MANDIBLES FROM THE PERMIAN RUHUHU AND USILI FORMATIONS (SONGEA GROUP), RUHUHU BASIN, TANZANIA

KENNETH D. ANGIELCZYK*1 and C. BARRY COX2

1Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, U.S.A., kangielczyk@fieldmuseum.org;
2Forge Cottage, 11 Blacksmith Close, Ashtead KT21 2BD, United Kingdom, barrycox1931@gmail.com

ABSTRACT—Dicynodont therapsids were discovered in the Permian Usili Formation (Ruhuhu Basin, Tanzania) in the 1930s and in the Permian Ruhuhu Formation in the 1960s, with further collections being made in 2007, 2008, and 2012. Here we describe two fragmentary mandibles that represent a new morphotype of emydopoid dicynodont. One specimen was collected in the middle fossiliferous horizon of the Ruhuhu Formation, and the other originated in the overlying Usili Formation. Three synapomorphies support the placement of these specimens in the emydopoid subclade Kingoriidae: mandibular fenestra occluded by the dentary; curved ridge that follows the profile of the symphysis present on the edge between the anterior and lateral surfaces of the dentary; and posterior dentary sulcus absent. The specimens may represent a new dicynodont species, a previously known species for which mandibular material was unknown, or an intraspecific variant of Dicynodontoides nowacki. Regardless of which of these options is correct, the specimens constitute the first taxon with a stratigraphic range extending from the likely middle Permian middle fossiliferous horizon of the Ruhuhu Formation into the late Permian Usili Formation. They also improve our understanding of the middle Ruhuhu tetrapod fauna, which previously consisted only of Endothyridon tolani.

http://zoobank.org/urn:lsid:zoobank.org:pub:E560DB91-177E-4AEC-8379-DBA8F19C5335

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Angielczyk, K. D., and C. B. Cox. 2015. Distinctive emydopoid dicynodont (Therapsida, Anomodontia) mandibles from the Permian Ruhuhu and Usili formations (Songea Group), Ruhuhu Basin, Tanzania. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2015.1008699.

INTRODUCTION

The history of research on Permian therapsids from Tanzania begins with the discovery of tetrapod fossils in the Ruhuhu Basin in the early 1930s (Stockley, 1931, 1932, 1935; Stockley and Oates, 1931). Stockley’s initial therapsid material, as well as collections made in the 1930s by Parrington and Nowack, minor collections by Stockley in the 1950s, and the collections of the 1963 British Museum (Natural History)–University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, served as the subject of a series of publications that span from the 1930s to the present day (e.g., Haughton, 1932; Broili and Schröder, 1936; Parrington, 1936, 1946, 1955; Nowack, 1937; von Huene, 1942, 1950; Boonstra, 1953; Cox, 1959, 1972; Kemp, 1969a, 1969b, 1972a, 1972b; Maisch, 1995, 2000, 2002, 2003, 2004, 2005, 2009; Gay and Cruickshank, 1999; Abdala and Allinson, 2005; Maisch and Gebauer, 2005; Angielczyk, 2007; Gebauer, 2014). All of the Permian material described in these papers originated in the upper Permian Usili Formation (sensu Kaaya, 1992; formerly the K6 or Kawinga Formation: Charig, 1963; Wopfner, 2002), which probably represents a time period equivalent to the Cistecephalus Assemblage Zone of South Africa (Angielczyk et al., 2014a). Additional collecting in 2007, 2008, and 2012 by a team including one of us (K.D.A.) has produced new material from the Usili Formation (Angielczyk et al., 2009; Sidor et al., 2010; Weide et al., 2010), much of which is still under study.

In addition to collecting in the Usili Formation, members of the 1963 British Museum (Natural History)–University of London Joint Palaeontological Expedition discovered fossils in the underlying Ruhuhu Formation (Attridge et al., 1964; Cox, 1964, 1991; Bishop, 1968; Cruickshank, 1986; Gay and Cruickshank, 1999). Much of this material pertains to the recently described dicynodont *Endothyridon tolani* (Cox and Angielczyk, 2015), although they also collected specimens of other taxa in a horizon above that which produced the *E. tolani* specimens (Angielczyk et al., 2014b). Recent work in the Ruhuhu Formation has uncovered the first dinocephalians known from Tanzania (Simon et al., 2010), as well as the new dicynodont *Abajudon kaayai*, and provided an improved understanding of the stratigraphic occurrences of fossils in the formation (Angielczyk et al., 2014b).

Among the material collected by the 1963 expedition at their Ruhuhu Formation Locality L3 (Cox, 1991) is a small, fragmentary dicynodont mandible (NH MukPV R12453) that bears ‘postcanine’ teeth. This locality samples the middle fossiliferous horizon of the Ruhuhu Formation (Angielczyk et al., 2014b), and most of the specimens it has produced represent *E. tolani* (Cox and Angielczyk, 2015). However, NH MukPV R12453 shows clear differences from the mandible of *Endothyridon* and instead has characters that are similar to members of the clade Emydopidea, although it cannot be accommodated within any currently recognized emydopoid species. A second specimen that displays the same combination of characters (NMT RB230)
was collected in 2008 from a locality in the Usili Formation. Here we describe these specimens, discuss their identification and phylogenetic affinities, and investigate how they fit into the emerging picture of the litho- and biostratigraphy of the Ruhuhu and Usili formations.

**Institutional Abbreviations**—BP Evolutionary Studies Institute, Johannesburg, South Africa; NHMUK, Natural History Museum, London, U.K.; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; SAM, Iziko: South African Museum, Cape Town, South Africa.

**Anatomical Abbreviations**—Den dentary; Dr?, dentary table–like structure; Lds, lateral dentary shelf; Sp, splenial.

**GEOLOGIC CONTEXT**

The Ruhuhu Basin (Fig. 1) is one of a series of Paleozoic rift basins that extends through southern and eastern Africa to the Arabian Peninsula (Catuneanu et al., 2005). The basin fill consists of rocks of the Songea Group, which together comprise over 3000 m of strata spanning the Upper Carboniferous to the Middle Triassic (Kreuser et al., 1990; Kaaya, 1992; Kreuser, 1995; Wopfner, 2002; Catuneanu et al., 2005). The Ruhuhu Formation is approximately 500 m thick and is a lacustrine mudrock succession with interbedded stromatolitic carbonate beds (e.g., Kaaya, 1992; Angielczyk et al., 2014b). Nearshore oolitic horizons are present in the lower and middle portions, whereas conglomeratic fluvial sandstone wedges become more common in the upper part of the formation. The age of the Ruhuhu Formation has generally been considered to be late middle Permian, and new data on tetrapod occurrences suggest that the Ruhuhu Formation spans the middle-late Permian boundary (Angielczyk et al., 2014b). The Usili Formation is approximately 260 m thick and is predominantly fluvial lacustrine in origin (e.g., Kaaya, 1992; Sidor et al., 2010). The lowermost portion of the formation consists of a conglomeratic interval that grades upward into strata primarily composed of coarse-grained, trough cross-bedded sandstones. In turn, these are overlain by massive nodular siltstones and laminated mudstones with minor ribbon sandstones. The age of the Usili Formation has generally been regarded as late Permian, and correlations with rocks of the *Dicynodon* Assemblage Zone of South Africa frequently have been suggested (e.g., Wild et al., 1993; Gay and Cruickshank, 1999). We favor a slightly older age, with the formation correlating with the rocks of the *Cistecephalus* Assemblage Zone of South Africa (Sidor et al., 2010; Angielczyk et al., 2014a).

Angielczyk et al. (2014b) georeferenced the localities of the 1963 expedition using the map presented in Cox (1991), a topographic map of the relevant region of the Ruhuhu Basin (Surveys and Mapping Division, 1972), and satellite imagery. Based on this work, and their observations of the geology of the area, they concluded that Locality L3 sampled the middle fissiliferous horizon of the Ruhuhu Formation. This level consists of a siltstone with calcareous nodules and stromatolitic concretions, and tetrapod fossils occur almost exclusively within nodules (Angielczyk et al., 2014b).

Specimen NMT RB230 was collected at a locality in the middle gray mudrocks of the Usili Formation. Fossils occur along with rhizocretions and large calcareous nodules at this level (Angielczyk et al., 2014b). The specimen was found weathering on the surface...
as part of an accumulation of cranial and postcranial material representing multiple individuals of *Oudenodon bainii* and *Dicynodontoides nowacki*. None of the additional material from the locality can be definitively associated with NMT RB230.

**SYSTEMATIC PALEONTOLOGY**

ANOMODONTIA Owen, 1860  
DICYNODONTIA Owen, 1860  
THEROCHELONIA Seeley, 1894  
EMYDOPOIDEA (van Hoepen, 1934) Cluver and King, 1983  
KINGORIIDAE King, 1988  
Gen. et sp. indet.  
(Fig. 2A, B, D, E, G, H)

**Referred Specimens**—NHMUK PV R12453, NMT RB230.

**Locality and Horizon**—Specimen NHMUK PV R12453 was collected at Locality L3 in the middle tetrapod-bearing horizon of the Permian Ruhuhu Formation, Ruhuhu Basin, Tanzania. The locality is close to the heads of the Matamondo and Rupaha streams, about 5.5 km north of the village of Litumba Ndyosi (Fig. 1). Georeferenced coordinates for this locality are available to qualified researchers from K.D.A. Specimen NMT RB230 was collected from the middle gray mudrocks of the Usili Formation at a locality approximately 3.3 km northwest of the southeastern end of Usili Mountain and 1.85 km northeast of the closest approach of the Mngaka River (Fig. 1). Detailed locality information for NMT RB230 is available to qualified researchers from the National Museum of Tanzania or from K.D.A.

**DESCRIPTION**

**NHMUK PV R12453**

This specimen (Fig. 2A, E, H) consists of the posterior portion of the symphyseal region of the mandible and the anterior portions of the left and right mandibular rami. It is mostly composed of the left and right dentaries, although the splenial is preserved on the ventral and medial surfaces of the symphysis. A repaired FIGURE 2. Unusual emydopoid dicynodont mandibles from the Permian Ruhuhu and Usili formations and comparative material of *Dicynodontoides* from South Africa and Tanzania. A, NHMUK PV R12453, dorsal view; B, NMT RB230, dorsal view; C, NMT RB427, *Dicynodontoides*, dorsal view; D, NHMUK PV R12453, left lateral view; E, NMT RB230, right lateral view; F, NMT RB427, *Dicynodontoides*, right lateral view; G, NHMUK PV R12453, ventral view; H, NMT RB230, right medial view; I, SAM-PK-K8069, *Dicynodontoides*, dorsal view. Note dentary table-like structures. NMT RB247 was collected in the Ruhuhu Basin (Tanzania), whereas SAM-PK-K8069 is from the Karoo Basin (South Africa). White arrows in A, B, and H indicate teeth.
longitudinal break is present close to the midline of the symphysis, but this does not seem to represent a suture between the dentaries, which appear to have been firmly fused together. The anterior portion of the dentary is missing, making it uncertain whether the specimen possessed the ‘shovel-shaped’ jaw symphysis typical of most emydopoids. The anteroventral surface of the symphysis bears numerous vascular foramina, suggesting the presence of a keratinous beak. A weak, rounded ridge that extends posteroventrally delimits the anterior edge of the lateral surface of the symphysis on each side of the jaw.

In dorsal view, a dentary table and a posterior dentary sulcus (sensu Angielczyk and Rubidge, 2013) are absent. Instead, the dorsal surface of the dentary tapers to a narrow, ridge-like edge, similar to the morphology present in *Dictynodontoides* (Fig. 2C). A small medial projection arises from the medial side of the dentary near the posterior edge of the symphysis and extends slightly past the level of the anterior edge of the lateral dentary shelf. The broken bases of ‘postcanine’ teeth are present on this medial projection; two teeth are visible on the better-preserved left side, whereas one tooth is visible on the right side. As preserved, the teeth are round in cross-section, but no part of the crown is present, making it uncertain whether the teeth were laterally compressed or had serrations or other ornamentation (see Angielczyk et al., 2014b, for a review of dicynodont tooth morphology).

A prominent lateral dentary shelf is present. It arises at the level of the posterior edge of the symphysis and widens posteriorly. The broken posterior edge of the mandible truncates the shelf posteriorly, indicating that the shelf originally extended along a significant portion of the lateral surface of the dentary. The lateral edge of the shelf is smoothly rounded and lacks the rugose anterolateral muscle scar found in *Emydops* (Angielczyk et al., 2005; Fröbisch and Reisz, 2008). The dorsal surface of the shelf bears a well-developed fossa with a rounded anterior edge that is very similar in morphology to that seen in *Dictynodontoides* (Fig. 2C, I; also see Cox, 1959). The somewhat more complete right side of the specimen suggests that a lamina of the dentary occluded the mandibular fenestra beneath the lateral dentary shelf, but there is not enough of the specimen preserved to state this with absolute certainty.

The splenial forms the posterior surface of the symphysis and extends along the medial surfaces of the dentary rami. It also bears a long, pointed anterior process that makes a substantial contribution to the ventral surface of the symphysis. Like the dentaries, it is broken along its midline, but appears to have originally been a single fused element.

**NMT RB230**

This specimen consists of a portion of the right mandibular ramus that extends from the posterior part of the symphysis to near the posterior end of the dentary (Fig. 2B, E, H). Only the dentary and the splenial are preserved in the specimen.

As in NHMUK PV R12453, the anterior portion of the symphysis is missing in NMT RB230, making its original shape uncertain. A rounded ridge delimits the anterior edge of the lateral surface of the symphysis, and is slightly more prominent in NMT RB230 than in NHMUK PV R12453. The vascular foramina on the external surface of the symphysis end at the ridge, suggesting that it may mark the posterior extent of the beak. The nature of the broken medial surface of the symphysis suggests that the dentaries were fused. For example, ridges and grooves that would interlock with the left dentary in a sutureal connection are absent; instead, the bone has a roughened, uneven surface consistent with a weathered break.

Posterior to the symphysis, the dorsal surface of the dentary tapers to a rounded edge. This edge is less ridge-like than that of NHMUK PV R12453, but a dentary table and posterior dentary sulcus clearly are absent. Two small ‘postcanine’ teeth are present on the medial surface of the dentary just posterior to the posterior edge of the symphysis and close to the level of the anterior edge of the lateral dentary shelf. They are round in cross-section but complete crowns are not preserved. The medial swelling from which they erupt is less pronounced than in NHMUK PV R12453.

A well-developed lateral dentary shelf is present in NMT RB230, and seems to be preserved in its entirety. The shelf arises at about the level of the ‘postcanine’ teeth and rapidly expands to its maximum width, although proportionally it is somewhat narrower than the shelf in NHMUK PV R12453. The lateral edge of the shelf is slightly roughened, but this appears to reflect weathering of the bone surface more than the development of a strong muscle scar. The dorsal surface of the shelf bears a well-developed, rounded fossa that is about one third of the total length of the shelf. Anterior to the fossa, the shelf narrows towards its anterior junction with the lateral surface of the dentary, and the dorsal surface of this anterior section is smoothly rounded. Posterior to the fossa, the shelf narrows and takes on the form of a rounded ridge on the lateral surface of the dentary. The lateral surface of this ridge bears a shallow fossa that is somewhat reminiscent of the fossa on the posterior portion of the lateral dentary shelf in *Kombuisia* (Fröbisch, 2007; Fröbisch et al., 2010), although it is much deeper and dorsoventrally taller in the latter taxon. A greater portion of the dentary is preserved below the lateral dentary shelf than in NHMUK PV R12453, and this indicates that a lamina of the dentary did occlude the mandibular fenestra.

Part of the splenial is preserved on the medial surface of the mandible. It is plate-like, with a smooth medial surface, and is narrowly exposed in lateral view along the ventral edge of the mandible. The broken surface of the symphysis shows that the splenial possessed an anterior process that contributed to the symphysis. This contribution was quite substantial: the process is not a superficial feature limited to the external surface but instead extends upwards into the interior of the symphysis.

**DISCUSSION**

**Comparison**

Although they display some minor differences (e.g., slightly wider lateral dentary shelf in NHMUK PV R12453), the specimens described here are extremely similar and it seems obvious that they represent the same morphotype. Furthermore, this morphotype does not conform exactly to the mandibles of any well-characterized dicynodont species. Comparisons with other toothed dicynodonts and to endentulous emydopoid dicynodonts provide a useful illustration of this fact.

A total of 15 dicynodont species with mandibular teeth are well-described and/or have been included in recent phylogenetic analyses: *Eodicynodon oosthuizeni*, *Chelydontops allidentalis*, *Pristerodon mackayi*, *Endothiodon bathystoma*, *Endothiodon mahalanobisi*, *Endothiodon tolani*, *Eosimops newtoni*, *Prosictodon dubii*, *Robertia broomiana*, *Niassodon mjumu- kasi*, *Emydops arctatus*, *Emydops oweni*, *Australobarbarus kotelnitschi*, *Australobarbarus platycephalus*, and *Tropidostoma dubium*. Angielczyk and Rubidge (2013) presented comparative figures of the mandibles of nearly all of these genera. The Tanzanian specimens do not represent *Eodicynodon oosthuizeni*, based on the absence of a dentary table and the more anteromedial placement of the teeth. They differ from *Chelydontops*, *Pris- terodon*, *Endothiodon*, *Niassodon*, *Emydops*, *Australobarbarus*, and *Tropidostoma* in lacking a posterior dentary sulcus. The specimens can be differentiated from *Eosimops*, *Prosictodon*, and *Robertia* by the absence of a well-developed dentary table that is bounded medially by a tall blade.
Thirteen emydopoid species with known mandibles are recognized: Emydops arctatus, Emydops oweni, Niassodon mfumukasi, Dicynodontoides recurvidens, Dicynodontoides nowacki, Kombuisia herensis, Kombuisia antarctica, Digalodon rubidgei, Myosaurus gracilis, Cistecephalus microrhinus, Cistecephaloidea boonstrai, and Kowingasaurus fossils. All but Myosaurus miura have been included in recent phylogenetic analyses. Angielczyk et al. (2014a; also see Freeman, 1993) briefly noted a new cistecephalid from Zambia for which mandibles are known. Different combinations of characters distinguish the Tanzanian specimens from the known emydopoids. The presence of teeth and the apparent occlusion of the mandibular fenestra indicate that the specimens do not represent Myosaurus, Myosaurus, Cistecephalus, Cistecephaloidea, Kowingasaurus, or the Zambian cistecephalid (e.g., Cox, 1972; Keyser, 1973; Cluver, 1974a, 1974b). As noted above, the absence of a posterior dentary sulcus differentiates the Tanzanian specimens from Emydops and Niassodon. The only known mandible of Digalodon (BP/1/157; see Kammerer et al., 2015) is very poorly preserved and prepared, making detailed comparisons difficult. However, there is no conclusive evidence for the presence of ‘postcanine’ teeth in BP/1/157, and the symphyal region seems to be deeper than in the Tanzanian specimens.

Among emydopoids, the new specimens show the closest resemblance to Dicynodontoides and Kombuisia, e.g., in the absence of a posterior dentary sulcus and in the occlusion of the mandibular fenestra by the dentary. The presence of dentary teeth and the very weak development of a fossa on the lateral surface of the lateral dentary shelf show that the specimens are not part of Kombuisia (Fröbisch, 2007; Fröbisch et al., 2010). The Tanzanian mandibles conform almost exactly to the morphology of Dicynodontoides. The absence of a dentary table and posterior dentary sulcus, the size and shape of the lateral dentary shelf, the presence of a fossa on the dorsal surface of the lateral dentary shelf, and the occlusion of the mandibular fenestra by the dentary all are consistent with the morphology of Dicyonodontoides (e.g., Cox, 1959). The only significant difference is the presence of dentary teeth in the Tanzanian specimens: no specimens of Dicynodontoides with ‘postcanine’ teeth have been described in the literature, and we are unaware of any undescribed specimens in museum collections that possess teeth.

Phylogenetic Analysis

To assist with the identification and interpretation of NHMUK PV R12453 and NMT RB230, we used them to code an operational taxonomic unit (OTU) that we added to the data matrix of Cox and Angielczyk (2015). With this addition, the data set included 100 OTUs and 175 characters. The list of characters and a copy of the data matrix can be found in Supplementary Data; more information on the data set can be found in Cox and Angielczyk (2015). We analyzed the data set using TNT 1.1 (October 2010 version) (Goloboff et al., 2008), and two search strategies were employed. The first search used the new technology methods of TNT. We employed a driven search with the initial search level set at 65, which was checked every three hits. The initial number of addition sequence replicates was 500, and the search was required to find the trees of shortest length 20 times. The analysis started with default settings for sectorial searching, tree drifting, parsimony ratchet, and tree fusing. In the second analysis, we used the traditional search method of TBR (tree bisection and reconnection) branch swapping with 10,000 replicates and 10 trees held per replicate. Biarmosuchus served as the outgroup to root the most parsimonious clademgrams from both analyses. Because we only were able to code 13 characters for the new OTU, we consider the analysis to be preliminary and we did not conduct symmetric resampling or decay analyses.

A single most parsimonious cladogram was discovered by the searches (length = 1011.816 steps, consistency index [CI] = 0.240, retention index [RI] = 0.713). The position of the new OTU in the tree is shown in Figure 3, and the complete topology of the tree can be found in Supplementary Data. The new OTU falls within Emydopoidae as the most basal member of Kingoriiidae (i.e., it is the sister taxon of Dicynodontoides + Kombuisia). Three synapomorphies support this placement: mandibular fenestra occluded by the dentary (char. 100, state 2); curved ridge that follows the profile of the symphysis present on the edge between the anterior and lateral surfaces of the dentary (char. 107, state 1); and posterior dentary sulcus absent (char. 109, state 0).

Overall, the topology of the tree is rather different from those of Kammerer et al. (2011, 2013), Castanhinha et al. (2013) and Cox and Angielczyk (2015), despite being based on a very similar data set. We suspect that these differences stem largely from the...
very large amount of missing data for the new OTU, so we will not discuss most of the topological differences in detail. However, the reconstruction of a broadly defined Endothiodontia (here composed of Endothiodon bathystoma, E. tolanis, and Niassodon; see Kammerer and Angielczyk, 2009, for information on the definition of Endothiodontia) as the sister taxon of Emydopoidea is novel and worthy of some consideration.

The Endothiodontia + Emydopoidea clade is supported by four discrete-state synapomorphies: anterior margin of orbit extended posteromedially to partly close off the snout from the rest of the skull (char. 14, state 1); keel-like extension of the palatal rim posterior to the caniniform process (char. 28, state 1); symphysis region of mandible shovel-shaped with a rounded or squared-off edge and a weak depression on its posterior surface (char. 106, state 3); and four sacral vertebrae (char. 124, state 1). The width of the interorbital skull roof relative to basal skull length (char. 157) and the length-to-height ratio of the mandibular fenestra (char. 156) also support this clade. Niassodon is particularly interesting in this context. In many ways, it resembles the expected morphology for a generalized emydopoid, with characters such as a postcaniniform keel, a broad temporal bar, bimodal temporal portions of the postorbitals, a pineal foramen located relatively posteriorly on the skull roof, a shovel-shaped mandibular symphysis, and a large lateral dentary shelf. At the same time, it also has two characters otherwise seen among dicyodonts only in Endothiodon: premaxillary teeth and elongate palatine pads that bear paired depressions on their ventral surfaces. This raises the possibility that the highly distinctive morphology of Endothiodon was derived from an Emydops- or Niassodon-like ancestor, but additional fossil discoveries will be needed to corroborate this phylogenetic hypothesis and reveal how this transition proceeded.

The combination of character states preserved in the new Tanzanian mandibles and the data that are missing from them doubtlessly affected patterns of character optimization and thus the topology of the shortest cladograms for our data set. There is not an obvious link between their morphology and the Endothiodontia + Emydopoidea clade, though. For example, two characters (char. 108 and 112) preserved in the Tanzanian mandibles are synapomorphies of Emydopoidea on our tree, but they are widely distributed among emydopoids, including kingorids, such that the new mandibles do not dramatically change our view of their evolutionary history. The most distinctive feature of the mandibles, the presence of ‘postcanine’ teeth, is reconstructed as a symplesiomorphy that is shared with many basal dicyodonts as well as Niassodon, Endothiodon, and Emydops. The topology of our cladogram does imply a separate loss of ‘postcanines’ in Kingoridae and Kistecephalidae (here Myosaurus + Cistecephalidae; see Kammerer and Angielczyk, 2009, for definition), and the implied presence of a toothed basal kingorid apparently facilitates moving that clade out of Kistecephalidae.

**Interpretation**

Based on the comparisons listed above and the phylogenetic analysis, it seems clear that NHMUK PV R12453 and NMT RB230 represent a previously unknown morphotype of emydopoid dicyodont. However, several factors, including the incompleteness of the specimens and the nature of the locality at which NMT RB230 was found, make us hesitant to simply describe the specimens as a new taxon. Instead, we consider three hypotheses to be equally well-supported at this time: (1) NHMUK PV R12453 and NMT RB230 represent a new taxon; (2) NHMUK PV R12453 and NMT RB230 represent the mandible of a toothed dicyodont previously known only from skull material, such as Compsodon; and (3) NHMUK PV R12453 and NMT RB230 represent a rare and previously unknown variant of Dicyodontoides nowaki.

The main argument in favor of NHMUK PV R12453 and NMT RB230 representing a new taxon is the fact that they possess a combination of characters that is not found in other known dicyodonts (see above). We have refrained from erecting a new name for two reasons. First, although the specimens represent a distinctive morphotype, they do not possess any truly autapomorphic features and it seems premature to name a new taxon based on such a limited part of the animal’s anatomy without a unique diagnostic feature. Second, NMT RB230 was found among a large amount of material that can be unequivocally diagnosed as Oudenodon and Dicyodontoides. Although none of the material can be associated definitely with NMT RB230, if the specimen represents a new taxon, it is curious that only a fragment of mandible would be preserved in such an otherwise productive locality. On the other hand, we cannot eliminate the possibility that NMT RB230 is associated with some of the cranial and/or postcranial material at the locality. Given that NMT RB230 shows a high degree of overall similarity to Dicyodontoides, such a scenario would imply that the specimen likely is part of that taxon, with the presence of ‘postcanine’ teeth representing a rare form of individual variation.

As noted above, there are 13 emydopoid species that have mandibles of known morphology. In addition to these species, there are two other poorly known species that have recently been suggested to be emydopoids: Cryptocynodon simus and Compsodon helmoedi (Castanhinha et al., 2013; Angielczyk et al., 2014a; see Seeley, 1894, and van Hoepen, 1934, for the original descriptions of these taxa). The holotypes of these species do not preserve mandibles, and newly discovered specimens of Cryptocynodon and Compsodon only consist of skulls as well. Because NHMUK PV R12453 and NMT RB230 show clear affinities to Emydopoidea, but include a combination of characters not found in other known emydopoid jaws, it is conceivable that they represent the ‘missing’ jaw of Compsodon or Cryptocynodon. This hypothesis is impossible to fully refute or confirm, however, until specimens of these taxa that possess mandibles are discovered so that they can be compared with NHMUK PV R12453 and NMT RB230. The hypothesis is also complicated by the fact that Compsodon and Cryptocynodon are not known to occur in the Ruhuhu Basin, although Compsodon is present in the nearby Luangwa Basin of Zambia (Angielczyk et al., 2014a).

The third possibility is that NHMUK PV R12453 and NMT RB230 represent a rare form of individual variation in Dicyodontoides. The primary data supporting this interpretation are the close overall resemblance of the new specimens to more complete mandibles of Dicyodontoides, and the fact that NMT RB230 was collected at a locality that has produced a number of fragmentary Dicyodontoides specimens, including partial skulls (e.g., NMT RB41, NMT RB242), mandibles (e.g., NMT RB249, NMT RB250, NMT RB251), and postcrania (e.g., NMT RB40, NMT RB236, NMT RB237). In addition, atavistic variation in Dicyodontoides is not unprecedented. Angielczyk (2001) noted two Dicyodontoides specimens (SAM-PK-K8069, SAM-PK-K1269a; Kingoria in that paper) that possessed small dentary table-like expansions of the dorsal surface of the dentary (Fig. 21), a seeming reversal to a character state lost in most Dicyodontoides individuals. Apparently random variation in the presence of tusks and ‘postcanine’ teeth also has been reported for some cryptodont dicyodonts (e.g., Angielczyk, 2002; Botha and Angielczyk, 2007), and rare instances of the presence of two erupted tusks on the same side of the skull have been documented in Eodicynodon and Emydops (Jinnah and Rubidge, 2007; Frösch and Reisz, 2008). However, this variation seems to be confined to the maxillary dentition. In our observations, the presence or absence of teeth in the mandible is a very stable character among dicyodont taxa, and we are unaware of toothed specimens of otherwise edentulous taxa.
Regardless of whether NMUK PV R12453 and NMT RB230 represent a new or previously known species, the specimens are noteworthy in providing the first evidence of a species-level taxon that ranges from the middle fossiliferous horizon of the Ruhuhu Formation into the Usuli Formation, likely crossing the middle-late Permian boundary in the Ruhuhu Basin (Angielczyk et al., 2014b). The genus *Endothiodon* has a similar range, but it is represented by distinct species in the lower Ruhuhu Formation and the upper Ruhuhu and Usuli Formations (Cox and Angielczyk, 2015). Given the long time interval represented, it is unlikely that the specimens will be able to clarify biostratigraphic correlations between the Ruhuhu and Usuli formations and rock units outside of the Ruhuhu Basin. However, if they represent a previously known taxon such as *Compsodon*, they could provide a downward stratigraphic range extension. Alternatively, if they represent a variant of *Dicynodontoides*, that taxon’s range in the Ruhuhu Basin would be consistent with its range in the Karoo Basin, where it extends from the middle Permian *Pristerognathus* Assemblage Zone (Rubidge et al., 2013) to near the Permo-Triassic boundary in the *Dicynodon* Assemblage Zone (Angielczyk et al., 2009; Botha-Brink et al., 2014; Smith and Botha-Brink, 2014).

The taxonomic and stratigraphic questions surrounding NMUK PV R12453 and NMT RB230 will only be definitively answered with the discovery of new, more complete material. However, documentation of these specimens provides a search image for future collecting efforts and increases the known dicynodont diversity of the middle fossiliferous horizon of the Ruhuhu Formation.

**ACKNOWLEDGMENTS**

We thank A. Milner, S. Chapman, S. Kaal, and R. Smith for access to specimens. P. Hurst photographed NMUK PV R12453. M. Graham prepared and conserved NMUK PV R12453, and C. Van Beek prepared NMT RB230. Fieldwork in Tanzania in 2007, 2008, and 2012 was supported by National Geographic Society grants 7787-05 and 8962-11 (to C. Sidor) and The Grainger Foundation (to K.D.A.). Additional support for this work provided by NSF EAR-1337291 (to K.D.A.). We thank C. Saanane (University of Dar es Salaam) as well as A. Tibajjuka and L. Nampanju (Antiquities Division, Ministry of Natural Resources and Tourism) for assistance in arranging and carrying out the field work. M. Abdalla, S. Nesbitt, C. Sidor, R. Smith, S. Steyer, M. Stocker, W. Simpson, N. Tabor, and L. Tsuji contributed to productive field seasons in 2007, 2008, and 2012. J. Fröbisch and C. Kammerer provided helpful reviews of the manuscript. Finally we inadvertently included incorrect information in the acknowledgements of Cox and Angielczyk (2015) and offer the following correction: We thank the following staff of the NMUK: S. Chapman and A. Milner of the Department of Earth Sciences, for their unfailing help, advice and curation; P. Hurst, Image Resources, for his expert photography; M. Graham of the Conservation Centre for detailed preparation and conservation.

**LITERATURE CITED**

Abdala, F., and M. Allinson. 2005. The taxonomic status of *Pararhinecodon proops* (Therapsida: Cynodontia), with comments on the morphology of the palate in basal cynodonts. Palaeontologia africana 41:45–52.

Angielczyk, K. D. 2001. Preliminary phylogenetic analysis and stratigraphic congruence of the dicynodont anomodonts (Synapsida: Therapsida). Palaeontologia africana 37:53–79.

Angielczyk, K. D. 2002. Redescription, phylogenetic position, and stratigraphic significance of the dicynodont genus *Odontocyclops* (Synapsida: Anomodontia). Journal of Palaeontology 76:1047–1059.

Angielczyk, K. D. 2007. New specimens of the Tanzanian dicynodont “Cryptocynodon parringtoni” von Huenne, 1942 (Therapsida, Anomodontia), with an expanded analysis of Permian dicynodont phylogeny. Journal of Vertebrate Palaeontology 27:116–131.

Angielczyk, K. D., and B. S. Rubidge. 2013. Skeletal morphology, phylogenetic relationships, and stratigraphic range of *Eosimops newtoni* Broom, 1921, a palaeccephalid dicynodont (Therapsida, Anomodontia) from the middle Permian of South Africa. Journal of Systematic Palaeontology 11:191–231.

Angielczyk, K. D., J. Fröbisch, and R. M. H. Smith. 2005. On the stratigraphic range of the dicynodont taxon *Emydops* (Therapsida: Anomodontia) in the Karoo Basin, South Africa. Palaeontologia africana 41:23–33.

Angielczyk, K. D., C. A. Sidor, S. J. Nesbitt, R. M. H. Smith, and L. A. Tsuji. 2009. Taxonomic revision and new observations on the post-cranial skeleton, biogeography, and biostratigraphy of the dicynodont genus *Dicynodontoides*, the subjective senior synonym of *Kingoria* (Therapsida, Anomodontia). Journal of Vertebrate Paleontology 29:1174–1187.

Angielczyk, K. D., J. Steyer, J.-S., C. A. Sidor, R. M. H. Smith, R. L. Whatley, and S. Tolan. 2014a. Permian and Triassic dicynodont (Therapsida: Anomodontia) faunas of the Luangwa Basin, Zambia: taxonomic update and implications for dicynodont biogeography and biostratigraphy; pp. 93–138 in C. F. Kammerer, K. D. Angielczyk, and J. Fröbisch (eds.), Early Evolutionary History of the Synapsida. Springer, Dordrecht, The Netherlands.

Angielczyk, K. D., S. Huertas, R. M. H. Smith, N. J. Tabor, C. A. Sidor, J. S. Steyer, and L. A. Tsuji. 2014b. New dicynodonts (Therapsida, Anomodontia) and updated tetrapod stratigraphy of the Permian Ruhuhu Formation (Songea Group, Ruhuhu Basin) of southern Tanzania. Journal of Vertebrate Paleontology 34:1408–1426.

Attridge, J., H. W. Ball, A. J. Charig, and C. B. Cox. 1964. The British Museum (Natural History)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, 1963. Nature 201:445–449.

Bishop, W. W. 1966. The evolution of fossil environments in east Africa. Transactions of the Leicester Literary and Philosophical Society 67:22–44.

Boonstra, L. D. 1953. A report on a collection of fossil reptilian bones from Tanganyika Territory. Annals of the South African Museum 42:5–18.

Botha, J., and K. D. Angielczyk. 2007. An integrative approach to distinguishing the late Permian dicynodont species *Oudemodon bainii* and *Tropidostoma microtrema* (Therapsida: Anomodontia). Palaeontology 50:1175–1209.

Botha-Brink, J., A. K. Huttonlocker, and S. P. Modesto. 2014. Vertebrate palaeontology of Nooitgedacht 68: a *Lystrosaurus maccarighi* rich Permio-Triassic boundary locality in South Africa; pp. 289–304 in C. F. Kammerer, K. D. Angielczyk, and J. Fröbisch (eds.), Early Evolutionary History of the Synapsida. Springer, Dordrecht, The Netherlands.

Broili, F., and J. Schroder. 1936. Beobachtungen an Wirbeltieren der Karrooformation XXIV. Über Theriodontier-Reste aus der Karrooformation Ostafrikas. Sitzungsberichte der Mathematisch-naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München 1936:311–355.

Castanhinha, R., R. Araújo, L. C. Júnior, K. D. Angielczyk, G. G. Martins, R. M. S. Martins, C. Chaouiya, F. Backmann, and F. Wilde. 2013. Bringing dicynodonts back to life: paleobiology and anatomy of a new emydopoid genus from the Upper Permian of Mozambique. PLoS ONE 8:e60974.

Catuneanu, O., H. Wopfner, P. G. Eriksson, B. Cairncross, B. S. Rubidge, R. M. H. Smith, and P. J. Hancox. 2005. The Karoo basins of southern Africa. Journal of African Earth Sciences 43:211–253.

Charig, A. J. 1963. Stratigraphical nomenclature in the Songea Series of Tanganyika. Records of the Geological Survey of Tanganyika 10:47–53.

Cluver, M. A. 1974a. The skull and mandible of a new cistecephalid dicynodont. Annals of the South African Museum 64:137–155.

Cluver, M. A. 1974b. The cranial morphology of the Lower Triassic dicynodont *Myosaurus gracilis*. Annals of the South African Museum 66:35–54.

Cluver, M. A., and G. M. King. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new
classification of dicynodonts. Annals of the South African Museum 91:195–273.

Cox, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. Proceedings of the Zoological Society of London 132:321–367.

Cox, C. B. 1964. On the palate, dentition, and classification of the fossil reptile *Endothiodon* and related genera. American Museum Novitates 2171:1–25.

Cox, C. B. 1972. A new digging dicynodont from the upper Permian of Tanzania; pp. 173–189 in K. A. Joysey and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Oliver and Boyd, Edinburgh, U.K.

Cox, C. B. 1991. The Pangaca dicynodont *Rechnisaurus* and the comparative biostatigraphy of Triassic dicynodont faunas. Palaeontology 34:767–874.

Cox, C. B., and K. D. Angielczyk. 2015. A new endodontid dicynodont (Therapsida, Anomodontia) from the Permian Ruhuhu Formation (Songea Group) of Tanzania and its feeding system. Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2014.935388.

Crickshank, A. R. I. 1986. Biostatigraphy and classification of a new Triassic dicynodont from east Africa. Modern Geology 10:121–131.

Freeman, L. 1993. The cranial morphology of a new tasked species of the genus *Cistecephalus* (Therapsida, Dicynodonta). Unpublished B. Sc. Honours thesis, University of the Witwatersrand, Johannesburg, South Africa.

Froßch, J., and H. D. Reisz. 2008. A new species of *Emydopsis* (Synapsida, Anomodontia) and a discussion of dental variability and pathology in dicynodonts. Journal of Vertebrate Palaeontology 28:770–787.

Froßch, J., K. D. Angielczyk, and C. A. Sidor. 2010. The Triassic dicynodont *Kombuisia* (Synapsida, Anomodontia) from Antarctica, a refuge from the terrestrial Permian-Triassic mass extinction. Naturwissenschaften 97:187–196.

Gay, S. A., and A. R. I. Crickshank. 1999. Biostatigraphy of the Permian tetrapod faunas from the Ruhuhu Valley, Tanzania. Journal of African Earth Sciences 29:195–210.

Gebauer, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Gebauer, E. V. I. 2014. Re-assessment of the taxonomic position of the specimen GPT/RE/7113 (Sauroctonus parringtoni comb. nov., Gorgonopsia); pp. 185–207 in C. F. Kammerer, K. D. Angielczyk, and J. Frößch (eds.), Early Evolutionary History of the Synapsida. Springer, Dordrecht, The Netherlands.

Goebisch, J., K. D. Angielczyk, and C. A. Sidor. 2015. A comprehensiive taxonomic revision of *Cryptocynodon parringtoni* (Therapsida: Dicynodontia) from the upper Permian of Tanzania. Neues Jahrbuch für Geologie und Paläontologie, Monatsshefte 2015:99–104.

Goloboff, P. A., T. Farris, and C. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Haughton, S. H. 1932. On a collection of Karroo vertebrates from Tanga-

Kammerer, C. F., K. D. Angielczyk, and J. Frößch. 2015. Redescription of *Digalodon rubidgei*, an emydopoid dicynodont (Therapsida, Anomodontia) from the late Permian of South Africa. Fossil Record 18:43–55.

Kammerer, C. F., J. Frößch, and K. D. Angielczyk. 2013. On the validity and phylogenetic position of *Eubrachiosaurus browni*, a kannemeyeriiform dicynodont (Anomodontia) from Triassic North America. PLoS ONE 8:e64203.

Kemp, T. S. 1969a. On the functional morphology of the gorgonopian skull. Philosophical Transactions of the Royal Society B 256:1–83.

Kemp, T. S. 1969b. The atlas-axis complex of the mammal-like reptiles. Journal of Zoology 159:223–248.

Kemp, T. S. 1972a. Whatiids Therocephalia and the origin of cynodonts. Philosophical Transactions of the Royal Society B 264:1–54.

Kemp, T. S. 1972b. The jaw articulation and musculature of the whatiids *Therocephalia*; pp. 213–230 in K. A. Joysey, and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Oliver and Boyd, Edinburgh, U.K.

Keyser, A. W. 1973. A preliminary study of the type area of the *Cistecepha-

Huene 1942) (Therapsida: Dicynodontia) from the upper Permian of Tanza-

Kemp, T. S. 1995. Rift to drift evolution in the Permian-Jurassic basins of east Africa; pp. 297–315 in J. J. Lambiase (ed.), Hydrocarbon Habit-

King, G. M. 1988. Anomodontia. Handbuch der Paläoherpetologie, 17 C. Gustav Fischer Verlag, Stuttgart, Germany, 174 pp.

Reusser, K. J. 1995. Rift to drift evolution in the Permian-Jurassic basins of east Africa; pp. 297–315 in J. J. Lambiase (ed.), Hydrocarbon Habitat in Rift Basins. Geological society of London Special Publication 86.

Reusser, K. J. 1995. Rift to drift evolution in the Permian-Jurassic basins of east Africa; pp. 297–315 in J. J. Lambiase (ed.), Hydrocarbon Habitat in Rift Basins. Geological society of London Special Publication 86.

Reusser, K. J. 1995. Rift to drift evolution in the Permian-Jurassic basins of east Africa; pp. 297–315 in J. J. Lambiase (ed.), Hydrocarbon Habitat in Rift Basins. Geological society of London Special Publication 86.

Reusser, K. J. 1995. Rift to drift evolution in the Permian-Jurassic basins of east Africa; pp. 297–315 in J. J. Lambiase (ed.), Hydrocarbon Habitat in Rift Basins. Geological society of London Special Publication 86.
Angielczyk and Cox—Tanzanian emydopoid mandibles (e1008699-9)

Tethysuchia. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 185:987–1018.
Sidor, C. A., K. D. Angielczyk, D. M. Weide, R. M. H. Smith, S. J. Nesbitt, L. A. Tsuji. 2010. Tetrapod fauna of the lowermost Usili Formation (Songea Group, Ruhuhu Basin) of southern Tanzania, with a new burnetiid record. Journal of Vertebrate Paleontology 30:696–703.

Simon, R. V., C. A. Sidor, K. D. Angielczyk, and R. M. H. Smith. 2010. First record of a tapinocephalid (Therapsida: Dinocephalia) from the Ruhuhu Formation (Songea Group) of southern Tanzania. Journal of Vertebrate Paleontology 30:1289–1293.

Smith, R. M. H., and J. Botha-Brink. 2014. Anatomy of a mass extinction: sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 396:99–118.

Stockley, G. M. 1931. Reptilian remains of Karroo age. Annual Report of the Tanganyika Geological Survey 1930/6.

Stockley, G. M. 1932. The geology of the Ruhuhu coalfields Tanganyika Territory. Quarterly Journal of the Geological Society of London 88:610–622.

Stockley, G. M. 1935. A further contribution on the Karroo rocks of Tanganyika Territory. Quarterly Journal of the Geological Society of London 92:1–31.

Stockley, G. M., and F. Oates. 1931. Report on geology of the Ruhuhu Coalfields. Bulletin of the Geological Survey of Tanganyika 2:1–68.

Surveys and Mapping Division. 1972. Matomondo. Series Y742. Sheet 286/3. Edition 1-TSD. Ministry of Lands, Housing, and Urban Development, Dar es Salaam, Tanzania.

van Hoepen, E. C. N. 1934. Oor die indeling van die Dicynodontidae na aanleiding van nuwe vorme. Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein 2:67–101.

Weide, D. M., C. A. Sidor, K. D. Angielczyk, and R. M. H. Smith. 2010. A new record of Procynosuchus delaharpeae (Therapsida: Cynodontia) from the upper Permian Usili Formation, Tanzania. Palaeontologia africana 44:21–26.

Wild, R., C. Kaaya, T. Kreuser, S. Markwort, and P. Z. Semkiwa. 1993. Discovery of a skull of Dicynodon lacerticeps in the uppermost Permian (Tatarian) of Tanzania. Sonderveröffentlichungen, Geologisches Institut der Universität zu Köln 70:231–242.

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

Submitted September 11, 2014; revisions received December 7, 2014; accepted January 11, 2015.

Handling editor: Jennifer Botha-Brink.