

A new vertebrate fauna from the Cretaceous Red Sandstone Group, Rukwa Rift Basin, Southwestern Tanzania

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Abstract

The Rukwa Rift Basin Project was initiated to conduct exploratory field paleontology in poorly sampled terrestrial strata in southern and western Tanzania. Here we report the discovery of a series of new fossiliferous localities from Red Sandstone Group deposits in the Rukwa Rift Basin. These localities contain a diverse Cretaceous terrestrial/freshwater vertebrate fauna that consists of members of several major clades, including fishes, turtles, crocodyliforms, dinosaurs and mammals. Expeditions conducted in the austral summers of 2002–05 have identified numerous fossil-bearing localities, with specimens ranging from isolated elements to semi-articulated sauropod and theropod dinosaurs. Notable among the finds are the most complete mammal specimen recovered from the Cretaceous of continental Africa, megaloolithid dinosaur eggshell, and both theropod and sauropod dinosaurs. Given the scarcity of Cretaceous terrestrial faunas from sub-equatorial Africa, this portion of the East Africa Rift System holds great promise for providing new paleontological data that will contribute to testing and refining a number of biogeographic hypotheses that have been advanced to explain Gondwanan vertebrate distributions in the latter half of the Mesozoic.

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1. Introduction

In recent years, increasing attention has focused on expanding the record of fossil vertebrates from Gondwanan landmasses. Intensive field research in South America, Australia, Antarctica, India, circum-Saharan Africa, and Madagascar has resulted in myriad hypotheses regarding the biogeographic histories of many late Mesozoic Gondwanan vertebrate groups (Bonaparte and Powell, 1980; Molnar, 1980; Rich et al., 1983, 1999; Archer et al., 1985; Prasad and Sahni, 1988; Prasad and Godinot, 1994; Rauhut and Werner, 1995; Krause et al., 1997; Sampson

et al., 1998; Ross et al., 1999; Rougier et al., 2000; Krause, 2003; and numerous others). Indeed, a Cretaceous Gondwanan origin has been proposed for neornithine birds (Cracraft, 2001), and Late Cretaceous faunal similarities between Madagascar, India, and South America have been attributed to a physical connection between Indo-Madagascar and South America via Antarctica (as proposed by Hay et al. (1999)) that excluded continental Africa during the Late Cretaceous (e.g., Krause et al., 1997, 1999; Sampson et al., 1998, 2001; Krause, 2003; Turner, 2004; also see Rage, 2003, Sereno et al., 2004; Krause et al. (accepted for publication)).

Concurrent with increasing data derived from recent fossil discoveries, many molecular studies have advanced a key role for continental Africa as the geographic

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backdrop for the evolution of numerous vertebrate clades. For example, an African center of origin is hypothesized for not only placental mammals (e.g., Murphy et al., 2001 and references therein), but also for a number of eutherian clades including strepsirrhine primates (Seiffert et al., 2003), and the putatively monophyletic Afrotheria (e.g., Springer et al., 1997; Madsen et al., 2001; van Dijk et al., 2001). Finally, a Cretaceous–Paleogene African origin has been proposed for many components of the extant Malagasy fauna (e.g., the endemic Malagasy radiation of cichlid fishes—Vences et al., 2001; lemuriform primates—Yoder et al., 2003).

It is in this context that a surge in paleontological research over the last 15 years is beginning to incorporate data from previously undersampled regions, particularly Jurassic and Cretaceous strata of continental Africa and Madagascar (e.g., Jacobs et al., 1990, 1992, 1993; Sereno et al., 1994, 1996, 1998, 2004; Krause et al., 1997, 1999, 2003; Flynn et al., 1999; Gomani, 1999; Goodwin et al., 1999; Smith et al., 2001; O'Connor et al., 2003; Gottfried et al., 2004; O'Leary et al., 2004; Suberbiola et al., 2004). Such work has significantly refined hypotheses regarding the phylogenetic and biogeographic histories of many Gondwanan vertebrate clades (e.g., fishes—Gottfried and Krause, 1998; crocodyliforms—Buckley and Brochu, 1999; Buckley et al., 2000; Turner, 2004; mammals—Jacobs et al., 1988; Bonaparte, 1990; Brunet et al., 1990; Krause et al., 1997, 2003; and dinosaurs—Jacobs et al., 1993; Sereno et al., 1994, 1996, 1998, 2004; Russell, 1996; Sampson et al., 1998, 2001; Forster, 1999; Curry, 2001; Curry Rogers and Forster, 2001; Upchurch et al., 2001; Carrano et al., 2002).

Historically, Cretaceous-age terrestrial deposits on the African continent have been recovered predominantly from supra-equatorial regions, with localities in Algeria, Cameroon, Egypt, Ethiopia, Mali, Morocco, Niger, Libya, and the Sudan receiving most attention (e.g., Lavocat, 1954; Lapparent, 1960; Taquet, 1976, 1982; Jacobs et al., 1988, 1989, 1996; Brunet et al., 1990; Sereno et al., 1994, 1996, 1998, 2004; Rauhut and Werner, 1995, 1997; Nesson et al., 1998; Sigogneau-Russell et al., 1998; Goodwin et al., 1999; Smith et al., 2001; Rage and Cappetta, 2002; O'Leary et al., 2004). The most glaring geographic deficiency in this emerging story remains sub-equatorial Africa. Non-marine Cretaceous strata in sub-equatorial Africa are extremely rare and low in vertebrate diversity (Dingle et al., 1983; Mateer et al., 1992), with two notable exceptions: the Berriasian–Valanginian Kirkwood Formation of South Africa (Broom, 1904; Galton and Coombs, 1981; Rich et al., 1983; Ross et al., 1999; de Klerk et al., 2000), and the ~Aptian Dinosaur Beds of Malawi (Dixey, 1928; Haughton, 1928; Colin and Jacobs, 1990; Jacobs, 1990; Jacobs et al., 1990, 1992, 1993; Gomani, 1999).

Because many paleobiogeographic inferences are based not only on the presence, but also the absence (or apparent absence) of taxa in a given region, hypotheses concerning Gondwanan-wide Cretaceous terrestrial faunas have relied overwhelmingly on negative evidence. These inferences

suffer from the paucity of fossil evidence recovered from sub-equatorial Africa during this critical time period. We refer to this problem as the 'African Gap', reflecting both temporal and geographic deficiencies in data available to test competing hypotheses. Sub-equatorial Africa represents the largest missing piece in the Cretaceous Gondwanan puzzle (at least of the non-Antarctica landmasses that are logistically feasible to sample), and various aspects of vertebrate paleobiogeography can only be rigorously tested by developing an African fossil record that approaches the expanding data set from other regions of Gondwana.

Our team is working to fill this 'African Gap' through recent expeditions to Cretaceous strata in the Mbeya Region of southwestern Tanzania (the Cretaceous effort being one component of the Rukwa Rift Basin Project—RRBP). Prior to our initial expedition, this area had not been extensively explored for fossil vertebrates. Mesozoic terrestrial vertebrates previously recorded from Tanzania most notably include dinosaurs, mammals and other taxa recovered from the Upper Jurassic Tendaguru site in southeastern Tanzania (Janensch, 1914, 1922, 1961; Russell et al., 1980; Galton, 1988; Heinrich, 1991, 1998, 1999, 2001; Heinrich et al., 2001; Aberhan et al., 2002; Arratia et al., 2002). Our initial interest in the Mbeya Region (~850 km west of Tendaguru) was prompted by legend notes mentioning fossil bones on geological maps of the region (e.g., Harkin and Harpum, 1957; Grantham et al., 1958; Pallister, 1963), a popular press report of dinosaur eggshell (Swinton, 1950), and the suggestion that the Dinosaur Beds of Malawi might extend into Tanzania (Haughton, 1963; Jacobs et al., 1990).

2. Geographical and geological setting

The fossils described herein were recovered from Unit I (*sensu* Roberts et al., 2004) of the Red Sandstone Group (RSG) in the Songwe Valley portion of the Rukwa Rift Basin, southwestern Tanzania (Fig. 1, Table 1). The main field area is located southwest of Mbeya town at approximately 8°56'S, 33°12'E (precise locality coordinates are on file with the authors). Four field seasons have been conducted during the austral winters of 2002–05, resulting in the identification of 35 vertebrate fossil-bearing localities. Some localities contain a range of isolated vertebrate remains, typically located within basal pebble conglomerates in fluvial sandstones. In contrast, other localities preserve associated to partially articulated specimens in finer sediments that clearly demonstrate the in situ nature of fossil material within this sequence. One locality (TZ-07) includes over 150 m of vertical exposure that is laterally continuous for over 0.5 km (Fig. 2). Fossils of particular significance from this locality include associated and semi-articulated sauropod and theropod dinosaurs, one of the most complete mammal specimens recovered from the Cretaceous of continental Africa (Krause et al., 2003), and abundant megaloolithid (dinosaur) eggshell (Gottfried et al., 2004). Significantly, fossils are present

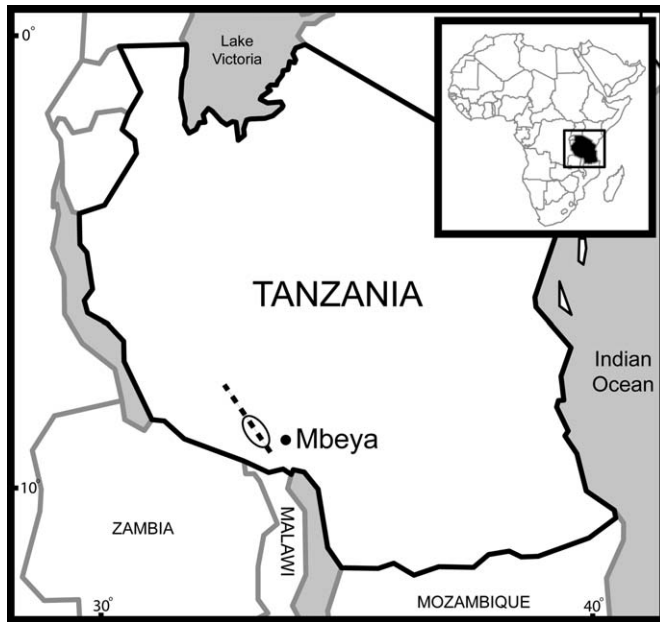


Fig. 1. Map showing location of study area in the Songwe Valley (oval) of the Rukwa Rift Basin (approximate location indicated by dashed line) in southwestern Tanzania.

Table 1
Songwe Valley Fauna—Red Sandstone Group (Unit I) southwestern Tanzania

Osteichthyes
Sarcopterygii
Dipnoiformes
Dipnoi
Ceratodontidae
Actinopterygii
Teleostei
Osteoglossomorpha
Teleostei indet
Sauropsida
Testudines
Crocodyliformes
Dinosauria (non-avian)
Saurischia
Theropoda indet
Sauropoda
Lithostrotia
*Dinosaur Eggshell (Parataxonomic Oospecies = Megaloothidae)
Mammalia
Gondwanatheria?

throughout most of the exposed section (Fig. 2). The majority of fossils described in this contribution were recovered from locality TZ-07, with additional materials recovered from locality TZ-06.

Abbreviations—Tanzanian National Museums, Dar es Salaam (TNM).

2.1. Rukwa Rift Basin and the Red Sandstone Group

Recent work by our group (O'Connor et al., 2003; Roberts et al., 2004; Stevens et al., in press^a) has confirmed at

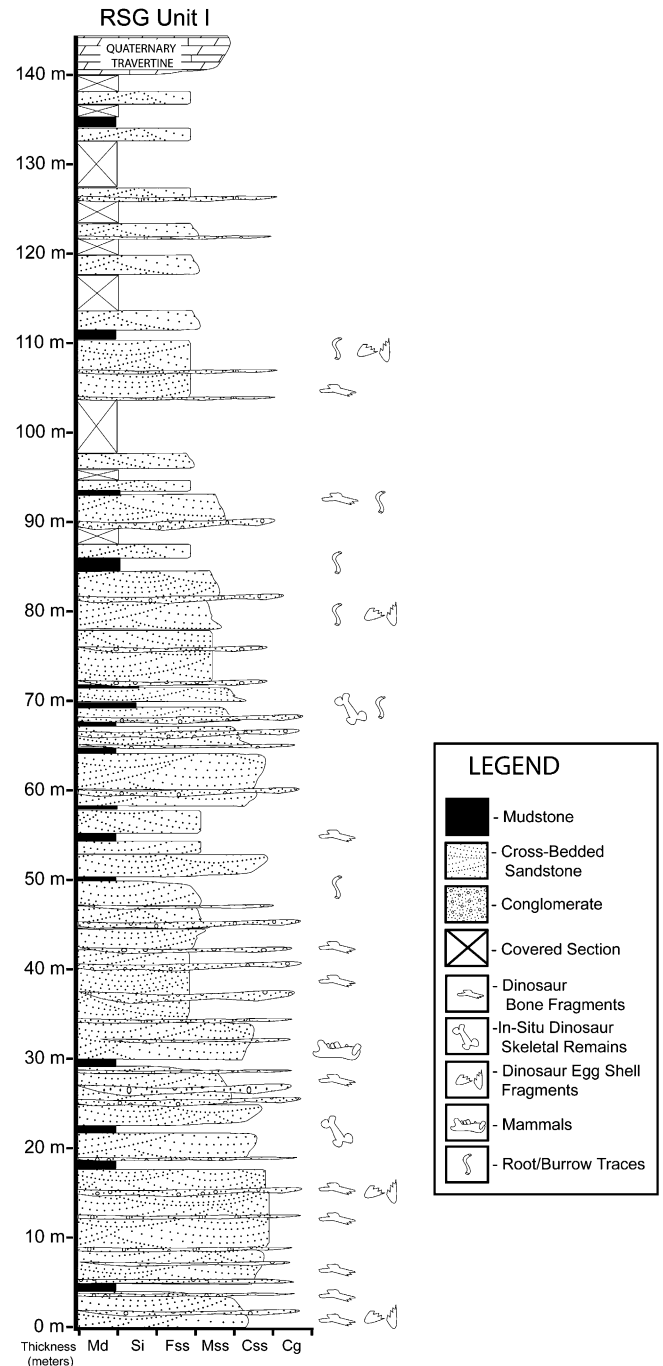


Fig. 2. Stratigraphic section measured at locality TZ-07 in Unit I of the Red Sandstone Group in the Songwe Valley (modified from Roberts et al., 2004). Abbreviations: Cg, conglomerate; Css, coarse sandstone; Fss, fine sandstone; Md, mudstone; Mss, medium sandstone.

least two temporally distinct depositional episodes for the Red Sandstone Group, clarifying certain aspects of the contentious debate surrounding the nature and age of these strata in the RRB (e.g., Spence, 1954; Spur, 1954; Tiercelin et al., 1988; Ebinger et al., 1989; Wescott et al., 1991; Kilembe and Rosendahl, 1992; Damblon et al., 1998; Morley et al., 1999). Deposits associated with the older of these two events [Unit I] consist of a series of red

sandstones and mudstones considered to be Cretaceous in age, based in part on faunal and lithological similarities with ~Aptian Dinosaur Beds of Malawi (Dixey, 1928; Spence, 1954; Colin and Jacobs, 1990; Jacobs et al., 1990; Mateer et al., 1992). These deposits are dominated by medium grained, dark red (5R 2/6) to grayish purple (5P 4/2) sandstone with occasional basal pebble conglomerate and thin, lenticular dark red (5R 2/6) mudstone and siltstone. The presence of lithologically similar, yet younger “red beds” (Unit II of the Red Sandstone Group) in the Songwe Valley has been discussed elsewhere (e.g., Stevens et al., 2004, *in press-a*, *in press-b*; also, see Roberts et al., 2004 for a detailed review of the Red Sandstone Group). Exposures of the Red Sandstone Group strata are located in the Western Branch of the East African Rift System (EARS) and were deposited in a fully alluvial setting, well inland from the Indian Ocean. As such, intercalated marine sequences with potentially time-restrictive biostratigraphic index taxa are not present.

3. Fossil materials recovered

3.1. Fishes

Fish remains are very rare in RSG Unit I strata. One of the more diagnostic specimens recovered to date is an isolated scale (TNM 02071) collected at locality TZ-07. The scale is referred to Osteoglossomorpha (Teleostei) on the basis of its cycloid shape combined with well-developed radial furrows along its (presumed) anterior field and fine circuli (Fig. 3a and b). It measures 9.7 by 7.4 mm, with ca. 15 well-developed radial furrows that diverge symmetrically along the anterior field of the scale (terminology follows Hilton, 2003). The furrows penetrate approximately halfway into the body of the scale, converging towards the center of the scale. The scale lacks reticulate furrows, but does have very fine circuli preserved over part of its surface. Within osteoglossomorphs, this combination of features is found in extant and fossil Hiodontidae and Notopteridae (Arratia, 1997), both relatively basal families, and is considered the primitive condition for the group as a whole (Hilton, 2003). Cretaceous osteoglossomorphs are known from other locales in Africa (e.g., the notopterid *Palaeonopterus greenwoodi* from the Albian/Cenomanian Kem Kem Beds of Morocco; Cavin and Forey, 2001). Given the predominantly Gondwanan freshwater distribution for the clade and a fossil record extending back to the Early Cretaceous (Arratia, 1997), it is not unexpected to have a relatively basal osteoglossomorph represented as part of this East African Cretaceous freshwater fauna.

Other fish discoveries include a single, small (5.3 mm long) tooth (TNM 03059) from TZ-07 assigned to Teleostei indet. (Fig. 3c). In addition, a small fragment of dermal bone (TNM 02058, recovered from locality TZ-06), measuring ca. 10.6 by 7 mm, is assigned to the lungfish family Ceratodontidae (Dipnoi) on the basis of its distinctive cosine ornament.

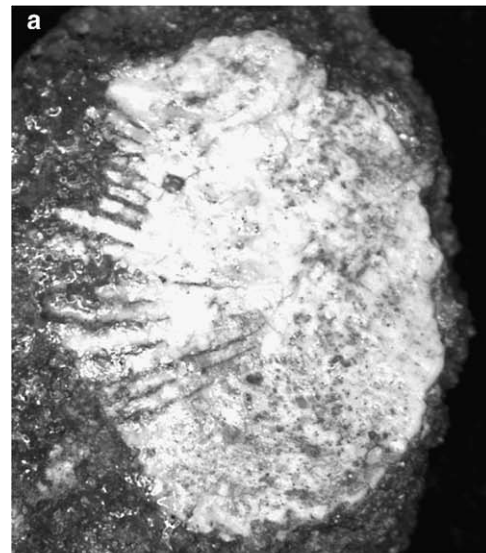


Fig. 3. Photograph (a) and line drawing (b) of osteoglossomorph scale (TNM 02071) and photograph (c) of an indeterminate teleost tooth (TNM 03059). Anterior is the left in (a, b) and to the right in (c). Scale equals 2 mm in all images.

3.2. Turtles

Although relatively uncommon, a number of specimens referable to Testudines have been recovered, including

elements of both plastron and carapace. Incomplete preservation precludes a more specific taxonomic assignment at this time.

3.3. *Crocodyliforms*

Crocodyliforms from the Red Sandstone Group are also rare, with only a single, fragmentary tooth (TNM 02080) recovered to date. This tooth is referred to Crocodyliformes on the basis of its conical crown with apically directed grooves. Taken together, the low abundance of both crocodylian and turtle fossils in this depositional environment distinguishes it from many contemporaneous upland faunas (e.g., Jacobs et al., 1990, 1996; Gomani, 1997). A more thorough understanding of whether this represents sampling or taphonomic bias, or reflects the actual faunal composition of this paleoenvironment, awaits additional field collection.

3.3.1. *Sauropod dinosaurs*

Sauropod dinosaurs are represented by multiple specimens collected from throughout the field area, including a partially articulated specimen from locality TZ-07. The specimen preserves components of both the axial and appendicular skeleton, and is still undergoing preparation and study. Additional, isolated vertebral specimens (TNM 02065, TNM 02072; Fig. 4) have also been collected from locality TZ-07, including caudal vertebrae referable to lithostrotian titanosaurs (Table 2). Although incompletely preserved, proximal and middle caudal vertebral centra are procoelous (i.e., with a cranially facing concavity) and exhibit a moderately well-developed “ball” caudally. They are also characterized by a neural arch attachment restricted to the cranial half of the centrum (Fig. 4a, d, e and h). Taken together, these traits demonstrate possible lithostrotian affinities (Upchurch et al., 2004). Yet the possession of procoelous middle caudal vertebrae excludes the Tanzanian lithostrotian from assignment to the potentially contemporaneous form *Malawisaurus dixeyi* from the nearby Dinosaur Beds of Malawi, a taxon which lacks this character (Jacobs et al., 1993; Gomani, 1999; Wilson, 2002). Moreover, RSG caudal vertebrae (Fig. 4d and h) do not possess the ventrally protruding chevron facets present in *Malawisaurus*. It is possible that specimens TNM 02065 and/or TNM 02072 pertain to the Malawi lithostrotian “undesignated morph 1” (based on the presence of procoelous middle caudal vertebrae; Gomani, 1999); however, additional, better-preserved materials from both the Malawi Dinosaur Beds and the RSG are required to verify this assessment. The recovery of two isolated sauropod teeth, characterized by narrow, cylindrical, non-flaring crowns, with wrinkled enamel and high-angle wear facets, also support a titanosaurian assignment for at least some of the sauropod materials.

Locality TZ-07 preserves abundant and well-preserved megaloolithid dinosaur eggshell throughout the exposed

section (Fig. 2). This may derive from the same taxon as the titanosaurian skeletal material found throughout the same locality, given that the parataxonomic Oofamily Megaloolithidae has been linked with titanosaurs in other locales (e.g., Cousin et al., 1994; Sahni et al., 1994; Chiappe et al., 1998, 2001). Morphological characteristics specific to Megaloolithidae (e.g., tuberculate surface ornamentation, single structural layer of calcite, etc.) are detailed in Gottfried et al. (2004). However, until intact eggshell with identifiable embryonic remains are recovered, as in Chiappe et al. (2001), definitive taxonomic associations cannot be made. Recovery of eggshell has thus far been limited to locality TZ-07.

3.4. *Non-avian theropod dinosaurs*

Non-avian theropod dinosaurs are represented by a pair of articulated proximal caudal vertebrae (TNM 03041), also recovered from locality TZ-07 (Fig. 5a–c; see Table 2 for vertebral metrics). TNM 03041 consists of a centrum and associated neural arch, along with a portion of the succeeding vertebra. The amphicoelous centra are slender and elongate, with moderate constriction of the corpus between the intercentral articulations. The ventral surface of the centrum exhibits a broad, shallow longitudinal sulcus (Fig. 5b), characteristic of many theropod taxa. Intercentral articulations are dorsoventrally ovoid (Fig. 5c), with moderately well-developed chevron facets, particularly on the caudoventral end of the centrum.

Neural arches of both vertebrae are partially preserved, with the proximal portion of each transverse process and neural spine present. The neural canal is asymmetric, with the dorsal half of the canal transversely broader than the ventral half (the incomplete second vertebra reveals a clear cross-sectional view of the canal). Neural arches are characterized by a pedicle attaching along the cranial four-fifths of the centrum, a transverse process projecting laterally just caudal to midcentral length, and a postzygapophysis extending caudally to a position just dorsal to the cranial intercentral facet of the succeeding vertebra (Fig. 5a). Distinct cranial centrodiapophyseal and prezygodiapophyseal laminae demarcate a substantial infraprezygapophyseal fossa on the neural arch (Fig. 5a). Although the lack of precise character data preclude a specific taxonomic assignment, overall morphology is broadly similar to that of medium to large-sized, non-coelurosaurian theropods (e.g., *Dilophosaurus*—Welles, 1984; *Ceratosaurus*—Gilmore, 1920; Madsen and Welles, 2000).

Non-avian theropod dinosaurs are also represented by 11 isolated, partially preserved teeth, all of which derive from locality TZ-07 (Fig. 5d). As with the eggshell described above, theropod teeth have been recovered from throughout the exposed section at TZ-07. Several isolated teeth were discovered during the excavation of a semi-articulated sauropod dinosaur, suggesting a possible scavenging event. All teeth are gently recurved, exhibit serrations on both mesial and distal carinae (~13–16 denticles/5 mm;

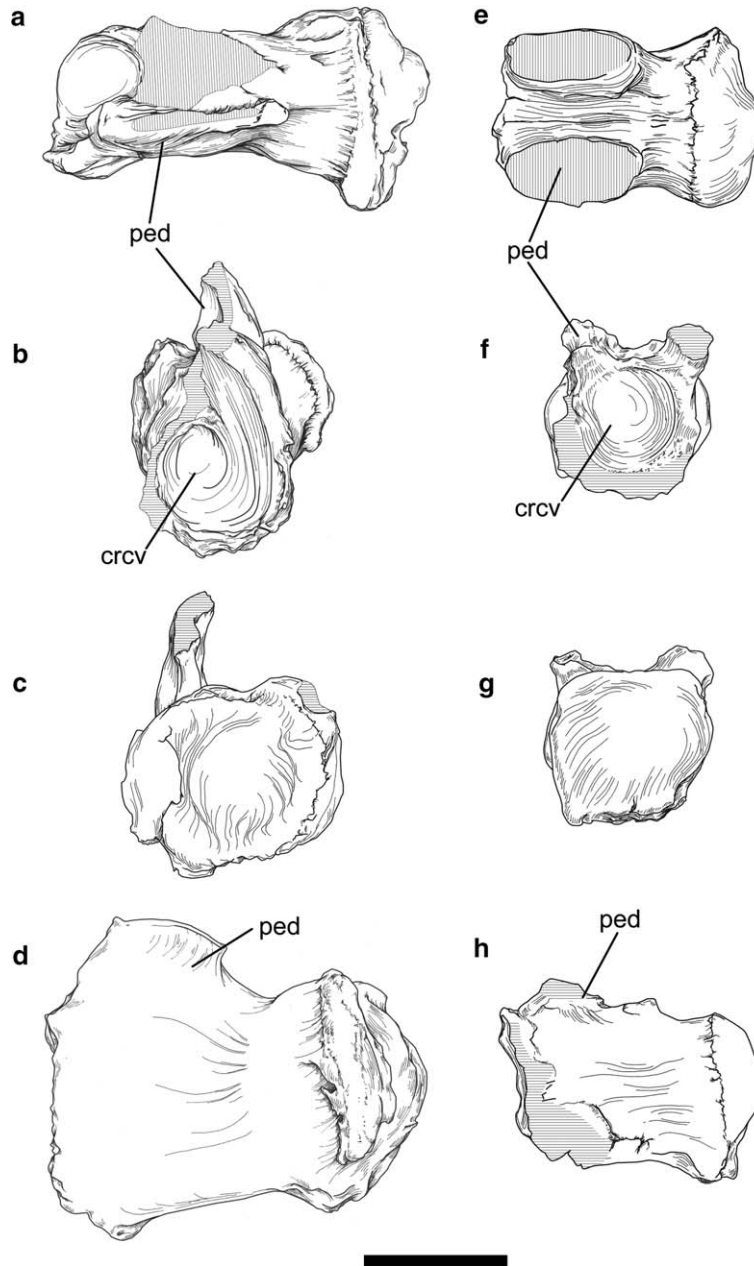


Fig. 4. Proximal (TNM 02072; a–d) and middle (TNM 02065; e–h) caudal vertebrae of lithostrotian sauropods in dorsal (a, e), cranial (b, f), caudal (c, g), and left lateral (d, h) views. Abbreviations: crcv, cranial concavity; ped, pedicle. Scale equals 5 cm.

Fig. 5d), and belong to the same approximate size class (~11.5 mm mesiodistally by 4.5 mm labiolingually) Two

Table 2
Measurements of sauropod and theropod caudal vertebrae (in mm)

Specimen	CL	CH	CW
Sauropod			
TNM 02065	84	54	50
TNM 02072	140	76	59
Theropod ^a			
TNM 03041	80	46	30

CL, centrum length; CH, centrum height; CW, centrum width.

^a The caudal (posterior) vertebra of the pair is incomplete, thus only measurements for the cranial member are included here.

teeth are D-shaped in cross-section, indicating a position in the rostralmost portion of either the dentary or premaxilla.

3.5. Mammals

Mammals are represented in the fauna by specimen TNM 02067 (Fig. 6—referred to as NMT 02067 in Krause et al., 2003) that has been tentatively assigned to the sudamericid gondwanatherians (Gottfried et al., 2003; Krause et al., 2003). The specimen consists of a short (19.5 mm) and deep (11.4 mm), moderately abraded left dentary exhibiting a single, laterally compressed procum-

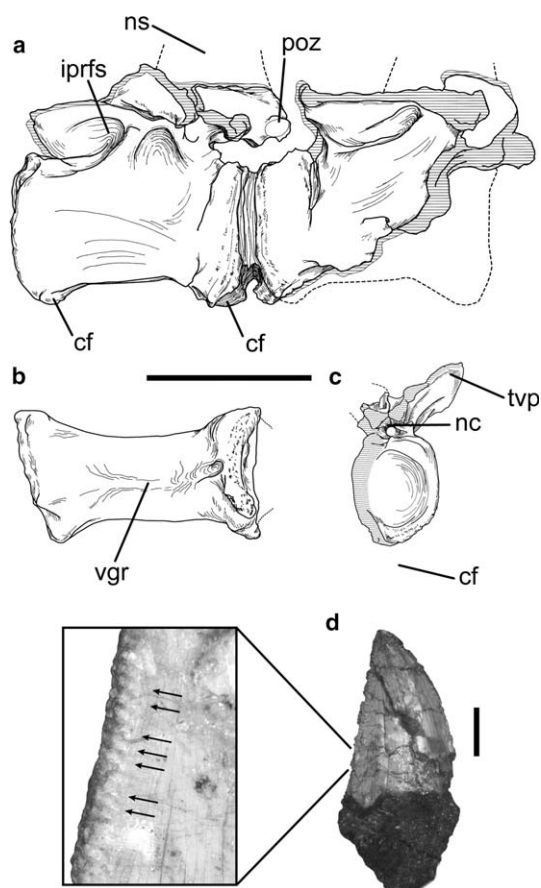


Fig. 5. Two proximal caudal vertebrae of a non-avian theropod dinosaur (TNM 03041) in left lateral (a), ventral (b), and cranial (c) views; and an isolated theropod dinosaur tooth (TNM 02088) in labial (d) view, with black arrows in inset illustrating close-set serrations (i.e., ~13–16 denticles/5 mm). Abbreviations: cf, chevron facet; iprfs, infraprezygapophyseal fossae; nc, neural canal; ns, neural spine; poz, postzygapophysis; tvp, transverse process. Scale equals 5 cm for (a)–(c); 5 mm for (d).

bent central incisor that is separated by a small (~2.5 mm) diastema from five columnar, hypsodont, single-rooted cheek teeth. This specimen represents the largest and most complete mammal specimen recovered from Cretaceous deposits on continental Africa. Its relatively large size and unique combination of characters (e.g., extreme hypsodonty) make it notable among Cretaceous-age Gondwanan mammals in general (also see Kielan-Jaworowska et al., 2004; Krause, 2004), and in particular, those recovered from Africa.

4. Discussion

4.1. Age of Unit I—Red Sandstone Group, Rukwa Rift Basin

Based on preliminary faunal analyses, our group has documented at least two different depositional episodes for the Red Sandstone Group within the Songwe Valley portion of the Rukwa Rift Basin (O'Connor et al., 2003; Gottfried et al., 2004; Roberts et al., 2004; Stevens et al.,

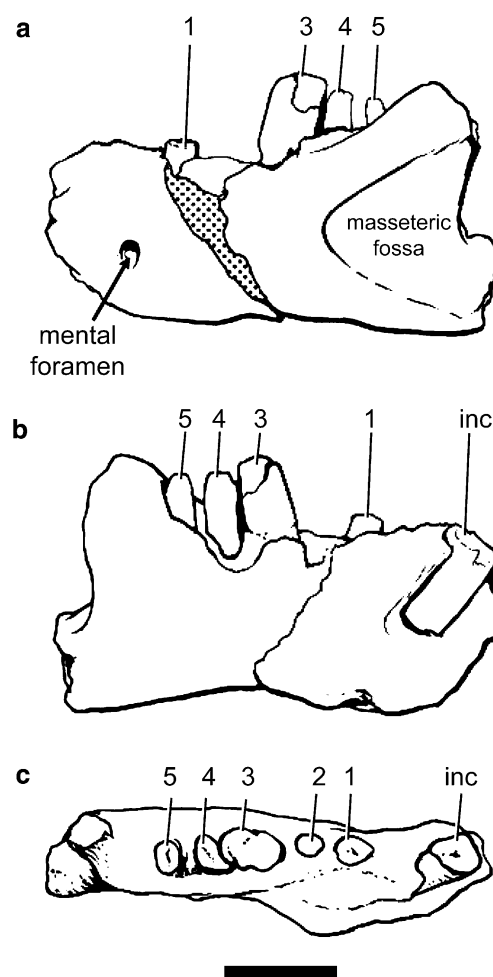


Fig. 6. A left dentary (TNM 02067) recovered from locality TZ-07 that has been tentatively referred to the poorly known mammalian clade, Gondwanatheria, illustrated in labial (a), lingual (b), and (c) occlusal views. Abbreviations: inc, incisor; 1–5 cheek teeth 1–5. Scale equals 5 mm (modified from Krause et al., 2003).

2004; Stevens et al., in press-a, in press-b). These two units were informally referred to as Units I and II by Roberts et al. (2004). Unit I contains articulated non-avian dinosaurs, whereas Unit II preserves Paleogene-restricted mammals (e.g., the phiomorph rodent *Metaphiomys*; Stevens et al., in press-a). These new faunal data, combined with the wide range (i.e., Middle Jurassic to Miocene) of previous age assignments for the Red Sandstone Group in southwestern Tanzania (e.g., Tiercelin et al., 1988; Ebinger et al., 1989; Wescott et al., 1991; Kilembe and Rosendahl, 1992; Damblon et al., 1998; Morley et al., 1999), emphasize that additional work is necessary to fully characterize the temporal and depositional history of this sedimentary sequence.

A Cretaceous age assignment for Unit I is consistent with many previous geological assessments of the RSG in Tanzania (e.g., Spence, 1954; Spur, 1954; Grantham et al., 1958; Pallister, 1963; Haughton, 1963; Mondeguer et al., 1989; Kilembe and Rosendahl, 1992). Moreover, a number of studies have suggested a correlation between

'red sandstones' in Tanzania and the Early Cretaceous (~Aptian) Dinosaur Beds of Malawi (Dixey, 1928; Jacobs et al., 1990; Mateer et al., 1992). The most convincing faunal evidence for a Cretaceous age of Unit I as opposed to either a Jurassic or a Cenozoic assignment is the co-occurrence of dinosaurs (e.g., lithostrotian titanosaurs, non-avian theropods) and osteoglossomorph fishes, the latter taxon being known exclusively from the Early Cretaceous to recent times (Arratia, 1997). Whereas lithostrotians are not restricted exclusively to Cretaceous strata, it was during this period that the clade diversified and radiated throughout the much of the world (Curry, 2001; Wilson and Upchurch, 2003; Upchurch et al., 2004).

4.2. Biogeographic context—Gondwanan vertebrate distributions in the Cretaceous

Two dominant paleobiogeographic scenarios have been proposed in recent years to account for the distribution of terrestrial vertebrates in Gondwana during the Cretaceous Period, with continental Africa playing a pivotal role in each scenario. The 'Africa-first' hypothesis (*sensu* Sereno et al., 2004) posits a scenario whereby subaerial connections between Indo-Madagascar, Antarctica, and South America, to the exclusion of continental Africa, persisted well into the Late Cretaceous allowing certain groups of closely related taxa (e.g., abelisaurid theropod dinosaurs) to disperse among the conjoined landmasses (Sampson et al., 1998, 2001; Krause et al., 1999). The apparent absence of these clades from Africa, along with geophysical models depicting the continent's isolation prior to the Early-Late Cretaceous boundary, has been used as additional support for this model. Although the proposed physical connections between Indo-Madagascar and Antarctica contrast with most traditional paleogeographic reconstructions (Smith et al., 1994; Scotese, 2001), geophysical evidence consistent with the Africa-first hypothesis has been provided by the tectonic modeling of Hay et al. (1999). Importantly though, the entire faunal dataset used in support of this hypothesis was derived from uppermost Cretaceous (i.e., Campanian-Maastrichtian) terrestrial strata of South America, India, and Madagascar, a time period that remains virtually absent in the terrestrial rock record of both continental Africa and Antarctica.

The recently proposed 'Pan-Gondwana' hypothesis, which has been presented as an alternative to the 'Africa-first' model, posits intermittent connections among Gondwanan landmasses, including Africa and South America, up through the Early-Late Cretaceous boundary (Sereno et al., 2004). Developed to account for the recent discovery of Cretaceous-age abelisauroid theropods from the African continent (e.g., *Rugops primus* from the Albian-Cenomanian? Echkar Formation of Niger), new taxa featured in this scenario have been interpreted to refute the Africa-first model. An appropriate test of this biogeographic hypothesis requires two elements: temporal and phylogenetic relevance. First, the basis of the Cenomanian age determination

for the Echkar Formation (Sereno et al., 2004) must be clarified in light of previous estimates that have assigned it an Albian age (i.e., pre-Late Cretaceous; Lapparent, 1960; Taquet, 1976). Moreover, from a phylogenetic perspective, only a taxon nesting within the derived abelisaurids would effectively refute the Africa-first hypothesis. As such, the presence of a basal abelisaurid on continental Africa may instead indicate that the clade as a whole had a lengthy history on Gondwana predating the initial breakup of the supercontinent. In sum, time-equivalency of fossil-bearing strata and well-resolved phylogenetic hypotheses are critical components for rigorously testing and refining biogeographic models to account for the distribution of terrestrial vertebrates in the Cretaceous of Gondwana (see Krause et al. (accepted for publication) for a discussion of Africa-first and Pan-Gondwana hypotheses).

4.3. Biogeographic implications of fossils from Unit I of the Red Sandstone Group

Cretaceous fossils recovered from the RSG deposits are already beginning to have a direct impact upon regional, continental and even supercontinent-level biogeographic hypotheses. For example, the tentatively identified gondwanatherian mammal (TNM 02067; Krause et al., 2003) from Unit I provides a new geographic datum for this clade of Gondwanan mammals, representing the only occurrence of the group on continental Africa. Prior to its discovery, gondwanatherians were known only from Campanian to Eocene deposits in Madagascar, India, South America, and Antarctica (Kielan-Jaworowska and Bonaparte, 1996; Krause et al., 1997; Reguero et al., 2002; Krause et al., 2003). However, the tentative taxonomic assignment of TNM 02067, and temporal ambiguity of Unit I strata, serve to limit biogeographic inferences at this time. If the RSG deposits are pre-Campanian (e.g., if they are actually contemporaneous with the Aptian Dinosaur Beds of Malawi), not only would TNM 02067 represent the sole gondwanatherian occurrence from Africa, but it would represent a significant increase in the temporal range of the clade. And if RSG deposits are Campanian or later, from the standpoint of testing competing biogeographic hypotheses, the uncertain phylogenetic relationships among known gondwanatherians renders TNM 02067 functionally equivalent to the basally positioned abelisaurid *Rugops*; basal or ambiguously positioned taxa do not provide phylogenetic resolution sufficient for discriminating between the 'Africa-first' and 'Pan-Gondwana' hypotheses.

The comparison of other Unit I fossils (e.g., sauropod dinosaurs) with contemporaneous faunas of both sub-equatorial (e.g., the Malawi Dinosaur Beds) and circum-Saharan Africa (e.g., Gadoufaoua, Niger; Kem Kem Beds, Morocco) may be useful for distinguishing among other biogeographic hypotheses. In particular, they offer insights into whether Cretaceous terrestrial vertebrate faunas exhibit continent-level cosmopolitanism or whether they reflect

patterns of regional endemism, as proposed by Jacobs et al. (1996). Red Sandstone Group deposits in the Rukwa Rift Basin have been thought to represent northern extensions of the Early Cretaceous Dinosaur Beds of Malawi (e.g., Dixey, 1928; Jacobs et al., 1990), although the latter are actually contained within a different rift segment (i.e., the Malawi Rift Basin). Given the proximity (~200 km) and potentially contemporaneous nature of the two sequences, an initial hypothesis of 'Regional Biotic Similarity' predicts that the assemblage recovered from Unit I of the RSG will exhibit faunal overlap with the Malawi Dinosaur Beds.

For example, lithostrotian titanosaurs are present in both the Dinosaur Beds and RSG deposits as evidenced by specimens including thin, cylindrical teeth with high-angle wear facets, and procoelous proximal caudal vertebrae (Upchurch, 1998; Wilson, 2002; Upchurch et al., 2004). Tanzanian sauropod vertebrae from the middle portion of the tail, however, are procoelous (e.g., TNM 02065), distinguishing them from *Malawisaurus*, a taxon characterized by the absence of middle caudal procoely (e.g., Gomani, 1999). As such, at least some of the Tanzanian sauropod material represents a more derived form than *Malawisaurus* within Lithostrotia (e.g., see Gomani, 1999; Wilson, 2002; Upchurch et al., 2004). Notably, the Tanzanian form may be conspecific with another of the Malawi sauropods (e.g., Malawi "undesignated morph 1"; Gomani, 1999) based on the identification of middle caudal vertebrae exhibiting the procoelous condition; yet as both Tanzanian and Malawian 'vertebral taxa' are based on non-diagnostic materials, this assessment is clearly premature. In short, initial comparisons do not refute broad taxonomic overlap between Tanzanian and Malawi faunas.

Finally, regional patterns of faunal similarity emerge from the examination of Cretaceous vertebrates from other parts of Africa, particularly the dinosaurian taxa (e.g., spinosaurid and carcharodontosaurid theropods; ornithomimid and ornithomimid-like theropods; ornithomimid-like theropods) represented in the late Early and early Late Cretaceous faunas of circum-Saharan Africa (Weishampel et al., 2004). Interestingly, these dinosaurian elements very common to northern Africa have yet to be recovered from either the penecontemporaneous Dinosaur Beds of Malawi (Jacobs et al., 1996) or the Red Sandstone Group deposits in southwestern Tanzania. Whether this reflects an actual biogeographic signal or sampling bias can only be revealed by continued exploration of Cretaceous-age sequences in other regions of the continent.

5. Conclusions

We report the discovery of new Cretaceous-age vertebrate-bearing localities from Red Sandstone Group exposures in the Rukwa Rift Basin of Southwestern Tanzania. These new sites preserve a diverse terrestrial/freshwater fauna including fishes, turtles, crocodyliforms, dinosaurs and mammals. Recent expeditions have identified a number of fossiliferous localities, with specimens ranging from

isolated elements to semi-articulated non-avian dinosaurs. Other finds include one of the most complete mammal specimens recovered from the Cretaceous of continental Africa, abundant dinosaur eggshell, and both theropod and sauropod dinosaurs. This portion of the East Africa Rift System offers great promise for the discovery of new Cretaceous fossils crucial for evaluating biogeographic hypotheses proposed to explain Gondwanan vertebrate distributions in the latter half of the Mesozoic.

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