

Paleontological Exploration in Africa

A View from the Rukwa Rift Basin of Tanzania

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Introduction

The Mesozoic – Cenozoic transition was a period of dramatic global change during which time the Earth's continents were in the process of fragmenting from a large, relatively continuous landmass to assume a configuration similar to that seen today. The most significant tectonic activity in the southern hemisphere occurred during the Cretaceous-Paleogene interval, when the large Gondwanan sub-regions of Africa, South America, Australia, Indo-Madagascar and Antarctica became increasingly isolated from one another (Smith et al., 1994; Scotese, 2001). Continental dynamics of this scale are not only geologically significant, they also profoundly influenced the evolution of both terrestrial and marine biotas (Forster, 1999; Krause et al., 1999; Sereno, 1999; Lieberman, 2000; Upchurch et al., 2002; Humphries and Ebach, 2004). Indeed, the Cretaceous-Paleogene transition marks large-scale faunal turnover of major vertebrate and invertebrate taxa (e.g., extinction of nonavian dinosaurs, radiation of “modern” mammals and birds; Cracraft, 2001; Springer et al., 2003, 2004; Archibald and Fastovsky, 2004; Kielan-Jaworowska et al., 2004; Rose and Archibald, 2004; Clarke et al., 2005).

Numerous hypotheses have been proposed to explain the origin, diversification, and extinction of many vertebrate groups living on, or dispersing through, Gondwana during the Cretaceous and Paleogene. For example, molecular studies have postulated a Cretaceous-Paleogene African origin for a number of higher-level amniote clades, including Placentalia (Murphy et al., 2001 and references therein), Afrotheria (Hedges et al., 1996; Springer et al., 1997, 2003,

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2005; Madsen et al., 2001; van Dijk et al., 2001), and neornithine birds (Cracraft, 2001). In particular, an ancient (\sim Cretaceous/Paleocene) Gondwanan primate origin has been proposed, with a strepsirrhine-haplorhine divergence occurring shortly thereafter (e.g., Tavaré et al., 2002). African origins have also been proposed for a number of Malagasy terrestrial and freshwater groups (e.g., etropline cichlids (Vences et al., 2001); lemurs (Yoder et al., 2003, Poux et al., 2005); tenrecs (Poux et al., 2005)). Yet divergence time estimates retrieved by molecular studies for various clades often vastly predate the first occurrences of those groups in the fossil record (e.g., Smith and Peterson, 2002), instigating considerable debate as to the time of origin and path of dispersal for a broad range of taxa (e.g., Martin, 2000; de Wit, 2003; Schrago and Russo, 2003; Rose and Archibald, 2004; de Queiroz, 2005; Masters et al., 2006). This is perhaps not surprising, as Martin and others have demonstrated that by any measure, the vertebrate fossil record (particularly in places like Africa) is dismayingly incomplete, such that dates derived from paleontological data alone are likely to significantly underestimate true divergence times (Martin, 1993, 2000; Paul, 1998; Tavaré et al., 2002; Miller et al., 2005). Whereas questions remain regarding the reliability of molecular clocks with respect to calibration and rate heterogeneity (Smith and Peterson, 2002), it is also clear that sustained work is needed to improve sampling of the fossil record and test molecular hypotheses by providing fossil data that can be used to more rigorously calibrate and refine divergence time estimates (Seiffert et al., 2003; Yoder et al., 2003). This is particularly true of undersampled regions where new discoveries can have a profound effect on hypotheses based on presence/absence data (e.g., a Cretaceous gondwanatherian mammal from Tanzania; Krause et al., 2003b; O'Connor et al., 2006). Moreover, recent studies examining the robusticity of biogeographic reconstructions demonstrate that even a single new outgroup or ingroup fossil can powerfully influence area-of-origin interpretations (e.g., Stevens and Heesy, 2004, 2006; Heesy et al., 2006).

Uneven Paleontological Sampling

Much of our knowledge of terrestrial communities during the Cretaceous-Paleogene transition has been based on research conducted on northern continents. These studies have sought to address global-level issues such as species diversity and extinction, in addition to providing information concerning the phylogenetic and biogeographic histories of major terrestrial vertebrate groups. In recent decades, efforts have increased to improve the fossil record from Gondwanan landmasses and rectify the Laurasian sampling bias. Field research in South America, supra-equatorial Africa, India, and Madagascar has significantly improved the Southern Hemisphere vertebrate record over the last thirty years (e.g., Bonaparte and Powell, 1980; Molnar, 1980; Rich et al., 1983; Archer et al., 1985; Flynn et al., 1987; Prasad and Sahni, 1988; Godinot, 1994; Prasad and

Godinot, 1994; Sereno et al., 1996, 2004; Sampson et al., 1998; Sigogneau-Russell et al., 1998; Krause et al., 1999, 2006; Chiappe et al., 2001; Kay et al., 2001; Smith et al., 2001; Flynn et al., 2003; Krause, 2003b; Prasad et al., 2005; Rana et al., 2005), but large portions of the former supercontinent remain relatively unexplored. Especially problematic is the patchiness of terrestrial sequences on continental Africa and its surrounding islands, rendering early Cenozoic vertebrate diversification in many of these locales a virtual mystery.

African Vertebrate Paleontology—A Cretaceous-Paleogene Perspective

Historically, African Mesozoic terrestrial vertebrate assemblages have been recovered from only select portions of the continent, notably the Permo/Triassic-Jurassic Karoo basins in southern Africa, the Upper Jurassic Tendaguru series in southeastern Tanzania, and a number of “middle” Cretaceous locales scattered throughout circum-Saharan Africa (Fig. 1A). Such faunas bear witness to pioneering paleontological exploration during the last century by workers such as Lavocat (1954), Lapparent (1960), and others, for example, in Niger, Algeria, Tunisia, and Morocco. A few Cretaceous-age fossil-bearing sequences are known from sub-equatorial Africa, although only the ~Aptian Dinosaur Beds of Malawi (Dixey, 1928; Jacobs et al., 1990, 1993; Gomani, 2005) and the Berriasian-Valanginian Kirkwood Formation of South Africa (Rich et al., 1983; De Klerk et al., 2000) have revealed diverse vertebrate assemblages. Until recently, Paleogene sampling has largely been restricted to a few isolated localities, mostly concentrated in the northern Saharan arc (Fig. 1B), along with a single locality in the southwestern portion of the continent (Pickford, 1986). Cenozoic faunas recovered from East Africa have traditionally been limited to deposits of Miocene and later age, but recent work has demonstrated that this region also preserves a deeper record of vertebrate evolutionary history (Leakey et al., 1995; Harrison et al., 2001; Gunnell et al., 2002; Kappelman et al., 2003; Stevens et al., 2004). Yet few places in Africa have received the sustained, long-term paleontological effort that has been dedicated to the Eocene-Oligocene deposits of Egypt.

A Window into the Early Cenozoic of Africa

Without doubt, the exemplar for intensive fossil collecting in the African Paleogene has been the work of Elwyn Simons and his collaborators in the Fayum Depression of Egypt. Prior to these expeditions, a modest number of fossils from the Fayum had been collected and described (e.g., Andrews, 1901, 1902; Beadnell, 1902; Osborn, 1908; Matsumoto, 1921). However, since 1961,

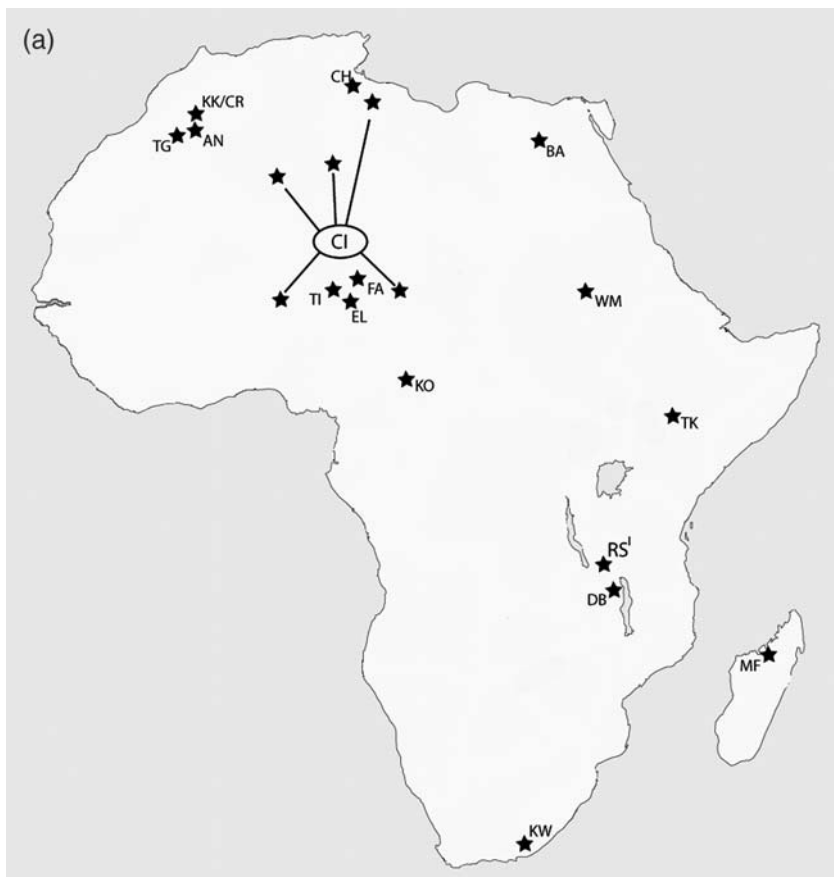


Fig. 1 Map of Africa and its surrounding islands illustrating the principal Cretaceous (A) and Paleogene (B) sequences preserving terrestrial vertebrates. Note: only locales preserving relatively diverse terrestrial vertebrate assemblages are indicated. Abbreviations for **Fig. 1A** as follows: AN, Anoual, Lower Cretaceous, Morocco; BA, Baharija Fm., Upper Cretaceous, Egypt; CH, Chenini Fm., Lower Cretaceous, Tunisia; CI, "Continental Intercalaire," Lower Cretaceous-lowermost Upper Cretaceous, multiple locations throughout circum-Saharan Africa; CR, Continental Red Beds, Upper Cretaceous, Morocco; DB, Dinosaur Beds, Lower Cretaceous, Malawi; EL, Elrhaz Fm., Lower Cretaceous, Niger; FA, Farak Fm., Lower Cretaceous, Niger; KK, Kem Kem Beds, Upper Cretaceous, Morocco; KO, Koum Fm., Lower Cretaceous, Cameroon; KW, Kirkwood Fm., Lower Cretaceous, South Africa; MV, Maevarano Fm., Upper Cretaceous, Madagascar; RS^I, Red Sandstone Group (Unit I), "mid" Cretaceous, Tanzania; TI, Tiourarén Fm., Lower Cretaceous, Niger; TG, Tegana Fm., Lower Cretaceous, Morocco; TK, Turkana Grits, Upper Cretaceous, Kenya; WM, Wadi Milk Fm. Upper Cretaceous, Sudan.

Abbreviations for **Fig. 1B** as follows: AM, Adrar Mgorn, Paleocene, Morocco; BZ, Buel Haderait/Zella, Dor et Talha, Eocene-Oligocene, Libya; CG, Chambi/Gebel Bou Gobrime, Eocene-Oligocene, Tunisia; CH, Chilga, Oligocene, Ethiopia; FD, Fayum Depression, Eocene-Oligocene, Egypt; GN, Glib Zegdou/El Kohol/Nementcha, Eocene, Algeria; MH, Mahenge, Eocene, Tanzania; ML, Malembe, Oligocene, Angola; RS^{II}, Red Sandstone Group (Unit II), Oligocene, Tanzania

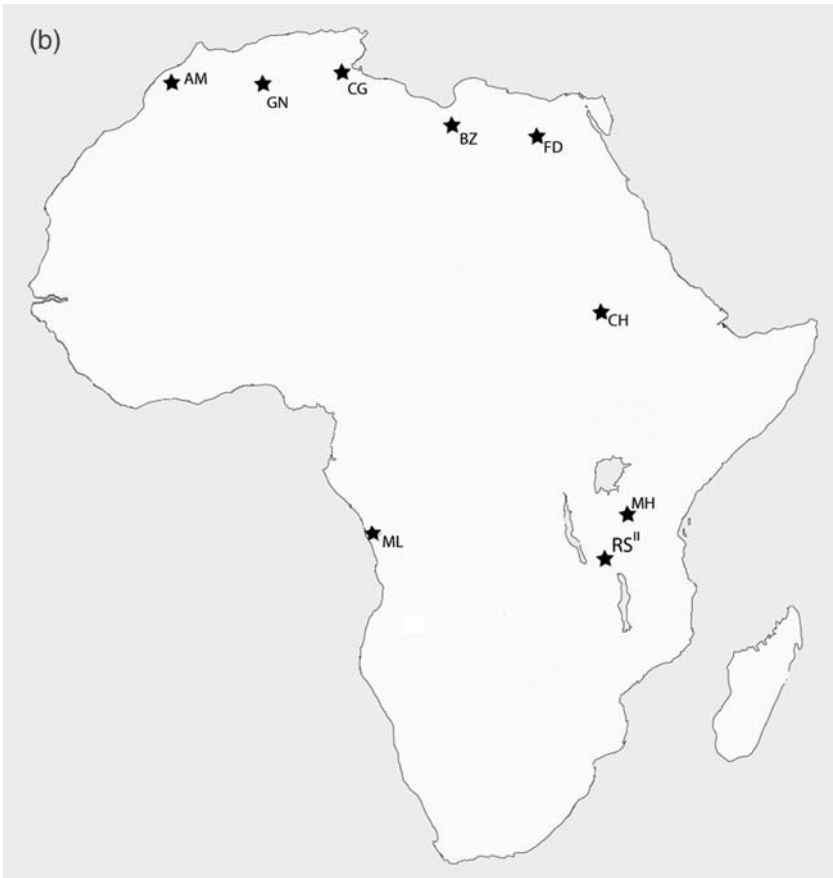


Fig. 1 (continued)

each of the 38 (~7-week) Fayum expeditions organized by Simons has assembled a crew of approximately 17 members, resulting in over 207,000 ‘*person-hours of collecting effort*’ on the ground searching for fossils. This effort has yielded tens of thousands of vertebrate fossil specimens, which have in turn formed the basis for hundreds of publications. From a new order of mammals (Ptolemaiida Simons and Bown, 1995), to primitive elephant shrews (Simons et al., 1991) and abundant rodents (Wood, 1968; Holroyd, 1994), from the minute *Wadilemur* (Simons, 1997; Seiffert et al., 2005) and *Widanelfarasia* (Seiffert and Simons, 2000) to *Megalohyrax* (e.g., Thewissen and Simons, 2001), the Fayum Depression has provided a tantalizing glimpse into Africa’s past. This collection has inspired a generation of researchers to muse over aspects of the paleoecological setting (Bown, 1982; Bown et al., 1982; Simons et al., 1994), incorporating studies

of plants, fish (Murray and Attia, 2004), tortoises (Holroyd and Parham, 2003), birds (Rasmussen et al., 2001), hyraxes (Rasmussen and Simons, 2000; De Blieux and Simons, 2002), anthracotheres (Holroyd et al., 1996), creodonts (Holroyd et al., 1996; Holroyd, 1999), and especially primates (e.g., Simons and Rasmussen, 1995; Simons, 1998). The diversity and abundance of the primate sample alone has permitted important reconstructions of diets (e.g., Kirk and Simons, 2001), locomotor habits (e.g., Fleagle and Simons, 1982, 1983, 1995; Hamrick et al., 1995; Rasmussen et al., 1998, Ankel-Simons et al., 1998), and activity patterns and social systems (e.g., Fleagle et al., 1980; Fleagle, 1999), fleshing out the inhabitants of an Oligocene forest in striking detail.

Work by Simons and colleagues in the Jebel Qatrani Formation has fostered the development of other significant projects in the region, for example in Wadi Hitan (Gingerich et al., 1990); Wadi Moghara (Miller, 1999), and Birket Qarun (Seiffert et al., 2003). Perhaps most importantly, the continued discovery of new species and additional localities even after so much dedicated effort in the Fayum serves to underscore the importance of this area for providing exciting windows into the past, and offering encouragement for long-term projects in other parts of Africa.

Expanding the Cretaceous Record on a Neighboring Isle

As another recent example of sustained paleontological exploration, eight field seasons conducted since 1993 in the Upper Cretaceous Maevarano Formation of northwestern Madagascar have yielded similarly striking results. Since its inception, the Mahajanga Basin Project has more than quadrupled the known vertebrate diversity (>40 species) from the Late Cretaceous of Madagascar (Krause et al., 1999, 2006; Krause, 2003b). Although fossils from the Maevarano Formation were first discovered and published in the late 1800s (Depéret, 1896), intensive field research with large crews was not undertaken until the early 1990s. Several ~6 week expeditions, with crew sizes ranging between 15 and 20 individuals, transformed a virtually unknown terrestrial fauna into one of the most comprehensive Late Cretaceous assemblages in all of Gondwana (e.g., Sampson et al., 1998; Krause et al., 1999). This diversity encompasses fishes (Gottfried et al., 2001), frogs (Asher and Krause, 1998), turtles (Gaffney and Forster, 2003), lizards (Krause et al., 2003a), crocodyli-forms (Buckley and Brochu, 1999; Buckley et al., 2000), nonavian dinosaurs (Sampson et al., 1998; Curry Rogers and Forster, 2001; Carrano et al., 2002; O'Connor, 2007), birds (Forster et al., 1996, 1998), and mammals (Krause et al., 1997; Krause, 2001, 2003a). Hand in hand with announcements of species new to science, contributions have detailed the geological and paleoenvironmental context of the Maevarano Formation (Rogers et al., 2000; Rogers, 2005), exploring paleobiological aspects of the fauna (e.g., Buckley et al., 2000; Rogers et al., 2003; O'Connor and Claessens, 2005). Krause et al. (1999, 2006) provide a more comprehensive overview of the project's history.

The abovementioned projects have set a standard for how to conduct and sustain successful field projects in historically undersampled regions. Over the years both projects have included numerous student participants, graduates and undergraduates alike. Perhaps most significant is the fact that so many of these former student participants have pursued paleontological projects in other locales (e.g., Fleagle and Bown, 1983; Covert and Hamrick, 1993; Wing et al., 1993; Kay et al., 2001; Kappelman et al., 2003; Rasmussen, 2008). One such project still in its early stages is discussed below.

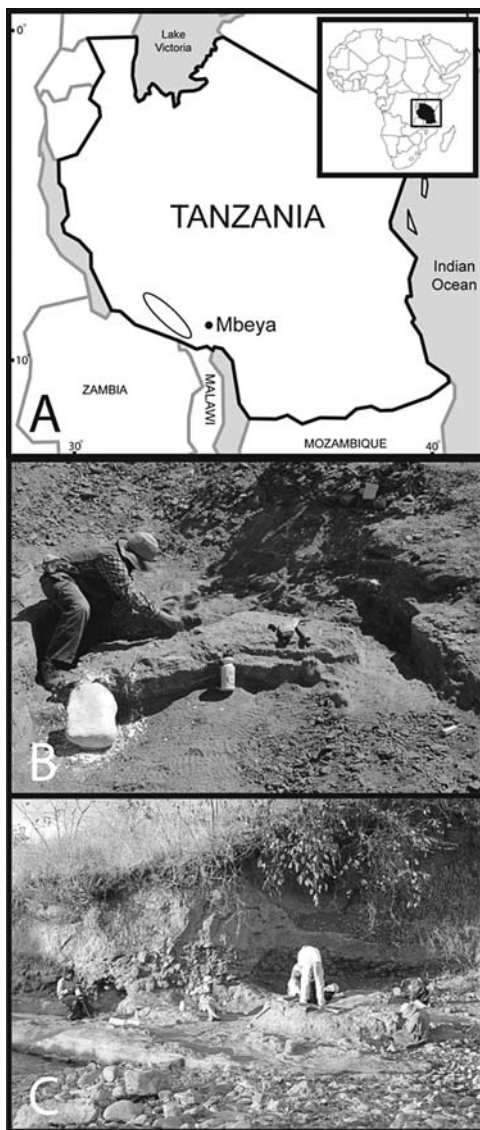
New Views into Vertebrate Evolutionary History: The Rukwa Rift Basin Project, Southwestern Tanzania

Developed in the spirit of the aforementioned endeavors, the Rukwa Rift Basin Project (RRBP) is seeking to expand the record of Cretaceous and Paleogene terrestrial vertebrates in sub-equatorial Africa. Situated in southwestern Tanzania between Lakes Nyasa (Malawi) and Tanganyika, the Rukwa Rift Basin (Fig. 2A) forms part of the western branch of the East African Rift System (EARS), and contains some of the thickest sedimentary deposits in East Africa (Wescott et al., 1991; Kilembe and Rosendahl, 1992; Morley et al., 1999). At least three major sedimentary episodes are recorded in the RRB, resulting from intermittent Permian to Recent tectonic events (Quenell et al., 1956; Wheeler and Karson, 1994). The middle sedimentary sequence, commonly referred to as the Red Sandstone Group (RSG), has been poorly understood in terms of depositional timing, with age assessments ranging from the Middle Jurassic through the late Cenozoic (e.g., Damblon et al., 1998; Morley et al., 1999). Since 2002, work by our group has revised the geological context of the RSG, uncovering nearly 40 fossil-bearing localities that clearly document the presence of both Cretaceous (Unit I) and Oligocene (Unit II) sequences (O'Connor et al., 2003, 2006; Gottfried et al., 2004; Roberts et al., 2004; Stevens et al., 2004, 2005 [a, b]; 2006). Fossils from both units are typically recovered from laterally extensive sandstone bodies, with occasional lenticular mudstones (Figs 2B–C; see Roberts et al., 2004 for a discussion and historical overview of the RSG). Table 1 provides a faunal list for Units I and II.

Cretaceous Finds from the Rukwa Rift Basin

Cretaceous (Unit I) localities are characterized by specimens ranging from small, isolated elements such as teeth and jaws to large, articulated dinosaur skeletons (Fig. 3; O'Connor et al., 2006). The close of the 2005 field season witnessed the discovery of the first multi-taxon bonebeds; initial analyses suggest that these densely packed accumulations contain specimens representing multiple dinosaurian taxa. Notable finds from other localities include

Fig. 2 Map of Tanzania (inset of Africa depicting position of Tanzania) illustrating general location and orientation of the Rukwa Rift Basin (oval outline) between Lake Nyasa (Malawi) to the southeast and Lake Tanganyika to the northwest (A), and representative photographs of Unit I—Cretaceous (B) and Unit II—Oligocene (C) exposures of the Red Sandstone Group (Note: informal Unit designation follows that outlined in Roberts et al., 2004; the definition of formal type sections is currently underway; Roberts et al., *In Prep*)



articulated theropod and sauropod dinosaurs (O'Connor et al., 2003, 2006), megaloolithid dinosaur eggshell (Gottfried et al., 2004), one of the most complete mammal specimens yet recovered from the Cretaceous of continental Africa (Krause et al., 2003a), as well as crocodyliform, testudine, ceratodontid lungfish, and osteoglossomorph teleost representatives (e.g., Gottfried et al., 2005).

Saurischian dinosaurs include a theropod (Fig. 3A) and at least two titanosaurian sauropod taxa distinguishable on the basis of dental morphology. Two

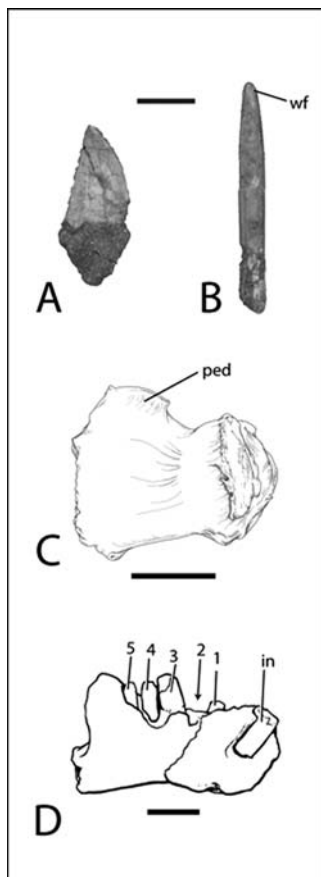
Table 1 Faunal list of vertebrate and invertebrate groups recovered from Unit I (Cretaceous) and Unit II (Oligocene) of the Red Sandstone Group in the Rukwa Rift Basin, southwestern Tanzania

Unit I:	Unit II
Mammalia	Mammalia
Gondwanatheria	Primates
Mammalia <i>incertae sedis</i>	Macroscelideans (x2)
	Phiomorph Rodents (x4)
Dinosauria	
Theropoda (x2)	Avialae
Sauropoda (x3)	
Crocodyliformes	Crocodyliformes
Testudines	Testudines
Osteichthyes	Osteichthyes
Sarcopterygii	Sarcopterygii
Ceratodontidae	Ceratodontidae
Actinopterygii	Actinopterygii
Osteoglossomorpha	Teleostei <i>incertae sedis</i>
Mollusca	Mollusca
Gastropoda	Gastropoda
Bivalvia	Bivalvia
	Arthropoda
	Decapoda

tooth morphs are represented, one exhibiting the thin, cylindrical crowns with high-angle wear facets typical of many titanosaurs (Fig. 3) and a second characterized by a crown exhibiting moderate apical-flattening (i.e., a crown that is less convex lingually than labially) reminiscent of *Malawisaurus dixeyi* from the Aptian Dinosaur Beds of Malawi (Gomani, 2005). Multiple vertebral morphologies are also present, some preserving features (e.g., procoelous middle caudal vertebrae; Fig. 3C) consistent with a titanosaurian assignment (see O'Connor et al., 2006 for additional information on the RRBP dinosaurian fauna).

During the 2002 field season, the team also recovered a small (~2 cm) left dentary (TNM 02067; Fig. 3D) tentatively referred to sudamericid gondwanatherians, a poorly-known group of Cretaceous-Paleogene mammals restricted to Madagascar, India, South America, and Antarctica (Krause et al., 2003). Although moderately abraded, it is clear that the specimen possessed a single, laterally compressed, procumbent central incisor and at least four (likely five) columnar, extremely hypsodont, single-rooted cheek teeth (Fig. 3D). If the gondwanatherian assignment of TNM 02067 stands with the recovery of additional specimens, it represents the first occurrence of the group on the African continent. Moreover, it would extend the clade into the 'mid' Cretaceous (~Aptian-Cenomanian; see O'Connor et al., 2006 for a

Fig. 3 Fossils recovered from Unit I (Cretaceous) of the Red Sandstone Group, including: (A) Nonavian theropod dinosaur tooth (TNM 02088); (B) sauropod dinosaur tooth (TNM 02093); (C) titanosaurian sauropod caudal vertebra (TNM 02072), left lateral view (modified from O'Connor et al., 2006); (D) left gondwanatherian(?) dentary (TNM 02067), lingual view (modified from Krause et al., 2003). Abbreviations as follows: in, incisor; ped, pedicle; wf, wear facet; 1–5, cheek teeth. Scale equals 1 cm in A and B, 5 cm in C, and 5 mm in D

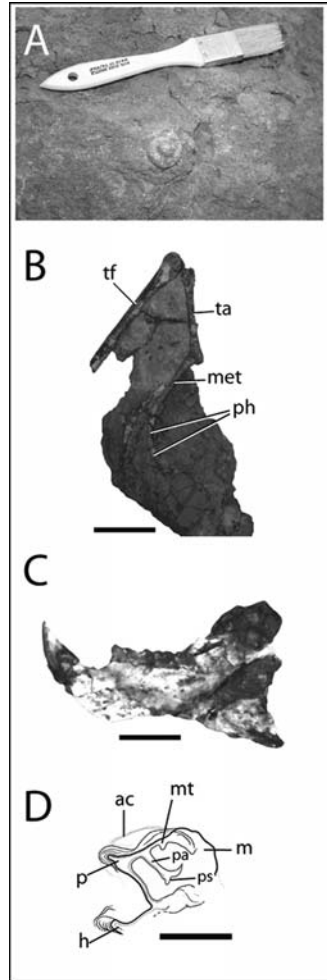


discussion of the likely temporal affinities of Unit I taxa), a notable range extension for the group as all other gondwanatherians have been recovered from Campanian to Eocene deposits. With considerable debate surrounding the timing and location of the origin of ‘modern’ placental groups (e.g., Hedges et al., 1996; Stanhope et al., 1998; Foote et al., 1999a, b; Rich et al., 1999; Ji et al., 2002; Springer et al., 2003, 2004), recovery of mammalian fossils (e.g., TNM 2067) from Unit I may provide critical new data for evaluating and/or refining competing hypotheses.

Paleogene (Oligocene) Finds from the Rukwa Rift Basin

Oligocene (Unit II) localities are dominated by small (<4 cm) vertebrate and invertebrate remains (Fig. 4). These sites have produced articulated crustacean specimens, in addition to dozens of well-preserved gastropods, ranging in size

Fig. 4 Fossils recovered from Unit II (Oligocene) of the Red Sandstone Group, including (A) *in situ* gastropod (TNM 04008); (B) anuran hind limb (TNM 03014); (C) right phiomorph rodent mandible (TNM 04150), lingual view; (D) partial lower left molar of *Metaphiomys beadnelli* (TNM 03111), occlusal view (drawing modified from Stevens et al., 2006). Abbreviations as follows: ac, anterior cingulum; h, hypoconid; m, metaconid; met, metatarsus; mt, metalophid; p, protoconid; pa, posterior arm of protoconid; ph, phalanges; ps, protospur; ta, tarsoastragalus; tf, tibiofibula. Scale equals 1 cm in B, 5 mm in C, and 1 mm in D



between 1 mm and 3 cm (Fig. 4A). Numerous vertebrate gnathic elements and postcranial specimens have also been recovered. For example, Unit II localities have revealed an abundance of well-preserved anuran cranial and postcranial elements (Holman et al., 2004). Some of these materials are found still in articulation, with limbs found in postures ranging from flexed to extended (e.g., Fig. 4B). A number of isolated teeth representing small crocodyliforms have also been found.

Micromammals are well-represented in the fauna, including a number of phiomorph rodents previously restricted to deposits in North Africa and the Arabian Peninsula (Fig. 4C, Stevens et al., 2006). *Metaphiomys* preserves hystricognathous mandibular morphology and low-crowned lower molars exhibiting acute buccal cusp margins and a posterior arm of the protoconid

that ends in a weak protospur (Fig. 4D). Upper molars of *Metaphiomys* similar to specimens recovered from Zalla, Libya (Fejfar, 1987) and the Fayum Depression of Egypt (Holroyd, 1994) have also been found. Multiple species of *Phiomys* are present, one with lower molar morphology featuring a small cuspid on the anterior cingulum, an anteriorly-positioned metacoid and broad shallow basins that open lingually. A diminutive humerus (TNM 03100; Stevens et al., 2005b) bears strong resemblance to early anthropoid specimens from the Fayum (e.g., Seiffert et al., 2000). This specimen preserves an entepicondylar foramen and a dorso-epitrochlear fossa (Stevens et al., 2005b), features commonly observed in parapithecids and platyrrhines (Fleagle and Simons, 1982). Finally, Unit II localities have produced dental and postcranial elements representing multiple novel macroscelidean taxa, offering rare documentation of the diversification of the sengis, or elephant shrews (Stevens et al., 2005a).

To date, specimens recovered from the RRPB study area are limited to taxa characteristic of Afro-Arabia prior to the faunal exchange with Eurasia that began around 24 Ma with no evidence of the small-bodied immigrant taxa such as cricetodontids, sciurids, murids, or leporids that began to appear in the Miocene (e.g., Winkler, 1994). All Oligocene finds in the first two field seasons were restricted to a single locality, yet three additional highly fossiliferous Unit II sites discovered during the 2004 field season indicate promise for future discoveries.

Outcrops

Like much of sub-equatorial Africa, the Rukwa Rift Basin consists of a mixed vegetation-rock surface cover; hence outcrops of the RSG are unlike the badlands typically explored for vertebrate fossils in other parts of the world. For this reason, we have employed remote-sensing technology (computer-assisted satellite photographic analysis) to assist with the identification of outcrops throughout the region. To do so, a ratio operation is performed to emphasize contrast between outcrops and vegetated surfaces, and an image classification procedure is performed on the ratio data to produce a land cover map of the study area. Known outcrops and ground cover information recorded by GPS during previous field expeditions are overlaid on base maps, resulting in a refined plan for prospecting regions for new outcrops. A pilot study utilizing these methods conducted prior to the 2004 field season successfully identified new RSG exposures in the heavily vegetated southern end of the study area, clearly demonstrating that such approaches are useful not only to help refine search areas, but also to identify access points into more remote regions. We wholeheartedly agree with Miller et al. (2005), regarding the need for paleontological exploration of “non-traditional” deposits.

Potential for Future Discoveries

In short, four brief (2–4 week) field seasons in southwestern Tanzania have significantly expanded the Cretaceous and Oligocene vertebrate record in sub-equatorial Africa. This increased sampling is providing the requisite comparative data for evaluating regional, continental, and supercontinent-level biogeographic hypotheses related to the distribution of Gondwanan vertebrates during the Cretaceous and Paleogene (O'Connor et al., 2006; Stevens et al., 2006). A comparison of the RRBP's discoveries and '*person hours of collecting effort*' with estimates from projects such as the Fayum suggests that the developing RSG fauna still occupies a basal position on the discovery asymptote (Meehl, 1983), underscoring the role of the Rukwa Rift Basin for producing many more fossils in years to come.

Prospectus

Clearly, continental Africa still holds many secrets about long extinct biotas, with great promise for discovery of novel faunas and floras, as demonstrated by sustained efforts in locales such as the Fayum Depression. The Rukwa Rift Basin in southwestern Tanzania preserves a situation found in few other places in Africa, the presence of co-localized Cretaceous and Paleogene fossil-bearing sequences. In addition to expanding our knowledge of the relatively patchy African vertebrate fossil record, paleontological efforts can:

- Continue developing technological approaches (e.g., satellite-assisted photographic survey) to expand search areas into *less typical* environments (e.g., forested and bush environments with minimal sedimentary exposures).
- Serve a role in training not only US students, but also African geoscientists and paleobiologists to facilitate the development of natural resource maintenance infrastructure in host-countries. This is consistent with efforts in other fields (e.g., <http://africaarray.psu.edu/>) to support scientific infrastructure throughout Africa¹.
- Provide unique opportunities for student training, not only in aspects of paleontology, but ideally, in how to develop and maintain strong international research collaborations that will benefit the field for years to come.

Conducted in collaboration with faculty and students from the University of Dar es Salaam, the RRBP has resulted in the development of multiple research projects for both Tanzanian and US participants. During the field season we

¹ Editorial. (2005). Africa 2005. Nature 433:669.

liaise with a representative from the Antiquities Division of the Tanzanian National Museums, who accompanies the expedition and facilitates interactions with the local communities in order to explain the project goals and outcomes. In this regard, we have spent 1–2 days in each of the last two field seasons conducting workshops and lectures on biology, geology, paleontology and biogeography at local primary and secondary schools, reaching dozens of teachers and hundreds of students. US faculty are active in the African Studies programs at their respective universities, taking advantage of language courses and mentoring African students studying in the US. These activities maintain an interactive learning environment, not only with regard to fossil vertebrates, but also in promotion of international scientific exchange.

Members of the Rukwa Rift Basin Project participated in field work in the Fayum (NJS) and/or the Mahajanga Basin Projects (PMO, EMR, NJS, MDG), inspiring them to develop a project in East Africa. Realizing the importance of such involvement early in an academic career, the RRBP routinely includes US and Tanzanian graduate and undergraduate students as part of the field crew and in laboratory based research, in hopes that they too will begin projects of their own.

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