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Cretaceous mammals of India–Stratigraphic distribution, diversity and intercontinental affinities

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ABSTRACT

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Extensive research carried out on the Cretaceous deposits of Laurasia has revealed an overwhelming presence of eutherian, metatherian and multituberculate groups of mammals in the Cretaceous ecosystems of Northern Hemisphere continents. In contrast, the relatively poorly documented fossil record of Cretaceous mammals from Gondwanan continents is represented by gondwanatherians, dryolestoids, and a few multituberculates and haramiyidans. Until now, no undoubted eutherian mammals have been reported from the Cretaceous strata of the southern continents except for India. In this context, Indian Cretaceous mammals assume great significance for understanding the origin and evolution of these mammals in Gondwana. Currently, the Cretaceous mammals of India include three groups, viz., eutherians, gondwanatherians, and haramiyidans. These three mammalian groups were recovered primarily from the Upper Cretaceous Deccan infra–and inter–trappean beds of peninsular India exposed near Bacharam, Naskal and Rangapur (Telengana), Upparhatti (Karnataka) and Kisalpuri (Madhya Pradesh) villages. Eutheria is by far the most diverse clade comprising three named genera (*Deccanolestes*, *Sahnitherium*, *Kharmerungulatum*) and one unnamed taxon (Eutheria *incertae sedis*). The gondwanatherians are known by *Bharattherium bonapartei* and Sudamericidae gen. et sp. indet. The third mammalian group, a possible haramiyidan, is represented by a solitary species *Avashishta bacharamensis*. Overall, the Cretaceous mammal fauna of India presents a complex biogeographic history with eutherians of Laurasian affinity, pan–Gondwanan gondwanatherians and a possible late surviving haramiyidan. Numerically abundant and speciose *Deccanolestes*, identified as an adapisoriculid, has been interpreted to have had originated in northward drifting Indian Plate in the Late Cretaceous and dispersed out of India into Africa and Europe over island arc systems (Oman–Kohistan–Dras) and the Ladakh magmatic arc at or near the Cretaceous–Paleogene boundary. A similar dispersal mode has also been visualized for *Kharmerungulatum* and Eutheria *incertae sedis* of Laurasian affinities. The close similarity of dental morphology between Madagascan and Indian gondwanatherians attests to the fact that these taxa derived from a common endemic Gondwanan stock had evolved in isolation following the separation of Indo–Madagascar from other Gondwanan continents. *Avashishta* represents a late Gondwana survivor of a group that had a Pangaean distribution until the Early Cretaceous.

Key-words—Mammals, Eutherians, Gondwanatherians, Haramiyidans, Cretaceous, Laurasia, Gondwana.

INTRODUCTION

MESOZOIC mammals are one of the most fascinating prehistoric animals that coexisted with dinosaurs. Their study will offer an insight into the lifestyles of these strange animals which lived prior to the ascent of modern groups of mammals (placental, marsupials, and monotremes). Majority of these mammals are known in the fossil record primarily from isolated teeth, jaws and skeletal remains. It is primarily in Mongolia and more recently in China that these mammals were documented by complete skeletons. Several new finds from China had revealed the ecomorphological diversity and range of dietary adaptations in early mammals, and their role in the evolution of modern mammalian groups.

The fossil record of Mesozoic mammals is highly skewed towards Laurasian continents, viz. North America, Europe and Asia. These are also the continents where maximum number of palaeontologists are working on Mesozoic mammals. As a consequence, most of our understanding of their diversity, adaptive radiations, and phylogenetic relationships comes from the fossils documented from Laurasian continents. In contrast, very limited number of Mesozoic mammals are known from Gondwanan continents which can be attributed to fewer palaeontologists working in the southern continents and vast areas of this part of the world remaining unexplored. However, this scenario is fast changing in recent years with many new and significant Mesozoic mammalian discoveries coming from this part of the globe.

Though Late Triassic mammaliaforms and Jurassic mammals are significant in their own right, it is the Cretaceous mammals which received greater attention as the eutherian and metatherian mammals of this period gave rise to later placental and marsupial clades. At present, the Cretaceous fossil record of mammals in Gondwana is restricted to the Lower Cretaceous Dinosaur Cove and Flat Rocks sites of the Eumeralla and Wonthaggi formations, respectively, of Australia, the Upper Cretaceous (Turonian–Campanian) Galula Formation in the Rukwa Rift Basin of southwestern Tanzania, the Upper Cretaceous (Campanian) Los Alamitos, La Colonia and Allen formations of Argentina, the Upper Jurassic–Lower Cretaceous Ksar Metlili Formation of Morocco, the Upper Cretaceous Maevarano Formation of Madagascar, and the Upper Cretaceous Deccan infra–and inter–trappean beds of India. The Early Cretaceous mammals from Australia are mainly represented by monotremes and supposed placentals (Rich *et al.*, 1997, 1999; see Kielan–Jaworowska *et al.* (1998) for an opposing view). The Upper Cretaceous Maevarano Formation has yielded primarily gondwanatherian mammals, some multituberculates and a contested marsupial (Krause & Grine, 1996; Krause *et al.*, 1997; Averianov *et al.*, 2003; Krause, 2001, 2013, 2014; Krause *et al.*, 2014a, b; 2017, 2020). A solitary gondwanatherian left dentary is known from the Galula Formation, Tanzania (O'Connor *et al.*, 2019). The Late Cretaceous mammalian fauna of Argentina consists of dryloestoids, enigmatic ferugliotherid and sudamericid gondwanatherians, and multituberculates (Rougier *et al.*, 2009, 2010). Dryolestoid–like forms and non–tribosphenic mammals have also been documented from the Late Cretaceous of Bolivia (Gayet *et al.*, 2001; Rougier *et al.*, 2010). In all these Gondwanan Cretaceous mammalian faunas, there is a conspicuous absence of eutherian mammals. Prior to 1980, no Mesozoic mammals were known from India. At that time, the general perception was that mammals did not exist in India during its insolation phase when it was drifting towards

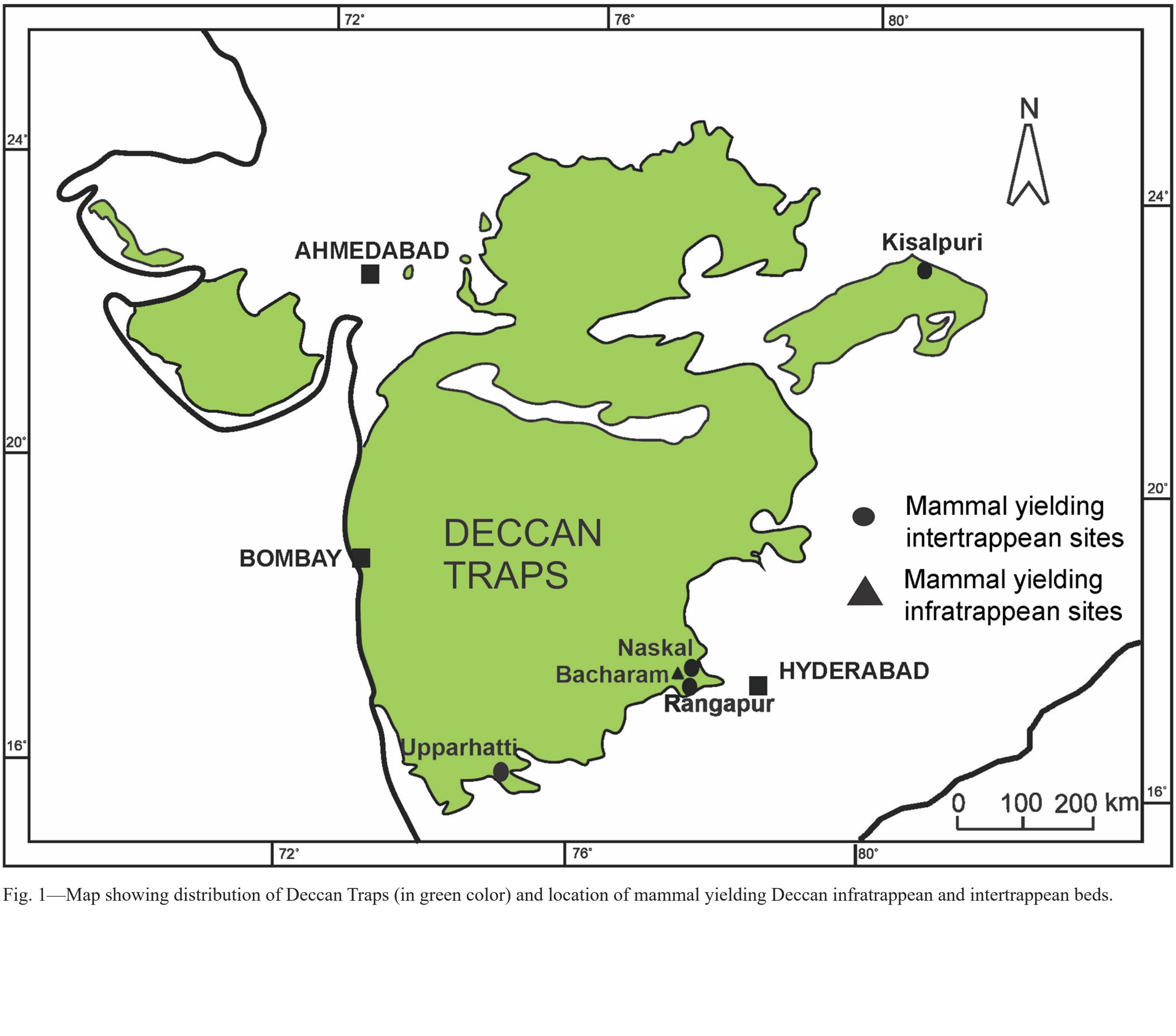

Fig. 1—Map showing distribution of Deccan Traps (in green color) and location of mammal yielding Deccan infratrappean and intertrappean beds.

north and mammals arrived in India only after India's suturing with Asia. However, in 1981, the first Jurassic mammal was reported from the Kota Formation of the Pranhita–Godavari Basin (Datta, 1981). This report raised the hopes of finding Cretaceous mammals in India. As a result of concerted efforts and extensive field exploration in the Deccan Volcanic Province (DVP), the first Cretaceous mammal of India was discovered in the intertrappean beds of Naskal, situated about 70 km to the west of Hyderabad City in Telengana (Prasad & Sahni, 1988). The first Cretaceous mammal tooth, an upper first molar (M^1), was found while trying to remove calcareous sediment matrix attached to some lower vertebrate microfossils by subjecting them to acid treatment. This became the holotype for *Deccanolestes hislopi*, the first named Cretaceous mammal from India (Prasad & Sahni, 1988). Subsequently, a third upper molar (M^3) was found from the same site. The research on Cretaceous mammals in India took off with these findings. It should be mentioned here that India is unique in being the sole Gondwanan landmass that hosted unquestioned eutherian mammals. In the following sections, the distribution, geological context, age of different Cretaceous mammal yielding sites along with the diversity and intercontinental affinities of recovered mammalian taxa are presented.

Institutional Abbreviations—GSI/SR/PAL–Geological Survey of India, Southern Region (Hyderabad), Palaeontology Division catalogue numbers; ITV/R/Mm–Intertrappean Vertebrates/Rangapur Mammal catalogue numbers of the Department of Geology, HNB Garhwal University, Srinagar, Uttarakhand; PL/IGNOU–Palaeontological Laboratory, Indira

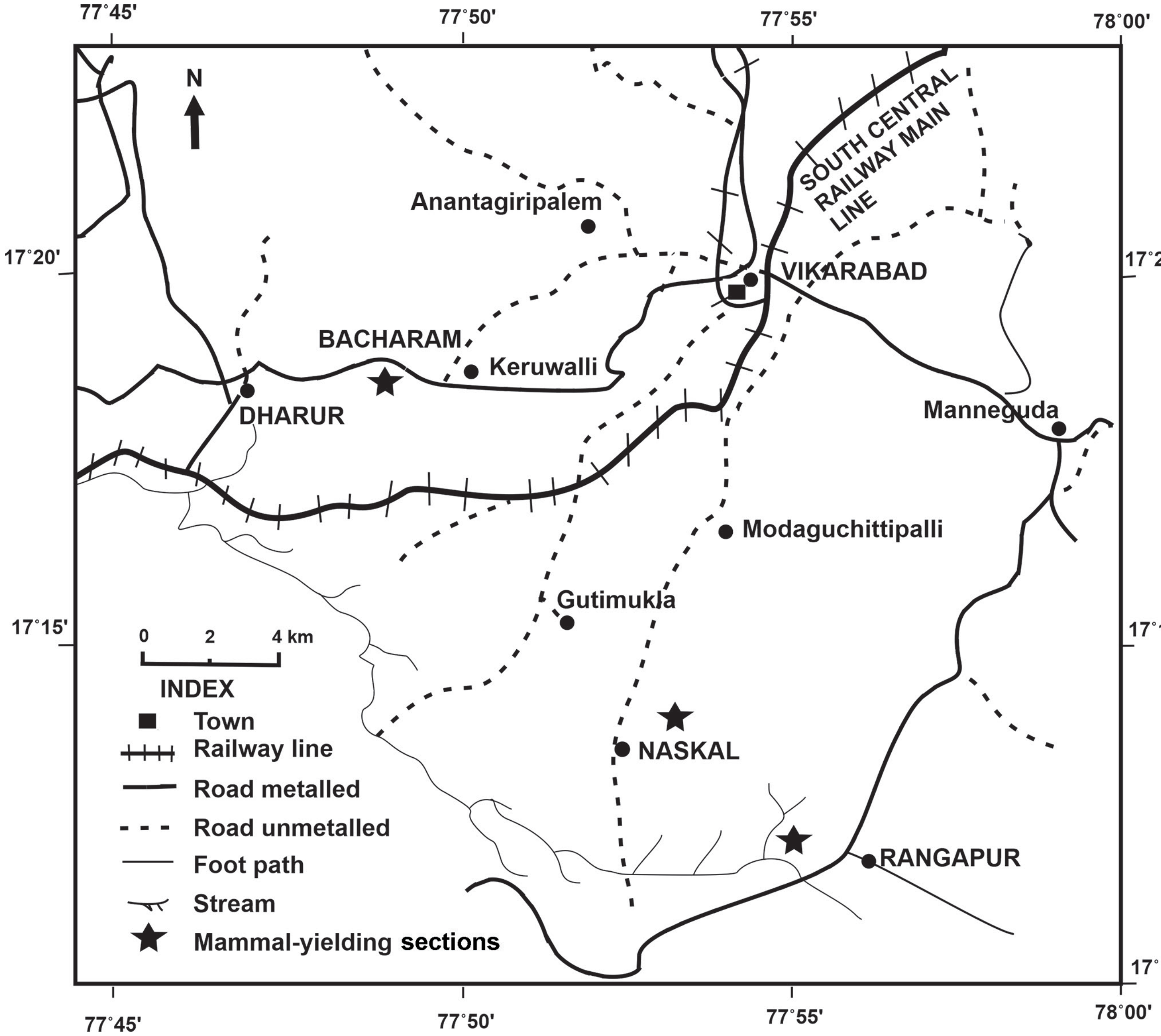

Fig. 2—Location map of the mammal–yielding infratrappean beds of Bacharam and intertrappean beds of Naskal and Rangapur in Rangareddi District, Telengana.

Gandhi National Open University catalogue numbers, New Delhi; VPL/JU/IM–Vertebrate Palaeontology Laboratory, Jammu University Intertrappean Mammal catalogue numbers, Jammu; VPL/JU/NKIM–Vertebrate Palaeontology Laboratory, Jammu University Naskal Intertrappean Mammal catalogue numbers, Jammu.

STRATIGRAPHIC DISTRIBUTION OF CRETACEOUS MAMMAL–YIELDING HORIZONS

One of the major difficulties that a Mesozoic mammalian palaeontologist commonly faces is the rarity of mammalian specimens in the fossil collections. Even when present, they occur in such a small number that disaggregation and wet screen–washing of several thousands of kilograms of rock samples and scanning of a large quantity of screen–washed residue under the microscope may lead to the collection of a few specimens. In India, continental Cretaceous rocks occur mainly in the Deccan Volcanic Province (DVP) as sediments occurring below the oldest lava flow (infratrappean beds or Lameta Formation) and those occurring intercalated with the lava flows (intertrappean beds), and the Kallamedu Formation of the Cauvery Basin. Despite of the study of a large number of infratrappean and intertrappean sections in the DVP in the last 30 years or so, only a few have yielded mammals. Subsequent to the discovery of first Cretaceous mammals from the Deccan intertrappean beds of Naskal, five more additional sites yielding Cretaceous mammals, viz. the infratrappean beds of Bacharam, the intertrappean beds of Rangapur, Kisalpuri, and Upparhatti in the DVP (Fig. 1), and the Upper Cretaceous Kallamedu Formation in Cauvery Basin have been identified.

Intertrappean beds of Naskal

The intertrappean section of Naskal is located 2 km northeast of Naskal Village in Pargi Mandalam of Rangareddi District in Telengana State (Figs 2, 3). Here the intertrappean beds occur intercalated with basaltic flows 4 and 5 and measure 2 m in thickness. The intertrappean sequence begins with a gleyed mudstone unit at the bottom and is followed upwards by yellow mudstone, marlstone, chert, impure marlstone and calcareous mudstone in this order of superposition (Prasad & Khajuria, 1996). A rich

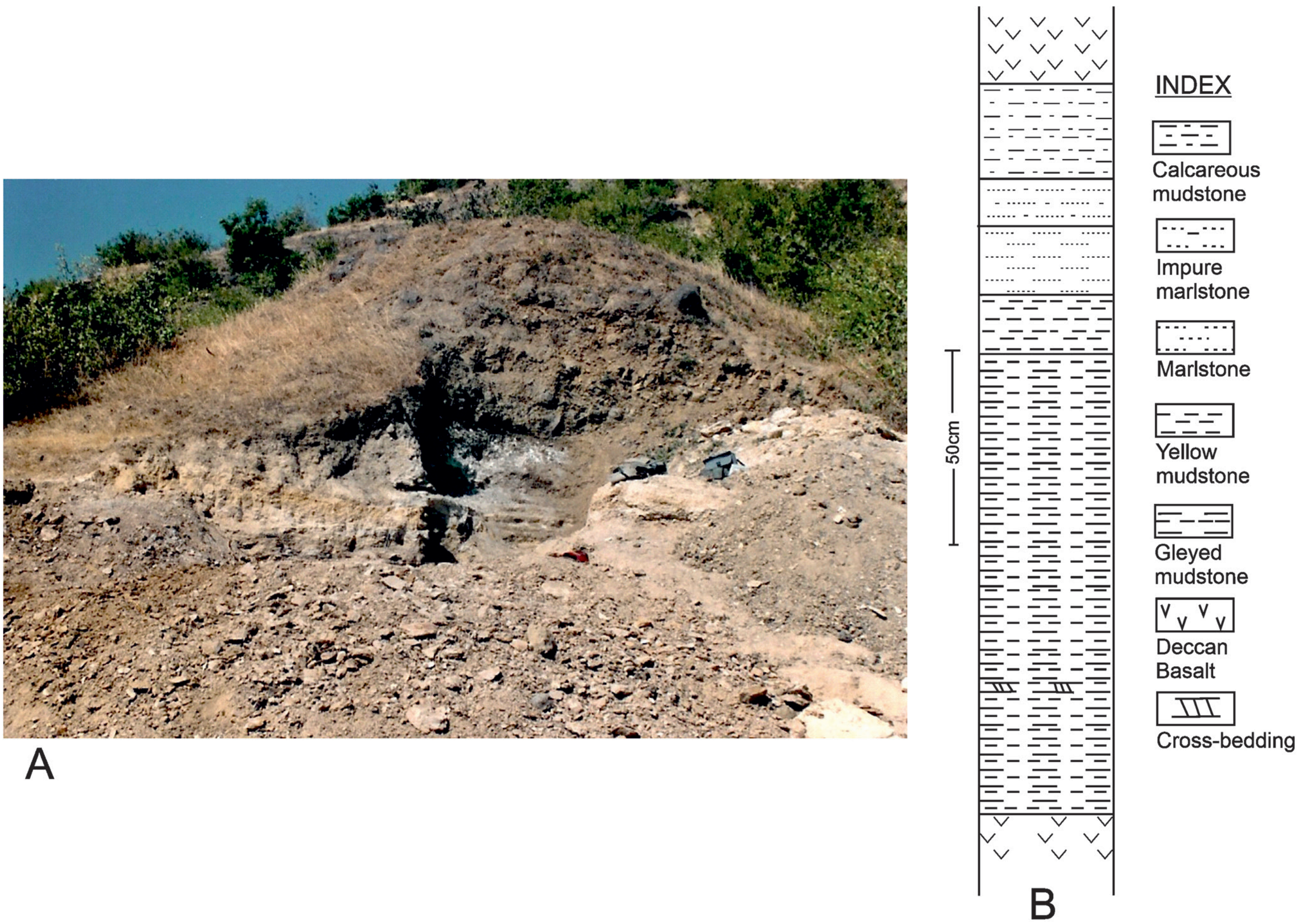

Fig. 3—A. Field photograph of excavated intertrappean beds of Naskal and overlying basalts. B. Stratigraphic column of the excavated Naskal intertrappean section.

microvertebrate assemblage represented by fish (*Igdabatis indicus,* cf. *Lepisosteus indicus*, Osteoglossidae indet; Siluriformes indet., Pycnodontiformes indet., Otolith taxa: *Heterotidinarum heterotoides*, *Osteoglossidarum deccanensis*, *O. intertrappus, Notopteridarum nolfi, Gonorynchidarum rectangulus,* ?Ariidae, *Anthracoperca bhatiai*, *Percoideorum citreum*, *Percoideorum rangapurensis*, Percoidei sp. 1, *Apogonidarum curvatus*), anurans (?Gobiatinae/Costata, ?Leptodactylidae, Ranoidea indet., ?Hylidae), lizards (Anguidae, non–anguid indeterminate Lacertilia), turtles (Chelonia indet.), snakes *Indophis sahnii*, *Coniophis* sp., ?Cholophidia, Serpentes *incertae sedis*), crocodiles (Crocodylia indet.) and mammals (*Deccanolestes hislopi*, *Deccanolestes* cf. *D. hislopi*, *D. robustus, Bharattherium bonapartei*) (Prasad, 1987; Prasad & Khajuria, 1990; Prasad & Sahni, 1988; Prasad & Rage, 1991, 1995; 2004; Rage & Prasad, 1992; Prasad *et al.*, 1994; Prasad & Godinot, 1994; Godinot & Prasad, 1994; Sahni *et al.*, 1996; Krause *et al.*, 1997; Prasad & de Lapparent de Broin, 2002; Cione & Prasad, 2002; Rage *et al.*, 2004; Prasad *et al.*, 2007a, Nolf *et al.*, 2008; Prasad *et al.*, 2010; Boyer *et al.*, 2010; Goswami *et al.*, 2011; Fabre *et al.*, 2014) has been documented from the calcareous mudstone. Two cheek teeth and one incisor of gondwanatherian mammals (*B. bonapartei*) were also described from the intertrappean beds of Naskal by Wilson *et al.* (2007). According to their description, the teeth were recovered from a 1–2 m thick grey sandy siltstone that overlies a less than1m thick greenish chert layer.

In addition to vertebrate microfossils, pulmonate gastropods, bivalves, ostracods, charophytes and palynofossils were also recovered from this intertrappean site (Sahni *et al.*, 1996; Singh *et al.*, 2006). Palaeontological and sedimentological data from this section indicate the presence of a freshwater, shallow, floodplain lake that was subjected intermittently to subaerial exposure and accompanying pedogenic processes (Prasad & Khajuria, 1996; Khajuria & Prasad, 1998). Because of the absence of marine fossils except for occasional brackish–marine myliobatid (*Igdabatis*) and pycnodontiform fishes, it was suggested that this intertrappean floodplain lake existed in a distal position to the seacoast (Prasad & Khajuria, 1996; Khajuria & Prasad, 1998).

Among the Pisces, marginal teeth of *Igabatis indicus*, a Campanian–Maastrichtian species known from a number of infra–and inter–trappean beds, has been occasionally recovered from this intertrappean section. *Igdabatis* together with a palynological assemblage comprising *Ariadnaesporites, Gabonisporites* cf. *G. vigourouxii, Triporoletes, Mulleripollis, Azolla* and *Minerisporites* favoured a Maastrichtian age for the intertrappean beds of Naskal (Sahni *et al.*, 1996; Singh *et al.*, 2006).

Intertrappean beds of Rangapur

Another mammal–bearing intertrappean section is located within the neighborhood of the Naskal Intertrappean site. This intertrappean section is situated along a stream cutting about 1.5 km southwest of Rangapur Village in Rangareddi District (Telengana) and about 4 km southeast of Naskal site as the crow flies (Figs 2, 4). As in the case of the Naskal Intertrappean beds, the intertrappean sequence of Rangapur also occurs between basaltic flows 4 and 5 (Dutt, 1975). The intertrappean sedimentary sequence begins with a white marl unit which is followed upwards by black chert, blackish–brown marl, black chert, greenish–pink marl, grey marl with whitish–grey cherty nodules, and whitish–grey marl beds. Rana (1988, 1990) reported the occurrence of

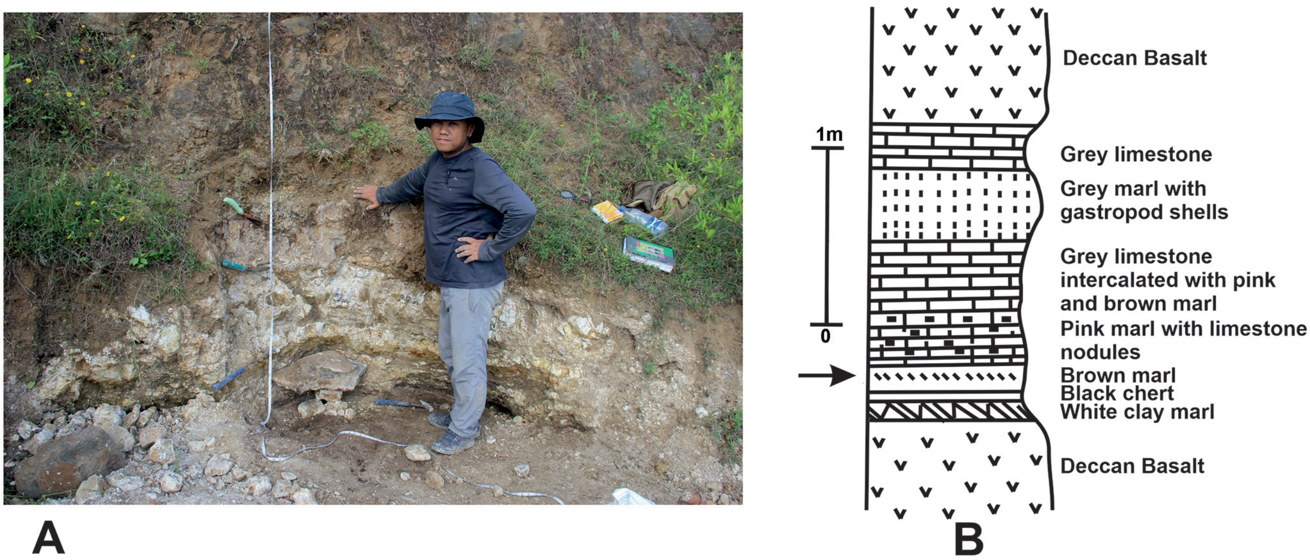

Fig. 4—A. Field photograph of excavated intertrappean beds of Rangapur. B. Stratigraphic column of the Rangapur intertrappean section (adapted from Fig. 2 of Nolf *et al.*, 2008). Arrow points to the mammal–bearing horizon.

freshwater ostracods, molluscs, and charophytes in the white marl, blackish–brown marl, and whitish−grey marl beds. Leaf impressions, silicified ostracods, molluscs, and charophytes were also documented from the black chert beds (Rana,1988, 1990; Bhatia *et al.*, 1989). Vertebrate microfossils, particularly micromammals, were reported from the blackish–brown marl and whitish–grey marl units (Rana 1988, 1990; Rana & Wilson, 2003). Rana (1988) described a suite of otolith based fish species from these intertrappean beds which have been revised in a subsequent work by Nolf *et al.* (2008). The otolith taxa include "*Osteoglossidarum*" *deccanensis,* "*Osteoglossidarum" intertrappus*, "*Notopteridarum*" *nolfi,* "*Clupeidarum*" *sahnii*, "*Gonorynchidarum*" *rectangulus*, "*Gonorynchidarum*" sp. "*Ariidarum*" sp., *Anthracoperca bhatiai*, "*Percoideorum*" *rangapurensis*, Percoidei sp. 1, Percoidei sp. 2, *Dapalis erici*, "*Apogonidarum*" *curvatus*, and "*Blenniidarum*" sp. Two charophyte species *Platychara perlata* and *Nemegtichara grambasti* were also documented from the intertrappean beds of Rangapur (Bhatia *et al.*, 1989). Although the presence of crocodilian teeth of Alligatorinae affinity were reported from the intertrappean beds of Rangapur by Rana (1990) and Rana & Sati (2000), later they have been identified as Crocodylia *incertae sedis* (Prasad & de Lapparent de Broin, 2002). The mammalian fauna of this site comprises *Deccanolestes* cf. *hislopi*, *Deccanolestes* cf. *robustus*, *Deccanolestes*? sp., *Sahnitherium rangapurensis* and Theria *incertae sedis* (Rana & Wilson, 2003). Because of its stratigraphic position in between flows 4 and 5 (as is the case with the intertrappean beds of Naskal), the Rangapur Intertrappean site is regarded as coeval to that of Naskal and accordingly a Maastrichtian age was assigned. The intertrappean beds of Rangapur yielding essentially freshwater fish, amphibian and crocodilian remains, molluscs, ostracods, and charophytes, and terrestrial mammals are interpreted to have been deposited in a freshwater lacustrine environment.

Intertrappean beds of Kisalpuri

The mammal yielding Kisalpuri Intertrappean beds are located about 1.5 km southwest of Kisalpuri Village in Dindori District in Madhya Pradesh (Fig. 5A). The intertrappean section occurs on the right bank of Kharmer River, a tributary of the Narmada River. This site is located about 700 km to the north of Naskal and Rangapur Intertrappean sites. The Kisalpuri Intertrappean section is 4.5 m thick and comprises brownish–yellow, green and red clays, brownish–green siltstone, pebbly green mudstone, yellowish–green clay, red gravely clay, hard mudstone and chocolate brown clays in this order of superposition (Fig. 5B–D). The clays are relatively poor in fossils. The brownish–green siltstone is richly fossiliferous and on wet screen–washing of four tons of sediments from this horizon, a highly diverse assemblage of vertebrate microfossils has been recovered. The fauna is represented by batoid (*Igdabatis indicus*), lepisosteid (*Lepisosteus* cf. *indicus*), Osteoglossidae gen. et sp. indet., Siluriformes *incertae sedis*, and pycnodontiform fishes, anurans (?Costata, leptodactyloid–hemisotids, ranoid–myobatrachoid, ?ranoid morphotypes), Bothremydidae turtles, indeterminate squamates, indeterminate snakes, crocodilian teeth, crocodilian and dinosaur eggshells, and mammals (eutherians and gondwanatherians) (Khosla *et al.*, 2004; Prasad *et al.*, 2007a, b; Verma, 2008; Khosla *et al.*, 2009; Prasad *et al.*, 2010; Verma *et al.*, 2012; Prasad *et al.*, 2015; Verma *et al.*, 2016; Rage *et al.*, 2020). Freshwater ostracods and gastropods were also recovered along with these vertebrate microfossils. Based on the occurrence of Campanian–Maastrichtian batoid fish *Igdabatis indicus* and Maastrichtian freshwater ostracods, a Maastrichtian age was assigned to the intertrappean beds of Kisalpuri (Khosla *et al.*, 2004).

The microvertebrate fauna from this intertrappean section includes both freshwater and brackish water/marine elements and is very similar to the fossil assemblages described from the Lameta Formation of Jabalpur, Pisdura and Marepalli, and the intertrappean beds of Piplanarayanwar, Nagpur and Asifabad. As the microvertebrate assemblage predominantly consists of freshwater taxa in association with a few brackish water/marine forms, it is inferred that these intertrappean beds were deposited in a lacustrine basin close to the seacoast so that the brackish water/marine taxa could venture into the freshwater lake (Khosla *et al.*, 2004). From this section, two distinct mammalian groups (eutherian and gondwanatherians) represented by 50 dental and postcranial bones have been documented (Prasad *et al.*, 2007a, b; Verma, 2008; Prasad *et al.*, 2010; Verma *et al.*, 2012).

Intertrappean beds of Upparhatti

Wilson *et al.* (2007) described three cheek teeth (GSI/SR/PAL–G074, a right mf4; GSI/SR/PAL–G059, left mf3; GSI/SR/PAL–G070, right mf4) of a gondwanatherian mammal from an intertrappean section near Gokak in Karnataka (Fig. 1). The mammalian teeth were reported to have been collected from a 1 m thick, red silty–mudstone that overlies 2–3 m thick, grey silty–sandstone (Wilson *et al.*, 2007). The authors mentioned that the fossils come from the Maastrichtian Intertrappean beds near Gokak, but no specific information on the location of the site with respect to Gokak Town or location map and litholog of the mammal–yielding section were provided. The longitude and latitude given in the publication places the site about 5.5 km northwest of Upparhatti village on google maps. In the past, some intertrappean beds have been reported near Upparhatti village near Gokak (Foote, 1876; Kelkar & Gupte, 1943). The presence of *Unio* shells in these intertrappean beds was first reported by Foote (1876). The *Unio* shells from this site were later identified as belonging to the genus *Indonaia* (Prashad, 1918). Subsequently, Kelkar & Gupte (1943) reported shells of *Unio*, *Physa*, *Lymnaea* and

Paludina along with some chelonian bones. More recently, De Lapparent de Broin & Prasad (2020) described a large number of shell, limb, and a few skull and neck elements of turtles belonging to three indeterminate taxa of Bothremydidae from the intertrappean beds of Upparhatti. It is not clear from the locality information given in the paper of Wilson *et al.* (2007) whether the fossils reported come from this intertrappean section or some other section.

Infratrappean beds of Bacharam

Anantharaman *et al.* (2006) reported the occurrence of an upper molariform tooth of a possible haramiyidan, *Avashishta bacharamensis* (Allotheria: ? Haramiyidae), from a Maastrichtian Infratrappean sequence exposed near the village Bacharam, in unified Andhra Pradesh. This publication does not include any information on the location of the infratrappean site except for the coordinates (17°20' N, 79°50' E). We are puzzled by the fact that the coordinates given in the publications of Wilson *et al.* (2007) and Anantharaman *et al.* (2006) do not match the ground realities with discrepancies ranging from 5 to over a hundred kilometers (e.g., Bacharam). To our knowledge, a village by name Bacharam occurs about 13 km to the west of Vikarabad Town in Rangareddi District where the infratrappean outcrops are present in fullers earth quarries (Figs 1, 2). These infratrappean sediments, comprising sandstone and gritty clays or siltstones, are somewhat similar to the lithological units mentioned by Anantharaman *et al.* (2006) and also yield vertebrate microfossils. Detailed palaeontological investigations need to be undertaken in this area to locate the mammal–bearing infratrappean section of Bacharam.

Kallamedu Formation

The Upper Cretaceous (Late Maastrichtian) Kallamedu Formation of the Cauvery Basin comprising sandstones, clays and siltstones is known to yield vertebrate fossils since the latter half of 19th Century (Blanford, 1862; Matley, 1929; Yadagiri & Ayyasami, 1979, 1989; Gaffney *et al.*, 2001; Prasad *et al.*, 2013; Goswami *et al.*, 2013; Halliday *et al.*, 2016). Presence of a fragmentary gondwanatherian mammal tooth has been reported by Goswami *et al.* (2012) from the Kallamedu Formation. Pending its description, we refrain from discussing it in this paper.

DIVERSITY OF INDIAN CRETACEOUS MAMMALS

As evident from their stratigraphic distribution, Cretaceous mammals of India are primarily known from the Upper Cretaceous infra–and inter–trappean beds and the Kallamedu Formation. No mammals have been documented from the Cretaceous rocks older than the Maastrichtian. Currently, the Late Cretaceous mammalian fauna of India is represented by three groups, viz., eutherians (Infraclass Eutheria), gondwanatherians (Order Gondwanatheria), and haramiyidans (Order Haramiyida).

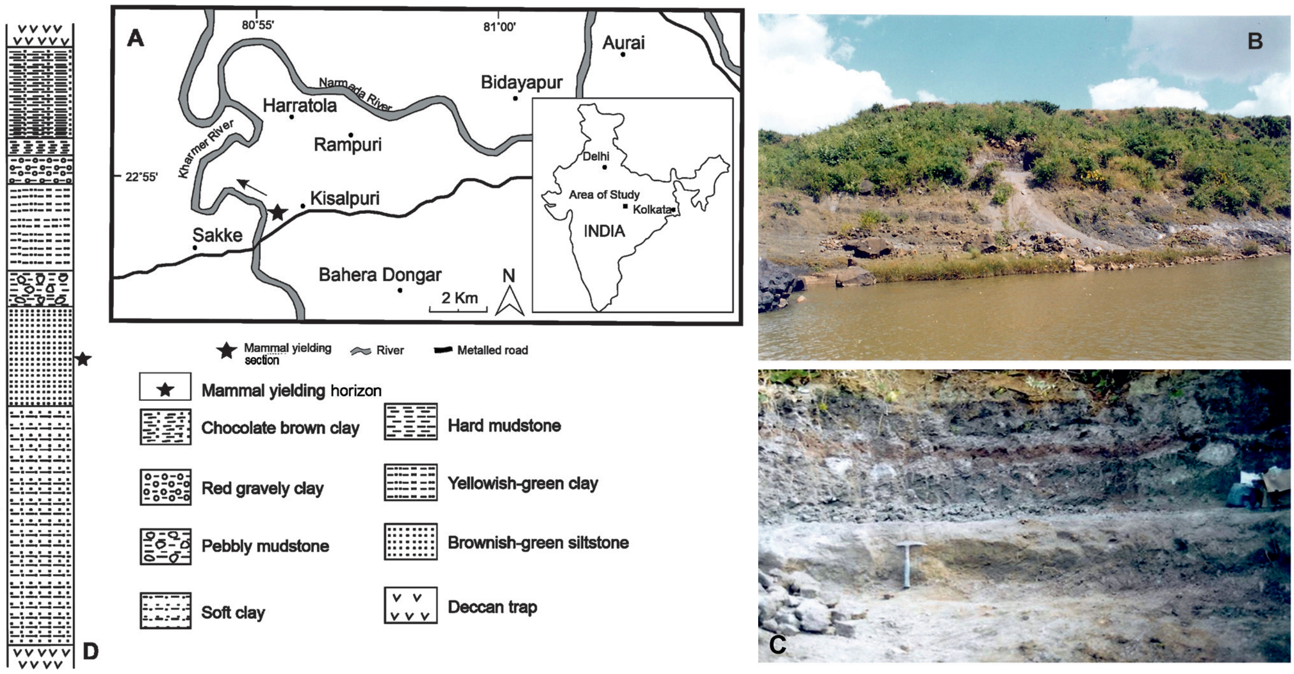

Fig. 5—Location map of the mammal yielding Kisalpuri Intertrappean beds in Dinodori District, Madhya Pradesh. B. Field photo of excavated Kisalpuri Intetrappean section on the right bank of Kharmer River. C. Close–up view of the intertrappean section with hammer placed against the mammal–bearing brownish–green siltstone horizon. D. Measured stratigraphic column of the Kisalpuri I ntetrappean section.

Table 1—Stratigraphic distribution of Cretaceous mammals of India.

Mammalian group	Name of the taxon	Stratigraphic horizon	Age
Eutheria	Adapisoriculidae: *Deccanolestes hislopi* Prasad & Sahni, 1988 *Deccanolestes* cf. *hislopi* (Prasad *et al*., 1994; Rana & Wilson, 2003) *D. robustus* Prasad *et al*., 1994	Intertrappean beds of Naskal and Rangapur, Rangareddi District, Telengana	Maastrichtian
	Sahnitherium rangapurensis Rana & Wilson, 2003	Intertrappean beds of Rangapur, Rangareddi District, Telengana	Maastrichtian
	D. narmadensis Prasad *et al*., 2010 *Kharmerungulatum vanvaleni* Prasad *et al*., 2007b Eutheria *incertae sedis* Khosla *et al*., 2004	Intertrappean beds of Kisalpuri, Dindori District, Madhya Pradesh	Maastrichtian
Gondwanatheria	*Bharattherium bonapartei* Prasad *et al*., 2007a (Wilson *et al*., 2007) Sudamericidae gen. et sp. indet. (Wilson *et al*., 2007; Verma *et al*., 2012)	Intertrappean beds of Naskal (Telengana), Kisalpuri (Madhya Pradesh) and Upparhatti (Karnataka)	Maastrichtian
Haramiyida	*Avashishta bacharamensis* Anantharaman *et al*., 2006	Infratrappean beds of Bacharam, Andhra Pradesh (Rangareddi District, Telengana?)	Maastrichtian

Infraclass Eutheria

Eutherian mammals, the stem group for modern placental mammals, are present in great abundance and diversity in the Cretaceous deposits of Laurasia (Kielan–Jaworowska *et al*., 2004). In comparison, no undoubted eutherian mammals are known from the Cretaceous deposits of Gondwana with the exception of India. In this context, the eutherian mammalian fauna of India is highly significant for understanding the biogeographic origins and evolution of this group in the southern continents. In the Cretaceous fossil record of India, the eutherian clade is relatively more diverse and species rich than the other clades. Currently there are three named genera represented by five species. These are *Deccanolestes* (*D. hislopi* Prasad & Sahni, 1988) (Fig. 6A–B, E–F), *Deccanolestes* cf. *hislopi* (Fig. 6C–D, Fig. 8A–E), *D. robustus* Prasad *et al*., 1994 (Fig. 7A–D), *D. narmadensis* Prasad *et al*., 2010 (Fig. 9A–F), *Sahnitherium* (*S. rangapurensis* Rana & Wilson, 2003) (Fig. 10A–D), *Kharmerungulatum* (*K. vanvaleni* Prasad *et al*., 2007b (Fig. 11A–E)). In addition to these, there is one lower molar (Fig. 12A–E) referable to Eutheria *incertae sedis* (Khosla *et al*., 2004). Of the three named eutherian genera, *Deccanolestes* is numerically abundant (known by more than 100 dental and postcranial remains) and speciose as compared to *Sahnitherium, Kharmerungulatum* and Eutheria *incertae sedis* which are represented by one specimen each. *D. hislopi* and *D. robustus* were reported from both Naskal and Rangapur Intertrappean beds, *S. rangapurensis* was documented from the intertrappean beds of Rangapur, while *D. narmadensis*, *K. vanvaleni* and Eutheria *incerate sedis* were described from the intertrappean beds of Kisalpuri (Table 1).

Order Gondwanatheria

Gondwanatherians are an enigmatic group of mammals with exclusive Gondwanan distribution in the Upper Cretaceous–Paleogene deposits of Argentina (Scillato–Yané & Pascual, 1984, 1985; Bonaparte, 1986a, b, 1990; Pascual *et al*., 1999; Gurovich, 2008; Gurovich & Beck, 2009; Goin *et al*., 2012; Chimento *et al*., 2020, 2021), Chile (Goin *et al*., 2020), Madagascar (Krause *et al*., 1997; Krause 2013, 2014; Krause *et al*., 2014a, b; 2020), India (Das Sarma *et al*., 1995; Krause *et al*., 1997; Prasad *et al*., 2007a; Wilson *et al*., 2007; Verma *et al*., 2012), Tanzania (Krause *et al*., 2003; O'Connor *et al*., 2019), and Antarctica (Goin *et al*., 2006). With chisel–like incisors and molariform cheek teeth, gondwanatherians present a wide range of morphological variability in their cheek teeth. Ferugliotheriids (Ferugliotheriidae) represented by *Ferugliotherium* (Krause *et al*., 1992) and *Trapalcotherium*

(Rougier *et al.* 2009) are low–crowned teeth with longitudinal rows of multiple cusps connected by transverse ridges. Sudamericids (Sudamericidae) comprising *Sudamerica*, *Gondwanatherium*, *Bharattherium*, *Lavanify*, and *Vintana* (Pascual *et al.* 1999; Prasad *et al.* 2007a; Gurovich 2008; Krause 2013, 2014; Krause *et al.* 2014a, b) though exhibit distinctive tooth morphologies share high, hypsodont cheek teeth with vertical furrows, infundibula, and cementum–filled enamel islets. *Greniodon* from the Middle Paleocene of Patagonia has protohypsodont teeth with a distinctive occlusal morphology (Goin *et al.*, 2012) and was placed in Sudamericidae (Krause *et al.*, 2014a).

The first gondwanatherian mammal from India, reported from the intertrappean beds of Naskal based on a single, poorly preserved high–crowned tooth (VPL/JU/NKIM/25), was not named because of its incomplete preservation (Krause *et al.*, 1997). Prior to this, similar teeth were briefly reported by Das Sarma *et al.* (1995) from the same intertrappean beds. Later, a well preserved cheek tooth recovered from the intertrappean beds of Kisalpuri was named as *Bharattherium bonapartei* (Fig. 13A–H) (Prasad *et al.*, 2007a) and the unnamed VPL/JU/NKIM/25 from Naskal was also referred to it. In the same year, Wilson *et al.* (2007) described four gondwanatherian lower cheek teeth and one lower incisor from the intertrappean beds of Gokak and Naskal under a new genus and new species *Dakshina jederi*. As the holotypes of *B. bonapartei* and *D. jederi* are morphologically indistinguishable from each other and as the publication of *Bharattherium* pre–dates that of *Dakshina*, Verma *et al.* (2012) synonymized *D. jederi* with *B. bonapartei*. A left mf4 recovered from the intertrappean beds of Kisalpuri was described under Sudamericidae gen. et sp. indet. (Verma *et al.* 2012) (Fig. 13I–K). As mentioned earlier, there is another yet to be described gondwanatherian tooth from the Kallamedu Formation, Cauvery Basin, Tamil Nadu.

Order Haramiyida

Haramiyidans known primarily by isolated teeth and mandibles resemble the multituberculates in their dental morphology. It is one of the longest lived group among Mesozoic mammals with fossil record extending from Late Triassic to Early Cretaceous (Kielan–Jaworowska *et al.*, 2004) with one possible report from the Late Cretaceous of India (Anantharaman *et al.*, 2006). Most of the haramiyidan fossils have been reported from Europe (Simpson, 1947; Sigogneau–Russell *et al.*, 1986; Kermack *et al.*, 1998; Butler, 2000; Butler & Hooker, 2005) with a few taxa also known from Greenland (Jenkins *et al.*, 1997), Morocco (Sigogneau–Russell, 1991) and Tanzania (Heinrich, 1999). In recent years, they have also been documented by articulated skeletons from the Middle–Upper Jurassic strata of China which revealed greater diversity in this group (Zheng *et al.*, 2013; Zhou *et al.*, 2013; Bi *et al.*, 2014; Han *et al.*, 2017). The recent discoveries from China and North America stirred a debate on their phylogenetic relationship with multituberculates, whether they represent a paraphyletic assemblage of crown mammals related to multituberculates (Zheng *et al.*, 2013) or a close sister group to Mammalia (mammaliaforms) (Huttenlocker *et al.*, 2018).

Anantharaman *et al.* (2006) described one right upper molariform tooth under Haramiyida and named it as *Avashishta bacharamensis* (Fig. 14A–C) from the infratrappean beds of Bacharam,Telengana.

INTERCONTINENTAL AFFINITIES OF THE MAMMALIAN FAUNA

Eutherian Mammals

Adapisoriculidae

Prasad & Sahni (1988) described the first Cretaceous mammal from the Naskal Intertrappean beds based on a right upper first molar and a right upper third molar. This was named as *Deccanolestes hislopi* (Fig. 6A–B, E–F). Six years later, a larger species *D. robustus* represented by right upper second molar and left lower first molar (Fig. 7A–D*)* and a worn right upper second molar placed under *Deccanoleste*s cf. *hislopi* (Figs 6C–D) have been documented (Prasad *et al.*, 1994). In addition to these, postcranial bones (astragali and calcanea) referable to both the gracile and robust species of *Deccanolestes* were also documented (Prasad & Godinot, 1994; Godinot & Prasad, 1994).

Ever since their discovery in 1988, the systematic position *Deccanolestes* within the Eutherian clade has remained a subject of debate because of isolated nature and poor preservation of the teeth. Prasad & Sahni (1988) noticed some significant similarities in dental morphology

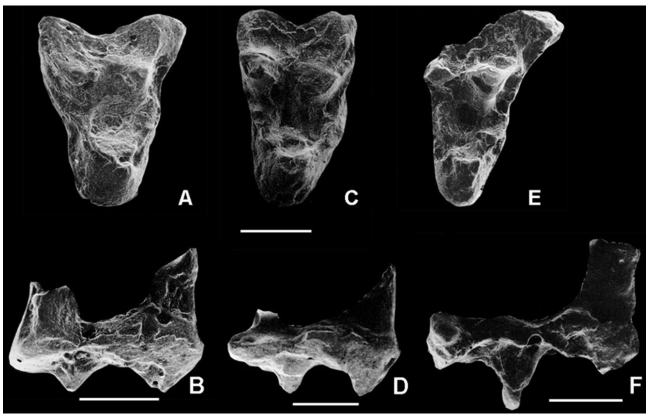

Fig. 6—A–B. *Deccanolestes hislopi* Prasad & Sahni, 1988 from the intertrappean beds of Naskal. A–B. VPL/JU/NKIM/10, right M1, A. occlusal view, B. anterior view; C–D. *Deccanolestes* cf. *hislopi*, VPL/JU/NKIM/15, right M2, C. occlusal view, D. anterior view; E–F. *Deccanolestes hislopi*, VPL/JU/NKIM/11, right M3, E. occlusal view, F. anterior view. Scale bar equals 0.5 mm (adapted from Fig. 6 of Prasad *et al.*, 1994)

of *D. hislopi* and *Kennalestes* of Mongolia and *Cimolestes* of North America and suggested palaeoryctoid affinity. After a comprehensive analysis of their morphology and comparison with North American *Cimolestes magnus* and *Procerberus formicarum*, Prasad *et al.* (1994) observed that the distinct dental structure of *Deccanolestes* warrants its placement in a subfamily of Palaeoryctidae or in its own family. On the other hand, functional analysis of calcanea and astragali referred to *D. hislopi* and *D. magnus* indicated that these animals had adapted for arboreal mode of life and are possibly related to Archonta or Euarchonta (dermopterans, tree shrews, Plesiadapiformes and the Primates) (Prasad & Godinot, 1994; Godinot & Prasad, 1994). Based on the early descriptions of *Deccanolestes hislopi,* Wible *et al.* (2007) included it in a phylogenetic analysis of Cretaceous eutherians which returned it as a stem eutherian consistent with 'palaeoryctid'–like dental morphology of Prasad & Sahni (1988). Alternatively, phylogenetic analysis based on tarsal bone characters alone placed arboreal *Deccanolestes* as a stem member of Euarchonta (Hooker, 2001). In the meanwhile, a new intertrappean bed discovered near Kisalpuri Village, Dindori District, Madhya Pradesh in 2004 has yielded comparatively well preserved mammalian teeth and postcranial bones (Khosla *et al.*, 2004; Verma, 2008). On comparison of the mammalian teeth from Naskal and Kisalpuri with those *Afrodon chleuhi* (Family Adapisoriculidae) from the Late Paleocene (Thanetian) Adrar Mgorn site of Morocco and *A. germanicus* from the Late Paleocene of Walbeck, Germany, and Cernay and Berru localities of France, Prasad *et al.* (2010) erected a new species of *Deccanolestes* (*D. narmadensis*) (Fig. 9A–F) and suggested that *Deccanolestes* is an adapisoriculid. Simultaneously, Smith *et al.* (2010) also arrived at a similar conclusion that *Deccanolestes* is closely related to African and European adapisoriculids based on the similarity of their tarsal bone morphology and identified it as a stem euarchontan. Functional study of fore limb bones (humerus and ulna) of *Deccanolestes* also supported an arboreal mode of life for *Deccanolestes*. These bones were found to be morphologically intermediate between those of Cretaceous 'condylarths' and Paleogene euarchontans, while European adapisoriculids represent morphological intermediates between *Deccanolestes* and definitive euarchontans (Boyer *et al.*, 2010). This conforms the fact that *Deccanolestes* coming from relatively older Upper Cretaceous deposits has more primitive dental and tarsal morphology than that of Paleocene African and European adapisoriculids. A cladistic analysis carried out to resolve these competing hypotheses on the phylogeny of *Deccanolestes* by integrating both dental and postcranial characters has shown that *Deccanolestes* (including *D. hislopi*, *D. robustus*, *D. narmadensis* + *S. rangapurensis*) and the African and European Paleogene adapisoriculids form a monophyletic group among the most basal eutherians (Goswami *et al.*, 2011). Thus, they were assigned to the family Adapisoriculidae and it was also suggested that dispersal of adapisoriculid mammals took place between India, Africa and Europe across the Tethys Sea at or near the Cretaceous–Paleogene (K/Pg) boundary. Goswami *et al.* (2011) further remarked that the presence of many Cenomanian taxa in the sister clade to Adapisoriculidae points to a hidden or ghost lineage of ~30 Ma for Adapisoriculidae either in India or Africa. More recently, Kapur *et al.* (2017a, b) documented an adapisoriculid right dentary with preserved p4, m2, and m3 (*Bharatlestes kalami*) from the Lower Eocene Cambay Shale of Vastan Lignite Mine, Gujarat. This find

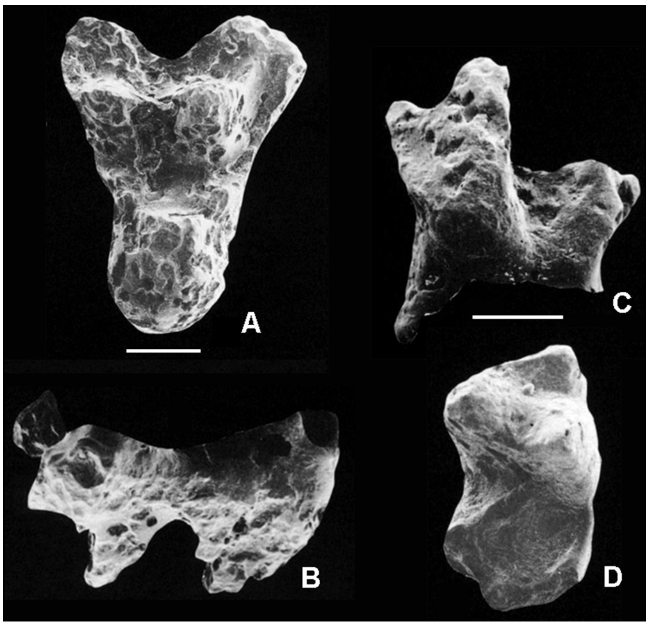

Fig. 7—A–D. *Deccanolestes robustus* Prasad *et al.*, 1994 from the intertrappean beds of Naskal. A–B. VPL/JU/NKIM/13, right M2, A. occlusal view, B. anterior view; C–D. VPL/JU/NKIM/14, left m1, C. labial view, D. occlusal view. Scale bar equals 0.5 mm (adapted from Fig. 7 of Prasad *et al.*, 1994).

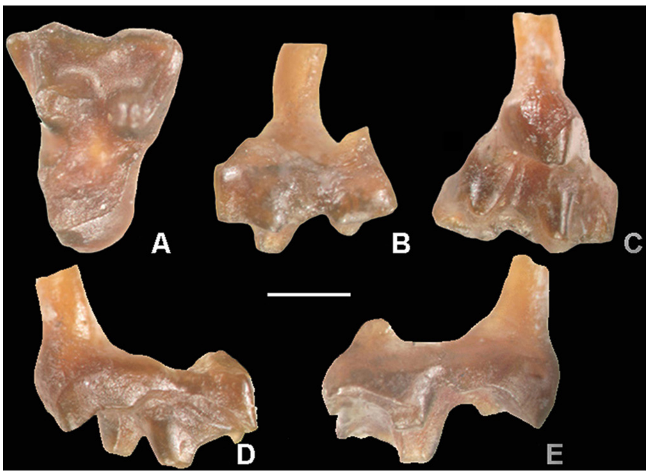

Fig. 8—A–E. *Deccanolestes* cf. *hislopi* from the intertrappean beds of Kisalpuri (Prasad *et al.*, 2010), VPL/JU/IM/17, left M1, A. occlusal view, B. labial view, C. lingual view, D. anterior view, E. posterior view. Scale bar equals 1 mm.

provides evidence for the crossing of the K/Pg boundary by adapisoriculid mammals and their survival into the Eocene in India. Phylogenetic analysis has recovered *Bharatlestes* as more derived than *Deccanolestes* and *Afrodon* which represent an unresolved primitive clade with respect to European *Bustylus* and *Adapisoriculus*. *Bharatlestes* with *Bustylus* + *Adapisoriculus* forms a sister group to *Deccanolestes–Afrodon* unresolved clade (Kapur *et al.* 2017a, b)

In light of the long history of adapisoriculids in Gondwana and the occurrence of the primitive adapisoriculid *Afrodon chleuhi* in the Paleocene of Africa, Africa was suggested as a centre of origin for adapisoriculids (Gheerbrant & Russell, 1989). However, De Bast *et al.* (2012) favoured Europe as a possible centre of origin for adapisoriculids in view of their high diversity in the European Paleocene fauna. Further, they argued that the high diversity of European Paleocene adapisoriculids points to the possible presence of an unknown Cretaceous European adapisoriculid clade. From the presence of the oldest adapisoriculid (*Deccanolestes*) in the Maastrichtian of India, more primitive nature of *Deccanolestes*'s dental morphology with respect to the African and European adapisoriculids, and absence of Cretaceous adapisoriculids in Africa and Europe, it appears more likely that adapisoriculids originated in India and subsequently dispersed out of it.

In the debate over India's biogeographic relationship with Laurasian landmasses, the eutherian mammals *Deccanolestes, Sahnitherium* and *Kharmerungulatum* figured invariably. The

Fig. 9—A–F. *Deccanolestes narmadensis* Prasad *et al.*, 2010 from the intertrappean beds of Kisalpuri. A–C. VPL/JU/IM/5, right m1 or m2, A. lingual view, B. labial view, C. anterior view; D–F, VPL/JU/IM/7, right m1 or m2, D. labial view, E. lingual view, F. posterior view. Scale bar equals 1mm.

much discussed phylogenetic relationships of *Deccanolestes* along with its close relative *Sahnitherium* is now settled with their inclusion in Adapisoriculidae (Prasad *et al.*, 2010; Smith *et al.*, 2010; Goswami *et al.*, 2011). Confirmation of *Deccanolestes* as the oldest adapisoriculid and its sister group relationship to *Afrodon* from Africa and Europe implies that overseas dispersals were possible between India and Africa–Europe at a time when India was drifting as an island landmass (Prasad *et al.*, 2010; Smith *et al.*, 2010; Goswami *et al.*, 2011). It has already been highlighted in the past that most of the taxa of Laurasian affinity reported from India were small–sized animals which could have dispersed across filter corridors or by sweepstakes mode of dispersal (Prasad & Sahni, 1999, 2009). Small–bodied mammals like *Deccanolestes* and *Kharmerungulatum* might have dispersed across the intervening Tethys sea making use of island arcs such as Oman, Kohistan and Dras, and Ladakh magmatic arc (Prasad & Sahni, 1999; Chatterjee *et al.*, 2017). The colonization of Madagascar at different times by the ancestors of modern mammals of Madagascar through similar overseas dispersals has been visualized (Samonds *et al.*, 2013).

Sahnitherium rangapurensis

Sahnitherium rangapurensis was erected on the basis of a solitary and worn upper right molar (Fig. 10A–D) and was distinguished from *Deccanolestes* because of its less transverse width, presence of stronger and longer postmetacrista carrying the supposed cusp 'C' and more posteriorly expanded metastylar area, absence of stylocone, the paracone slightly higher and more lingually expanded than the metacone, a large paraconule overhanging anterior part of the crown, moderate zalambdodonty of labial cusps, and anteroposteriorly unconstricted conular region (Rana & Wilson, 2003). But we observed that these features are also variably present or absent in the better preserved specimens of *Deccanolestes* from the intertrappean beds of Kisalpuri. As the holotype of *S. rangapurensis* (ITV/R/Mm–1) has a break at the anterolabial end of the crown and the specimen appears to be worn, the morphological differences observed between *Sahnitherium* and *Deccanolestes* cannot be properly evaluated. *Sahnitherium* is thus considered closely related to *Deccanolestes* and more well–preserved specimens are needed to establish distinctness of these two taxa. Because of the close relationship of *Sahnitherium* to *Deccanolestes*, it was also referred to the family Adapisoriculidae (Goswami *et al.*, 2011).

Kharmerungulatum vanvaleni

Ungulates are herbivorous animals that dominate terrestrial ecosystems. 'Condylarthra' is a paraphyletic group that was possibly ancestral or sister group to modern ungulates (Archibald, 1982). Prasad *et al.* (2007b) identified an isolated right lower molar (Fig. 11A–E) from the intertrappean beds of Kisalpuri as an archaic ungulate (*K. vanvaleni*). *Kharmerungulatum* differs from other Indian Cretaceous mammals, such as *Deccanoleste*s and *Sahnitherium* and North American Cretaceous eutherians, for example, *Cimolestes, Procerberus, Batodon* and *Gypsonictops* in having basally expanded molars with side wall convexity. The early ungulate molars exhibit reduced height difference between the trigonid and talonid, bunodont cusps, large hypoconid and typical abrasion causing bevelling of cusp apices (Archibald, 1982). These dental features enabled the ungulates to crush and grind food material (Archibald, 1982). *Kharmerungulatum* with these and several other primitive characters compares well with some of the archaic ungulates, such as *Protungulatum, Oxyprimus, Baioconodon* and *Mimatuta* known from the Early Paleocene (Puercan) of North America (Prasad *et al.*, 2007b). The molar morphology of *Kharmerungulatum* indicates that it had incipiently adapted for herbivorous diet. Prasad *et al.* (2007b) based on its primitive dental morphology and its Maastrichtian age concluded that *Kharmerungulatum* represents an early stage of ungulate evolution. Though recent phylogenetic analyses have placed *Protungulatum* within crown Placentalia (Spaulding *et al.*, 2009; O'Leary *et al.*, 2013), other phylogenetic studies recovered it as a stem eutherian close to Placentalia (Wible *et al.*, 2007; Goswami *et al.*, 2011; Halliday *et al.*, 2015). The phylogenetic analysis of Cretaceous eutherian mammals from India did not support the placement of *Kharmerungulatum* in the placental crown group (Goswami *et al.*, 2011). In a more recent phylogenetic analysis of Eocene ungulate mammal *Pahelia mysteriosa* (Zack *et al.*, 2019) from India, *Kharmerungulatum* emerged as a sister taxon to basal mesonychian *Oxyprimus cuspidatus* or the mioclaenine hyopsodontid *Mioclaenus turgidus* underscoring close faunal links with Laurasia.

The presence of an archaic ungulate comparable to *Protungulatum*, *Oxyprimus* and *Mioclaenus* in northward drifting Indian Plate raises some questions on its place of origin and dispersal across the continents. A Pangaean distribution for archaic ungulates cannot be ruled out. Absence of these mammals in the Cretaceous fossil record of other continents might be attributed to limited exploration in those continents. Secondly, at the time of publication of *Kharmerungulatum*, no Maastrichtian 'condylarth' was known from any other part of the world. Later a solitary occurrence of *Protungulatum* was reported from the Maastrichtian of North America (Archibald *et al.*, 2011). The morphological similarities between *Kharmerungulatum* and North American archaic ungulates suggests that dispersal between India and Laurasia was possible in the latest Cretaceous. Alternatively, since the tooth of *Kharmerungulatum* has primitive morphology in comparison to North American archaic ungulates, it is also possible that archaic ungulates had originated on the drifting Indian Plate and later dispersed to North America. But it is too early to support the latter hypothesis as the highly abraded molar of *Kharmerungulatum* preserves few characteristic features which can be used in a phylogenetic analysis. Future

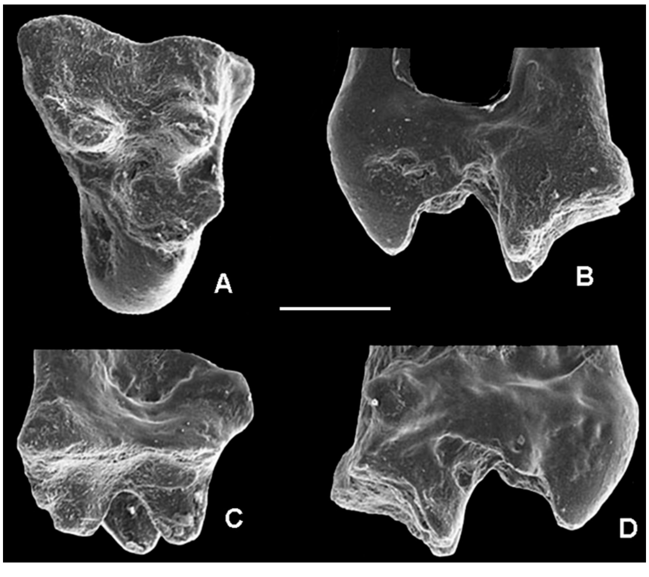

Fig. 10—A–D. *Sahnitherium rangapurensis* Rana & Wilson, 2003 from the intertrappean beds of Rangapur, ITV/right/RMm–1, right M1 or M2, holotype, A. occlusal view, B. posterior view, C. labial view, D. anterior view. Scale bar equals 0.5 mm (reproduced from Fig. 6 of Rana & Wilson, 2003 with permission from Acta Palaeontologica Polonica).

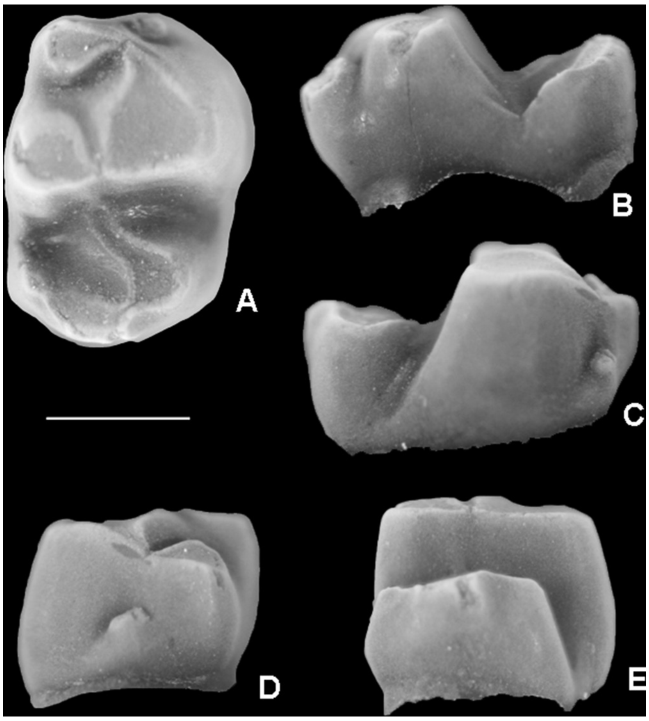

Fig. 11—A–E. *Kharmerungulatum vanvaleni* Prasad *et al.*, 2007b from the intertrappean beds of Kisalpuri. VPL/JU/IM/31, right m1 or m2, holotype, A. occlusal view, B. lingual view, C. labial view, D. anterior view, E. posterior view. Scale bar equals 1 mm (adapted from Fig. 1 of Prasad *et al.*, 2007b)

discovery of well–preserved specimens may help us in resolving the phylogenetic position of *Kharmerungulatum.* Notwithstanding the uncertainty surrounding the placement of the late Cretaceous *Kharmerungulatum* or *Protungulatum* in Placentalia, these taxa may represent putative archaic ungulates.

Eutheria *incertae sedis*

VPL/JU/IM/32 (Fig. 12A–E) is a partially preserved right lower third molar of an eutherian mammal which is quite distinct from all known species of *Deccanolestes* (*D. hislopi*, *Deccanolestes* cf. *hislopi*, *D. robustus*, *D. narmadensis*) and *S. rangapurensis* and basal eutherians *Prokennalestes trofimovi* Kielan–Jaworowska & Dashzeveg, 1989 and *Murtoilestes abramovi* Averianov & Skutschas, 2001, in its large size and having inflated cusps above roots, relatively reduced height difference of trigonid and taloned, anteriorly projecting paraconid as a distinct and well developed cusp, somewhat lingually deflected metaconid, large hypoconid (as large as the paraconid in cross section), and hypoconulid closer to the entoconid than to the hypoconid.

Though inflated cusps above the roots, lingually placed paraconid, hypoconulid closer to entoconid, reduced height difference between the trigonid and talonid, are also characteristic of *Protungulatum* and *Kharmerungulatum*, in these genera, the molars are relatively very large in size bearing bunodont cusps and a voluminous protoconid cusp of the trigonid. *Protungulatum* further has talonid wider than trigonid and a well–developed posterolabial cingulid.

The closest resemblance of VPL/JU/IM/32 is with *Bobolestes zenge* Nessov, 1985 (=*Otlestes meiman* Nessov, 1985a; Nessov *et al.*, 1994) reported from the early Cenomanian Khodzhakul Formation, Kyzylkum Desert, Uzbekistan (Averianov & Archibald, 2005). The characters shared between the two taxa include: trigonid cusps arranged in an acute–angled triangle (anteroposteriorly compressed), the trigonid wider than the longer and narrower talonid, relatively large paraconid connate with the metaconid at the base, and a voluminous hypoconid cusp with a deep hypoflexid. The lower molars of *Bobolestes* are, however, smaller than VPL/JU/IM/32 in size and the paraconid is slightly compressed anteroposteriorly in *Bobolestes,* whereas it is distinct, conical cusp in VPL/JU/IM/32. Despite some differences in molar morphology, the lower molars of *Bobolestes zenge* and VPL/JU/IM/32 have the same basic pattern of crown morphology, but the latter is more derived than *Bobolestes* in having a large paraconid cusp and inflated cusps. Because of the poor preservation of the trigonid, specifically the protoconid, more well–preserved specimens are needed to confirm the phylogenetic relationships of VPL/JU/IM/32 with *Bobolestes.*

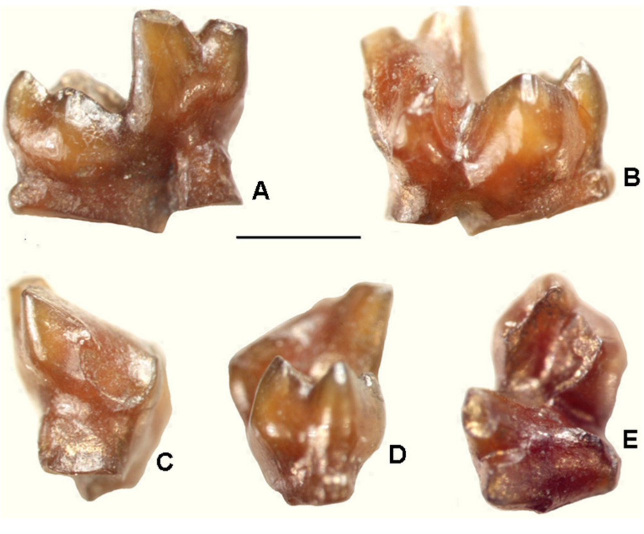

Fig. 12—Eutheria *incertae sedis* from the intertrappean beds of Kisalpuri. VPL/JU/IM/32, left m3, A. lingual view, B. labial view, C. anterior view, D. posterior view, E. occlusal view. Scale bar equals 1mm.

Gondwanatherians

Until now, no fossils of gondwanatherian mammals are known from extensively sampled Laurasia though they have been widely reported from all Gondwanan continents except Australia. They are known by isolated teeth, a few dentaries, a skull, and one complete skeleton (see O'Connor *et al.*, 2019 and Krause *et al.*, 2020 for references). Among Mesozoic mammals, Gondwanatherian are the only known mammals that had hypsodont dentition. The development of hypsodont dentition in gondwanatherians was possibly an adaptation to a diet of hard food material (von Koeningswald *et al.*, 1999; Patnaik *et al.*, 2001) or siliceous grasses (Prasad *et al.*, 2005). Their exclusive occurrence in Gondwana underscores their Gondwanan origin and radiation (Krause *et al.*, 2014). Of the two families of Gondwanatheria, Ferugliotheriidae and Sudamericidae, ferugliotheriids (*Ferugliotherium windhauseni, Trapalcotherium matuastensis*) are restricted to the Campanian–Maastrichtian deposits of Argentina (Bonaparte, 1986a; Krause *et al.*, 1992; Rougier *et al.*, 2009). Sudamericids have a wide geographic and stratigraphic distribution with known records from the Campanian–Maastrichtian of Argentina (*Gondwanatherium patagonicum, Magallanodon baikashkenke*) (Bonaparte, 1990; Chimento *et al.*, 2020, 2021), Chile (*Magallanodon baikashkenke*) (Goin *et al.*, 2020) and Paleogene (*Sudamerica ameghinoi,* Sudamericidae family indet*., Greniodon sylvaticus* (family indet.)) of Argentina (Scillato–Yané & Pascual, 1984; Gurovich, 2008; Gurovich & Beck, 2009; Goin *et al.*, 2012), Tanzania (*Galulatherium jenkinsi*) (Krause *et al.*, 2003; O'Connor *et al.*, 2019), Madagascar (*Lavanify miolaka*, *Vintana sertichi*, Sudamericidae gen. et sp. indet. (Krause *et al.*, 1997; Krause 2013, 2014; Krause *et al.* 2014a, b), India (*Bharattherium bonapartei* (Fig. 13A–H), Sudamericidae gen. et sp. indet. (Fig. 13I–K)) (Das Sarma *et al.*, 1995; Prasad *et al.*, 2007a; Wilson *et al.*, 2007;

Verma *et al.*, 2012), and Sudamericidae gen. et sp. indet., cf. *Sudamerica ameghinoi* of Antarctica (Goin *et al.*, 2006). More recently, a new gondwanatherian skeleton belonging to a new family Adalatheriidae (*Adalatherium hui*) was described from the Maastrichtian of Madagascar (Krause *et al.*, 2020). Phylogenetic analysis placed *Adalatherium* within Gondwanatheria, which emerged as a sister taxon to Multituberculata within Allotheria (Krause *et al.*, 2020). The new family Adalatheriidae appears more derived than Ferugliotheriidae and stemward relative to Sudamericidae (Krause *et al.*, 2020).

Initially gondwanatherians were considered as edentates (Scillato–Yané and Pascual, 1984, 1985; Bonaparte, 1986a, b, 1990; Mones, 1987) and then as multituberculates or closely related to allotherians (Krause & Bonaparte 1990, 1993; Krause *et al.* 1992; Bonaparte *et al.*, 1993; Kielan–Jaworowska & Bonaparte 1996; Gurovich & Beck 2009; Krause *et al.* 2014) or haramiyidans (Pascual & Ortiz Jaureguizar, 2007). In light of new discoveries of skull and postcranial remains of gondwanatherians from Madagascar, these mammals are now regarded as allotherians closely related to haramiyidans (Krause *et al.*, 2014, 2020). No matter what the phylogenetic relationships of this group are, gondwanatherians were considered to have originated in Gondwana following its break–up with Laurasia, but before the opening of South Atlantic (Rougier *et al.*, 2010).

As far as the Indian gondwanatherians are concerned, Wilson *et al.* (2007) suggested that *Lavanify* and *Bharattherium* share three possible derived characters, such as deep infundibula on molariform teeth not replaced by synclines (von Koenigswald *et al.* 1999), dental enamel showing well developed inter–row sheets of interprismatic matrix (Krause *et al.* 1997; von Koenigswald *et al.* 1999; Patnaik *et al.* 2001), and presence of transverse wave–like bands and grooves or perikymata on the enamel surface of molariform teeth. Krause (2013) agreed on the second character of enamel having inter–row sheets of interprismatic matrix as a shared derived character between *Bharattherium* and *Lavanify*, but observed that in addition to *Bharattherium* and *Lavanify*, *Gondwanatherium* and *Greniodon* have also the infundibula that penetrate deep into the crown (Krause *et al.*, 1997; Prasad *et al.* 2007a; Wilson *et al.* 2007; Goin *et al.* 2012; Krause, 2013), while *S. ameghinoi* lacks the infundibulum. They also questioned on the distribution and utility of presence or absence of perikymata as this feature was not observed in *Lavanify,* as wear would remove perikymata during individual's life, and preservational differences may also affect its presence.

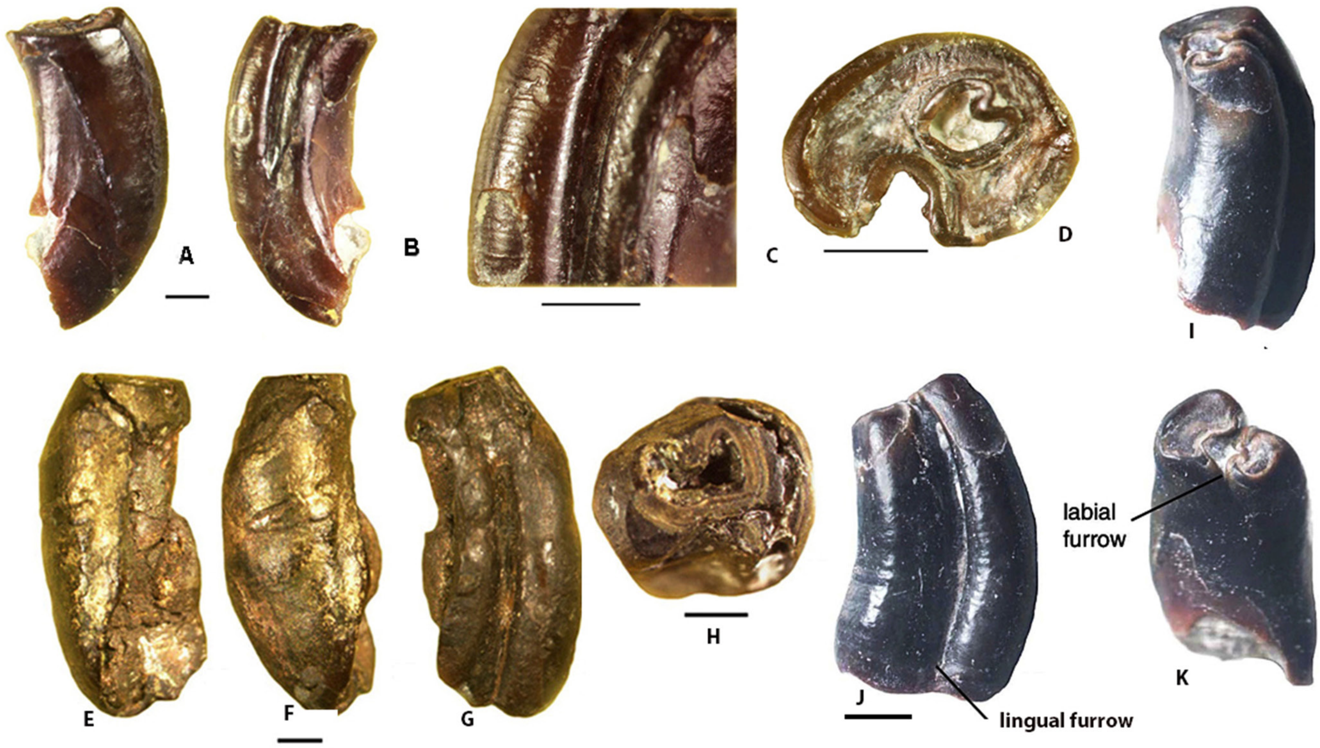

Fig. 13—A–H. *Bharattherium bonapartei* Prasad, Verma, Sahni, Krause, Khosla & Parmar, 2007a. A–D. VPL/JU/IM/33, cheek tooth, holotype, A–B. lateral views, C. enlarged lateral view showing incremental growth lines, D. occlusal view; E–H. VPL/JU/NKIM/25, cheek tooth, E–G. lateral views, H. occlusal view; I–K. Sudamericidae gen. et sp. indet. (Verma *et al.*, 2012), PL/IGNOU/103, left mf4, I. posterior view, J. lingual view, K. occlusolabial view. A–D, I–K from the intertrapperan beds of Kisalpuri, E–H from the intertrappean beds of Naskal. Scale bar equals 0.98 mm for A–B, 1.5 mm for C, 1.10 mm for D, 0.94 mm for E–G, 0.97 mm for H, and 1.0 mm for I–K.

In the beginning, gondwanatherians were considered as endemic to South America as they were known only from Campanian and Paleocene of Argentina (Bonaparte, 1990). Later discoveries of gondwanatherian teeth from the Upper Cretaceous (Maastrichtian) deposits India and Madagascar have shown their widespread distribution in the southern continents (Krause *et al.*, 1997). To explain the presence of gondwanatherian fossils in South America, India and Madagascar, Krause *et al.* (1997) proposed that Antarctica and Kerguelen Plateau provided a terrestrial connection between South America and Indo–Madagascar. They also anticipated the presence of gondwanatherians in Antarctica. Subsequently, gondwanatherian mammal remains were found in Antarctica but in younger Eocene rocks (Reguero *et al.*, 2002; Goin *et al.*, 2006). However, the presence of this southern biogeographic connection was refuted on geophysical grounds which indicated that Kerguelen Plateau was submerged under sea water by the Maastrichtian (Ali & Aitchison, 2009). Recent phylogenetic analysis of *Vintana* by Krause *et al.* (2014) identified a node (*Vintana*+ *Lavanify* + *Bharattherium*) to the exclusion of African and South American gondwanatherian taxa supporting the isolation of Indian and Madagascan forms from other gondwanatherians following the break–up of Gondwana. *Bharattherium* and *Lavanify* also resemble to some extent the cheek teeth of *Galulatherium* in lacking enamel on one side (*Galulatherium* teeth are fully enamel less), cheek teeth with nearly equal length and width somewhat similar to the peg–like cheek teeth of *Galulatherium*, and exceptionally high–crowned teeth curved along their length (O'Connor *et al.*, 2019). The distribution of Late Cretaceous gondwanatherians and their interrelationships not only reflect the endemic nature of the group but also insular evolution of Indo–Madagascar faunas.

Haramiyids

The fossil record of haramiyidans is known from the Upper Triassic and Middle Jurassic deposits of Laurasian landmasses but is unknown from extensively sampled Upper Jurassic and Cretaceous strata (Kielan–Jaworowska *et al.*, 2004). From the Gondwanan continents, the fossil record of haramiyidans comes from the Upper Jurassic Tendaguru beds (*Allostaffia enigmatica* Heinrich, 1999, 2001, 2004) and from the Upper Jurassic–Lower Cretaceous Ksar Metlili Formation, High Atlas Mountains, eastern Morocco (Sigogneau–Russell, 1991; Hahn & Hahn, 2003; Lasseron *et al.*, 2020). From the latter site, *Hahnodon taqueti* represented by a lower m2 was described as a multituberculate within the family Hahnodontidae (Sigogneau–Russell, 1991). Although its attribution to multituberculates was questioned in the past (Butler & Hooker, 2005), more conclusive evidence for its haramiyidan affinity came from the more recent discovery of a well preserved skull of a haramiyidan *Cifelliodon wahkarmoosuch* from the Lower Cretaceous Yellow Cat Member of Cedar Mountain Formation, Utah, USA (Huttenlocker *et al.*, 2018) with teeth having a morphology similar to that of *Hahnodon*. Based on the occurrence of *Cifelliodon* in the Early Cretaceous of USA and teeth with morphology similar to those of *Cifelliodon* in the Late Jurassic–Early Cretaceous of Morocco, it has been suggested that haramiyidan stem mammals survived into the Early Cretaceous of Laurasia and maintained broad geographic distributions in Laurasia and Gondwana at least up to the Early Cretaceous (Huttenlocker *et al.*, 2018).

Molariform tooth (GSI//SR/PAL–B215) of *Avashishta bacharamensis* from the Maastrichtian of India (Fig. 14 A–B) with its incomplete longitudinal grooves and concavities along the groove was interpreted to have an orthal chewing motion (Anantharaman *et al.*, 2006). As this chewing motion is typical of haramiyidans as contrasted with the palinal chewing motion of multituberculates (Butler & Hooker, 2005), it was placed under ?Haramiyidae. *Avashishta* was considered as closely related to the upper molariform of *Allostaffia* (Heinrich, 1999, 2004) known from the Upper Jurassic Tendaguru beds. Similarities observed between *Allostaffia* and *Avashishta* include saddle–like crown in lateral view, low and well separated cusps with blunt apices, main longitudinal groove that is the deepest at the distal end of the crown, the buccal wall of the main longitudinal groove steeper than the lingual wall and BB cusps at the mesial end of the crown (Anantharaman *et al.*, 2006). If these similarities represent true phylogenetic relationships between the two southern taxa, it can be concluded that the Gondwanan stock of haramiyidans survived late into the Cretaceous in the southern continents

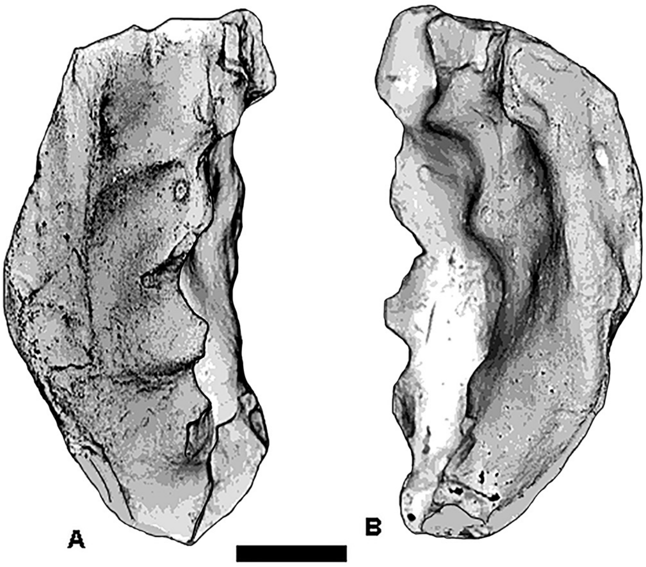

Fig. 14—A–B. *Avashishta bacharamensis* Anantharaman *et al.*, 2006, GSI/SR/PAL–B215, right upper molariform tooth from the infratrappean beds of Bacharam, Telengana. A. labial view, B. lingual view. Scale bar equals 0.5 mm (modified Fig.1 of Anantharaman *et al.*, 2006).

or this mammalian group was widely distributed in Panagaea (Huttenlocker *et al.*, 2018).

SUMMARY

Bonaparte & Kielan–Jaworowska (1987) proposed that Laurasian and Gondwanan continents developed distinctly different mammalian faunas in the Cretaceous because of their geographic isolation from each other. To a large extent, the Cretaceous mammalian faunas of Laurasian continents were characterized by multituberculates and diverse eutherian and metatherian groups and by the absence of triconodontids, dryolestoids, and spalacotheriid 'symmetrodontans'. Whereas in the southern continents, the mammalian faunas are dominated by endemics like gondwanatherians, some multituberculates and some relics of the Laurasian taxa that survived longer in Gondwana such as haramiyidans and dryolestoids. This is specifically true for South America and Africa (Morocco and Tanzania). In case of India, the Cretaceous mammalian fauna comprising both Laurasian and Gondwanan clades presents a complex biogeographic history for the Indian subcontinent. Currently, three mammalian groups, viz. eutherians, gondwanatherians and haramiyidans, are identified in the Cretaceous mammalian fauna of India. Among Gondwanan continents, India is the only southern landmass that preserves Cretaceous eutherian mammals, the fauna being overwhelmingly represented (in abundance and diversity) by the eutherians. The eutherians comprising the family Adapisoriculidae (*Deccanolestes hislopi*, *D. robustus*, *D. narmadensis*), an archaic ungulate (*Kharmerungulatum vanvaleni*), and an indeterminate eutherian (Eutheria *incertae sedis*) represent the most abundant and diverse group that demonstrates close biogeographic links with Laurasia. These mammals are highly significant from the point of understanding the evolutionary history of eutherians in the southern continents as they are the only unambiguously identified eutherians from Gondwana. The presence of closely related taxa in India (*Deccanolestes* and *Sahnitherium*) and Africa and Europe (*Afrodon*) and the older age and more primitive morphology of *Deccanolestes* argues in favour of Indian origin for adapisoriculids and subsequent dispersal to Africa and Europe close to the K/Pg boundary. A similar palaeobiogeographic picture emerges from the study of archaic ungulate *Kharmerungulatum* with close affinities to North American 'condylarths' and the unidentified eutherian sharing some morphological traits with *Bobolestes zenge* from Central Asia. Late Cretaceous Laurasian connection for India is also supported by other vertebrate groups such as pelobatid and Gobiatinae frogs, Anguidae lizards (Sahni *et al.*, 1982; Prasad & Rage, 1991; 1995, 2004; Rage *et al.*, 2020), troodontid dinosaur (Goswami *et al.*, 2013), charophytes (Bhatia *et al.*, 1989; Srinivasan *et al.*, 1994) and coryphoid palm (Srivastava *et al.*, 2014). The presence of these taxa of Laurasian affinities in India at a time when India was adrift in the Tethys can be explained by invoking dispersals across island arc systems as suggested in the past (Sahni *et al.*, 1982; Prasad & Sahni, 1999; 2009; Chatterjee *et al.*, 2013, 2017). Being very small in size, they might have made use of island arcs such as Oman, Kohistan and Dras, and Ladakh magmatic arc for a sweepstakes mode of dispersal to disperse from India to Europe via Africa or vice versa.

The fossil record of endemic gondwanatherian clade with a long stratigraphic range extending from Turonian to Eocene mirrors the tectonic history of Gondwana break–up. *Bharattherium*, the Indian Cretaceous gondwanatherian sharing some derived characters with *Lavanify* and *Vintana* from the Maastrichtian of Madagascar to the exclusion of gondwanatherian taxa from other Gondwanan landmasses highlights the evolution in isolation after separation from stem gondwanatherian stock. As the fossil record of haramiyidans was restricted to Late Triassic and Middle Jurassic of Laurasia (Kielan–Jaworowska *et al.*, 2004), their presence in the Upper Jurassic of Tanzania (Heinrich, 1999, 2001) was interpreted in the past as relict fauna that became extinct in Laurasia. The Indian Late Cretaceous *Avashishta bacharamensis* was interpreted as another haramiyidan that survived into the Late Cretaceous in Gondwana. However, recent discovery of a hahnodontid haramiyidan skull (*Cifelliodon wahkarmoosuch* Huttenlocker *et al.*, 2018) from the Early Cretaceous of North America pointed to the survival of haramiyidan stem mammals into the Early Cretaceous of Laurasia and a broad pangaean distribution of the group. At the moment, it is not clear whether the Indian Late Cretaceous haramiyidan represents a late survivor of the group in Gondwana or the one with broad distribution in Laurasia and Gondwana but without any fossils documented from the Upper Cretaceous deposits of Laurasia.

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