanzania, Malawi and Zambia, and terminating in Zimbabwe. The best and most complete

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exposures of Karoo-aged strata in these fault bounded basins are located in the Ruhuhu Basin, which is situated in southern Tanzania (Stockley & Oates 1931; Stockley 1932; Kreuser 1990; Kaaya 1992; Wopfner 2002; Catuneanu *et al.* 2005).

Within the Ruhuhu Basin, the rocks of the Songea Group range in age from Late Carboniferous to Middle Triassic and have been divided into six formations and one informally recognized unit (viz. Idusi, Mchuchuma, Mbuyura, Mhukuru, Ruhuhu and Usili formations and the informal Manda Beds, Wopfner 2002; Fig. 1). The Usili Formation (formerly K6 or Kawinga Formation) is considered Late Permian in age (Parrington 1936; Wopfner & Kreuser 1986; Wopfner 2002) and comprises alluvial fan conglomerates at the base followed by playa lake deposits of green and red mudrocks with interbedded fluvial siliciclastics (Wopfner & Markwort 1991).

The Usili Formation has been correlated with the Balfour and/or Teekloof formations of the South African Beaufort Group (Adelaide Subgroup) on the basis of their shared tetrapod fauna (Gay & Cruickshank 1999; Wopfner 2002; Catuneanu *et al.* 2005). In particular, dicynodonts such as *Dicynodon, Dicynodontoides* (formerly *Kingoria*; see Angielczyk *et al.*, in press), *Oudenodon* and *Rhachiocephalus* suggest a broad temporal correspondence between the Ruhuhu Basin and the upper parts of the Karoo Permian sequence (Angielczyk 2007; Angielczyk *et al.*, in press).

MATERIALS AND METHODS

The present specimen, NMT RB3, was collected in the Usili Formation near the base of Kingori Mountain in June, 2007. It was partially prepared at the South African Museum, with final cleaning at the Burke Museum of Natural History. Comparative data for *Procynosuchus* was based mainly on Parrington (1936), Broom (1938), Kemp (1979) and Abdala & Allinson (2005), with supplementary data from von Huene (1950) and Kemp (2005).

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Cynodontia Owen, 1861

Procynosuchus delaharpeae Broom, 1937

Holotype. RC 5, well-preserved cranium missing the temporal arches and anterior portion of the premaxilla.

Diagnosis. Cynodont with shallow fossa positioned high on lateral surface of coronoid process, multicusped lingual cingulum on lower postcanines and absence of labial cingulum, interpterygoid vacuity relatively broad (modified from Kemp 1979).

Referred specimen. NMT RB3, which consists of the postorbital portion of skull, posterior portions of both mandibles, and an isolated postcanine tooth.

Locality. Usili Formation, Songea Group, Ruhuhu Basin. Present specimen collected near the base of Kingori Mountain, Songea District, Tanzania at the following coordinates: 10°14.293'S, 35°3.591'E. This is in the general vicinity of Stockley's (1932) locality B19 and Nowack's (1937) Kingori Mountain localities, although both have proven difficult to relocate precisely.

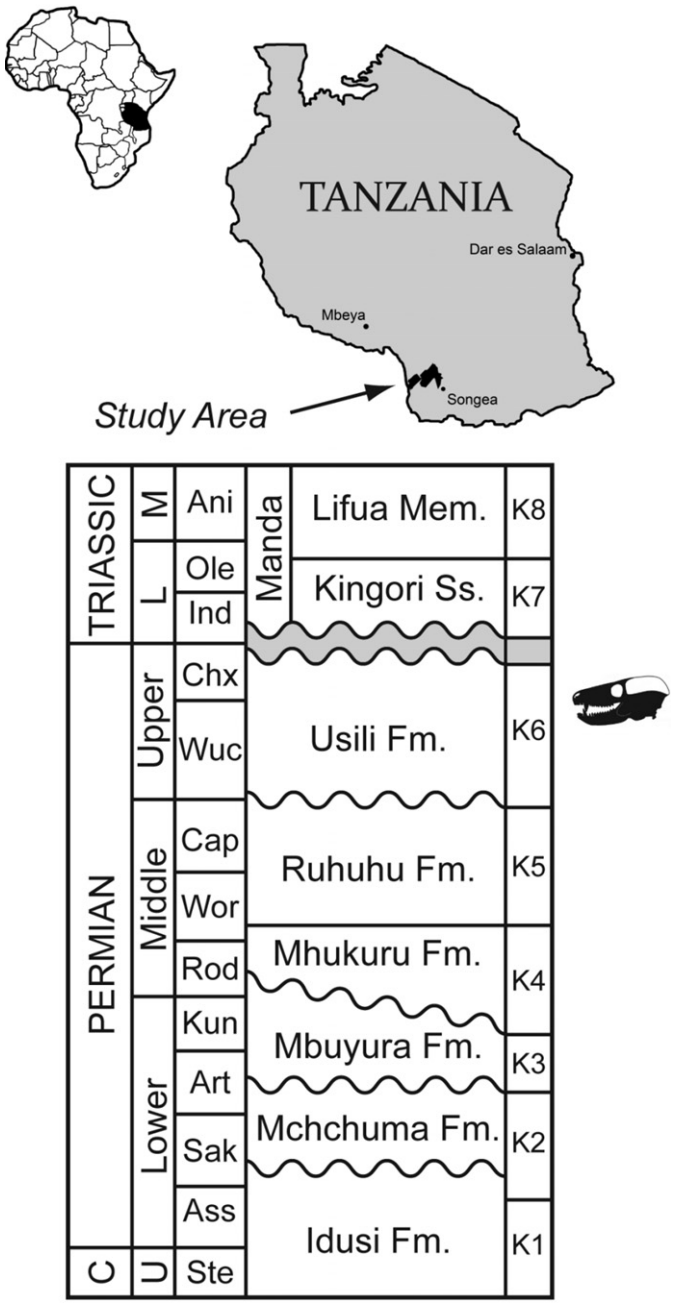

Figure 1. Generalized geology and geography of the Songea Group (Ruhuhu Basin). Correlations between lithostratigraphy and marine stages based on Wopfner (2002). Skull icon (modified from Hopson, 1994) denotes approximate stratigraphic position of *Procynosuchus*.

DESCRIPTION

General preservation

The partial cranium consists of the intertemporal region, the caudal part of the left zygomatic arch, and much of the braincase and occiput. Posterior sections of both lower jaws are also preserved, with both dentaries retaining postcanine teeth. In addition, a beautifully preserved postcanine was found suspended in matrix next to the parietal foramen.

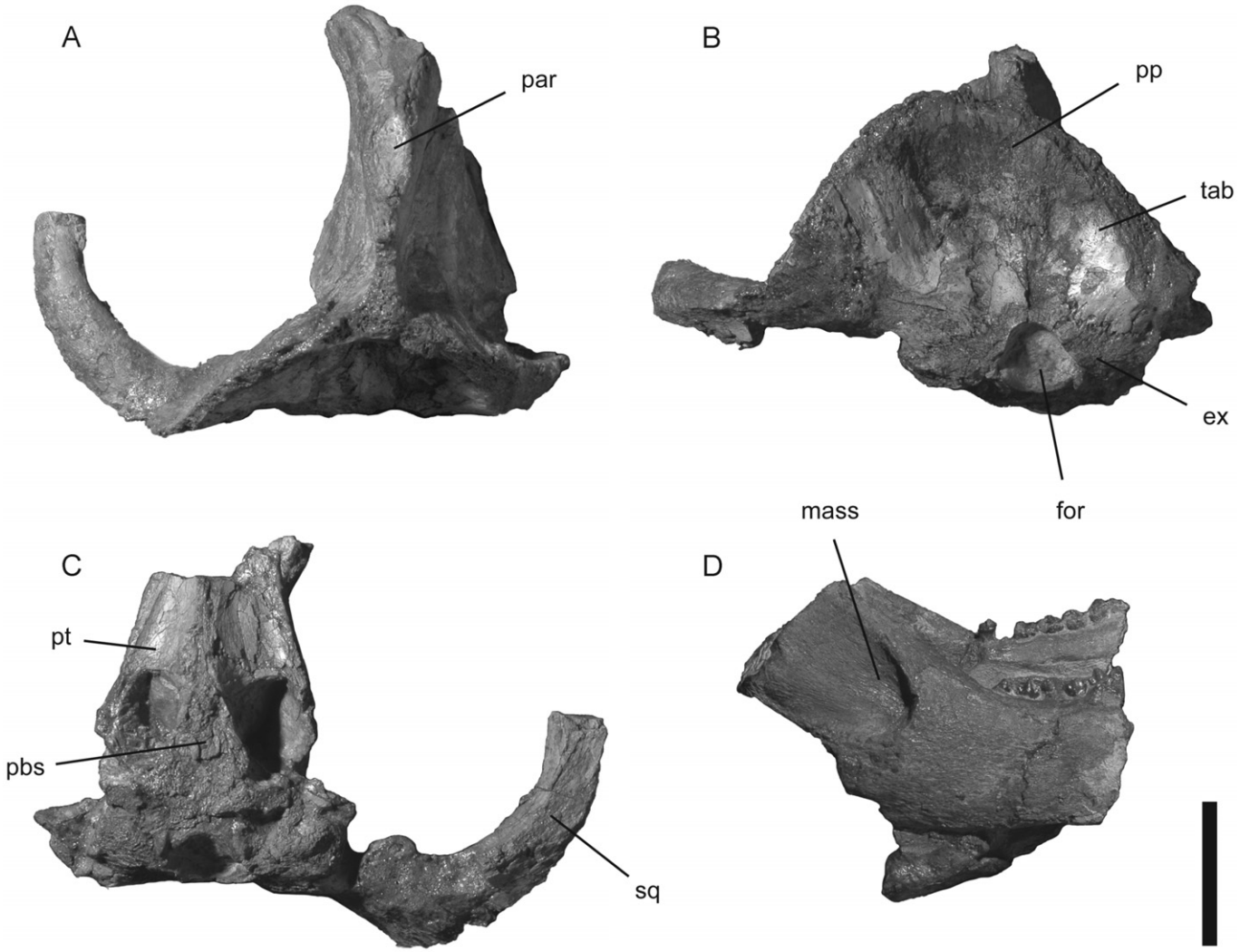

Figure 2. Partial skull of *Procynosuchus delaharpeae* (NMT RB3) in (**A**) dorsal, (**B**) occipital and (**C**) ventral views. Posterior portions of lower jaws of the same specimen in right lateral view (**D**). Scale bar = 2 cm.

Temporal region

Despite its fragmentary nature, the specimen retains the broad outlines of a cynodont temporal region in dorsal view, with a narrow sagittal crest between enlarged temporal fenestrae (Fig. 2A). An oval parietal foramen is incorporated into the sagittal crest, and is about twice as long as it is wide. Part of the temporal ramus of the left postorbital is preserved overlying the corresponding parietal. A midline suture between the parietals is impossible to discern, which, along with the specimen's large size, suggests that the fossil pertains to a mature individual. Comparison with complete skulls of *Procynosuchus* suggests a skull length of approximately 140 mm for NMT RB3.

The confluence of the sagittal and lamboidal crests is eroded dorsally, but more laterally the parietal-squamosal suture is visible on the left side and conforms to the arrangement shown in Kemp (1979, fig. 3). The posterior half of the left zygomatic arch is present. It is formed primarily by the squamosal, but a small wedge of the jugal remains attached to its medial surface. The ventral margin of the squamosal is weathered and incomplete.

Beneath the parietal, the medial wall of the temporal fenestra is formed by the descending lamina of the parietal, as well as by the expanded epipterygoid characteristic of cynodonts (Hopson & Barghusen 1986; Sidor & Smith 2004). The latter element is trapezoidal in outline, with its free anterior edge inclined anterodorsally and its more vertical, posterior margin sutured to the prootic. The venous channel is well developed on both sides, but is positioned relatively lower than depicted by Kemp (1979: fig. 16).

Basicranium

In ventral view, the braincase and posterior portion of the palate are present (Fig. 2C). The basicranial rami of the pterygoids are separated from one another by a very narrow interpterygoid vacuity. As noted by Kemp (1979), the retention of an interpterygoid vacuity is characteristic of *Procynosuchus* among cynodonts, although the relatively large opening present in the specimen that he described (TSK34) suggests that it belongs to a juvenile individual (Abdala & Allinson 2007; see also van Heerden 1972). Immediately anterior to the vacuity, the medial borders of the pterygoids are pinched together into a midline crest.

The cultriform process of the parasphenoid is visible for a short distance between the basipterygoid processes, before it disappears above the pterygoids. Further posteriorly, the ventral surface of the parabasisphenoid complex is quite eroded, such that internal carotid foramina are not

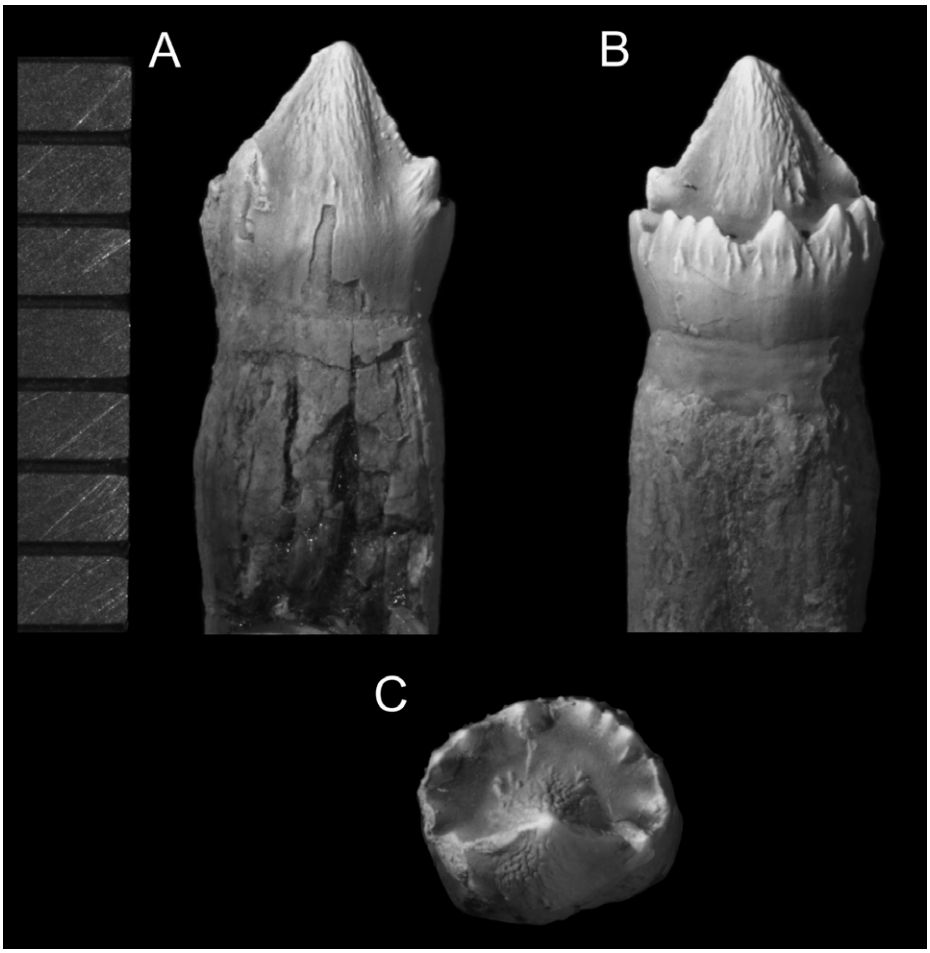

Figure 3. Isolated lower postcanine tooth of *Procynosuchus delaharpeae* (NMT RB3) in (**A**) labial, (**B**) lingual, and (**C**) occlusal views. Scale bar divisions in mm.

apparent. Additionally, both the external surface of the basioccipital as well as the entirety of the occipital condyles is missing. On the left side, the rugose lateral margin of the fenestra ovalis is preserved, along with part of the lateral process of the prootic.

Occiput

The occiput is nearly vertical and well preserved (Fig. 2B). The tabulars and supraoccipital form the bulk of the occipital surface and together create a large concave surface for the attachment of cervical muscles. Erosion has reduced the total height of the occiput, but the postparietal is still clearly visible above the supraoccipital. The upper margin of the foramen magnum is well preserved and formed by the supraoccipital. The dorsolateral margins of the foramen magnum are formed by the exoccipitals, but ventrally the occipital condyles are eroded away, leaving the eroded basioccipital on the ventral midline. Lateral to the foramen magnum, a suture separating the exoccipital and paroccipital process of the opisthotic is not discernible. The dorsal rim of the left post-temporal fenestra is intact and formed by the tabular.

Mandibles

The posterior portions of both mandibles were found closely associated, but displaced and positioned within the left temporal fenestra. As prepared, there are a few millimeters of matrix between the right and left rami, making identification of postdentary bones such as splenial and articular difficult. However, next to the ventral face of the left mandibular ramus is a thin sheet of bone attached to the matrix. We interpret this element as the left splenial, or possibly angular, that has slipped ventrally.

The lateral surface of both dentaries is completely exposed. On the right side (Fig. 2D), a conspicuous masseteric fossa is located relatively high on the coronoid process of the dentary, as is typical for *P. delaharpeae* and *Dvinia prima* (Tatarinov 1968: fig. 5; Kemp 1979: fig. 6). The horizontal rami of both dentaries are broken approximately halfway along their length.

Dentition

The right dentary retains five intact postcanines (Fig. 2D) whereas the left retains six. Each postcanine conforms to the general dental pattern of *Procynosuchus,* with a dominant cusp flanked by anterior and posterior accessory cusps, and bordered lingually by a well-developed cingulum studded with fine cuspules (Kemp 1979). In occlusal view, the lingual cingulum gives the postcanines an oval section (i.e., longer mesio-distally than labio-lingually). A labial cingulum is absent. The penultimate tooth position on the left dentary is represented by an edentulous gap.

An isolated postcanine tooth was found suspended in matrix next to the sagittal crest. This tooth is nearly pristine

(Fig. 3), and although its original position cannot be determined with confidence, the presence of eight lingual cingulum cuspules suggests that it came from the posterior portion of the tooth row. For descriptive purposes, we consider this tooth to belong to the lower jaw, although the upper and lower postcanines of *Procynosuchus* generally are very similar. If this position is accepted, the anterior accessory cusp is broken. Beyond this, however, the crown lacks visible wear, and thus was likely newly erupted.

Fine crenulations are visible on the lingual aspect of the main cusp as well as below the lingual cuspules. Similar crenulations are visible on the labial face of the principle cusp, but these are somewhat more muted. Interestingly, the crenulations were hardly visible before the specimen was smoked with magnesium for photography. Kemp (1979) makes no mention of enamel crenulations in his description, and we are unaware of this feature's recognition in the literature.

The crown is separated from its single, long root by a slight narrowing at the cervix. As preserved, the root forms approximately two-thirds of the total height of the tooth.

DISCUSSION

All of the available craniodental evidence indicates that NMT RB3 pertains to the well-known Permian cynodont *Procynosuchus.* For example, the lower postcanine teeth exhibit a dominant main cusp flanked by small anterior and posterior accessory cusps as well as a denticulated lingual cingulum (Kemp 1979). Likewise, the relatively small masseteric fossa, which does not reach the ventral edge of the dentary, corroborates its referral to *Procynosuchus,* although *Dvinia* also retains this feature (Tatarinov 1968).

NMT RB3 confirms the presence of *Procynosuchus* in the upper half of the Usili Formation. Unfortunately, because the specimen was found *ex situ,* we cannot place its occurrence more precisely. However, the specimen was found in close proximity to several partial gorgonopsian skulls, as well as a short-faced, tusked dicynodont likely referable to '*Dicynodon*', and a snout of the therocephalian *Theriognathus.* As noted by Angielczyk *et al.* (2008), our field observations have failed to find evidence for more than one tetrapod assemblage within the Usili Formation (contra von Huene 1950). The dicynodont component of the fauna is particularly uniform throughout the thickness of the formation, given our field observations and locality information available for specimens in museum collections.

Gay & Cruickshank (1997), Abdala & Allinson (2005) and Angielczyk (2007) all made note of the interesting mix of widespread [e.g. *Endothiodon, Kingoria* (now *Dicynodontoides*; Angielczyk *et al.,* in press), *Oudenodon*] and endemic (e.g. *Kawingasaurus, Katumbia, Peltobatrachus*) taxa recovered from the Usili Formation. The Usili fauna is also remarkable in its apparent lack of several genera commonly found in the Beaufort Group of South Africa (e.g. *Diictodon, Emydops*). One potential factor affecting faunal composition could be the influence of basin subsidence rates (e.g. retroarc sag basin in the Karoo versus fault-bounded rift in the Ruhuhu). The sedimentary facies of the Usili Formation show that initially high-energy alluvial fans prograded from the bounding fault scarps, depositing tongues of reworked conglomeratic sand into the margins of a deep stratified axial lake (see Wopfner 2002).

Later, as subsidence slowed, the alluvial fans amalgamated to form a fairly continuous alluvial plain with meandering channels and expansive floodplains dotted with shallow playa lakes. Under semi-arid climatic conditions, these floodplains likely supported perennial vegetation, including glossopterid trees, shrubs and ferns. The tetrapod fossils occur in two main taphonomic modes: concentrated pockets of disarticulated and broken elements in the basal conglomerates, and as isolated, more complete skeletons within the floodplain fines. The conglomerates contain numerous stromatolitic carbonate nodules that have clearly been eroded from the underlying Ruhuhu mudstones during a hiatus in sedimentation. It is likely that the bone concentrations were also generated at the same time as the conglomerates and as such they represent a much larger time interval than the overlying mudrock-hosted skeletons. However, despite this likely difference in time-averaging, there is no significant difference in the faunal composition of the two types of bone occurrence. Regardless of its basis, the Usili tetrapod fauna is unique and straightforward correlation with a particular assemblage zone of the Beaufort Group may not be possible.

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ABBREVIATIONS

Institutional

NMT	National Museum of Tanzania, Dar es Salaam
RC	Rubidge Collection, Graaff-Reinet
TSK	Collection of Thomas Kemp, currently housed in the Oxford University Museum of Natural History

Stratigraphic

Ani	Anisian
Art	Artinskian
Ass	Asselian
C	Carboniferous
Cap	Capitanian
Chx	Changhsingian
Fm	Formation
Ind	Induan
Kun	Kungurian
L	Lower
M	Middle
Mem	Member
Ole	Olenekian
Rod	Roadian
Sak	Sakmarian
Ss	Sandstone
Ste	Stephanian
Wor	Wordian
Wuc	Wuchiapingian

Anatomical

ex	Exoccipital
for	Foramen magnum
mass	Masseteric fossa
par	Parietal foramen
pbs	Parabasisphenoid
pp	Postparietal
pt	Pterygoid
sq	Squamosal
tab	Tabular

REFERENCES

ABDALA, F. & ALLINSON, M. 2005. The taxonomic status of *Parathrinaxodon proops* (Therapsida: Cynodontia), with comments on the morphology of the palate in basal cynodonts. *Palaeontologia africana* **41**, 45–52.

ABDALA, F. & DAMIANI, R. 2004. Early development of the mammalian superficial masseter muscle in cynodonts. *Palaeontologia africana* **40**, 23–29.

ANGIELCZYK, K.D. 2007. New specimens of the Tanzanian dicynodont '*Cryptocynodon*' *parringtoni* von Huene, 1942 (Therapsida, Anomodontia), with an expanded analysis of Permian dicynodont phylogeny. *Journal of Vertebrate Paleontology* **27**, 116–131.

ANGIELCZYK, K.D., SIDOR, C.A., NESBITT, S.J., SMITH, R.M.H. & L.A. TSUJI. In press. Taxonomic revision and new observations on the postcranial skeleton, biogeography, and biostratigraphy of the dicynodont genus *Dicynodontoides,* the subjective senior synonym of *Kingoria* (Therapsida, Anomodontia). *Journal of Vertebrate Paleontology*

ANGIELCZYK, K.D., SIDOR, C.A., TSUJI, L.A., NESBITT, S.J. & R.M.H. SMITH. 2008. The Permo-Triassic dicynodont fauna of the Ruhuhu Basin, Tanzania: new discoveries and their implications. *Journal of Vertebrate Paleontology* **28** (supplement to 3), 46A.

BOTHA-BRINK, J. & ABDALA, F. 2008. A new cynodont record from the *Tropidostoma* Assemblage Zone of the Beaufort Group: implications for the early evolution of cynodonts in South Africa. *Palaeontologia africana* **43**, 1–6.

BOTHA, J., ABDALA, F. & SMITH, R. 2007. The oldest cynodont: new clues on the origin and early diversification of the Cynodontia. *Zoological Journal of the Linnean Society* **149**, 477–492.

BROOM, R. 1938. The origin of the cynodonts. *Annals of the Transvaal Museum* **19**, 279–288.

CATUNEANU, O., WOPFNER, O., ERIKSSON, P.G., CAIRNCROSS, B., RUBIDGE, B.S., SMITH, R.M.H. & HANCOX, P.J. 2005. The Karoo basins of south-central Africa. *Journal of African Earth Sciences* **43**, 211–253.

GAY, S.A. & CRUICKSHANK, A.R.I. 1999. Biostratigraphy of the Permian tetrapod faunas from the Ruhuhu Valley. *Journal of African Earth Sciences* **29**, 195–210.

HOPSON, J.A. 1994. Synapsid evolution and the radiation of non-eutherian mammals. **In**: D.B. Prothero & R.M. Schoch (eds), *Major Features of Vertebrate Evolution,* 190–219. Knoxville, Paleontological Society.

HOPSON, J.A. & BARGHUSEN, H. 1986. An analysis of therapsid relationships. **In**: N. Hotton, P.D. MacLean, J.J. Roth and E.C. Roth (eds), *The Ecology and Biology of the Mammal-like Reptiles,* 83–106 Washington, Smithsonian Institution Press.

JOHNSON, M.R., VAN VUUREN, C.J., HEGENBERGER, W.F., KEY, R. & SHOKO, U. 1996. Stratigraphy of the Karoo Supergroup in southern Africa: an overview. *Journal of African Earth Sciences* **23**, 3–15.

KAAYA, C.Z. 1992. Depositional environment of Late Permian Karoo beds in the Ruhuhu Basin and Mikumi area of Tanzania. *Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln* **83**, 1–125.

KEMP, T.S. 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* **285**, 73–122.

KEMP, T.S. 1980. The primitive cynodont *Procynosuchus*: structure, function and evolution of the postcranial skeleton. *Philosophical Transactions of the Royal Society of London B,* **288**, 217–258.

KEMP, T.S. 2005. *The Origin and Evolution of Mammals.* Oxford, Oxford University Press.

KREUSER, T. 1990. Permo-Trias im Ruhuhu-Becken (Tansania) und anderen Karoo-Becken von SE-Afrika. *Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln* **75**, 1–123.

NOWACK, E. 1937. Zur kenntniss der Karru-formation in Ruhuhu-Graben (D.O.A.). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie (Abt B)* **78**, 380–412.

PARRINGTON, F.R. 1936. On the tooth-replacement in theriodont reptiles. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* **226**, 121–142.

RAY, S., BOTHA, J. & CHINSAMY, A. 2004. Bone histology and growth patterns of some nonmammalian therapsids. *Journal of Vertebrate Paleontology* **24**, 634–648.

RUBIDGE, B.S. & SIDOR, C.A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics* **32**, 449–480.

SIDOR, C.A. & SMITH, R.M.H. 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology* **46**, 535–556.

STOCKLEY, G.M. 1932. The geology of the Ruhuhu coalfields, Tanganyika territory. *Quarterly Journal of the Geological Society* **88**, 610–22.

STOCKLEY, G.M. & OATES, F. 1931. Report on geology of the Ruhuhu Coalfields. *Bulletin of the Geological Survey of Tanganyika* **2**, 1–68.

SUES, H-D. & BOY, J.A. 1988. A procynosuchid cynodont from central Europe. *Nature* **331**, 523–524.

SUES, H-D. & MUNK, W. 1996. A remarkable assemblage of terrestrial tetrapods from the Zechstein (Upper Permian: Tatarian) near Korbach (northwestern Hesse). *Paläontogische Zeitschrift* **70**, 213–223.

TATARINOV, L.P. 1968. Morphology and systematics of the northern Dvinia cynodonts (Reptilia, Therapsida; Upper Permian). *Postilla* **126**, 1–15.

VAN HEERDEN, J., 1972. Intraspecific variation and growth in the cynodont reptile *Thrinaxodon liorhinus* Seeley, 1984. *Navorsinge van die Nasionale Museum Bloemfontein* **2**, 307–347.

VON HUENE, F.R. 1950. Die Theriodontier der ostafrikanischen Ruhuhu-Gebietes in der Tübinger Sammlung. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **92**, 47–136.

WOPFNER, H. 2002. Tectonic and climatic events controlling deposition in Tanzanian Karoo basins. *Journal of African Earth Sciences* **34**, 167–177.

WOPFNER, H. & KREUSER, T. 1986. Evidence for late Palaeozoic glaciation in southern Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* **56**, 259–275.

WOPFNER, H., MARKWORT, S. & SEMKIWA, P.M. 1991. Early diagenetic laumontite in the Lower Triassic Manda beds of the Ruhuhu Basin, southern Tanzania. *Journal of Sedimentary Petrology* **61**, 65–72.