

New record of *Egertonia* (Elopiformes, Phyllodontidae) from the Late Cretaceous of South India

by THOMAS J.D. HALLIDAY^{1*}, ANDREW R. CUFF¹, GUNTUPALLI V.R. PRASAD²,
MECHEK S. THANGLEMMOI², and ANJALI GOSWAMI^{1,3}

¹Department of Genetics, Evolution, and Environment, University College London, Gower Street, London, WC1E 6BT, UK

emails: thomas.halliday.11@ucl.ac.uk, andrew.cuff@ucl.ac.uk, a.goswami@ucl.ac.uk

²Department of Geology, University of Delhi, Delhi 110 007, India

emails: guntupalli.vrprasad@gmail.com, moiyaas@gmail.com

³Department of Earth Sciences, University College London, Gower Street, London, WC1E 6BT, UK

*Corresponding author

Abstract: We report a new occurrence of the phyllodontid teleost fish *Egertonia* from the Late Cretaceous Kallamedu Formation of the Cauvery Basin, South India. This is the oldest occurrence of Phyllodontidae in India, and only the second Cretaceous Gondwanan occurrence of this genus, following a toothplate previously described from the Late Cretaceous Maevarano Formation, Madagascar. The presence of phyllodontid fish supports a fluvial-deltaic or brackish environment for the lower part of the Kallamedu Formation, a rich deposit including typically Gondwanan taxa, such as simosuchid crocodiles, bothremydid turtles, and abelisaurid dinosaurs, as well as an anomalous troodontid dinosaur. *Egertonia* adds another taxon of primarily Laurasian distribution to the Kallamedu fauna and further expands the list of taxa known from the Late Cretaceous of both India and Madagascar,

strengthening the degree of faunal similarity between the two landmasses in the latest Cretaceous.

Key words: Teleostei, Phyllodontidae, Late Cretaceous, Gondwana, India, Palaeobiogeography

DURING the Late Cretaceous, India was isolated from all other continental landmasses by several thousand miles, having most recently separated from Madagascar in the early Late Cretaceous (Briggs 2003; Melluso *et al.* 2009). The order and timing of breakup of the Gondwanan landmasses has inspired a variety of palaeobiogeographical hypotheses regarding vicariant and dispersive relationships of diverse taxa (e.g. Briggs 2003; Prasad and de Lapparent de Broin 2002; Van Bocxlaer *et al.* 2006). Among these, the relationships of India's Late Cretaceous fauna can be considered particularly unusual. The majority of Cretaceous Indian groups are known exclusively from Gondwanan continents, such as abelisaurid theropods (Novas *et al.* 2010), gondwanatherian and haramiyidan mammals (Anantharaman *et al.* 2006; Prasad *et al.* 2007a), and madtsoiid snakes (Wilson *et al.* 2010). Many of the Indian representatives of these clades are sister taxa of Madagascan taxa, for example *Majangasaurus* and *Rajasaurus* within Abelisauridae (Carrano and Sampson, 2008), *Kinkonychelys* and *Kurmademys* within Bothremydidae (Gaffney *et al.* 2009), and *Lavanify* and *Bharattherium* within the sudamericid Gondwanatheria (Prasad *et al.* 2007b). Additionally, there are some members of clades otherwise only known from Laurasian landmasses at this time. These include a probable troodontid theropod (Goswami *et al.* 2013), multiple species of eutherian mammal (Prasad and Sahni 1988; Prasad *et al.* 2007b; Prasad *et al.* 1994) and discoglossid frogs (Prasad and Rage 1991). In order to explain the presence of Laurasian taxa in the Late Cretaceous of India, at least 15 million years before the Indian

plate collided with Asia, it is necessary to either invoke dispersal events across the Tethys Sea or, in some cases, to suggest that several apparently Laurasian taxa radiated out of India after the collision with Asia (Krause and Maas 1990). The Late Cretaceous fauna of India, then, was a mosaic of Gondwanan clades, endemic radiations, and Laurasian immigrants, forming a complex combination of palaeobiogeographical histories (Prasad and Sahni 2009).

While most of the Cretaceous vertebrate fauna of India has been discovered in beds associated with the Deccan Volcanic Province (Fig. 1), recent fieldwork in the Cauvery Basin of Tamil Nadu, South India, has yielded a diverse assemblage of Cretaceous vertebrates. The latest Cretaceous (Maastrichtian) fossils of the Cauvery Basin's Kallamedu Formation include typically Gondwanan vertebrates, such as a tooth of a *Simosuchus*-like crocodyliform (Prasad *et al.* 2013), several teeth of abelisaurid dinosaurs (Prasad *et al.* 2013), multiple skulls and ample carapace elements of bothremydid turtles (Gaffney *et al.* 2001), and a large quantity of fragmentary limb bones that have been identified as titanosaurid sauropods (Lydekker 1877; Goswami *et al.* 2013), but also the anomalous troodontid tooth mentioned above (Goswami *et al.* 2013). These new discoveries have expanded our understanding of the Indian fauna in the Late Cretaceous and provided compelling new information on evolution on the Indian plate in a region distant from but contemporary with the Deccan volcanism. Here we further add to the known diversity of the Kallamedu Formation with the discovery of a phyllodontid fish, *Egertonia*. Phyllodontids are primarily known from Laurasian localities, with very few Cretaceous occurrences of the family from Gondwanan continents. This report is only the second Cretaceous and second Gondwanan record of *Egertonia* and further strengthens palaeobiogeographic links between the Late Cretaceous of South India with that of Madagascar.

GEOLOGICAL SETTING

The Cauvery Basin in Tamil Nadu, South India, formed during Late Jurassic-Early Cretaceous rifting of Eastern Gondwana, and represents an extensive sequence of Early Cretaceous-Paleocene deposits (Tewari *et al.* 1996; Sundaram *et al.* 2001). The Kallamedu Formation is late Maastrichtian in age and forms the uppermost part of the Ariyalur Group, conformably overlying the early Maastrichtian Ottakovil Formation, which in turn overlies the Kallankurichchi Formation and the late Campanian Sillakkudi Formation (Table 1., Ramkumar *et al.* 2013, Sugantha *et al.* 2015). The Kallamedu Formation is itself unconformably overlain by the Danian Niniyur Formation. An extensive exposure of the Kallamedu Formation is found approximately one km north of Kallamedu village, 10 km northeast of Ariyalur (Fig. 1). The fossiliferous exposures cover an area ~1.5 km from east to west and 0.5 km from north to south, although these beds are increasingly overrun by agricultural fields, including the locality that yielded the fossils described here and in recent publications (Goswami *et al.* 2013; Prasad *et al.* 2013; Gaffney *et al.* 2001).

The Kallamedu Formation is composed of red clays interbedded with sandstones and sandy clays. Cross-bedding in the sandstones indicates shallow deposition in moving channels, occurring largely during river flooding episodes (Ramkumar *et al.* 2013). Gaffney *et al.* (2001) interpreted part of the Kallamedu Formation as representing a freshwater pond on the basis of the presence of freshwater gastropods, although others have suggested the lower part of the Kallamedu Formation to have a minor marine influence (Tewari *et al.* 1996). The transition from lower, fossiliferous beds to upper, unfossiliferous beds of the Kallamedu Formation has been interpreted as representing a shift towards increasingly saline environments, from fluvial to brackish deltaic depositional environments, on the basis of quartz microstructure (Madhavaraju *et al.* 2006).

Vertebrate fossils are found throughout the lower beds of the Kallamedu Formation, with large dinosaur fossils and fragmentary turtle carapace common in the sandstones.

Screenwashing of the sandy clay layers has yielded many microvertebrate fossils, including theropod and crocodylomorph teeth, crocodylomorph scutes, anuran postcranial elements, and fish scales (Goswami *et al.* 2013; Prasad *et al.* 2013). The most complete fossils known from the area include several well-preserved skulls from a single species of side-necked turtle (Gaffney *et al.* 2001).

MATERIALS AND METHODS

The specimens described here were surface collected from ~1 m² of outcrop along the western edge of the Kallamedu Formation exposures approximately one km directly north of Kallamedu village during fieldwork in December 2014 – January 2015. These beds represent the lowest section of the eastwardly-dipping Kallamedu exposures. Surface collecting in the immediate area also yielded extensive quantities of fragmentary turtle carapace and a single ganoid fish scale. Previous collection in this particular site has also yielded several turtle skulls (Gaffney *et al.* 2001) and several theropod and crocodylian teeth (Prasad *et al.* 2013).

To clarify the internal structure of the toothplates, particularly the highly phylogenetically informative stacking arrangement of the teeth, without damaging the specimens, the two specimens described here were scanned in a Skyscan 1172 in the Anatomy Building in University College London. The smaller toothplate DUGF/145 was scanned with 80kV and 124µA using an aluminium and copper filter, resulting in 410 files with a pixel size of 9.95µm, whilst DUGF/146 was scanned with 94kV and 106µA using an aluminium and copper filter, resulting in 490 files with pixel size of 16.86µm. The resulting files were

reconstructed within *Mimics 16.0* (Materialise NV, Belgium), where the individual teeth were initially segmented using threshold values applicable to each specimen. However, due to the nature of the fossilized matrix and limitations with the scanner, manual segmentation was required to clarify the automated reconstructions.

INSTITUTIONAL ABBREVIATIONS

ChM – Charleston Museum, Charleston, South Carolina, United States of America

DUGF – Delhi University, Geology Department, Fossil Catalogue, Delhi, India

NHMUK – Natural History Museum, London, United Kingdom

SYSTEMATIC PALAEOLOGY

Class – Actinopterygii Cope, 1887

Order – Elopiformes Sauvage, 1875

Family – Phyllodontidae Sauvage, 1875

Subfamily - Phyllodontinae Darteville and Casier, 1943

Genus – *Egertonia* Cocchi, 1864

Egertonia sp.

Figs 2–3

Material

DUGF/145, DUGF/146

Description

The two new specimens, DUGF/145 and DUGF/146, are pharyngeal tooth plates. The former is 15.2 by 8.9 mm, and the latter 13.3 by 13.3 mm. Both are composed of a bony matrix in

which subcircular teeth are stacked in a near vertical arrangement, four and five teeth deep respectively. Individual teeth measure between 3 and 4 mm in diameter, and approximately 0.5 mm in depth. The teeth are slightly convex, with the convex surface facing away from the matrix in which the teeth are embedded. The thickness of the teeth is equal throughout without any tapering towards either edge.

Discussion

There are eight families of teleost which are known to have stacked (phyllodont) toothplates (Estes and Hiatt 1978). Of these, Carangidae, Diodontidae, and Labridae possess toothplates with long, thin teeth. Odacidae and Sciaenidae are characterized by conical teeth, and Scaridae possess a heavily fused plate, similar to those found in rays. Of the remaining two families, Phyllodontidae have smooth, round teeth, often with a circular depression in the centre of the tooth, while members of the family Oplegnathidae have a cutting edge on each tooth. Additionally, the genus *Casierius*, a member of Albulidae, is known to have phyllodont dentition which closely resembles those of basal phyllodontids (Estes 1969a). The combination of stacked, round teeth, lacking any form of cutting edge (albeit also lacking a circular depression), would favour inclusion of these specimens within either Phyllodontidae, or as a member of Albulidae as a close relative of *Casierius*. However, the phyllodont teeth of *Casierius* are alternately stacked, rather than directly above one another (Estes 1969a), as in specimens DUGF/145 and DUGF/146 (Figs 2–3, Figs S1-S2, online Supporting Information). Phyllodontidae consists of two subfamilies – Paralbulinae and Phyllodontinae. The latter subfamily is characterized by regularly stacked teeth, which are flattened. This is true of both members, *Phyllodus* and *Egertonia*, although the former possesses much flatter teeth than the latter. The genera included within Paralbulinae – *Paralbula* and *Pseudoegertonia* – have hemispherical, bulbous teeth, thought to be primitive to the family as

a whole (Estes 1969*b*), and *Pseudoegertonia* teeth are also typically larger than DUGF/145 or DUGF/146 (Becker *et al.* 2010). The teeth of specimens DUGF/145 and DUGF/146 are more broadly concave than *Phyllodus*, supporting inclusion as either a paralbuline or a primitive phyllodontine. However, paralbulines are also characterized by an irregular tooth stacking arrangement, while the teeth in these specimens are vertically stacked – a derived condition for phyllodontine phyllodontids. Additionally, there is no evidence of a basilar foramen for a separate pulp cavity, a trait that when present is indicative of *Paralbula*, suggesting further that the fossil is an early phyllodontine.

A basal phyllodontine which matches this description of a regularly stacked, slightly concave toothplate is *Egertonia*. This genus has only one diagnostic feature – a “sparse, punctate sculpture” (Estes and Hiatt 1978), but it is noted that phyllodontid teeth often wear down to become smooth and unornamented (Estes 1969*b*). Comparison of specimens DUGF/145 and DUGF/146 (Figs 2–3) with the holotype of *Egertonia isodonta* NHMUK 38814 (Fig. 4), as well as ChM PC4169 (Weems 1998), indicates that these specimens can be confidently assigned to the genus *Egertonia*.

DISCUSSION

Biogeography

Egertonia is known from only one other Cretaceous locality – the Maevarano Formation in Madagascar (Gottfried and Krause 1998; Ostrowski 2012) – where it occurs alongside another phyllodontid genus, *Paralbula*. Prior to these discoveries, the origin of phyllodontid fish was suggested to be in the Cretaceous of North America (Estes 1969*b*) or the Cretaceous of the shallow continental seas of the North Atlantic (Estes and Hiatt 1978). This latter biogeographic hypothesis was proposed on the basis of a supposed close relationship between

phylloodontids and the Cretaceous albuloid *Casierius*, and based on the known distribution of phylloodontid fish. The group is wholly extinct and known primarily from Cretaceous and Palaeogene deposits of North America and Europe. The majority of Cretaceous occurrences of the family are members of the subfamily Paralbulinae, although there are records of indeterminate phylloodontine phylloodontids from the late Maastrichtian of Europe (Laurent *et al.* 1999; Pereda-Suberbiola *et al.* 2015) and the Campanian of Canada (Peng *et al.* 2001), as well as *Phylloodus paulkatoii* from the Maastrichtian Hell Creek Formation of the Western United States (Estes and Hiatt 1978).

The last common ancestor of *Egertonia* and *Phylloodus* (both phylloodontine phylloodontids) was therefore predicted to be Cretaceous and Laurasian (Estes and Hiatt 1978), but both of the earliest representatives of *Egertonia* are Gondwanan. *Egertonia* is also known from the Eocene of India (Rana *et al.* 2004), based on a single tooth and two poorly preserved plates. Isolated teeth referable to another phylloodontid – *Pseudoegertonia* – were also documented from the Upper Cretaceous intertrappean beds of Asifabad (Prasad 1985). Within other Gondwanan localities, a specimen of *Pseudoegertonia* and a toothplate of *Paralbula* (Darteville and Casier 1943; Estes 1969b) are known from the Eocene of the Congo Basin in Africa, while the genus *Eodiaphyodus*, a basal phylloodontid (Estes 1969b) is known from the Late Cretaceous of the Congo (Darteville and Casier 1949) and Angola (Antunes and Cappetta 2002). A Moroccan species, *E. granulosus* (Arambourg 1952) was referred to *Pseudoegertonia* by Estes (1969b), reducing *Eodiaphyodus* to a single species, *E. lerichei*, but this assignment has not been exclusively followed, with *E. granulosus* also described from the Late Cretaceous of Nigeria (Vullo and Courville 2014) and considered part of *Eodiaphyodus*. These fossils demonstrate that early phylloodontids or their close relatives were

certainly present in the Cretaceous of Africa, regardless of the inclusion of *E. granulosis* within *Pseudoegertonia* or *Eodiaphyodus*.

The African, Madagascan and Indian occurrences of Cretaceous *Egertonia*, *Eodiaphyodus* and *Paralbula* illustrate that the biogeographic history of the group is decidedly more complex than a certain origin in the Cretaceous of North America or the North Atlantic. During the latest Cretaceous, India was isolated from all other continents by hundreds of kilometres of ocean (Ali and Krause 2011), having separated from Madagascar approximately 85 million years ago (Melluso *et al.* 2009). The presence of Late Cretaceous phyllodontids in the shallow seas and coastlines of North America, Europe, Africa, Madagascar, and now India suggests that the early geographical distribution of Phyllodontidae was much wider than previously supposed, and renders its geographical origin ambiguous. Specifically, *Egertonia* is the latest in a long list of clades shared between Mesozoic formations of Madagascar and South India, which further indicates that the similar complement of taxa in the two localities are a result of vicariant population division rather than subsequent dispersal and colonisation by taxa in either direction across the Seychelles Plateau.

Environmental implications for the Kallamedu Formation

Phyllodontids are known primarily from near-shore, littoral, or estuarine environments (Estes 1969b), typically in shallow water. This is consistent with interpretations of the Kallamedu Formation as a periodically flooding deltaic system of shallow channels (Ramkumar *et al.* 2013), and with the observation that the upper Kallamedu Formation shows evidence of salinity (Madhavaraju *et al.* 2006). The closest extant relatives of phyllodontids are considered to be bonefish (Albulidae) (Estes 1969a, b), which use their pharyngeal

toothplates to crush molluscs and other invertebrates (Crabtree *et al.* 1998). It is thought that the phyllodont morphology of toothplates is an adaptation which has arisen many times in shallow water environments for feeding on shelled invertebrates (Estes 1969a).

CONCLUSIONS

The specimens DGUF/145 and DGUF/146 are the second Gondwanan and second Cretaceous occurrence of *Egertonia*, otherwise only known from Madagascar at this time (Ostrowski 2012). The presence of *Egertonia* in the lower part of the Kallamedu Formation supports an interpretation of that site as a brackish or fluvial-deltaic depositional environment. This new occurrence expands the geographic distribution of *Egertonia*, and more generally suggests that phyllodontid fishes had a broader Cretaceous distribution than previously recognised. Lastly, the presence of *Egertonia* in the Cretaceous of South India further supports strong faunal similarity between the Late Cretaceous of South India and Madagascar.

Acknowledgements. This work was supported by Leverhulme Trust grant RPG-2010/129 to AG, Leverhulme Trust grant RPG-2014/364 to AG and TJDH, and a J.C. Bose National Fellowship (DST, New Delhi) to GVRP. We thank M. Richter for access to comparative specimens at the Natural History Museum, London.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository

SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

Figure S1. Interactive pdf of the CT scan of DGUF/145

Figure S2. Interactive pdf of the CT scan of DGUF/146

REFERENCES

- ALI, J. R. and KRAUSE, D. W. 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography*, **38**, 1855-1872.
- ANANTHARAMAN, S., WILSON, G. P., DAS SARMA, D. C. and CLEMENS, W. A. 2006. A possible Late Cretaceous "Haramiyidan" from India. *Journal of Vertebrate Paleontology*, **26**, 488-490.
- ANTUNES, M. T. and CAPPETTA, H. 2002. Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola. *Palaeontographica Abteilung A: Palaeozoologie-Stratigraphie*, **264**, 85-146.
- ARAMBOURG, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service géologique du Maroc*, **92**.
- BECKER, M.A., MALLERY JR, C.S. and CHAMBERLAIN JR, J.A. 2010. Osteichthyans from an Arkadelphia Formation-Midway Group Lag Deposit (Late Maastrichtian-Paleocene), Hot Spring County, Arkansas, USA. *Journal of Vertebrate Paleontology*, **30**, 1019-1036.
- BRIGGS, J. C. 2003. The biogeographic and tectonic history of India. *Journal of Biogeography*, **30**, 381-388.
- CARRANO, M.T. and SAMPSON, S.D. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, **6**, 183-236.
- COCCHI, I. 1864. Monografia dei Pharyngodopilidae, nuova famiglia di pesci labroidi. *Studi Paleontologica*, **4**, 88pp.
- COPE, E. D. 1887. Zittel's Manual of Palaeontology. *American Naturalist*, **21**, 1014-1019.
- CRABTREE, R. E., STEVENS, C., SNODGRASS, D. and STENGARD, F. J. 1998. Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida Keys. *Fishery Bulletin*, **96**, 754-766.
- DARTEVELLE, E. and CASIER, E. 1943. Les poissons fossiles du Bas-Congo et des régions voisines (première partie). *Annales du Musée du Congo Belge A, Série 3*, 1-200.
- 1949. Les poissons fossiles du Bas-Congo et des régions voisines (deuxième partie). *Annales du Musée du Congo Belge A, Série 3*, 201-256.
- ESTES, R. 1969a. Studies on fossil phyllodont fishes: *Casierius*, a new genus of albulid from the Cretaceous of Europe and North America. *Eclogae Geologicae Helvetiae*, **62**, 751-755.
- 1969b. Studies on fossil phyllodont fishes - interrelationships and evolution in Phyllodontidae (Albuloidei). *Copeia*, 317
- ESTES, R. and HIATT, R. 1978. Studies on fossil phyllodont fishes - A new species of *Phyllodus* (Elopiformes, Albuloidea) from the Late Cretaceous of Montana, USA. *Paleobios*, 1-10.
- GAFFNEY, E. S., CHATTERJEE, S. and RUDRA, D. K. 2001. Kurmademys, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India. *American Museum Novitates*, **3321**, 1-16.
- GAFFNEY, E. S., KRAUSE, D.W. and ZALMOUT, I.S. 2009. *Kinkonychelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar. *American Museum Novitates* **3662**, 1-25.
- GOSWAMI, A., PRASAD, G. V. R., VERMA, O., FLYNN, J. J. and BENSON, R. B. J. 2013. A troodontid dinosaur from the latest Cretaceous of India. *Nature Communications*, **4**.
- GOTTFRIED, M. D. and KRAUSE, D. W. 1998. First record of gars (Lepisosteidae, Actinopterygii) on Madagascar: Late Cretaceous remains from the Mahajanga Basin. *Journal of Vertebrate Paleontology*, **18**, 275-279.
- KRAUSE, D. W. and MAAS, M. C. 1990. The biogeographic origins of the late Paleocene-early Eocene mammalian immigrants to the western interior of North America. 71-105. In BOWN, T. M. and ROSE, K. D. (eds). *Dawn of the Age of Mammals in the Northern part of the Rocky Mountain Interior, North America*. Geological Society of America, pp. Custom 7.

- LAURENT, Y., CAVIN, L. and BILOTTE, M. 1999. A new Late Maastrichtian vertebrate locality in the French Petites-Pyrenees. *Comptes Rendus De L Academie Des Sciences Serie Ii Fascicule a-Sciences De La Terre Et Des Planetes*, **328**, 781-787.
- LYDEKKER, R. 1877. Notices of new and other Vertebrata from Indian Tertiary and Secondary rocks. *Records of the Geological Survey of India*, **10**, 30-43.
- MADHAVARAJU, J., LEE, Y. I., ARMSTRONG-ALTRIN, J. S. and HUSSAIN, S. M. 2006. Microstructures on detrital quartz grains of upper Maastrichtian-Danian rocks of the Cauvery Basin, Southeastern India: implications for provenance and depositional environments. *Geosciences Journal*, **10**, 23-34.
- MELLUSO, L., SHETH, H. C., MAHONEY, J. J., MORRA, V., PETRONE, C. M. and STOREY, M. 2009. Correlations between silicic volcanic rocks of the St Mary's Islands (southwestern India) and eastern Madagascar: implications for Late Cretaceous India-Madagascar reconstructions. *Journal of the Geological Society*, **166**, 283-294.
- NOVAS, F. E., CHATTERJEE, S., RUDRA, D. K. and DATTA, P. M. 2010. *Rahiolisaurus gujaratensis*, n. gen. n. sp., a new abelisaurid theropod from the Late Cretaceous of India. In BANDYOPADHYAYA, S. (ed.). *New aspects of Mesozoic biodiversity*. Lecture Notes in Earth Sciences, **132**, Springer, 134pp.
- OSTROWSKI, S. A. 2012. The teleost ichthyofauna from the Late Cretaceous of Madagascar: Systematics, distribution, and implications for Gondwanan biogeography. PhD thesis, Michigan State University.
- PENG, J., RUSSELL, A. P. and BRINKMAN, D. B. 2001. Vertebrate microfossil assemblages (exclusive of mammals) from the Foremost and Oldman Formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide. *Provincial Museum of Alberta Natural History Occasional Paper*, **25**, 1-54.
- PEREDA-SUBERBIOLA, X., CORRAL, J. C., ASTIBIA, H., BADIOLA, A., BARDET, N., BERRETEAGA, A., BUFFETAUT, E., BUSCALIONI, A. D., CAPPETTA, H., CAVIN, L., DIEZ DIAZ, V., GHEERBRANT, E., MURELAGA, X., ORTEGA, F., PEREZ-GARCIA, A., POYATO-ARIZA, F., RAGE, J. C., SANZ, J. L. and TORICES, A. 2015. Late Cretaceous continental and marine vertebrate assemblages of the Lano Quarry (Basque-Cantabrian Region, Iberian Peninsula): an update. *Journal of Iberian Geology*, **41**, 101-124.
- PRASAD, G. V. R. 1985. Microvertebrates and associated microfossils from the sedimentaries associated with Deccan Traps of the Asifabad region, Adilabad District, Andhra Pradesh. Panjab University, Chandigarh.
- PRASAD, G. V. R. and DE LAPPARENT DE BROIN, F. 2002. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Annales de Paleontologie*, **88**, 19-71.
- PRASAD, G. V. R., JAEGER, J. J., SAHNI, A., GHEERBRANT, E. and KHAJURIA, C. K. 1994. Eutherian mammals from the Upper Cretaceous (Maastrichtian) intertrappean beds of Naskal, Andhra Pradesh, India. *Journal of Vertebrate Paleontology*, **14**, 260-277.
- PRASAD, G. V. R. and RAGE, J. C. 1991. A discoglossid frog in the latest Cretaceous (Maastrichtian) of India - further evidence for a terrestrial route between India and Laurasia in the latest Cretaceous. *Comptes Rendus De L'Academie Des Sciences Serie II*, **313**, 273-278.
- PRASAD, G. V. R. and SAHNI, A. 1988. First Cretaceous mammal from India. *Nature*, **332**, 638-640.
- 2009. Late Cretaceous continental vertebrate fossil record from India: Palaeobiogeographical insights. *Bulletin De La Societe Geologique De France*, **180**, 369-381.
- PRASAD, G. V. R., VERMA, O., FLYNN, J. J. and GOSWAMI, A. 2013. A new Late Cretaceous vertebrate fauna from the Cauvery Basin, South India: implications for Gondwanan paleobiogeography. *Journal of Vertebrate Paleontology*, **33**, 1260-1268.
- PRASAD, G. V. R., VERMA, O., SAHNI, A., KRAUSE, D. W., KHOSLA, A. and PARMAR, V. 2007a. A new late cretaceous gondwanatherian mammal from central India. *Proceedings of the Indian National Science Academy*, **73**, 17-24.
- PRASAD, G. V. R., VERMA, O., SAHNI, A., PARMAR, V. and KHOSLA, A. 2007b. A Cretaceous hoofed mammal from India. *Science*, **318**, 937-937.

- RAMKUMAR, M., SUGANTHA, T. and RAI, J. 2013. Lithofacies and Granulometric Characteristics of the Kallamedu Formation, Ariyalur Group, South India: Implications on Cretaceous-Tertiary Boundary Events. In RAMKUMAR, M. (ed.) *On a Sustainable Future of the Earth's Natural Resources*. Springer-Verlag Berlin, Heidelberg, Germany, 21 pp.
- RANA, R. S., KUMAR, K. and SINGH, H. 2004. Vertebrate fauna from the subsurface Cambay Shale (Lower Eocene), Vastan Lignite Mine, Gujarat, India. *Current Science*, **87**, 1726-1733.
- SAUVAGE, H. E. 1875. Essai sur la fauna ichthyologique de la période Liasique suivi d'une notice sur les poissons du Lias de Vassy, deuxième mémoire. *Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles*, **14**, 1-24.
- SUGANTHA, T., RAMKUMAR, M., BALARAM, V., RAI, J. and SATYANARAYANAN, M. 2015. Environmental and climatic conditions during the K-T transition in the Cauvery Basin, India: Current understanding based on chemostratigraphy and implications on the KTB scenarios In: (M. Ramkumar, ed.) *Chemostratigraphy: Concepts, Techniques, and Applications*, Elsevier, Amsterdam, Netherlands, pp 131-168
- SUNDARAM, R., HENDERSON, R. A., AYYASAMI, K. and STILWELL, J. D. 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., HART, M. B. and WATKINSON, M. P. 1996. A revised lithostratigraphic classification of the Cretaceous rocks of the Trichinopoly District, Cauvery Basin, southeast India. *Contributions to 15th Indian colloquium on micropaleontology and stratigraphy.*, 789-800.
- VAN BOCKLAER, I., ROELANTS, K., BIJU, S. D., NAGARAJU, J. and BOSSUYT, F. 2006. Late Cretaceous Vicariance in Gondwanan Amphibians. *Plos One*, **1**.
- VULLO, R. and COURVILLE, P. 2014. Fish remains (Elasmobranchii, Actinopterygii) from the Late Cretaceous of the Benue Trough, Nigeria. *Journal of African Earth Sciences*, **97**, 194-206.
- WEEMS, R. E. 1998. Actinopterygian fish remains from the Paleocene of South Carolina. *Transactions of the American Philosophical Society*, **88**, 147-164.
- WILSON, J. A., MOHABEY, D. M., PETERS, S. E. and HEAD, J. J. 2010. Predation upon Hatchling Dinosaurs by a New Snake from the Late Cretaceous of India. *Plos Biology*, **8**.

FIGURE LEGENDS

Fig. 1 – Location map of the Kallamedu Formation within India. Modified from Prasad *et al.*

(2013), reproduced by permission of the Society of Vertebrate Paleontology

www.vertpaleo.org.

Fig. 2. CT scans of DGUF/145 (A-C) and DGUF/146 (D-F) in lateral (A, D), occlusal (B, E), and basal (C, F) views. The bony matrix has been digitally removed to illustrate the stacking of the teeth. Convex teeth are organized in vertical stacks; each stack is arranged in a row offset from adjacent rows. The basal surface of the teeth shows no foramen housing a pulp cavity, as is also true for NHM-UK 38814. Scale bar = 1 cm

Fig. 3 – Photographs of DGUF/145 (A-C) and DGUF/146 (D-F) in lateral (A, D), occlusal (B, E), and basal (C, F) views. Scale bar = 1 cm.

Fig. 4 – Lateral (A), occlusal (B) and basal (C) views of the holotype of *Egertonia isodonta* (NHM-UK 38814). Note the organized vertical stacking and slight convexity of the teeth, and the alternating arrangement. Scale bar = 1 cm.