A DIVERSE DINOSAUR TOOTH ASSEMBLAGE FROM THE UPPER JURASSIC OF ETHIOPIA: IMPLICATIONS FOR GONDWANAN DINOSAUR BIOGEOGRAPHY.

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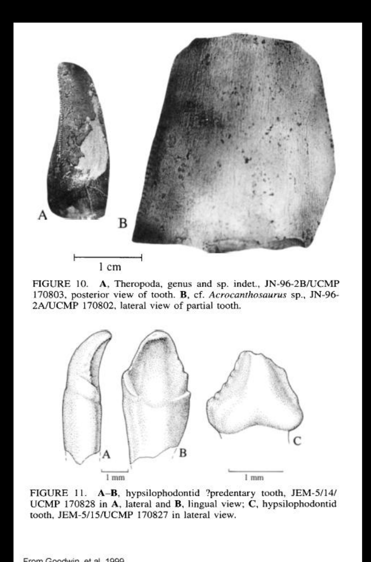
ABSTRACT

Dinosaur-bearing Gondwanan Upper Jurassic deposits are under represented in the fossil record and thus signify a gap in our understanding of the biogeographic radiation of several non-avian dinosaur clades. Here we present an analysis and description of dinosaur teeth from the Upper Jurassic (Tithonian) Mugher Mudstone Formation, Ethiopia, collected during several expeditions by the University of California Museum of Paleontology, Berkeley. Significantly, several teeth are referable to the Dromaeosauridae and represent the oldest skeletal remains of this group in Gondwana. Teeth referrable to the stegosaur *Paranthodon africanus* extend the stratigraphic range of this taxon into the Late Jurassic and expand the geographic range of African stegosaurs north beyond the Tanzanian record at Tendaguru. The presence of hypsilophodontids is confirmed. With the description of these dinosaur teeth from the Late Jurassic of Ethiopia, the Mugher dinosaur fauna approaches the taxonomic diversity represented by the historically important and rich Tendaguru deposits of eastern Africa. Future exploration of this formation and the northwestern plateau of Ethiopia is ongoing, and critical to deciphering evolutionary and biogeographic patterns in Jurassic nonavian dinosaurs across Gondwana.

INTRODUCTION

In contrast to cretaceous dinosaur assemblages, Africa's jurassic dinosaur record has rarely yielded new material for consideration. Early Jurassic dinosaurs in Africa are known from a fairly broad range of countries: Lesotho (Gauffre, 1993; Gow, 1975; Kitching and Raath, 1984), South Africa (Gow, 1975; Kitching and Raath, 1984), Zimbabwe (Cooper, 1981; Raath, 1972; Raath, 1969) and Morocco (Allain, et al. 2007). The dinosaur faunal assemblage from these localities consists of ornithischians (*Heterodontosaurus sp*., *Abrictosaurus sp*., *Lycorhinosaurus sp*., *Lanasaurus sp*.), a prosauropod (*Massospondylus carinatus*), sauropods (*Melanorosaurus thabanensis*, and *Vulcanodon karaensis*), and theropods (*Megapnosaurus rodiensis* and *Berberosaurus liassicus*). The Middle Jurassic record is sparse in comparison, and consists solely of sauropod remains from Morocco (*Atlasaurus imelakei*; Monbarron et al. 1999) and Madagascar (*Lapparentosaurus madagascariensis*; Bonaparte, 1986). The Late Jurassic bears a substantially more robust record than the middle and currently contains at least as many taxa as the early. However, much of the currently known Late Jurassic African dinosaur material originates from a single locality in Tanzania: the Tendaguru beds. While a fairly diverse fauna (admittedly mostly sauropods) is preserved at this locality, the simple presence of the Tendaguru assemblage alone does not indicate the extent or the degree to which dinosaurs radiated throughout Africa before the Cretaceous. Thus, late Jurassic dinosaur localites outside of Tendaguru are incredibly important for understanding the extent of geographic ranges and evolutionary successes of extinct taxa. The list of Late Jurassic dinosaurs found outside of Tendaguru is strikingly brief, consisting of a partial theropod femur from Zimbabwe (Raath and McKintosh, 1987) and isolated dinosaur teeth from Ethiopia's Mugher Mudstone (Werner, 1995; Goodwin, et al. 1999).

There is a detailed account of previous work done in Ethiopia in Goodwin, et al.(1999), so it will not be covered here. Pertaining to this study, in the mid 1990's the University of California Museum of Paleontology (UCMP) collected and studied vertebrate fossils from the Late Jurassic (Tithonian) Mugher Mudstone and found remains of chondrichthyans (*Hybodus*), osteicthyans (*Lepidotes* and *Pycnodus*), the dipnoan *Asiatoceratodus*, and fragmentary skeletal remains of turtles and crocodilians (Goodwin, et al. 1999). In addition to work on the vertebrate assemblage, the age of the northwestern Ethiopian Mesozoic beds which produced these fossils was correlated with the Late Jurassic by the presence of the Tithonian-occuring dinoflagellate *Leptodinium acneum*, which was found in the lowest section of the Mugher Mudstone.



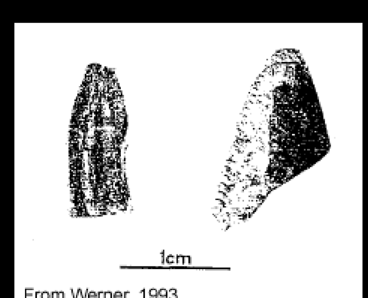


FIGURE 1 (above). ?Sauropod and theropod teeth figured in Werner, 1993 from the Mugher Mudstone.

FIGURE 2 (left). Previously described dinosaur teeth from the Mugher Mudstone reveal both theropod and hypsilophodontid material.

The UCMP expeditions also recovered numerous dinosaur teeth, found while picking screened sediments from microvertebrate localities. Six of the teeth were described in Goodwin et al. (1999), and include four partial theropod teeth (three specimens identified as "cf. *Acrocanthosaurus* sp." based on denticle morphology, and one possible dromaeosaurine) and two identified as possible hypsilphodontids. Here, nine additional teeth- picked from the original sediment samples collected by the UCMP Ethiopia expeditions- are described for the first time. To date, this is the largest and most complete record of dinosaur fossils from a Late Jurassic African locality outside of Tendaguru.

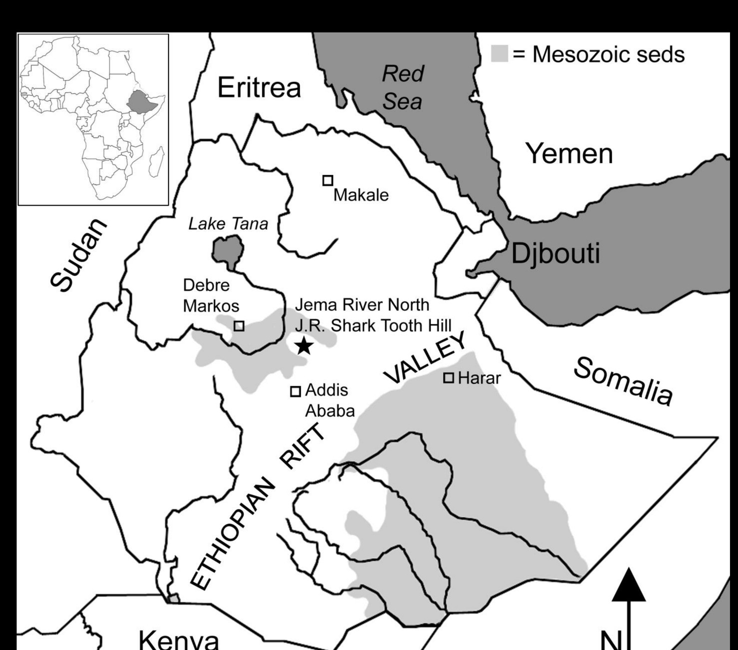


FIGURE 3. Map of Ethiopia showing exposures of Mesozoic sediments (light gray). Specimens from this study were collected from the Mugher Mudstone on the northwestern plateau, indicated by the star. Modified after Goodwin, et al. (1999).

GEOLOGIC AND GEOGRAPHIC SETTING

The geologic context of the Mugher Mudstone was reviewed in detail by Goodwin, et al. (1999) based in part on previous work by Getaneh (1991). The Mugher is directly underlain by the 420 m thick Lagajima Limestone (formerly the Antalo Limestone) which records a "regressional marine transgression" sequence. The Mugher Mudstone is a 320 m section of brackish water and terrestrial deposits. More specifically, the lower part of the section is composed of subtidal and lagoonal facies which transition into fine-grained, muddy fluvial sediments deposited by meandering river systems. There may also be evidence for seasonal rainfall and drought events in an overall semi-arid climate. The Mugher records a drop in sea level near the beginning of the Tithonian, followed by an onset of sandy, braided stream deposits in the overlying Early Cretaceous Debre Libanos Sandstone (Goodwin, et al., 1999; Getaneh, 1991).

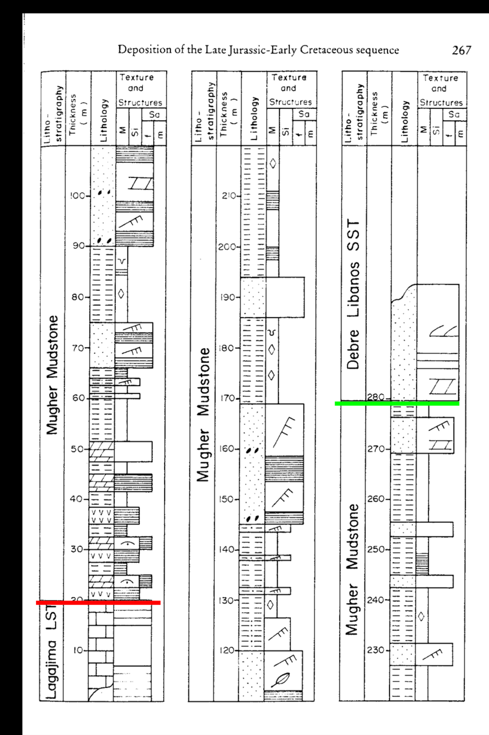


FIGURE 4. Stratigraphic section of the Mugher Mudstone records the transition from marine to terrestrial deposits with recession of sea level.

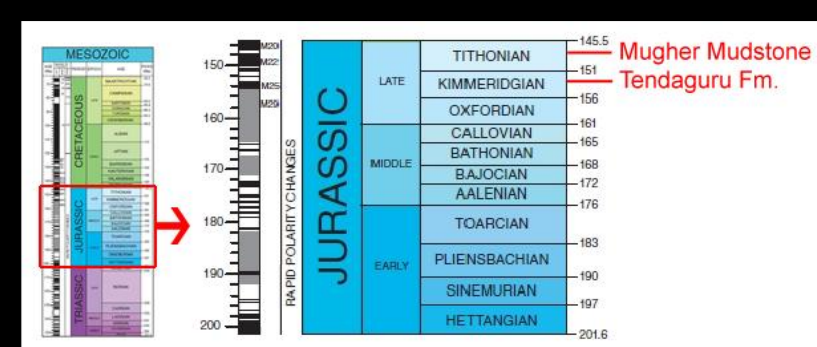


FIGURE 5. The Tithonian Mugher Mudstone records a unique interval in time not represented by the terrestrial portion of the Tendaguru Fm.

MATERIALS AND METHODS

These teeth were picked from a screen-washed geological hand sample (<10lbs) and mounted on pin heads inserted into cork plugs. For photography, the teeth were removed from the pinheads. Photomicrographs were taken in labial, lingual, mesial, and distal perspectives (not all perspectives were possible with all specimens- the increasingly small size of some made mesial and distal photography difficult or impractical) using a Nikon DS-U2 Digital Sight Camera Controller and polarized light microscope station with modified stage lighting in the Gabriel Laboratory for Cellular and Molecular Paleontology (MOR). Tooth measurements were taken on UCMP 152573 after Longrich (2008) and Sankey (2002).

SYSTEMATIC PALEONTOLOGY
DINOSAURIA Owen 1842
ORNITHISCHIA Seeley 1887
ORNITHOPODA Marsh 1881
HYPSILOPHODONTIDAE (Dollo, 1882)
GEN ET SP. INDET.

Morphotype A (Fig. 6 A-F)
Referred Specimens: UCMP 152567 (Fig. 2A, B, C); UCMP 152579 (Fig. 2D, E, F).

Description— The "A" morphotype exhibits a weakly spatulate, sub-triangular crown, 3 mm tall, with thick-edged lateral carinae. . The crown enamel is smooth with a convex labial surface.The lingual edge of lateral carinae of UCMP 152579 exhibit what may be very weakly expressed denticles. There is no denticulation on the flat mesial or distal surfaces of the carinae, nor on the lingual edges. It is therefore difficult to determine if these features are true denticles, are artifacts of wear from processing food or taphonomic transport, or the remnants of denticles that have been worn to the base. As the rest of the crown does not appear to be heavily worn, it seems unlikely the latter is the case. The apex is blocky and stout. There is a lingual cingulum and the lingual face is convex. The crown is weakly recurved lingually The single root is partially preserved, is bulbous and cylindrical in transverse section, and is situated asymmetrically from the crown midline.

Morphotype B (Fig. 6 G-R)
Referred Specimens: UCMP 152571 (Fig. 2G, H, I), UCMP 152576 (Fig. 2J, K, L), UCMP 152577 (Fig. 2M, N), UCMP 152578 (Fig. 2O, P, Q, R).

Description— The "B" morphotype consists of a rounded triangular, semi-spatulate crown with a maximum height of 1.3 mm. The crown is recurved lingually and the enamel is smooth. The lateral carinae exhibit subtle denticulation. The denticles are low ovoid hemispheres and decrease in size from the apical position towards the base. The carinae terminate basally in prominent cusps which transition into a lingual cingulum. These cusps may be low and rounded or more distinctly hook-like. UCMP 152577 exhibits heavy wear on one of its lateral carinae, to the point where the enamel is effectively gone and the tooth has a strikingly asymmetrical appearance. Similarly, UCMP 152576 has asymmetrical crown wear, with denticles preserved on the less worn carina. UCMP 152578 has wear concentrated to the apical portion of the crown, and both lateral carinae are intact, but denticles are not present. Due to the transparent nature of the enamel in these specimens, it is possible to compare relative enamel thickness of the carinae. The carinae of 152578 are indeed symmetrical, but when comparing enamel thickness to the carinae of UCMP 152576, it is plainly visible that the carinae of UCMP 152578 have worn down past the denticles. The labial face of the teeth is convex and the overall crown is strongly recurved lingually. The teeth appear to be single-rooted. A portion of the proximal root is present in UCMP 152571, is mesio-distally ovoid in cross section and exhibits smooth enamel as well

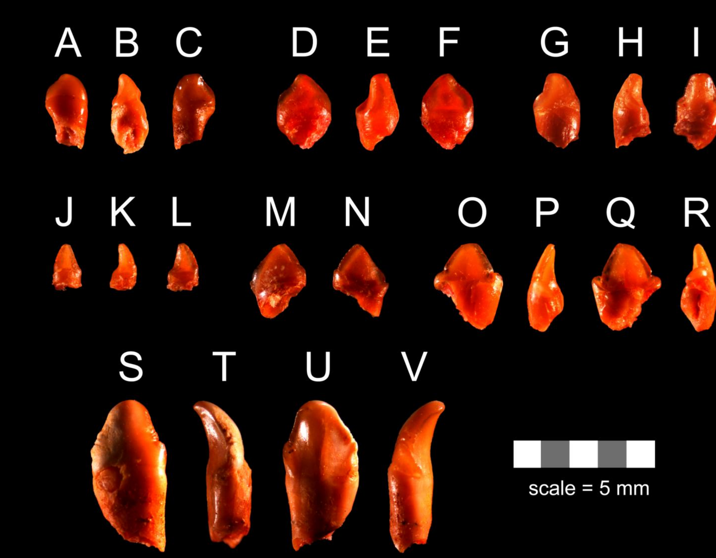


FIGURE 6. Hypsilophontid teeth of the Mugher Mudstone. Morphotype 'A' teeth: **A-C**, hypsilophodontid tooth, UCMP 152567, in **A**, labial, **B**, lateral, and **C**, lingual view; **D-F**, hypsilophodontid tooth, UCMP 152579, in **D**, labial, **E**, lateral, and **F**, lingual view; **G-I**, hypsilophodontid tooth, UCMP 152571, in **G**, labial, **H**, lateral, and **I**, labial view; Morphotype 'B' teeth: **J-L**, hypsilophodontid tooth, UCMP 152576, in **J**, labial, **K**, lateral and **L**, labial view; **M-N**, hypsilophodontid tooth, UCMP 152577 in **M**, labial and **N**, libual view; **O-R**, hypsilophodontid tooth, UCMP 152578 in **O**, labial, **P**, left lateral, **Q**, lingual and **R**, right lateral view; **S-V**, hypsilophodontid ?predentary tooth, UCMP 170827, in **S**, labial, **T**, right lateral, **U**, lingual and **V**, left lateral view. Scale is 5mm.

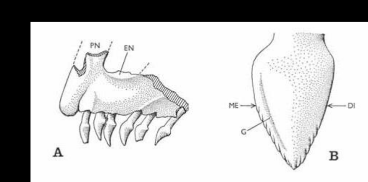


FIGURE 7. A- Left premaxilla of the South African hypsilophodontid *Fabrosaurus australis*. B- Detail of tooth crown belonging to *Fabrosaurus australis*. Image from Thulburn, 1970.

STEGOSAURIA Marsh 1877
STEGOSAURIDAE Marsh 1880
PARANTHODON Nopsca, 1929
AFRICANUS Broom 1912

(Fig. 8)
Specimens--UCMP 152570 (Fig. 8 A, B, C) and UCMP 152574 (Fig. 8 D, E, F), partial maxilla or dentary tooth crowns.

Description-- UCMP 152570 exhibits a broad (4 mm wide), asymmetrical, triangular crown with prominent, triangular denticles on the lateral carinae (3.5 denticles preserved on the mesial carina and 2.5 denticles preserved on the distal carina), and lacks a root Both the labial and lingual sides of the crown exhibit rounded, vertical ridges that descend from each denticle to the cingulum. The crown bears a large, prominent median ridge and a bulbous cingulum at its base on both sides. The apex is not preserved. UCMP 15274 is a 1.5 mm long fragment of distal (convex) carina that also exhibits prominent triangular denticles (4 preserved) which are identical to those on the distal carina of UCMP 152570. A portion of UCMP 152574's lingual crown surface is preserved along with part of the characteristic central ridge.

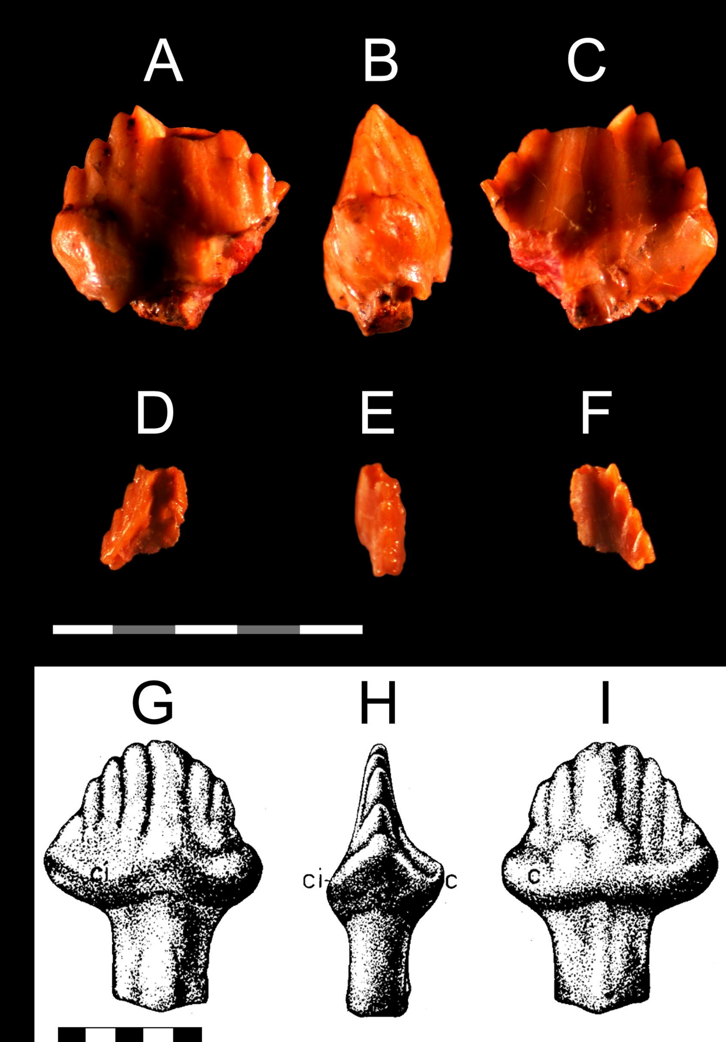


FIGURE 8. Teeth of *Paranthodon africanus*. **A-C**, *Paranthodon* tooth crown, UCMP 152570, in **A**, labial, **B**, lateral and **C**, lingual view; **D-F**, partial *Paranthodon* tooth crown, UCMP 152574, in **D**, ?labial, **E**, lateral, and **F**, ?lingual view; **G-I**, *Paranthodon* tooth, BMNH R4992, modified from Galton and Coombs (1981) in **H**, labial, **I**, lateral and **J**, lingual view. Scale is 5mm. **Abbreviations**: **c**, larger cingulum; **ci**, smaller cingulum.

SAURISCHIA
THEROPODA Marsh 1881
DROMAEOSAURIDAE Matthew and Brown, 1922
Gen et. Sp. Indet.

(Fig. 4)
Specimen—UCMP 152573 (Fig. 4A, B, C, D)
Description—UCMP 152573 is a tall (6.22 mm), D-shaped (in lateral aspect) theropod tooth crown lacking a root. The fore-aft basal length (FABL) is 3.86 mm. The mesial surface recurves distally towards the apex of the crown and bears tiny (6.39 per mm), flattened, weakly-raised, rectangular denticles; the distal carina is straight and bears larger (3-4 per mm; 5.03/17= .295882353 mm per denticle overall; 17/5.03=3.37972167 denticles per mm overall), rectangular and sub-apically inclined denticles which gradually decrease in size toward the apex. In transverse cross section the tooth is tear-drop shaped with a broad, rounded mesial edge and tapered distal carina. Half of the crown's base is fractured and missing, and therefore cross sectional thickness could not be measured. The apex of the crown is heavily worn, exhibiting significant wear and rounding of the tip and apical denticles, along with fracturing of the enamel.

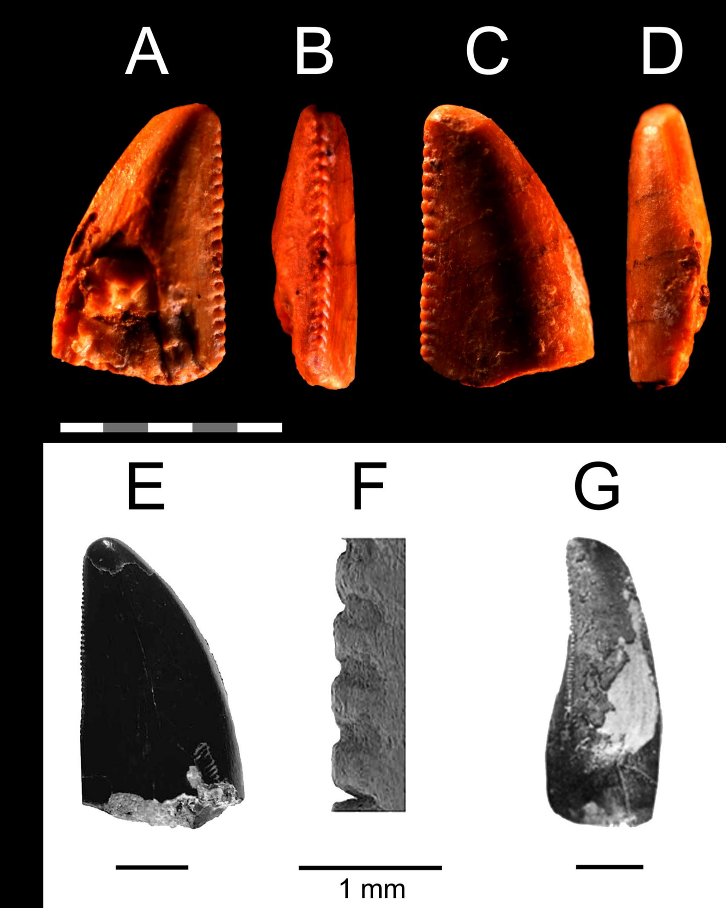


FIGURE 9. Dromaeosaurid teeth. **A-D**, velociraptorine tooth crown, UCMP 152573, in **A**, ?lingual, **B**, distal, **C**, ?labial, and **D**, mesial view; **E**, Isle of Wight velociraptorine tooth crown, IWCMS.2002.3, reproduced from Sweetman (2004) in ?labial view; **F**, SEM detail of distal denticles from **E** in ?labial view; **G**, possible dromaeosaurine premaxillary tooth, UCMP 170803, reproduced from Goodwin et al. (1999) in distal view. Scale is 5mm unless indicated.

DISCUSSION

The Mugher Mudstone is Tithonian in age (Goodwin, et al. 1999), and is potentially chronologically equivalent to the sandstone-dominated, marine *Trigonia smeei* member of the Tendaguru formation (Sames, 2008). The Mugher Mudstone is equivalent to time not represented by dinosaur-bearing strata in Tendaguru or elsewhere in Africa, which makes the formation a temporal interval of terrestrial deposition not preserved in the Tendaguru beds, and thus a unique record of evolution for Late Jurassic African vertebrates.

The analysis of teeth in this study combined with stratigraphic resolution is significiant because information gained from dentition is typically applied to species identification and may be used to answer biological and behavioral questions such as size and diet of single individuals or as evidence for gregarious behavior (Ostrom, 1969; Maxwell & Ostrom, 1995; Bakker, 1997). Less common and more pertinent to this study, stratigraphic and biogeographic analysis can provide information on temporal and spatial taxon ranges (DeValias, et al., 2003; Buffetaut, et al., 2008; Buffetaut, et al. 2005; Vickers-Rich, et al. 1999; Ray & Chinsamy, 2002; Smith & Della Vecchia, 2006). Further, isolated teeth are often the first fossil evidence indicating the presence of a taxon in a region (Salisbury, 2003; Godfroit & Lambert, 2007; Lim, et al., 2002; Sanz, 1982; Barrett, 2006; Fowler, 2007), and proper analysis of isolated teeth can prove very useful.

The specimens described in this study include hypsilophodontids with a unique dental morphology that has not been previously described. The confirmation of Hypsilophodontids in this study and in Goodwin, et al. (1999) mark a dramatic range extension, both geographically and stratigraphically, for the clade. Prior to their discovery in the Mugher Mudstone, hypsilophodonts were restricted to the Early Jurassic of Lesotho and South Africa (Gow, 1975). Their discovery in Ethiopia is evidence that Africa is no exception to the clade's success in Gondwana.

The presence of Stegosauria in Late Jurassic northern Africa comes as no surprise, as the clade is found on every continent in the northern hemisphere during that time (Dong, 1990). Previously, stegosaurs were unknown from northern Africa but had been documented in Early Cretaceous of south Africa (*Paranthodon africanus*; Galton and Coombs, 1981) and in the Late Jurassic of east-central Africa (*Kentrosaurus aethiopicus*; Heinrich, et al. 2002). As of this study, the geographic range of stegosaurs in Africa now extends across nearly the entire eastern margin of the continent in an almost continuous distribution. Additionally, the stratigraphic longevity of *Paranthodon africanus* is extended back almost 14 million years (Valengian to Tithonian). Taken into consideration with other records of the clade (Dong, 1990), this is strong evidence that Stegosauria enjoyed worldwide success into the Early Cretaceous, and that their Late Jurassic extinction in North America may have been the exception. Given that stegosaurs were so widely distributed in the African portion of Gondwana, it is highly plausible that their fossils are awaiting discovery in South America and somewhat plausible for Antarctica and Australia

Previously described theropods from Late Jurassic Africa outside of Ethiopia include *Elaphrosaurus bambergi* (Janensch, 1920) and ?*Allosaurus tendagurensis* (Janensch, 1925) from Tendaguru and a possible allosaurid from the Gokwe Formation of Zimbabwe (Raath and McKintosh, 1987). Work done in the Late Jurassic of Ethiopia by Goodwin, et al. (1999) showed that an allosauroid similar to *Acrocanthosaurus* was present, as well as a possible dromaeosaurine. Taken into consideration with the material from this publication, the Mugher Mudstone records a level of theropod diversity comparable to that of the famous Tendaguru locality. Further, the recovery of two dromaeosaurid teeth from the Mugher Mudstone adds to mounting evidence that dromaeosaurids were well established across northern Africa by the end of the Jurassic (Rauhut and Werner, 1995; Goodwin et al. 1999; Mudroch, et al. 2011).

Overall, the Mugher Mudstone records a degree of high level taxonomic diversity that more or less equals Tendaguru. Clades currently represented by the Tendaguru fauna include numerous sauropods, the theropods *Elaphrosaurus bambergi* and the enigmatic *Allosaurus tendagurensis*, the ornithopod *Dryosaurus lettowverbecki* and the charismatic stegosaur *Kentrosaurus aethiopicus*. By comparison, the Mugher fauna is represented by allosauroid and dromaeosaurine theropods, a probable sauropod, hypsilophodontids, and the stegosaur *Paranthodon africanus.*

Late Jurassic Fauna	Mugher	Tendaguru	Laurasia
Stegosaurids	🙂	🙂	🙂
Hypsilophodontids	🙂	🚫	🙂
Iguanodontids	🚫	🙂	🙂
Sauropods	?	🙂	🙂
Allosaurids	🙂	?	🙂
Ceratosaurids	🚫	🙂	🙂
Velociraptorines	🙂	🚫	🙂

Late Jurassic Fauna	Before	After (LJ Ethiopia)
Paranthodon africanus	EK South Africa	151~132 ma (+19 ma); + ~4600 km N
Hypsilophodontids	EJ South Africa	206-151 ma (+55 ma); + ~4600 km N
Iguanodontids	N/A	N/A
Sauropods	?EJ-LK Africa	Within existing strat/geo ranges.
Allosaurids	?LJ-EK Northern Afr.	Within existing strat/geo ranges.
Ceratosaurids	N/A	N/A
Dromaeosaurids	MJ & EK Northern Afr.	151-95 ma (+56 ma); + ~1500 km E

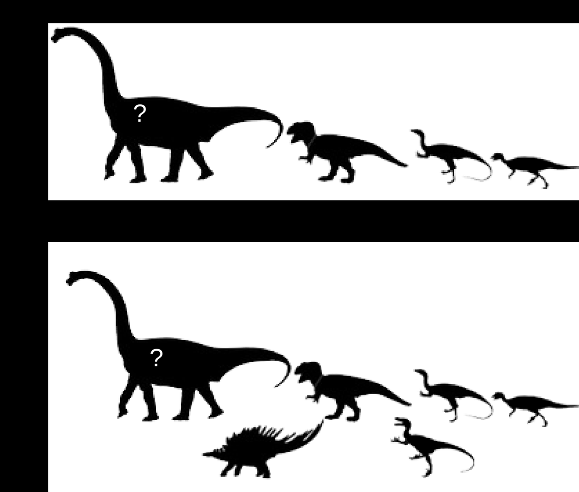


FIGURE 10. Representative faunal silhouettes of the Mugher Mudstone dinosaur fauna before this project (above) and including this study's findings (below).

FIGURE 11. The Jurassic of Ethiopia may have appeared similar to this scene representing Jurassic Portugal. Artwork by Allan Lam.

CONCLUSIONS

Prior to this study, dinosaur taxa known from Late Jurassic Africa were restricted to the Tendaguru fauna, a fragmentary theropod leg from Zimbabwe, and the small sample of teeth described by Werner (1995) and Goodwin, et al (1999). The Mugher specimens were composed of fairly typical Late Jurassic taxa, which included allosauroid theropods, hypsilophodontids, a possible sauropod and a possible dromaeosaurine. As of this study, analysis of isolated dinosaur teeth from the Mugher Mudstone has yielded new stratigraphic and geographic occurrences of the stegosaur *Paranthodon africanus*, new geographic ranges for dromaeosaurine theropods, and increased stratigraphic and geographic ranges for a hypsilophodontid with unique dental features.

The analysis of dinosaur teeth from the Mugher Mudstone of Ethiopia is an important case study that demonstrates why detailed descriptions and analyses of isolated dinosaur teeth are not only helpful, but necessary for understanding distribution patterns of extinct taxa, especially in poorly sampled formations. While at times it is a difficult and vexing task, combining the most basic tooth identifications with stratigraphic and geographic context provides valuable new information about taxon distribution and longevity. This makes isolated dinosaur teeth important tools for understanding the paleobiological variables of extinct taxa.

ACKNOWLEGEMENTS

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References available upon request.