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ARTICLE

A NEW LATE CRETACEOUS VERTEBRATE FAUNA FROM THE CAUVERY BASIN, SOUTH INDIA: IMPLICATIONS FOR GONDWANAN PALEOBIOGEOGRAPHY

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ABSTRACT—Late Cretaceous vertebrate faunas of India are known predominantly from intertrappean deposits in the Deccan volcanic province of the central and western parts of the country. A thick and nearly continuous sequence of Early Cretaceous–Early Paleocene fossiliferous sediments exposed in the Cauvery Basin of South India has been comparatively poorly explored. Here, we present a preliminary description of a new fauna consisting of vertebrate fossils discovered from the continental Upper Cretaceous (late Maastrichtian) Kallamedu Formation. The Kallamedu Fauna includes ganoid fishes, amphibians, turtles, crocodiles, and dinosaurs, with many taxa suggesting Late Cretaceous biotic links between India and other Gondwanan landmasses. Teeth of abelisaurid dinosaurs, known previously from the Middle Jurassic of South America and the Late Cretaceous of Africa, Madagascar, and central and western India, support a pan-Gondwanan distribution for this group of theropod dinosaurs. Of greatest significance, however, is the first discovery of a *Simosuchus*-like notosuchian crocodile outside of Madagascar. This report of the first Indian *Simosuchus*-like notosuchian crocodile further strengthens earlier evidence from other vertebrate groups for close biotic links between India and Madagascar in the Late Cretaceous, most likely through dispersal via the Seychelles block, Amirante Ridge, and Providence Bank.

INTRODUCTION

Upper Cretaceous continental, vertebrate-bearing horizons occur in two widely separated regions in peninsular India. These regions are the Deccan volcanic province, which occupies mainly the central and western parts of India, and the Cauvery Basin, which is restricted to the southeastern part of India. The vertebrate fauna of the volcano-sedimentary sequences (Lameta Formation and intertrappean beds) of the Deccan volcanic province has been extensively studied in the last three decades, and as a result knowledge of the vertebrate biodiversity of this region has substantially increased (see reviews by Khosla and Sahni, 2003; Prasad and Sahni, 2009). In contrast, despite documentation of a rich invertebrate fauna (Govindan, 2000), both the continental and marine vertebrate faunas of the Cauvery Basin are very poorly known, with only sporadic reports over the last few centuries (Egerton, 1845; Blanford, 1862; Matley, 1929; Sahni, 1957; Yadagiri and Ayyasami 1979; Yadagiri et al., 1983; Kohring et al., 1996; Underwood et al., 2011; Verma et al., 2012). The paucity of data for Cretaceous vertebrates from the Cauvery Basin is particularly surprising given its extensive Cretaceous outcrops (Sastry et al., 1972). For these reasons, since 2007 we have focused a comprehensive field program on exploration for sites yielding vertebrate fossils in the Barremian–Maastrichtian horizons of this basin, and have evaluated the recovered fossils for their biostratigraphic, paleoecological, and paleobiogeographic significance in the context of India's northward flight. The marine vertebrate fauna of the Albian–Turonian Karai Formation have been described elsewhere (Underwood et al., 2011; Verma et al., 2012), and comprise mainly elasmobranch and ichthyosaur remains. We describe here a new fauna of late Maastrichtian age recovered from the Kallamedu Formation near Kallamedu Village, Ariyalur District, Tamil Nadu. The Kallamedu Fauna consists of vertebrate fossils recovered through surface collection and screen-washing of microvertebrate sites during extensive surveys of the continental Upper Cretaceous (Maastrichtian) Kallamedu Formation in 2007 and 2009. Since 1862, fragmentary dinosaur bones have been reported from the Kallamedu Formation (Blanford, 1862; Matley, 1929; Yadagiri and Ayyasami, 1979, 1989). Blanford (1862) was the first to report a 'bone bed' near Kallamedu Village in Ariyalur District (Fig. 1). The reported bones were mostly friable and difficult to excavate in an identifiable condition. However, Blanford (1862) referred a carnivorous dinosaur tooth to *Megalosaurus* and therefore assumed that the other bones in the Kallamedu bone bed also belonged to *Megalosaurus*. The tooth was further described later by Lydekker (1879) as *Megalosaurus* sp. In a subsequent visit to the area, Matley (1929) also found large poorly preserved bone fragments. Based on their size, he referred them to sauropod dinosaurs. Yadagiri and Ayyasami (1989) reported the occurrence of an ilium, a tibia, a femur, and vertebrae from the Kallamedu bone bed and assigned them to a new theropod taxon *Bruhathkayosaurus matleyi*. However, the taxonomic assignment of the bones to a theropod dinosaur was later questioned by Krause et al. (2006), who considered them to represent a possible sauropod.

In addition to these dinosaur remains, a new genus of bothremydid turtle, *Kurmademys kallamedensis*, was described from the Kallamedu Formation (Gaffney et al., 2001). Despite these

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*Corresponding author.

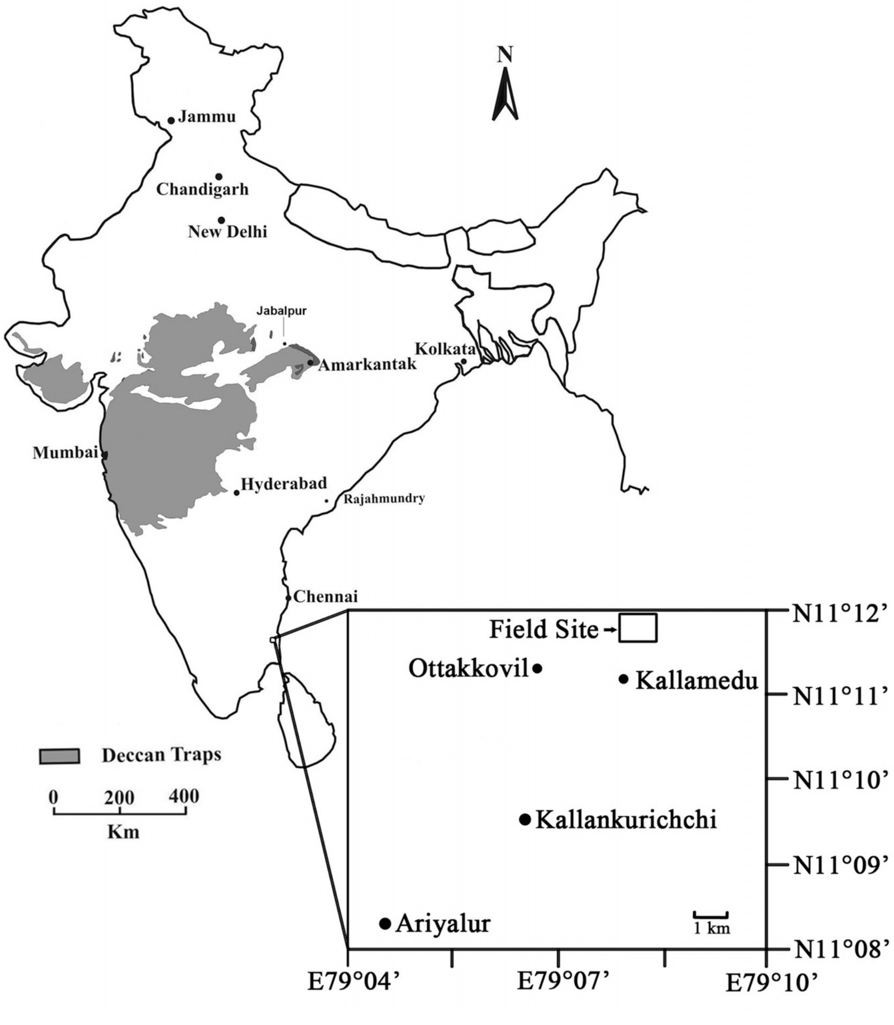

FIGURE 1. Location map of the vertebrate-bearing Kallamedu Formation.

promising initial reports, no extensive survey or description of the Kallamedu Formation's vertebrate fauna had ever been undertaken. Our field work has recovered numerous fish, amphibian, turtle, crocodyliform, and dinosaur specimens, which we report here in the first comprehensive description of the Kallamedu Fauna, recognizing its importance as the first well-studied Late Cretaceous Indian vertebrate fauna beyond the Deccan volcanic province.

GEOLOGIC SETTING

The Cauvery Basin trends NE–SW and formed as a result of Late Jurassic–Early Cretaceous rifting of Precambrian basement rocks between India and Australia-Antarctica (Powell et al., 1988). Pioneering work on the geology of this area was done by Blanford (1862), who divided the sedimentary succession of the basin into three lithostratigraphic units: the Uttatur Group, the Trichinopoly Group, and the Ariyalur Group, in order of superposition. The Ariyalur Group is exposed to the east and northeast of the town of Ariyalur and is the focus of the present study. Recent lithostratigraphic classification of the Cretaceous succession in the Cauvery Basin has divided the Ariyalur Group into the Sillakkudi, Kallankurichchi, and Kallamedu formations of Campanian, early Maastrichtian, and late Maastrichtian ages, respectively (Sundaram et al., 2001).

The Kallamedu Formation is exposed in badlands and along stream cuts to the east and northeast of Kallamedu, a small village approximately 10 km northeast of Ariyalur (Fig. 1). The formation is easily recognizable by its bright red clays overlain by a friable sandstone containing many sandy nodules and interspersed with sandy clays. The Kallamedu Formation has been interpreted to have been deposited in a fluvial, flood-plain environment in a coastal setting with a minor marine influence at the base (Tewari et al., 1996). Planktonic foraminifers from the basal marine part indicate a late Maastrichtian age for this formation (Srivastava and Tewari, 1967). The large dinosaur bones are generally found in the sandstone overlying the red clays. Screen-washing of the sandy clay layers within the sandstone bed led to the discovery of the small vertebrate fossils described here.

MATERIALS AND METHODS

Surface prospecting was undertaken in a large exposure of the Kallamedu Formation in the Cauvery Basin near Kallamedu Village, Ariyalur District, Tamil Nadu, South India (Fig. 1). During surface prospecting in the Kallamedu area, we found several highly fragmentary large bones, including one humerus, one possible scapula, three vertebrae, and other unidentifiable elements, presumably representing dinosaur taxa. As was the case with Blanford (1862) and Matley (1929), we noted that larger, presumably dinosaurian bones typically are fragile and crumble during excavation, despite the use of adhesives. In addition to these bones, we also found multiple theropod and crocodilian teeth during surface prospecting. We further screen-washed 300 kg of sediments from three different sites within the broad area of Kallamedu Formation exposures. Examination of the screen-washed residue yielded several ganoid fish scales, one fragmentary anuran ilium, and additional crocodilian and theropod teeth. A preliminary description of this microvertebrate assemblage and its paleobiogeographic significance is presented below.

Institutional Abbreviation—DUGF, Delhi University, Geology Department, Fossil Catalogue, Delhi, India.

SYSTEMATIC PALEONTOLOGY

ACTINOPTERYGII Klein, 1885
LEPISOSTEIFORMES Hay, 1929
LEPISOSTEIDAE Cuvier, 1825
Gen. et sp. indet.
(Fig. 2A–E)

Material—Eight isolated ganoid fish scales (DUGF/59–66).

Description—The eight scales recovered include three subcircular to subtriangular dorsal ridge scales, three scales with peg and socket structure, representing body scales, and two rhombic scales representing lateral line series. The dorsal ridge scales have rounded anterior margins with a slight concavity in the middle and a narrow, acutely rounded posterior end (Fig. 2A). The body scales are elongated anteroposteriorly and are roughly rhombic in outline with a long peg-like structure anteriorly. In two of these scales (DUGF/62–63), there is a small spur on the anterodorsal face of the peg (Fig. 2D–E). The lateral line scales (DUGF/65–66) are rhombic in outline and have a thick enamel covering externally.

Discussion—Scales with similar morphology were reported from the Upper Cretaceous Deccan intertrappean beds and have been assigned to the gar *Lepisosteus indicus* based on comparison with complete skeletons of this species from the Lameta Formation of central India (Mohabey and Udhoji, 1996). The intertrappean *Lepisosteus* scales often occur in association with isolated teeth. So far, no teeth have been found with the fish scales at the present site. For this reason, here they are tentatively assigned to the family Lepisosteidae.

AMPHIBIA Linnaeus, 1758
ANURA Fitzinger, 1843
Gen. et sp. indet.
(Fig. 2F, G)

Material—A fragmentary right ilium (DUGF/47).

Description—DUGF/47 is a fragmentary right ilium preserving part of the acetabulum and a small part of the iliac shaft (Fig. 2F–G). The iliac shaft has a vertically oval cross-section. The dorsal crest is not present. A scarcely developed dorsal prominence is present on the margin of the shaft in an anterodorsal position relative to the acetabulum. Because of the poor state of preservation, the dorsal protuberance and the nature of the supraacetabular expansion (pars ascendens) and the ventral acetabular expansion (pars descendens) (Fig. 2G) are not discernible. From the preserved part, the acetabulum appears to be a roughly spherical structure and clearly is large in size. The lateral face of the ilium on the opposite side of acetabulum is convexly rounded (Fig. 2F).

Discussion—Because of the fragmentary nature of the ilium and preservation of few distinguishing characters, this specimen is considered only to represent an indeterminate anuran.

TESTUDINES Linnaeus, 1758
Gen. et sp. indet.

Material—Several fragmentary pieces of carapace and one vertebral element.

Discussion—Although numerous small pieces of turtle carapace and one partial vertebral element were found in several localities of the Kallamedu Formation, their highly fragmentary nature does not allow any taxonomic identification beyond indeterminate Testudines. As detailed above, a new genus of bothremydid turtle, *Kurmademys*, has been previously described from the Kallamedu Formation, based on a complete skull, as well as postcranial material. Unfortunately, the carapace and vertebral fragments recovered during the survey reported here are not sufficiently complete to allow comparison with the published material of *Kurmademys*. In most cases, like this one, isolated shell fragments are poor indicators of taxonomic affiliation (Bonin et al., 2006), although some studies involving destructive sampling or identification of special features, not preserved in these specimens, have been able to identify group-specific traits (Scheyer and Anquetin, 2008; Pérez-Garcia et al., 2012). For this reason, more complete specimens, ideally representing cranial elements, or destructive sampling are required before more specific assignment of this material is possible.

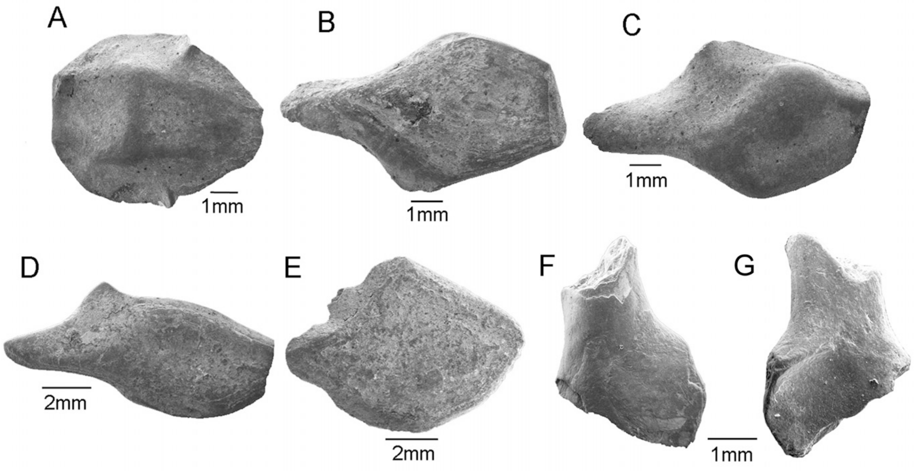

FIGURE 2. **A**–**E**, isolated scales of Lepisosteiformes indet. **A**, internal view of dorsal ridge scale (DUGF/59). **B**, **C**, body scale (DUGF/64) in external view (**B**) and internal view (**C**). **D**, **E**, body scales (**D**, DUGF/62 and **E**, DUGF/63) in external view. **F**, **G**, indeterminate anuran right ilium (DUGF/47) in medial view (**F**) and lateral view (**G**).

ARCHOSAURIA Cope, 1869
CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NOTOSUCHIA Gasparini, 1971
SIMOSUCHUS Buckley, Brochu, Krause, and Pol, 2000
cf. *SIMOSUCHUS* sp.
(Fig. 3A, B)

Material—One isolated multicuspid tooth (DUGF/48).

Description—This clove-shaped, multicuspid tooth has all the cusps lying in a single longitudinal row (Fig. 3A, B). The tooth is labiolingually compressed, with a pronounced constriction at the crown-root junction. The crown is twice as long as high. In occlusal view, the tooth is labiolingually symmetrical and thickened at the level of the cusp bases. The labial face of the crown is convex (Fig. 3A), whereas its lingual face is slightly concave (Fig. 3B). There are eight cusps in total, of which the mesial and distal cusps are broken and appear to be at a slightly lower level than the other cusps. The remaining cusps are nearly of the same size and height and are separated by shallow sulci on both the labial and lingual faces. These sulci terminate before reaching the basal thickening of the crown. The cusps are nearly parallel in orientation to each other. A small part of the root is preserved. The mesiodistal length of the root is less than that of crown; hence, the crown overhangs the root mesially and distally (Fig. 3A, B). The root is also labiolingually compressed and flares ventrally (cervically) from the crown-root junction. The basal cross-section is elliptical in outline. From the lingual view, the root appears to project anteriorly, whereas the crown juts posteriorly. We reconstruct DUGF/48 as a right dentary tooth, and in that position, attrition/wear facets are present on the tip of second cusp from the anterior side, on the occlusolabial face of cusps 3 and 4, on the occlusolingual face of cusp 5, and on the tip of cusps 6 and 7.

Discussion—This clove-shaped tooth with multiple homogeneous cusps and ventrally flaring root is reminiscent of the crown morphology of *Simosuchus clarki* Buckley, Brochu, Krause, and Pol, 2000, a notosuchian known from the Upper Cretaceous Maevarano Formation of Madagascar. In *Simosuchus*, the premaxillary teeth, anterior maxillary and dentary teeth all have a tripartite division of cusps, with a tall central prong with three cusps and two or three low cusps each on the mesial and distal prongs. Posteriorly, the teeth become progressively mesiodistally longer than high, and the cusps become lower and more homogeneous, being nearly equal in size (Kley et al., 2010). Based on these strong and distinctive similarities to the dental morphology of *Simosuchus clarki*, DUGF/48 is regarded as a tooth belonging to the posterior series of a notosuchian closely related to *Simosuchus*. The single known tooth is difficult to assign to the dentary or maxillary series. However, we tentatively place it within the posterior series of the right dentary, due to similar flaring of anterior part of the root relative to that described for some of the dentary teeth of *Simosuchus* (Kley et al., 2010:fig. 30H) and to the presence of eight cusps. In *Simosuchus*, the maxillary teeth have seven cusps instead of the

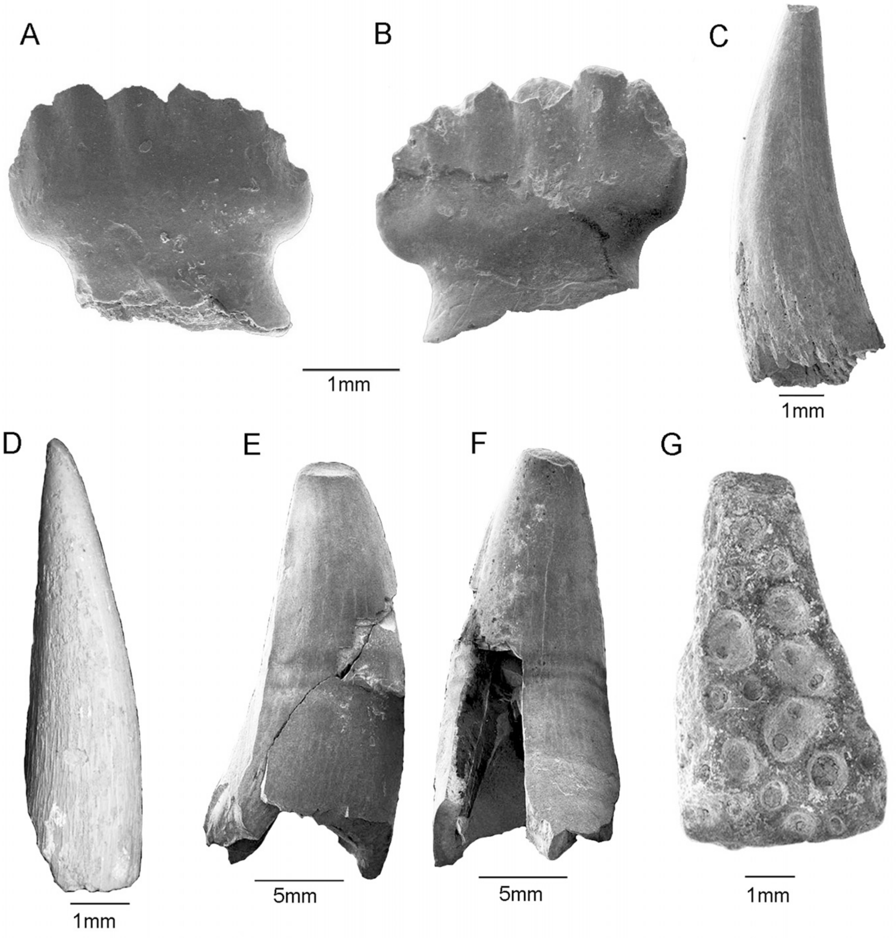

FIGURE 3. **A**, **B**, isolated distal tooth of notosuchid crocodile, cf. *Simosuchus* sp. (DUGF/48), in labial (**A**) and lingual (**B**) views. **C**–**F**, isolated teeth of Crocodylia indet. **C**, DUGF/50 in mesiolingual view. **D**, DUGF/49 in labial view. **E**, **F**, DUGF/51 in labial (**E**) and lingual (**F**) views. **G**, osteoderm of Crocodylia indet. (DUGF/58) in external view.

eight or nine cusps on all of the dentary teeth. In spite of the remarkable similarity of DUGF/48 to the teeth described for *Simosuchus* from Madagascar, we desist from assigning it to this taxon based on a single tooth. Further in mesiodistal length, DUGF/48 is much smaller (2.2 mm) than those of *Simosuchus* (5 mm).

CROCODYLIA Gmelin, 1789
Gen. et sp. indet.
(Fig. 3C–G)

Material—Three isolated teeth (DUGF/49–51) and one osteoderm (DUGF/58).

Description—Two teeth, DUGF/49 (Fig. 3D) and DUGF/50 (Fig. 3C), recovered from the screen-washed residue are conical in outline, with slightly lingually curved tips and non-serrated mesial and distal carinae. Lingually, the carinae are separated from the highly raised ridge of the crown body by shallow concavities both mesially and distally. The lingual face of the crown is ornamented with fine ridges in both the teeth, whereas the labial face of DUGF/49 has many tiny longitudinal ridges as compared with the nearly smooth (with relatively very few ridges) labial face of DUGF/50. The two carinae are located slightly lingual to the middle part of the mesial and distal faces. Thus, the highly convex labial face covers more crown area than the lingual one. These teeth have spherical basal cross-sections. As similar morphology is found in several crocodilian families, these specimens cannot be confidently assigned to any clade within Crocodylia.

A third and much larger crocodilian tooth (DUGF/51) (Fig. 3E, F) also was surface collected from this site. This tooth has a lingually bent apex, as in DUGF/49 and 50. The labial face of this tooth is strongly convex, whereas its lingual face is convex in the middle part, but less so on the mesial and distal margins. However, this tooth differs from DUGF/49 and 50 in having the worn mesial and distal carinae in the middle of the mesial and distal faces, with traces of eroded denticles. The labial face of the crown tip is worn flat. Approximately halfway along the tooth length, there are two slight transverse depressions that circumscribe the tooth, which may represent a developmental artifact; otherwise, the surface of the tooth is smooth. The tooth has a circular cross-section. In its large size, smooth crown surface, and presence of denticles on the mesial and distal carinae, DUGF/51 differs from DUGF/49 and 50.

DUGF/58 is a dermal osteoderm of a crocodile, with a number of spherical pits on the surface (Fig. 3G).

Discussion—It is not possible to allocate the isolated teeth or the osteoderm at any taxonomic level below Crocodylia.

THEROPODA Marsh, 1881
ABELISAURIDAE Bonaparte and Novas, 1985
Gen. et sp. indet.
(Fig. 4A–I)

Material—Five isolated teeth (DUGF/53–57).

Description—DUGF/53 is a 25 mm high, laterally compressed tooth with a mesiodistal length (17 mm) more than double the basal width (7 mm) (Fig. 4A). The mesial carina is moderately curved towards the distal end. The distal carina is almost straight but slightly angled mesially near the apex (Fig. 4A). The denticles on the mesial carina are approximately as high as long. These denticles are chisel-like in shape but are not oriented perpendicular to the long axis; rather, they are at an angle to it (Fig. 4B). Their distal ends are slightly pointed towards the apex of the crown. The denticles of the basal and apical parts of mesial carina are smaller than those of the middle part. The apex of the crown bears the smallest and most worn denticles. The basal and middle parts of the distal carina are broken. In the apical part of the distal carina, 17 denticles are preserved. Of these, the lower 12 denticles are relatively large in size and longer than high, in contrast to the denticles of the mesial carina, and their distal ends are apically curved (Fig. 4C). Interdenticular sulci are distinctly developed on both mesial and distal denticles. There are 2.5 denticles per mm in the mesial and distal carinae. As the tooth is labiolingually flattened, it has an oval or teardrop-shaped basal cross-section, with a slightly rounded mesial face and pointed distal face. The labial and lingual faces of the tooth are more or less equally convex except for a slight concavity on the lingual base. The enamel surface is smooth on both the labial and lingual faces.

DUGF/54 is the largest (height = 39 mm, mesiodistal length = 16 mm, labiolingual width = 8 mm) of the dinosaurian teeth in the Kallamedu vertebrate fossil collection described here (Fig. 4D). This tooth, except for its large size, is similar in morphology to DUGF/53. The enamel of DUGF/54 is not preserved; thus, the denticles are preserved only in the form of indentations on the mesial and distal carinae (Fig. 4E). This tooth is also labiolingually compressed, which renders an oval basal cross-section to the tooth.

DUGF/55 compares well with DUGF/53–54 in its overall morphology. In this tooth, the apex and distal base are broken. The mesial carina is worn, bearing broken denticles that are similar in shape (chisel-like) to those of DUGF/53. Only 11 denticles are present on the preserved distal carina. These denticles are longer than high, with their distal ends pointing apically (hook-like) (Fig. 4F), and distinct interdenticular sulci are present, as in DUGF/53. The surface of the crown is smooth. The preserved height of this tooth is 20 mm. There are 3 denticles per mm in the basal part and 2.5 denticles per mm in the middle part of the carinae.

In DUGF/56, the distal one-third of the crown and the apical tip are broken (preserved height = 18 mm) (Fig. 4G). The crown is convex both labially and lingually. The denticles on the mesial carina (Fig. 4H) are worn but somewhat similar to those of DUGF/53 in shape, size variation, and orientation with respect to the long axis of the tooth. There are 3 denticles per mm in the basal part and 2.5 per mm in the middle part of the carina. It appears that DUGF/56, although laterally flattened, is not as labiolingually compressed as are DUGF/53 and DUGF/54. The mesial basal cross-section presents a more rounded outline in comparison with that of DUGF/53 and 54; this may be attributable to its more anterior position on the dentition.

DUGF/57 is a fragmentary tooth in which only the distal carina and a small part of crown body are preserved (Fig. 4I). The lingual face of this tooth is concave, whereas the labial face is flat to convex. In the basal and middle parts of the tooth, the denticles are perpendicularly oriented relative to the long axis. The apical six denticles are slightly deflected apically. Interdenticular sulci are distinctly developed in this tooth. There are 4 denticles per mm in the basal part and 3–3.5 per mm in the middle part of the crown.

Discussion—Teeth with a mesiodistally oriented long axis that is almost twice the length of the short axis, a strongly curved mesial profile, and a straight distal profile slightly angling mesially towards the apex are characteristic of abelisaurid theropod dinosaurs, such as *Majungasaurus* and *Indosuchus*. In abelisaurid jaws, the premaxillary teeth are basally more rounded than those of the maxilla and dentary. Moreover, in premaxillary teeth the mesial and distal carinae are located lingual to the center of the crown base, and the labial face is more strongly convex than the lingual face. The convexity of the labial face decreases distally in maxillary and dentary teeth, and both faces are more or less equally convex in more distal teeth. The teeth described have equally convex labial and lingual faces and flat basal cross-sections and thus may represent more distally positioned maxillary or dentary teeth of abelisaurids. Of the abelisaurid dinosaurs, the dentitions of *Majungasaurus* and *Masiakasaurus* from the Late Cretaceous of Madagascar are the best known (Smith, 2007). In *Majungasaurus*, the mesial and distal denticles of distal teeth are roughly the same size, whereas in the best-preserved tooth (DUGF/53) of the Kallamedu collection, the mesial denticles are slightly smaller than those of distal carina, as in *Masiakasaurus*.

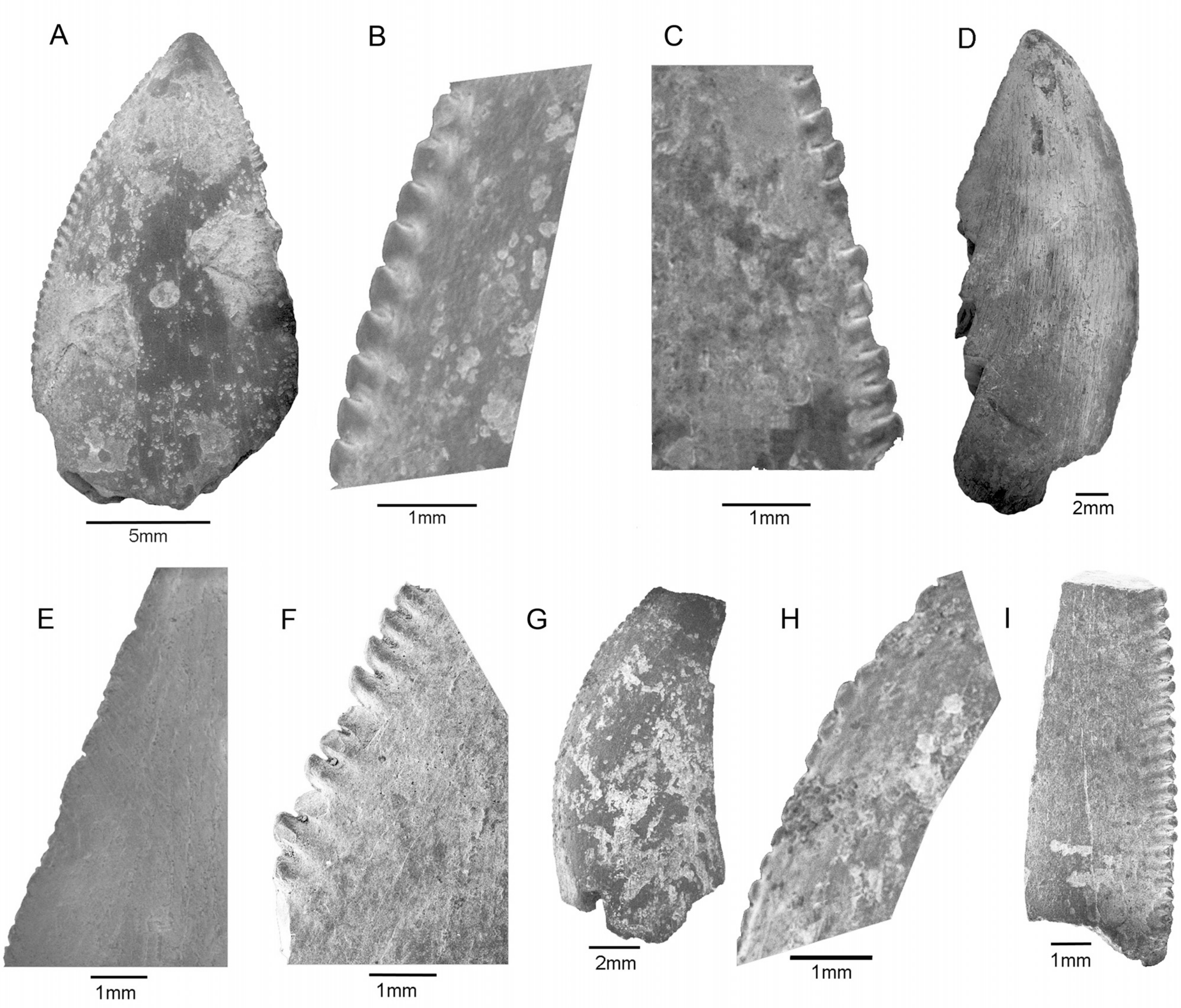

FIGURE 4. **A**–**I**, Abelisauridae indet. **A**–**C**, DUGF/53 in labial view (**A**); enlarged view of mesial carina (**B**) and enlarged view of distal carina (**C**). **D**, **E**, DUGF/54 in lingual view (**D**) and enlarged view of apical distal carina (**E**). **F**, distal carina of theropod dinosaur tooth (DUGF/55). **G**, **H**, fragmentary theropod tooth (DUGF/56) in labial view (**G**) and enlarged view of mesial carina (**H**). **I**, distal carina of a theropod tooth fragment (DUGF/57).

The interdenticular sulci are well developed and basally angled in *Majungasaurus*, whereas they are absent in *Masiakasaurus*. *Indosuchus* is supposed to represent an intermediate position between these two Madagascan taxa in having poorly developed interdenticular sulci (Smith, 2007). In the Kallamedu teeth, the interdenticular sulci are moderately well developed, but do not angle basally as in *Majungasaurus*. Overall, the crown morphology of the Kallamedu teeth most closely approaches that of ‘abelisaurid Morphotype 3’ (Fanti and Therrien, 2007) described from the Upper Cretaceous Maevarano Formation of Madagascar, in possessing 2.5–3.0 denticles per mm and in the slight recurving of the denticles towards the apex, particularly in the distal carinae of DUGF/53 and 55. However, better-preserved specimens are required for more accurate taxonomic assignment.

DISCUSSION

Paleobiogeographic Significance

The notosuchian crocodyliform tooth described here is highly significant from a paleobiogeographic perspective, because it presents additional evidence for a biotic link between India and Madagascar in the Late Cretaceous, approximately 15–20 million years after their separation. Previous studies of Late Cretaceous vertebrates have demonstrated that India, Madagascar, and South America have some common faunal elements, such as abelisaurid dinosaurs and gondwanatherian mammals. In fact, the Indian abelisaurid dinosaurs *Indosuchus raptorius* and *Rajasaurus narmadensis* (Wilson et al., 2003) from the Lameta Formation of Jabalpur, Madhya Pradesh (central India), and Rahioli, Gujarat (western India), respectively, have been considered to be sister taxa to *Majungasaurus crenatissimus* from Madagascar (Carrano and Sampson, 2008). In the most recent analysis, the Indo-Madagascan clade was also reconstructed as nested within South American abelisaurids, including *Carnotaurus sastrei* and *Abelisaurus comahuensis* (Carrano and Sampson, 2008). *Masiakasaurus knopfleri*, a smaller abelisaurid from Madagascar, has also been considered to be closely allied to *Laevisuchus indicus* of India and *Noasaurus leali* of South America (Sampson et al., 2001; Carrano et al., 2002). Similarly, *Bharattherium bonapartei*, a gondwanatherian mammal from India, is regarded as the sister group of *Lavanify miolaka* from Madagascar (Krause et al., 1997; Prasad et al., 2007). Most recently, *Kinkonychelys rogersi* (Gaffney et al., 2009), a bothremydid turtle from the Late Cretaceous of Madagascar, has been described as closely related to the Indian kurmademyinine bothremyid turtles *Sankuchemys sethnai* and *Kuramademys kallamedensis*, whereas *Kelyophis hechti* (Laduke et al., 2010), a nigerophiid snake also described from the Late Cretaceous of Madagascar, has been allied with the Indian snake genus *Indophis sahni*.

Prasad and Lapparent De Broin (2002) suggested resemblances between the uruguaysuchid notosuchian *Araripesuchus wegneri* and peirosaurid notosuchian *Hamadasuchus rebouli* from Africa, and isolated crocodyliform teeth recovered from the Deccan intertrappean beds of India. However, *Pabweshi pakistanensis*, a baurusuchid from the Upper Cretaceous Pab Formation of Pakistan (Wilson et al., 2001), is the only clearly assignable Cretaceous notosuchian known from the Indian subcontinent to date. The notosuchian tooth from the Kallamedu Formation presented here exhibits characteristic features for *Simosuchus*; hence, it can be confidently described as a *Simosuchus*-like notosuchian crocodile. This new discovery from Kallamedu adds another line of evidence to the growing number of vertebrate fossil groups, supporting a close biogeographic link between India and Madagascar in the Late Cretaceous. The question of how and when these groups arrived in India and Madagascar, and the polarity of any dispersal events, remains open. In the following section, we discuss three possible biogeographic scenarios proposed by prior workers.

Pan-Gondwanan Distribution—Late Cretaceous occurrences of abelisaurid dinosaurs, gondwanatherian mammals, and notosuchian crocodiles across South America, India, and Madagascar may reflect a formerly wide distribution for these groups across some or all Gondwanan landmasses. These Late Cretaceous occurrences in South America and Indo-Madagascar may then represent Gondwanan relicts. An ancestrally pan-Gondwanan distribution would be supported by older fossils in these and other Gondwanan continents. Abelisaurid dinosaurs were known from the Middle Jurassic of South America (Pol and Rauhut, 2012) and the early Late Cretaceous of Africa, supporting a pan-Gondwanan distribution for this clade (Ali and Krause, 2011). Similarly, notosuchian crocodyliforms are widespread across Gondwana from the middle Early Cretaceous through the Late Cretaceous, with reports from Africa, South America, Madagascar, and the Indian subcontinent. In contrast, the oldest gondwanatherians are from the Campanian of South America, with only Maastrichtian occurrences in Madagascar and India. Without more data from earlier Cretaceous localities, or from other Gondwanan landmasses, it is impossible to assess if gondwanatherians had an ancestrally pan-Gondwanan distribution or later dispersed among the Gondwanan landmasses using one of the hypothesized routes discussed below.

Nigerophiid snakes and bothremydid turtles are known from Africa, India, and Madagascar in the Late Cretaceous, and in all cases, the Indian and Madagascan taxa are more closely related to each other than either are to the African forms. *Simosuchus*-like notosuchian crocodyliforms, although members of a larger, pan-Gondwanan notosuchian clade, are known only from the Late Cretaceous of Madagascar and now India. Because none of these three groups are known earlier in the Cretaceous or from other Gondwanan landmasses, there is no direct evidence supporting a more widespread, i.e., pan-Gondwanan, distribution for any of them; thus, dispersal may be a more likely explanation for their Late Cretaceous occurrences.

Southern Dispersal Route—Krause et al. (1997) suggested a terrestrial dispersal route between Indo-Madagascar and South America via Antarctica and the Kerguelen Plateau to explain the presence of gondwanatherian mammals across South America, India, and Madagascar. The occurrence of abelisaurid dinosaurs in South America, India, and Madagascar also was attributed to the existence of this terrestrial route (Sampson et al., 1998). Case (2002) suggested a slight variant of this hypothesis, with the Gunnerus Ridge rather than the Kerguelen Plateau providing a subaerial connection between Antarctica, Madagascar, and India. However, serious doubts have been raised about the viability of either of these routes, because paleogeographic data for the Kerguelen Plateau and Gunnerus Ridge have reconstructed these aseismic tectonic structures as subaerially exposed only up to 90 Ma (Ali and Aitchison, 2009; Ali and Krause, 2011). According to these reconstructions, the proposed terrestrial routes instead would have been submerged during most of the Late Cretaceous and thus could not have served as corridor for the dispersal of terrestrial organisms at that time.

Dispersals across Intervening Tectonic Elements—With the refutation of a southern terrestrial link between South America and Indo-Madagascar via Antarctica and the Kerguelen Plateau or the Gunnerus Ridge, and in the absence of any fossil evidence supporting a pan-Gondwanan distribution for these vertebrate clades, dispersal is perhaps the most plausible explanation at present for many of these groups (Prasad et al., 2010; Goswami et al., 2011; but see Ali and Krause, 2011). Recent analyses allying *Deccanolestes*, eutherian mammals from the Late Cretaceous of India, with adapisoriculid mammals from the Paleocene of Europe and Africa also suggest that dispersal occurred between India and Africa in the Late Cretaceous (Prasad et al., 2010; Smith et al., 2010; Goswami et al., 2011), but again raise the question of how and when these dispersals took place.

Some of the vertebrate groups discussed here may have dispersed from South America to Africa as late as 90 Ma, as suggested by Sereno et al. (2004). This time frame implies that dispersal started from western Gondwana (i.e., from South America to Africa), with taxa subsequently dispersing from Africa to Madagascar across the Mozambique channel, and lastly from northeast Madagascar to India, presumably via the Seychelles block, Amirante Ridge, and Providence Bank (Ali and Aitchison, 2008). An alternative route between India and Africa was proposed in a recent publication by Chatterjee and Scotese (2010), who suggested that the Kohistan, Dras and Oman Island Arcs could have formed an important intermittent link between the Indian subcontinent and Africa in the Late Cretaceous, thereby facilitating dispersal of Gondwanan elements from Africa to India, or vice versa. Moreover, because Africa was faunistically connected with Europe in the Late Cretaceous (Gheerbrant and Rage, 2006), this route may also have facilitated dispersal between eastern Gondwanan and Laurasian landmasses (Goswami et al., 2011).

CONCLUSIONS

This detailed analysis of the Kallamedu Fauna, a new Late Cretaceous terrestrial vertebrate fauna recovered far from the well-studied Deccan volcano-sedimentary sequences of central India, provides an important new perspective on Late Cretaceous Gondwanan paleobiogeography and on the evolution of several vertebrate clades. The relatively diverse vertebrate fauna described here includes the first report of a *Simosuchus*-like notosuchian crocodyliform outside of Madagascar, and supports close biotic links between Madagascar and India in the latest Cretaceous. Abelisaurid dinosaurs such as those recovered from this fauna are predominantly Gondwanan in distribution and are also documented from central and western India. The expansion of their record to South India in this study provides further evidence of their widespread distribution in the Late Cretaceous of India. The Gondwanan signature of the Kallamedu Fauna provides important data on the Cretaceous vertebrate diversity and biogeographic relationships of the southern continents.

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LITERATURE CITED

Ali, J. R., and J. C. Aitchison. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth Science Review 88:145–166.

Ali, J. R., and J. C. Aitchison. 2009. Kerguelen Plateau and the Late Cretaceous southern continent bioconnection hypothesis: tales from a topographical ocean. Journal of Biogeography 36:1–7.

Ali, J. R., and D. W. Krause. 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. Journal of Biogeography 38:1855–1872.

Blanford, H. F. 1862. On the Cretaceous and other rocks of the South Arcot and Trichinopoly district, Madras. Memoirs of the Geological Survey of India 4:1–217.

Bonaparte, J. F., and F. E. Novas. 1985. *Abelisaurus comahuensis*, n.g., n.sp., Carnosauria del Crétacico Tardio de Patagonia. Ameghiniana 21:259–265.

Bonin, F., B. Devaux, and A. Dupré. 2006. Turtles of the World. John Hopkins University Press, Baltimore, Maryland, 416 pp.

Buckley, G. A., C. A. Brochu, D. W. Krause, and D. Pol. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. Nature 405:941–944.

Carrano, M. T., and S. D. Sampson. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). Journal of Systematic Palaeontology 6:183–236.

Carrano, M. T., S. D. Sampson, and C. A. Forster. 2002. The osteology of *Masiakasaurus knopfleri,* a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 22:510–534.

Case, J. A. 2002. A new biogeographical model for dispersal of Late Cretaceous vertebrates into Madagascar and India. Journal of Vertebrate Paleontology 22(3, Supplement):42A.

Chatterjee, S., and C. Scotese. 2010. The wandering Indian plate and its changing biogeography during the Late Cretaceous-Early Tertiary period; pp. 105–126 in S. Bandyopadhyay (ed.), New Aspects of Mesozoic Biodiversity. Lecture Notes in Earth Sciences 132.

Cope, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philosophical Society, New Series 14:1–252.

Cuvier, G. 1825. Recherches sur les ossemens fossiles, où l'on rétablit les caractèrs des plusieurs animaux dont les révolutions du globe ont détruit les espèces. Third Edition, Volume 3. G. Dufour et E. d'Ocagne, Paris.

Egerton, P. de M. G. 1845. On the remains of fishes found by Mr. Kaye and Mr. Cunliffe in the Pondicherry Beds. Quarterly Journal of Geological Society of London 1:164–171.

Fanti, F., and F. Therrien. 2007. Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaeosaurids in Madagascar. Acta Palaeontologica Polonica 52:155–166.

Fitzinger, L. 1843. Systema Reptilium. Fasciculus Primus. Amblyglossae. Apud Braumüller and Seidel Bibliopolas, Vienna, 106 pp.

Gaffney, E. S., S. Chatterjee, and D. K. Rudra. 2001. *Kurmademys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India. American Museum Novitates 3321:1–16.

Gaffney, E. S., D. W. Krause, and I. S. Zalmout. 2009. *Kinkonychelys*, A new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar. American Museum Novitates 3662:1–25.

Gasparini, Z. 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo Infraorden de los Mesosuchia (Crocodilia). Ameghiniana 8:83–103.

Gheerbrant, E., and J.-C. Rage. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia. Palaeogeography, Palaeoclimatology, Palaeoecology 24:224–246.

Gmelin, J. F. 1789. Regnum animale. Caroli a Linne Systema Naturae per regna tri naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio Decima Tertia, Aucta, Reformata, Leipzig, 1(3):1033–1516.

Goswami, A., G. V. R. Prasad, P. Upchurch, D. M. Boyer, E. R. Seiffert, O. Verma, E. Gheerbrant, and J. J. Flynn. 2011. A radiation of arboreal basal eutherian mammals beginning in the Late Cretaceous of India. Proceedings of the National Academy of Sciences of the United States of America 108:16333–16338.

Govindan, A. 2000. Cretaceous stratigraphy: an update. Memoirs of the Geological Society of India 46:1–14.

Hay, O. P. 1929. Second bibliography and catalogue of the fossil Vertebrata of North America. Publications of the Carnegie Institute of Washington 390(Part I):1–2003.

Hay, O. P. 1930. Second bibliography and catalogue of the fossil Vertebrata of North America. Publications of the Carnegie Institution of Washington 390(Part II):1–1074.

Khosla, A., and A. Sahni. 2003. Biodiversity during the Deccan volcanic eruptive episode. Journal of Asian Earth Sciences 21:895–908.

Klein, E. F. 1885. Beiträge zur Bildung des Schädels der Knochenfische, 2. Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 42:205–300.

Kley, N. J., J. J. W. Sertich, A. H. Turner, D. W. Krause, P. M. O'Connor, and J. A. Georgi. 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar; pp. 13–98 in D. W. Krause and N. J. Kley (eds.), *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Memoir of the Society of Vertebrate Paleontology 10.

Kohring, R., K. Bandel, D. Kortum, and S. Parthasarathy. 1996. Shell structure of a dinosaur egg from the Maastrichtian of Ariyalur (southern India). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1996:48–64.

Krause, D. W., G. V. R. Prasad, W. v. Koenigswald, A. Sahni, and F. E. Grine. 1997. Cosmopolitanism among Gondwanan Late Cretaceous mammals. Nature 390:504–507.

Krause, D. W., P. M. O'Connor, K. Curry Rogers, S. D. Sampson, G. A. Buckley, and R. R. Rogers. 2006. Late Cretaceous terrestrial vertebrates from Madagascar: implications for Latin American biogeography. Annals of the Missouri Botanical Garden 93:178–208.

Laduke, T. C., D. W. Krause, J. D. Scanlon, and N. J. Kley. 2010. A Late Cretaceous (Maastrichtian) snake assemblage from the Maevarano Formation, Mahajanga Basin, Madagascar. Journal of Vertebrate Paleontology 30:109–138.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Laurentii Salvii, Holmiae (Stockholm), 823 pp.

Lydekker, R. 1879. Fossil Reptilia and Batrichia. Palaeontologica Indica Series IV 1:1–36.

Marsh, O. C. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science, Series 3 21:417–423.

Matley, C. A. 1929. The Cretaceous dinosaurs of the Trichinopoly district and the rocks associated with them. Records of the Geological Survey of India 61:337–349.

Mohabey, D. M., and S. G. Udhoji. 1996. Fauna and flora from Late Cretaceous (Maastrichtian) non-marine Lameta sediments associated with Deccan volcanic episode, Maharashtra: its relevance to the K–T boundary problem, palaeoenvironment and palaeogeography. Gondwana Geological Magazine Special Volume 2:349–364.

Pérez-García, A., T. M. Scheyer, and X. Murelaga. 2012. New interpretations of *Dortoka vasconica* Lapparent de Broin and Murelaga, a freshwater turtle with an unusual carapace. Cretaceous Research 36:151–161.

Pol, D., and O. W. M. Rauhut. 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. Proceedings of the Royal Society B 279:3170–3175.

Powell, C. McA., S. R. Roots, and J. J. Veevers. 1988. Pre-breakup continental extension in east Gondwanaland and the early opening of the Indian Ocean. Tectonophysics 155:261–283.

Prasad, G. V. R., and F. Lapparent De Broin. 2002. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. Annales de Paléontologie 88:19–71.

Prasad, G. V. R., and A. Sahni. 2009. Late Cretaceous continental vertebrate fossil record from India: palaeobiogeographical insights. Bulletin de la Société Géologique de France 180:369–381.

Prasad, G. V. R., O. Verma, A. Sahni, D. W. Krause, A. Khosla, and V. Parmar. 2007. A new Late Cretaceous gondwanatherian mammal from Central India. Proceedings of the Indian National Science Academy 73:17–24.

Prasad, G. V. R., O. Verma, E. Gheerbrant, A. Goswami, A. Khosla, V. Parmar, and A. Sahni. 2010. First mammal evidence from the Late Cretaceous of India for biotic dispersal between India and Africa at the KT transition. Comptes Rendus Palévol 9:63–71.

Sahni, M. R. 1957. The fossil reptilian egg from Uttatur (Cenomanian) of south India, being the first record of vertebrate fossil egg in India. Records of the Geological Survey of India 87:671–674.

Sampson, S. D., M. T. Carrano, and C. A. Forster. 2001. A bizarre predatory dinosaur from Madagascar: implications for the evolution of Gondwanan theropods. Nature 409:504–505.

Sampson, S. D., L. M. Witmer, C. A. Forster, D. W. Krause, P. M. O'Connor, P. Dodson, and F. Ravoavy. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. Science 280:1048–1051.

Sastry, M. V. A., B. R. J. Rao, and V. D. Mamgain.1972. Ostracod fauna of the Ariyalur Group (Upper Cretaceous), Tiruchirapalli District, Tamil Nadu, part I. Lithostratigraphy of Ariyalur Group. Memoirs of the Geological Survey of India, Palaeontologica Indica, New Series 40:1–48.

Scheyer, T. M., and J. Anquetin. 2008. Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. Lethaia 41:85–96.

Sereno, P. C., J. A. Wilson, and J. L. Conrad. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. Proceedings of the Royal Society B 271:1325–1330.

Smith, J. B. 2007. Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 27:103–126.

Smith, T., E. De Bast, and B. Sigé. 2010. Euarchontan affinity of Paleocene Afro-European adapisoriculid mammals and their origin in the Late Cretaceous Deccan Traps of India. Naturwissenschaften 97:417–422.

Srivastava, R. P., and B. S. Tewari. 1967. Biostratigraphy of the Ariyalur Stage, Cretaceous of Trichinopoly. Journal of the Palaeontological Society of India 12:48–54.

Sundaram, R., R. A. Henderson, K. Ayyasami, and J. D. Stilwell. 2001. A lithostratigraphic revision and palaeoenvironmental assessment of the Cretaceous System exposed in the onshore Cauvery basin, southern India. Cretaceous Research 22:743–762.

Tewari, A., M. B. Hart, and M. P. Watkinson. 1996. A revised lithostratigraphic classification of the Cretaceous rocks of the Trichonopoly district, Cauvery basin, southeast India; pp. 789–800 in J. Pandey, R. J. Azmi, A. Bhandari, and A. Dave (eds.), Contributions to the XV Colloquium on Micropaleontology and Stratigraphy. Dehra Dun, India, 1996.

Underwood, C. J., A. Goswami, G. V. R. Prasad, O. Verma, and J. J. Flynn. 2011. Marine vertebrates from the 'mid' Cretaceous (early Cenomanian) of South India. Journal of Vertebrate Paleontology 31:539–552.

Verma, O., G. V. R. Prasad, A. Goswami, and V. Parmar. 2012. *Ptychodus decurrens* Agassiz (Elasmobranches: Ptychodontidae) from the Upper Cretaceous of India. Cretaceous Research 33:183–188.

Walker, A. D. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. Philosophical Transactions of the Royal Society B 257:323–372.

Whetstone, K. N., and P. J. Whybrow. 1983. A "cursorial" crocodilian from the Triassic of Lesotho (Basutoland), southern Africa. Occasional Papers of the Museum of Natural History, University of Kansas 106:1–37.

Wilson, J. A., M. S. Malkani, and P. D. Gingerich. 2001. New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous Pab Formation of Vitakri, Balochistan (Pakistan). Contributions of the Museum of Paleontology of the University of Michigan 30:321–336.

Wilson, J. A., P. C. Sereno, S. Srivastava, D. K. Bhatt, A. Khosla, and A. Sahni. 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. Contributions of the Museum of Paleontology of the University of Michigan 31:1–42.

Yadagiri, P., and K. Ayyasami. 1979. A new stegosaurian dinosaur from Upper Cretaceous sediments of South India. Journal of the Geological Society of India 20:521–530.

Yadagiri, P., and K. Ayyasami. 1989. A carnosaurian dinosaur from the Kallamedu Formation (Maastrichtian horizon), Tamil Nadu; pp. 523–528 in M. V. A. Sastry, V. V. Sastry, C. G. K. Ramanujam, H. M. Kapoor, B. R. J. Rao, P. P. Satsangi, and U. B. Mathur (eds.), Symposium on Three Decades of Development in Palaeontology and Stratigraphy in India. Volume 1. Precambrian to Mesozoic. Geological Society of India Special Publications 11.

Yadagiri, P., K. Ayyasami, and B. R. J. Rao. 1983. Cretaceous dinosaurs from southern India and their palaeogeographic significance. Records of the Geological Survey of India 112:51–57.

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