A new Cretaceous lungfish (Dipnoi: Ceratodontidae) from the Rukwa Rift Basin, Tanzania

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'Ceratodontid' lungfishes have a wide Gondwanan distribution during the Mesozoic, and are well-known from a variety of Cretaceous sites in northern and western Africa. Despite this relatively broad occurrence, significant gaps remain in our knowledge of Mesozoic African lungfish palaeodiversity and palaeogeography, particularly from subequatorial Africa. Ongoing field research in the Cretaceous Galula Formation (Red Sandstone Group), which outcrops in the Rukwa Rift Basin (a segment of the greater East Africa Rift System) of southwestern Tanzania, has led to the discovery of a diverse vertebrate fauna, including a well-preserved lungfish toothplate. This specimen is described here as a new taxon, *Lupaceratodus useviaensis* gen. et sp. nov., on the basis of its unique combination of morphological features relative to other 'ceratodontids.' *L. useviaensis* represents the first Cretaceous record of a 'ceratodontid' lungfish from Tanzania, and more broadly from the southwestern portion of the East African Rift System. The new Tanzanian form adds further diversity and a new datum to the evolutionary history of lungfishes in Africa, and it suggests possible regional differentiation between the Cretaceous fishes of East Africa and the better-known fish faunas of the period from northern and western Africa, perhaps related to the Cretaceous establishment of the Trans-Sahara Seaway.

Key words: *Lupaceratodus*, lungfish, Ceratodontidae, Cretaceous, Rukwa Rift Basin, Tanzania.

CONTENTS

INTRODUCTION

African Mesozoic 'ceratodontid' lungfish records are concentrated in the northern and northwestern parts of the continent (e.g. Haug 1905; Peyer 1925; Weiler 1930; Arambourg & Joleaud 1943; Tabaste 1963; Martin 1981, 1984; Churcher 1995; Churcher & De Iuliis 2001), reflective of a broader pattern in the African Cretaceous terrestrial and freshwater vertebrate fossil record. Apart from significant finds made in South Africa (e.g. de Klerk *et al.* 2000) and Malawi (Jacobs *et al.* 1990), our working knowledge of subequatorial African Cretaceous vertebrates is, in general, notoriously poor – a situation that we have previously referred to as the 'African Gap' (e.g. O'Connor *et al.* 2006). With this in mind, we began exploring the Rukwa Rift Basin (RRB) of southwestern Tanzania in 2002, and have conducted eight field seasons to date, recovering both Cretaceous and Palaeogene vertebrates, invertebrates, and plants from *ca.* 60 localities (Stevens *et al.* 2008).

The Cretaceous fauna from the RRB is beginning to close at least some portions of the aforementioned gap (Krause *et al.* 2003; Gottfried *et al.* 2004; O'Connor *et al.* 2005, 2006), and has the potential to provide data that are useful in assessing competing Gondwanan biogeographical hypotheses. For example, the 'Africa First' model (*sensu* Sampson *et al.* 1998; Krause *et al.* 1999, 2006) postulates that the (apparent) absence of several Gondwanan vertebrate clades in the

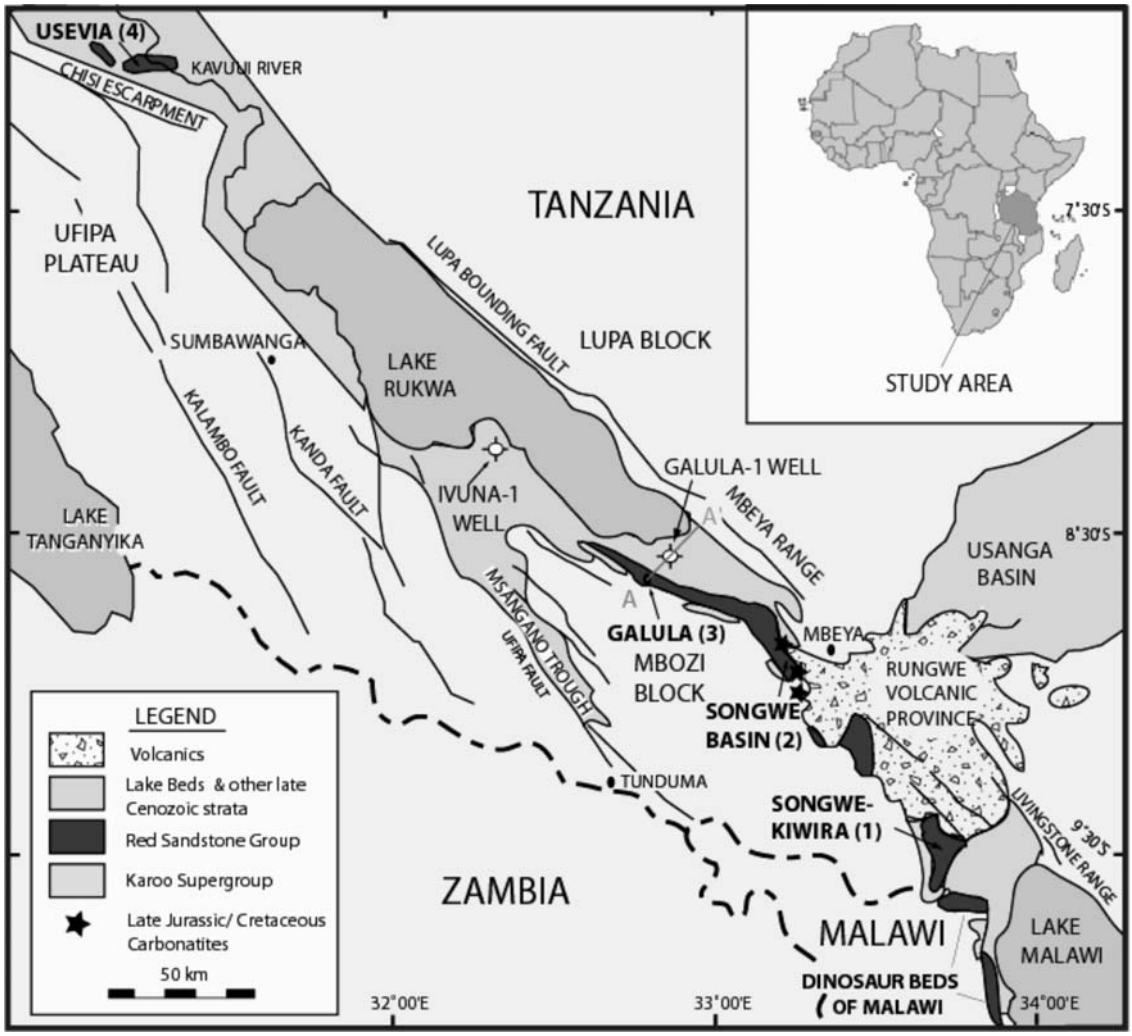

Fig. 1. General geological setting and outcrop area of the Red Sandstone Group in the Rukwa Rift Basin, southwestern Tanzania. The specimen described here was collected near Usevia (outcrop area 4), in the northwestern part of the Rukwa Rift Basin. Inset map shows Tanzania (shaded), study area depicted is indicated by the line denoting the southwestern corner of Tanzania.

African Cretaceous is the result of Africa being physically isolated from Indo-Madagascar, Antarctica, and South America and thus not part of a broadly distributed Gondwanan Cretaceous biota. The alternative 'Pan-Gondwana' model (*sensu* Sereno *et al*. 2004) predicts that certain clades will be present in the Cretaceous of Africa and other Gondwanan continents due to persistent, if somewhat intermittent, physical connections during the Cretaceous. More regionally focused biogeographical models (e.g. O'Connor *et al*. 2006) suggest possible provinciality between Saharan and subequatorial freshwater/terrestrial faunas, which could have resulted in part due to the hypothesized trans-Saharan seaway (Gebhardt 1999) acting as a marine barrier separating northwestern Africa from more southern and eastern regions of the continent. The primary challenge in testing these biogeographical models remains the lack of Cretaceous fossil data from subequatorial Africa.

The specimen reported here from the Cretaceous Galula Formation (Red Sandstone Group) in the RRB of western Tanzania (Fig. 1) establishes the presence of Mesozoic lungfish for the first time in the southwestern portion of the East African Rift System, and it expands the palaeodiversity of ceratodontid lungfishes in Africa. More broadly, it underscores the palaeontological potential of the Tanzanian RRB deposits in preserving diverse, and potentially biogeographically informative, Cretaceous freshwater and terrestrial vertebrates from subequatorial Africa.

SYSTEMATIC PALAEONTOLOGY

SUBCLASS **DIPNOI** Müller, 1844
ORDER **CERATODONTIFORMES** Berg, 1940
Family **CERATODONTIDAE** Gill, 1872

***Lupaceratodus* gen. nov.**
Fig. 2

Type species
***Lupaceratodus useviaensis* sp. nov.**
Fig. 2

Derivation of name

Generic name refers to the Lupa Bounding Fault, a prominent geological feature in the Rukwa Rift Basin, combined with 'ceratodus' in reference to its affinities with other

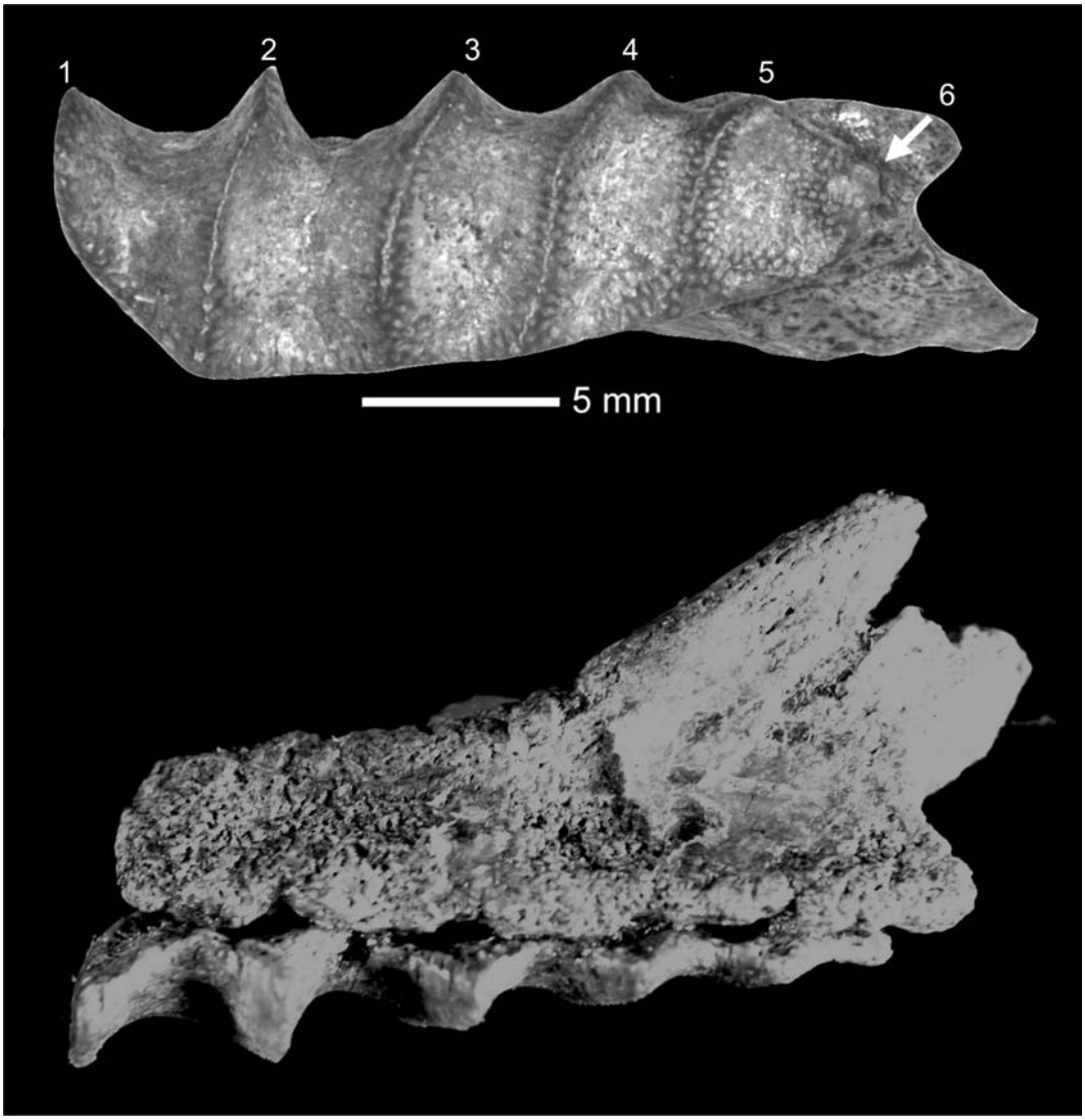

Fig. 2. *Lupaceratodus useviaensis* (gen. et sp. nov.) holotype – upper left toothplate and a portion of the pterygoid element (RRBP 04289), from the Cretaceous Galula Formation (Red Sandstone Group), Rukwa region, southwestern Tanzania. Top image in occlusal view, with anterior to the left and the lingual margin to the top; numbers 1–6 indicate ridges. Lower image shows holotype specimen rotated into lingual view.

ceratodontid lungfishes. Specific epithet refers to the town of Usevia, situated near the type locality.

Holotype

Ruka Rift Basin Project (RRBP) 04289 (National Museum of Tanzania), a moderately worn, complete upper left (pterygoid) toothplate with a portion of the pterygoid bone attached (Fig. 2).

Locality and geological setting

RRBP 04289 was collected on 30 June 2004 (by EMR) near the town of Usevia, in the Rukwa District of western Tanzania, at *ca.* 7°6′ south latitude, 31°10′ east longitude (see Fig. 1; precise locality coordinates are on file with the authors). The specimen was recovered from a sandstone outcrop designated by us as locality TZ-22 and assigned to the Galula Formation (Roberts *et al.,* in press) (formerly 'Unit I' *sensu* Roberts *et al.* 2004) of the Red Sandstone Group. The Galula Formation is Cretaceous in age based on its temporally distinctive vertebrate fauna, which includes sauropod and theropod dinosaurs, megaloolithid dinosaur eggshell, and osteoglossomorph fishes (Gottfried *et al.* 2004; Roberts *et al.* 2004; O'Connor *et al.* 2005, 2006). Detrital zircon analysis provides some independent support for this by demonstrating that the depositional age must be Late Jurassic or younger (Roberts *et al.* 2007), and this age interpretation is consistent with facies relationships and our geological mapping of the field area. Taken together these data indicate a Cretaceous age assignment, and further suggest that the majority if not all deposition of the Galula Formation transpired in the lower to middle Cretaceous. Further refinement of the age of the Galula Formation is the subject of ongoing research.

The Galula Formation, consisting of red sandstones and mudstones, accumulated in a freshwater fluvial/floodplain continental rift setting. Deposition of these sediments was along a northwest-flowing river system oriented parallel to the axis of the RRB. The Galula Formation exposures near

Usevia are situated towards the northwestern end of the basin (see Fig. 1), which is a roughly 300 km long by 50 km wide northwest–southeast trending segment of the southwestern branch of the East African Rift System (EARS).

The overall Cretaceous fauna recovered to date includes osteichthyans (osteoglossomorphs, fragments of an as yet unidentified teleost, and a 'ceratodontid' lungfish (this report)), turtles, crocodyliforms, at least four taxa of saurischian dinosaurs, megaloolithid dinosaur eggshell, and a (probable gondwanantherian) mammal (see Krause *et al.* 2003; Gottfried *et al.* 2004; O'Connor *et al.* 2005, 2006).

Diagnosis

Distinguished from other 'ceratodontid' lungfish upper toothplates by the following unique combination of features: Markedly slender (overall length:maximum width ratio 2.6:1) in proportion; first (anteriormost) ridge diverges at an angle of *ca.* 55 degrees from the next ridge and has distinct bend halfway along its length; second ridge slightly shorter but projecting further lingually than first; second and third ridges arcuate, fourth and fifth ridges sinusoidal along ridge crests; sixth ridge much shorter (no more than half the length of preceding ridges); labial margin of toothplate essentially straight (rather than curved) from second through sixth ridges and not strongly projecting at base of second ridge as in other ceratodontids; third through sixth ridges do not converge along labial margin.

Description

Lupaceratodus useviaensis (RRBP 04289, Fig. 2) is represented by a well-preserved, relatively small and slender, upper left toothplate, measuring 16.0 mm in length by 6.2 mm in (maximum) breadth (measured across the occlusal surface of the toothplate and including the crests of the ridges). As preserved, it is somewhat loosely ankylosed to the underlying preserved portion of the pterygoid element (Fig. 2). Five ridges (following the terminology of Churcher & De Iuliis 2001) are well-preserved; a notably shorter sixth posteriormost ridge (sometimes referred to as the posterior heel) is present but incompletely preserved. The anteriormost ridge diverges at an acute angle of *ca.* 55 degrees from the next ridge, and has a distinct bend approximately halfway along its length; the more posterior ridges are subparallel to one another, with the fourth and fifth sinusoidal along their crests. The four more posterior ridges do not converge along the labial margin of the toothplate as is common in many 'ceratodontid' toothplates, which thus have a 'palmate' appearance that is lacking in *L. useviaensis.* The angled anteriormost ridge is the longest at *ca.* 6.7 mm, the other ridges (with the exception of the much shorter sixth ridge) range from 6.3 to 5.2 mm in length and decrease rather evenly in length from anterior to posterior. The crest of the second ridge projects further lingually than does the first. The crests in general are well-defined, with relatively deep intervening sulci. The toothplate does not exhibit any resorption on its occlusal surface, which (along with its small size) suggests that it may be at a subadult stage of development (Kemp 1977). Closely spaced simple round to oval punctuations (~0.3 mm in diameter) are most apparent along the ridges and crests, and along the lingual and buccal margins, and are less distinctly developed in the deeper parts of the furrows between ridges.

Lupaceratodus exhibits similarities to upper toothplates of the extant Australian species *Neoceratodus forsteri* (Kemp & Molnar 1981; Kemp 1997), including the presence of a longer anteriormost divergent ridge followed by five ridges and a short posteriormost sixth ridge (= posterior heel). However, unlike *Neoceratodus, Lupaceratodus* has subparallel and curved (rather than straight) posterior ridges, and it differs in overall proportions. Toothplates that have been assigned to the problematic taxon '*Ceratodus'* are broader in proportion than *Lupaceratodus,* and characteristically bear fewer (4–5) and more radially divergent nonparallel ridges, resulting in an overall palmate appearance (see, e.g., *C. humei* in Churcher & De Iuliis 2001). The new taxon does bear some similarities in its relatively slender proportions and overall appearance to *Retodus* (formerly *Ceratodus*) *tuberculatus* (Churcher *et al.* 2006) from the Cretaceous of Egypt, Algeria, and Niger, but *R. tuberculatus* has four or perhaps five ridges, rather than six as in *Lupaceratodus,* and each of the ridges in *Retodus* has a similar posteriorly angled orientation, different from the situation in *Lupaceratodus* in which the anteriormost ridge is divergent from the others, and not posteriorly oriented.

DISCUSSION

The phylogenetic interrelationships and taxonomy of Mesozoic lungfishes remain problematic, and a comprehensive synthesis of the group's diversity and palaeogeographical distribution during the Mesozoic has yet to be achieved. Many taxa are based on isolated toothplates, with more complete material relatively rare, a situation that relates to poor mineralization of the skeleton, but robust development of petrodentine-reinforced toothplates in post-Palaeozoic lungfishes (Cavin *et al.* 2007). As a result, many of the species placed in the family Ceratodontidae have been assigned to the 'catch-all' genus *Ceratodus,* and in some cases species originally assigned to *Ceratodus* have more recently been placed in *Neoceratodus* (e.g. Churcher & De Iuliis 2001), *Atlantoceratodus* (Cione *et al.* 2007), or *Retodus* (Churcher *et al.* 2006), illustrating the current instability in the generic-level taxonomy of this group. Rather than placing the morphologically distinctive toothplate described here into *Ceratodus,* which is in need of a thorough revision, we have erected the new genus and species, *Lupaceratodus useviaensis,* to accommodate its distinctive and diagnosable combination of morphological features.

The presence of *Lupaceratodus* in western Tanzania adds a noteworthy new datum to dipnoan history in the Mesozoic of Africa. Its occurrence is not startling given the long geological time span and wide geographical distribution of 'ceratodontid' records in general (Obruchev 1964; Woodward 1906; Marshall 1986), including on Gondwanan continents. *Lupaceratodus* comprises another example of a morphologically relatively conservative lungfish in the African Mesozoic, conforming to the general 'ceratodontid' morphotype that was ultimately supplanted in the Cenozoic of Africa by the surviving lepidosirenid genus *Protopterus,* with its more specialized and simplified toothplate morphology.

Ceratodontid lungfishes are a geologically ancient and geographically widespread assemblage, the origin of which predates Gondwanan fragmentation (see e.g. Apesteguía

et al. 2007). The new taxon from Tanzania may shed some light on regional differentiation of the clade, in that *Lupaceratodus* is taxonomically distinct from the more typical 'ceratodontids' recovered from northern and western Africa. A possible abiotic mechanism that may account for at least some of this geographical separation, as reflected by the presence of *Lupaceratodus* in Tanzania, is the initial transgression of the Trans-Saharan seaway that divided the northwestern part of continental Africa from the rest of the continent during the Cretaceous (Gebhardt 1999), perhaps as early as pre-Albian (Al-Khashab 2000). Additional material is required to discern whether other components of the freshwater fish fauna in the southwestern portion of the EARS are also distinctive enough from those of northern and western Africa to posit intra-African biogeographical provincialism. The discovery of *Lupaceratodus* does underscore the continuing potential of the Rukwa Rift Basin and the Galula Formation of southwestern Tanzania to provide new and novel palaeontological data from the Cretaceous of subequatorial Africa.

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