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Review of the Cretaceous dinosaurs from India and their paleobiogeographic significance

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ABSTRACT:

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The Indian Mesozoic dinosaur record is famous for documenting significant aspects of dinosaur evolution during the Triassic, Jurassic and Cretaceous periods. The Cenomanian–Turonian Nimar Sandstone, Lower Narmada valley, has produced fragmentary skeletal remains of Sauropoda indet. The Maastrichtian Lameta Formation has yielded at least 5 valid sauropod taxa and indeterminate titanosaurid remains, and at least 11 named (but likely oversplit) theropod taxa, i.e., 3 smaller-bodied species and 8 medium-to-large sized theropods. Apart from skeletal remains, Infra- and Intertrappean beds of peninsular India have yielded more than 10,000 dinosaur eggs belonging to 5 oofamilies and 15 oospecies. Most of the Indian ootaxa show distinct affinities with the Late Cretaceous ootaxa of four other continental areas – Spain, France, Argentina and Morocco. The presence of the two dominant oofamilies, Fusioolithidae and Megaloolithidae, in the Infra- and Intertrappean localities of peninsular India and three different continents (South America, Europe and Africa) further shows an ancient Gondwanan affinity and basic terrestrial association among these three landmasses. Based on the phylogenetic analysis of skeletal material, the most plausible pathway of dinosaur dispersal between India and Madagascar took place during the Late Cretaceous. The other conceivable dispersal pathway for the small animals was between India and Asia by means of the Kohistan Dras Volcanic Arc or a northeast pathway through Somalia, while the very large vertebrates, like theropod dinosaurs, may have emerged as a component of a 'Pan Gondwanan' model.

Key words: Cenomanian–Turonian; Cretaceous; Dinosaurs; India; Paleobiogeography.

INTRODUCTION

The study of Indian Late Cretaceous dinosaur fossils is very important from the paleobiogeographic point of view because of the Mesozoic association of India with southern Gondwana landmasses such as Madagascar and South America (e.g., Khosla and Sahni 1995; Storey *et al.* 1995; Vianey-Liaud *et al.* 2003; Wilson *et al.* 2003, 2009, 2011; Wilson and Upchurch 2003; Novas *et al.* 2010; Mohabey 2011; Ezcurra and Agnolín 2012; Khosla and Verma 2015; Kapur and Khosla 2016, 2019; Krause *et al.* 2019; Langer *et al.* 2019; Khosla and Lucas 2020a–e; Khosla 2021; Khosla *et al.* 2021). The skeletal record of Indian dinosaurs is from two intervals of the Cretaceous: the Cenomanian–Turonian and the Maastrichtian. The older of these Cretaceous dinosaur-yielding intervals is the Nimar Sandstone (Bagh Beds) of Dhar district (Madhya Pradesh). In the Nimar Sandstone, sauropod dinosaur fossils occur in two unique paleoenvironmental conditions, including a basal, fluvial coarse-grained channel sandstone and an upper, largely intertidal environment with a close association of numerous well-preserved oysters, *Turritella* sp., shark teeth and fragmentary dinosaur bone material (Khosla *et al.* 2003). Maastrichtian dinosaur fossils are known mainly from the Lameta Formation in three areas, the Jabalpur (Madhya Pradesh), Nand-Dongargaon and Pisdura areas in Chandrapur district (Maharashtra), and the Kheda-Panchmahal districts in Gujarat (Matley 1921a, b, 1923, 1939; Huene and Matley 1933; Chatterjee 1978; Mohabey 1983; Srivastava *et al*. 1986; Vianey-Liaud *et al*. 1987, 2003; Loyal *et al*. 1996, 1998; Jain and Bandyopadhyay 1997; Wilson *et al*. 2003, 2009, 2011; Wilson and Mohabey 2006; Carrano *et al*. 2010; Mohabey 2011; Khosla and Verma 2015; Khosla and Lucas 2020a–e; Khosla 2021). Captain W.H. Sleeman (in Matley 1921a) was the pioneer worker who discovered solitary sauropod caudal vertebrae in the Lameta Formation near Jabalpur in 1828, which started the history of dinosaur collecting in central India (formerly the Central Provinces and Central India Agency). Following that, the area became a hotspot for fossil collecting, resulting in a flurry of new finds that continues to this day (Carrano *et al*. 2010).

Apart from W.H. Sleeman, in the 19th century there were numerous other geologists, i.e., Medlicott (1860, 1872), Hughes (1877), and Lydekker (1890), who made extensive contributions to the initial study of the Lameta Formation and dinosaur finds in India (Carrano *et al*. 2010). The majority of their discoveries were focused around Jabalpur or farther south near Pisdura and the Kheda-Panchmahal districts of Gujarat. Matley (1921a, b, 1939) and Huene and Matley (1933) extensively mapped and excavated the Lameta Formation exposed at the Chotta Simla and Bara Simla hills of the Jabalpur Cantonment area, and discovered numerous sauropods and theropod taxa there. Their initial work laid the foundation for dinosaur research in India (Mohabey 2011). The taxa erected by them are currently classified as Sauropoda (titanosaurians) and Theropoda (abelisaurids and noasaurids; Carrano *et al*. 2010; Table 1).

The Lameta Formation of the Nand-Dongargaon and Pisdura areas of the Chandrapur district (Maharashtra) yielded sauropod skeletal material (e.g., Chatterjee and Rudra 1996; Jain and Bandyopadhyay 1997; Wilson and Mohabey 2006) and egg nests (Mohabey 1996a, b, 1998; Vianey-Liaud *et al*. 2003; Fernández and Khosla 2015; Khosla 2017; Khosla and Lucas 2020d, e). Teeth and bones of sauropods and theropods were discovered in calcareous sandstones and conglomeratic layers beneath the egg-bearing limestones at Rahioli, Kheda district in Gujarat (Mathur and Srivastava 1987; Mohabey 1987, 1989; Wilson *et al*. 2003). Six unique theropod teeth were assigned to two taxa by Mathur and Srivastava (1987), but because tooth morphology in other ceratosaurs (Carrano *et al*. 2002) can change substantially along and between the tooth rows, these teeth may in fact belong to a single taxon (Wilson *et al*. 2003). The dinosaur eggs from the Kheda-Panchmahal districts of western India were excavated by numerous workers (e.g., Dwivedi *et al*. 1982; Mohabey 1983, 1996a, b,

Taxon		Lithostratigraphic unit	Age
Sauropoda	*Jainosaurus septentrionalis* (=*Antarctosaurus septentrionalis*)	Lameta Formation	Maastrichtian
	Jainosaurus cf. *septentrionalis*	Lameta Formation	Maastrichtian
	Isisaurus colberti	Lameta Formation	Maastrichtian
	Titanosaurus indicus	Lameta Formation	Maastrichtian
	Titanosaurus blanfordi	Lameta Formation	Maastrichtian
	indeterminate titanosaurid remains	Lameta Formation	Maastrichtian
	Sauropoda indet.	Nimar Sandstone	Cenomanian–Turonian
Theropoda	*Compsosuchus solus*	Lameta Formation	Maastrichtian
	Jubbulpuria tenuis	Lameta Formation	Maastrichtian
	Laevisuchus indicus	Lameta Formation	Maastrichtian
	Rajasaurus narmadensis	Lameta Formation	Maastrichtian
	Rahiolisaurus gujaratensis	Lameta Formation	Maastrichtian
	Indosuchus raptorius	Lameta Formation	Maastrichtian
	Indosaurus matleyi	Lameta Formation	Maastrichtian
	Ornithomimoides mobilis	Lameta Formation	Maastrichtian
	O. barasimlensis	Lameta Formation	Maastrichtian
	Dryptosauroides grandis	Lameta Formation	Maastrichtian
	Coeluroides largus	Lameta Formation	Maastrichtian

Table 1. Updated list of dinosaur taxa from the Cretaceous of India (Lameta Formation; Nimar Sandstone). From: Carrano and Sampson (2008), Wilson *et al*. (2011), Chatterjee *et al*. (2017), and Khosla and Bajpai (2021).

1998; Srivastava *et al*. 1986; Sahni *et al*. 1994; Sahni and Khosla 1994a–c; Khosla and Sahni 1995; Loyal *et al*. 1996, 1998; Khosla 2001, 2017, 2021; Fernández and Khosla 2015; Khosla and Lucas 2020d, e).

British and American paleontologists who discovered dinosaur bone material in the Lameta Formation of the east, west and central Narmada River region sent them to the Natural History Museum in London and the American Museum of Natural History in New York (Mohabey 2011). Carrano *et al*. (2010) have recently provided missing information about Indian dinosaurs, as well as a complete overview of the history of dinosaur collecting in central India in 1828–1947.

The main objective of this paper is to present a comprehensive overview of Cretaceous dinosaurs (Table 1) and the current status of the Late Cretaceous dinosaur fossil record (including skeletal fossils, nests and eggs) from India and also to discuss its paleobiogeographic significance.

Repositories

The following abbreviations are used to indicate the repositories of specimens cited in the text:

AMNH, The American Natural History, New York, USA;
GSI, Geological Survey of India, Kolkata, India;
ISIR, Indian Statistical Institute, Kolkata, India;
VPL/KH, Vertebrate Paleontology Laboratory, Khosla, Chandigarh, India.

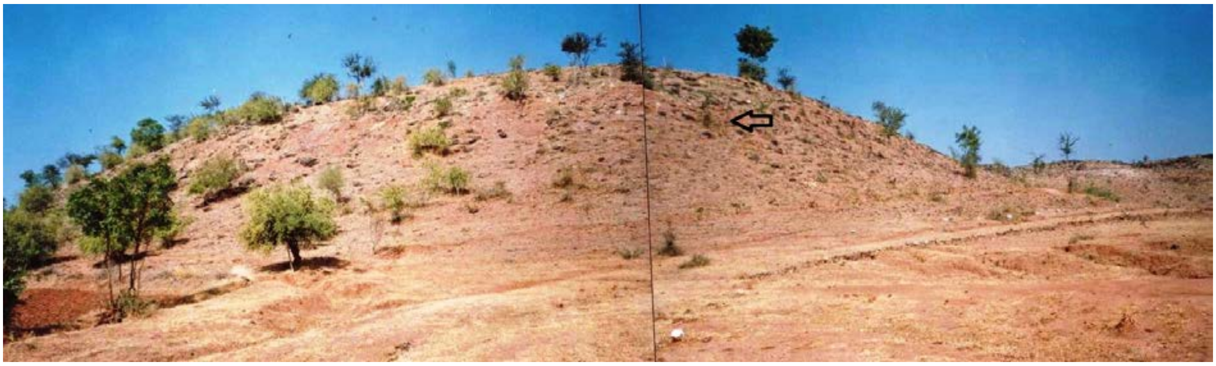
CENOMANIAN–TURONIAN DINOSAURS

Previous studies and geological context

The earliest Cretaceous dinosaurs from India are known from the Bagh Beds of the Lower Narmada Valley in west Madhya Pradesh, central India (Text-figs 1 and 2). Cenomanian–Turonian sauropods have been recorded from the Nimar Sandstone (Bagh Beds) of Dhar district (Madhya Pradesh). These are the first sauropods from the Bagh Beds and the oldest Cretaceous sauropods from India. Dinosaur bones have been recovered from both lower and upper portions of the Nimar Sandstone, and are here attributed to distinct paleoenvironments. The basal part of the coarse, conglomeratic and fluviatile Nimar Sandstone has yielded fragmentary bones, whereas the upper oyster band is associated with gritty and occasionally conglomeratic marine sandstones intercalated with red sandy shales and has yielded better preserved material of Cenomanian–Turonian age (Khosla *et al*. 2003).

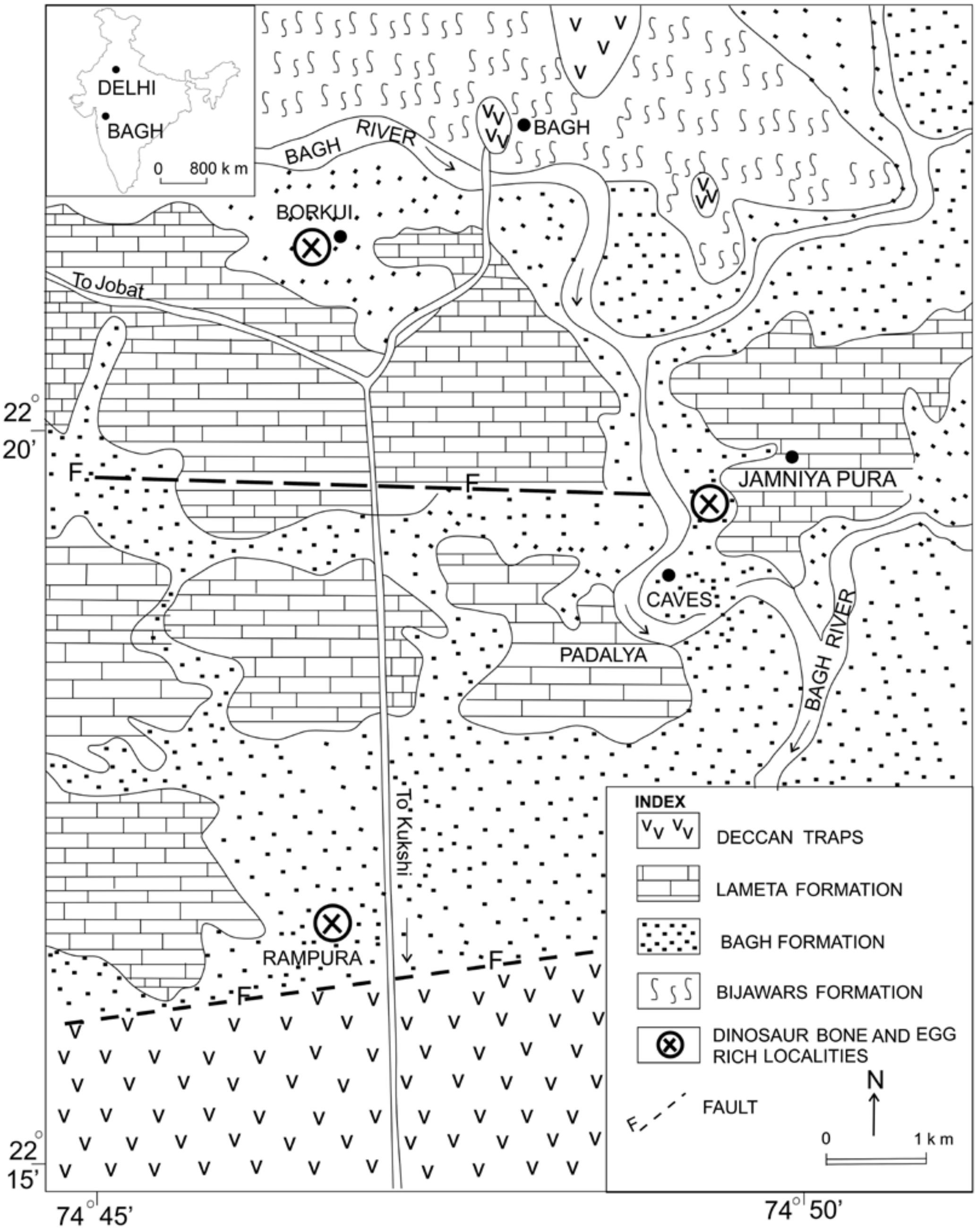
The fauna in the upper part of the Nimar Sandstone indicates marine influence (Badve and Ghare 1978; Singh and Srivastava 1981), and its depositional environment was diversely interpreted as shallow marine to nearshore with a shifting sandy substrate and turbulent waters (Badve and Ghare 1978; Nayak 2000), shallow sub-littoral (Chiplonkar *et al*. 1977a; Kundal and Sanganwar 2000), below low tide level (Kundal and Sanganwar 1998), intertidal to inner subtidal (Singh and Srivastava 1981), shallow shelf (Bose and Das 1986), macrotidal estuarine complex environment with tidal channels (Ahmad and Akhtar 1990), and intertidal-deltaic (Khosla *et al*. 2003).

This part of the Nimar Sandstone is ferruginous, hard, compact, gritty towards the top and also contains red shaly intercalations. *Ostrea* sp., *Turritella* sp., and a few shark teeth present at a number of localities (i.e., south of Bagh town along the Bagh-Kukshi Road, Amlipura and Ajantar) were reported from the upper part of this unit (Dassarma and Sinha 1975). A high-energy environment in a nearshore area is indicated by the thin oyster bed in the uppermost part (Kulshreshtha 1995). Short marine transgression and regression phases resulted in the



Text-fig. 1. Panoramic view of a section near Bagh Caves (Dhar district, Madhya Pradesh, India, showing the Cenomanian–Turonian dinosaur bone-bearing Nimar Sandstone horizon (arrowed; Khosla in preparation).

formation of trace fossil horizons, two oyster beds and an *Astarte–Turritella* bed within the upper part of the Nimar Sandstone near the Bagh Cave area (Chiplonkar and Badve 1972, 1973; Dassarma and Sinha 1975; Badve and Ghare 1978). Thus, intraformational units such as oyster beds within the Nimar Sandstone are the result of various regressive pulses of the sea along a shifting shoreline (Kulshreshtha 1995). The fauna in the uppermost part of the unit indicates marine influence (Badve and Ghare 1978; Singh and Srivastava 1981). The presence of algae (Badve and Nayak 1983, 1984a, b) representing the families Codiaceae, Corallinaceae, Cyanophyceae and Dasycladaceae, along with thick-shelled bivalve genera (*Granocardium* sp., *Jhabotrigonia* sp. and *Protocardium* sp.) in the uppermost part of the Nimar Sandstone in the Jhabua district, indicate that the top portion of the Nimar Sandstone must have been



Text-fig. 2. Simplified geological map of the Bagh area (Dhar district, Madhya Pradesh) showing the dinosaur bone and eggs, eggshells bearing localities (modified after Joshi 1995; Khosla *et al.* 2003).

Lithostratigraphic unit	Age	Lithology
Deccan Traps	Late Cretaceous	Basaltic flows
Lameta Formation	Late Cretaceous (Maastrichtian)	Red Sandstone Lameta Limestone
	disconformity	
Bagh Beds	Cenomanian to Turonian	Coralline Limestone Nodular Limestone Nimar Sandstone
	unconformity	
Archeans and Bijawars	Precambrian	Phyllites, quartzites and gneisses

Table 2. Generalized stratigraphic succession in the Bagh region (Dhar and Jhabua districts, Madhya Pradesh); after Khosla *et al.* (2003), Khosla and Lucas (2020c).

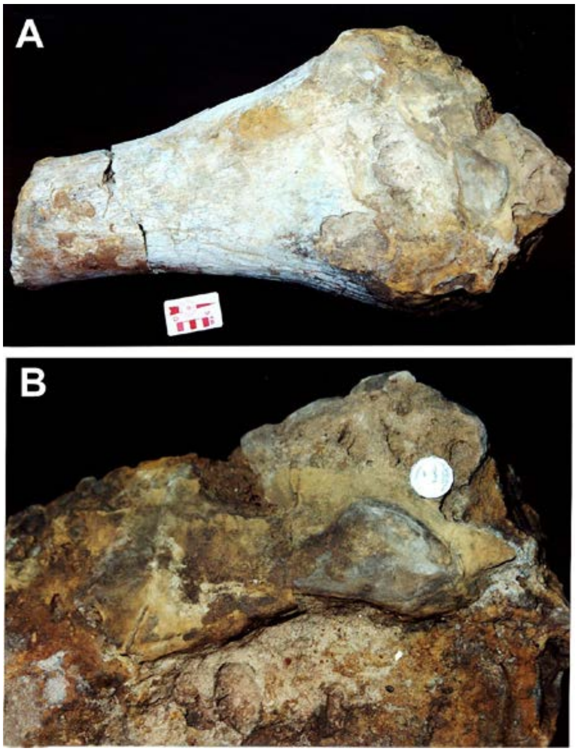
deposited in shallow marine conditions of a tropical region with normal salinity (Nayak 2000), while the bivalve assemblage indicates moderate to high energy nearshore conditions (Badve and Ghare 1978; Nayak 2000; Khosla *et al.* 2003). Documented records of calcareous algae belonging to Chlorophyta, Cyanophyta and Rhodophyta from the uppermost part of the Nimar Sandstone exposed at Pipaldehla (Jhabua district, Madhya Pradesh) also indicates that the topmost part was deposited in tropical waters at depths of 10–12 m (i.e., below tide level), suggesting a setting with moderate turbulence and normal water salinity (Kundal and Sanganwar 1998).

Thalassinoides isp. and crab burrows in the Nimar Sandstone at Man and Hatni river sections (Dhar district, Madhya Pradesh) were recorded by Singh and Srivastava (1981), which suggests deposition in a tidal flat area during a slow marine transgression in a shallow sublittoral to a nearshore environment with moderate to high energy levels. The rich and diverse ichnoassemblage from the uppermost part of the Nimar Sandstone recorded by Kundal and Sanganwar (2000) at Baria and Karondia (Manawar area, Dhar district, Madhya Pradesh) consists of 12 ichnospecies assigned to the *Cruziana* ichnofacies, which is generally indicative of a shallow sublittoral to nearshore environment with moderate to high energy levels (Khosla *et al.* 2003).

The basal part of the rocks exposed in the Bagh region (Dhar and Jhabua districts, Madhya Pradesh) comprise the Archean and Bijawar Supergroup, including phyllites, gneisses and quartzites, which are overlain by the Bagh Beds (Nimar Sandstone, Nodular Limestone and Coralline Limestone; Khosla *et al.* 2003; Khosla and Lucas 2020a, c; Table 2). The dinosaur bone-bearing Nimar Sandstone attains a thickness of about 27 m at Jamniya Pura and Borkui, and 22 m at the Bagh Caves (Text-fig. 2).

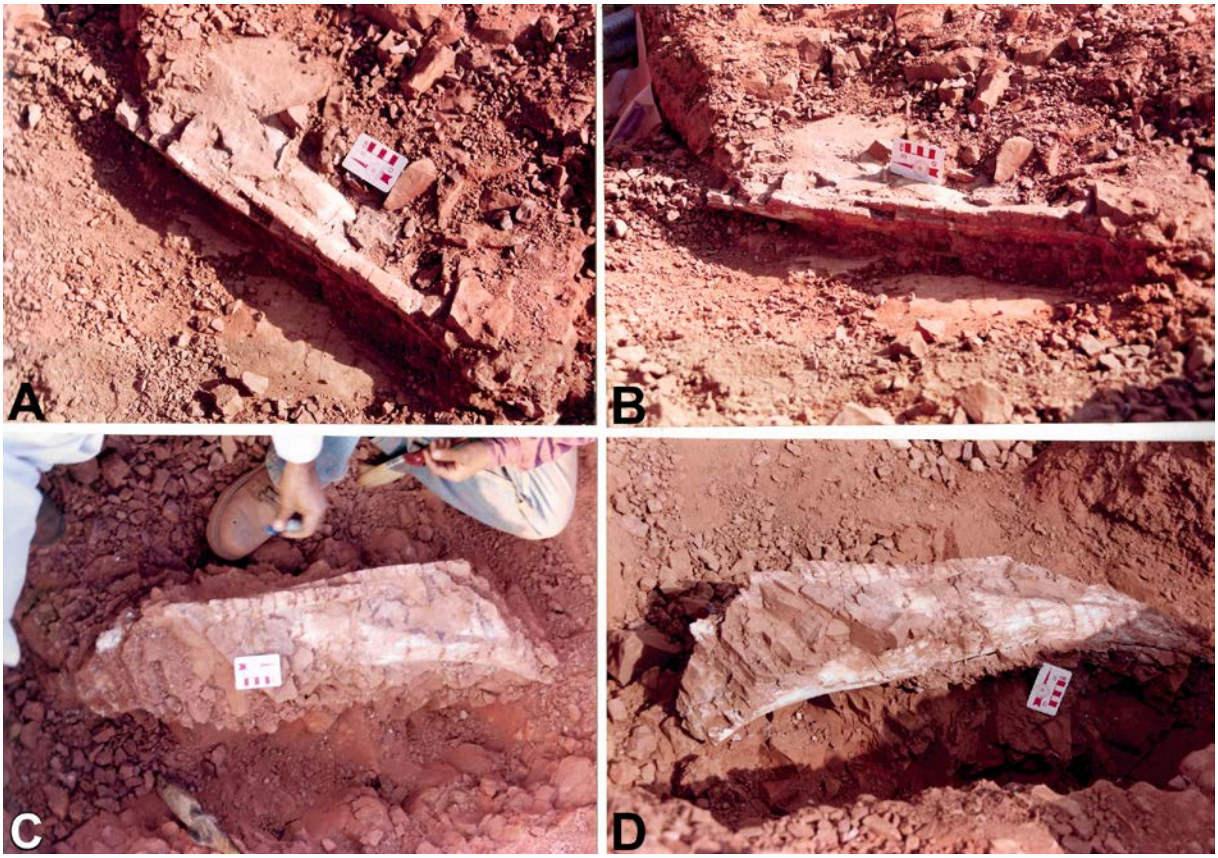
To summarize, the fossil data indicate that the deposition of the entire calcareous topmost portion of the Nimar Sandstone occurred in marine transgressive phase / deltaic-estuarine conditions, while deposition of the lower coarse conglomeratic sandstone part of the unit, which yielded dinosaur bones, began in fluviatile conditions (Khosla *et al.* 2003).

Regarding the age of the dinosaur bone-bearing Nimar Sandstone, the uppermost gritty portion of the Nimar Sandstone yielded shark teeth, *Ostrea* sp. and *Turritella* sp. (Dassarma and Sinha 1975) that indicate an age not earlier than the Cenomanian. In addition, marine fossils such as echinoids, ammonites and bivalves indicate a Cenomanian–Turonian age for the upper part of the Nimar Sandstone (Dassarma and Sinha 1975; Chiplonkar *et al.* 1977b); based on calcareous nannoplankton, Jafar (1982) assigned a Turonian age to the upper calcareous part of the Nimar Sandstone exposed in the Chikli and Sitapuri sections (Dhar district, Madhya Pradesh). A Cenomanian–Turonian age was assigned to the upper calcareous part of the Nimar Sandstone exposed at Pipaldehla (Jhabua district, Madhya Pradesh) based on fossil calcareous algae (Kundal and Sanganwar 1998).



Text-fig. 3. Sauropod indet. From the Cenomanian–Turonian of Borkui section (Dhar district, Madhya Pradesh). A – incomplete distal end of the right femur (VPL/KH/3500) in posterior view. Scale = 5 cm. B – enlarged view of the distal end of the femur showing the presence of embedded shells. Coin diameter = 3 cm.

Text-fig. 4. Panoramic view of the dinosaur bone-bearing (arrowed) red sandy soil (paleosol) in the Nimar Sandstone at Ratitalai section, Dhar district, Madhya Pradesh (scale = two boys sitting on the outcrop).



Text-fig. 5. Subsequent stages in the excavation of the fragmentary femur (VPL/KH/3502) recovered from the paleosol in the Nimar Sandstone at Ratitalai section, district Dhar, Madhya Pradesh. Scale = 5 cm.

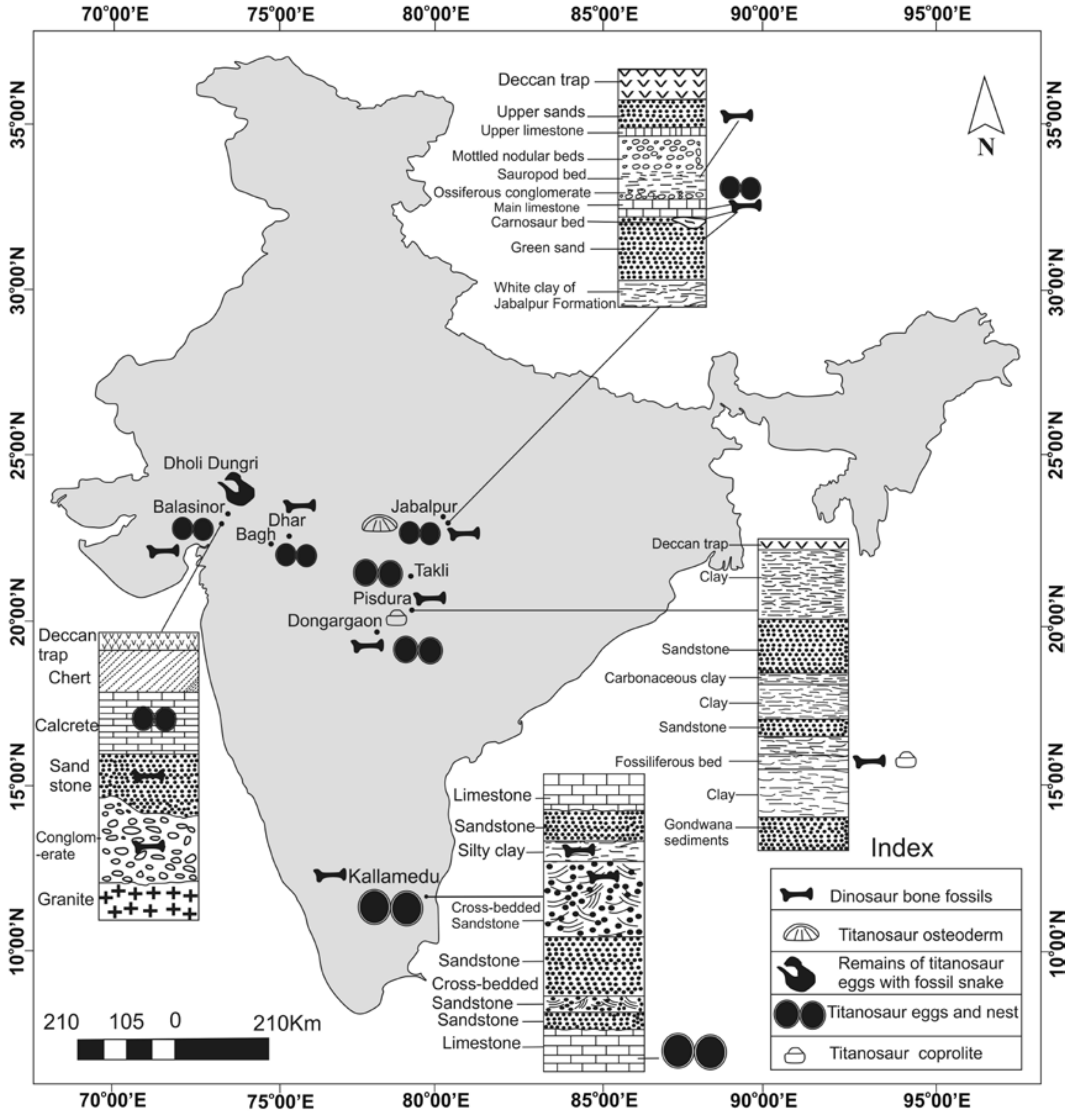
Nayak (2000) assigned a Cenomanian–Turonian age to the Nimar Sandstone based on the recovery of 15 bivalve species belonging to 10 genera from the uppermost part of the Nimar Sandstone exposed in the Akholi, Kanakakra, Ranapur, Rajla, Pipaldehla and Udaygarh sections (Jhabua district, Madhya Pradesh). The ages assigned on the basis of other biotic evidence such as ammonites, bivalves, bryozoans, calcareous algae, echinoids, planktonic foraminiferans and dinosaurs (Sharma 1976; Chiplonkar *et al.* 1977a; Jafar

1982; Taylor and Badve 1995; Nayak 2000; Bardhan *et al.* 2002; Khosla *et al.* 2003) clearly indicate a Cenomanian–Turonian age for the Nimar Sandstone.

Dinosaurs

The dinosaur fossils belong to at least to two individuals and include five broken femora, two incomplete humeri, radii, an ulna and several unidentified, broken bones (Khosla *et al.* 2003). The humerus recovered from Borkui is represented by the proximal end. The shaft is anteroposteriorly flattened in cross-section, and it further widens towards the distal condyle. In anterior and lateral views, the axis of the humerus is straight (Khosla *et al.* 2003). The distal end of the broken femur (Text-fig. 3) recovered from Borkui by AK and the National Geographic team in 2001, including professors Paul Sereno and Jeffrey Wilson, is well-preserved, and its maximum length and width are 0.77 m and 0.43 m, respectively.

The femoral shaft diameter is somewhat greater at the proximal end and half of the width across the distal end. On the posterior aspect of the femur, the distal condyles occupy subterminal positions. The second femur recovered from the Ratitalai section (Text-figs 4 and 5) is 1.08 m long, incomplete and thinner than the femora reported from the Borkui section. The ra-



Text-fig. 6. Map of India showing the principal Upper Cretaceous (Maastrichtian) dinosaur localities in the Lameta Formation with typical sections showing the position of the dinosaur-bearing beds (modified after Pal and Ayyasami 2022).

dius and ulna are incomplete, and the humeral articular surface of the ulna displays a rounded olecranon connected to the shaft of the ulna (Khosla *et al*. 2003).

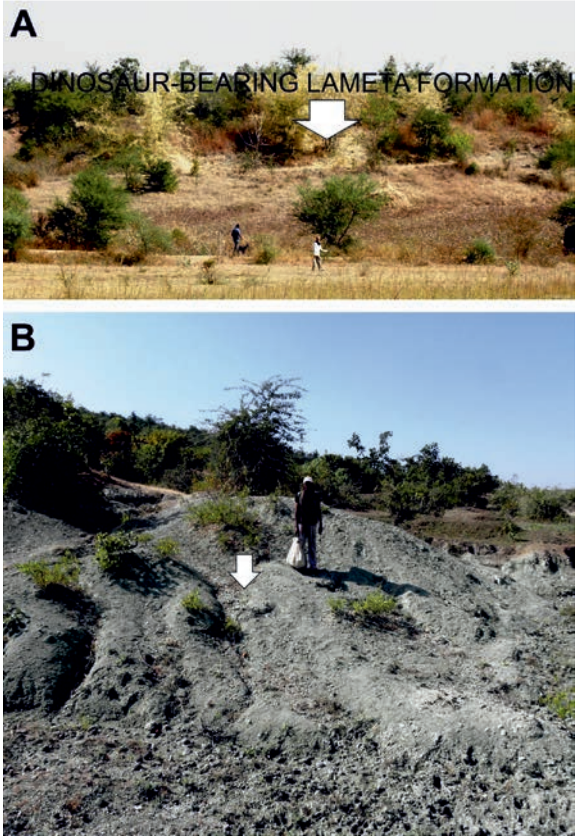
The sauropod bones from the Nimar Sandstone most likely belong to a new titanosaur species, possibly ancestral to the titanosaurs known from abundant remains from the younger (Maastrichtian) Lameta Formation of peninsular India (Chatterjee 2020). Chatterjee (2020) further suggested that the sauropod bones that have been reported from the Nimar Sandstone represent a dwarf titanosaur with an expected length of the femur surpassing >1.2 m. In addition to sauropods, several isolated abelisaurid teeth have been reported from the green sandstone, which constitutes the uppermost part of the Bagh beds (Prasad *et al*. 2016).

MAASTRICHTIAN DINOSAURS

Previous studies and geological context

The latest Cretaceous dinosaur skeletal material from India was first reported from Jabalpur in Madhya Pradesh, Pisdura and Dongargaon in Maharashtra, and Balasinor, Dholi Dungri and Rahioli in Gujarat (Text-fig. 6). Outcrops of the dinosaur-skeletal and egg-rich Lameta Formation cover an area of about 10,000 km, with thicknesses ranging from 3 to 12 m. The Infratrappean (lying below the Deccan traps) and Intertrappean Beds, which are intercalated between the Deccan traps, are well exposed in four areas: Jabalpur; Dhar and Jhabua districts, Madhya Pradesh; Kheda-Panchmahal district, Gujarat; and Pisdura, Nand-Dongargaon, Chandrapur district, Maharashtra (Khosla and Lucas 2020d; Pal and Ayyasami 2022; Text-fig. 6) where dinosaur remains occur in different geological contexts. The dinosaur-bearing Lameta Formation is a relic of an ancient soil cover that overlies several old shield basements in peninsular India along the Narmada River region, including the Archaeans, Aravalli metasediments, Godhra Granites, Bijawar metamorphics, Vindhyans, Gondwanas, and Bagh Beds, ranging in age from the Precambrian to the Early Cretaceous (Khosla and Lucas 2020c). The Godhra granitoids and the Aravalli metasediments form the basement rocks, which are unconformably covered by the 3–5 m thick Lameta Formation, rich in dinosaur skeletal remains, eggs and eggshells. Cherty limestones characterize the uppermost part of the Lameta Formation (Khosla and Lucas 2020c).

The Lameta Formation in the Jabalpur area rests directly on the Archaean basement and Gondwana Supergroup. In ascending order, it comprises the Green Sandstone, Lower Limestone, Mottled Nodular Bed, Upper Sandstone, and Upper Limestone. Skeletal material and many nests, including eggs and eggshells, were discovered in the Lower Limestone (Khosla and Lucas 2020c). The thickness of the dinosaur eggshell-rich part of the Lameta Formation varies from 1 to 11 m in the Pisdura and Nand-Dongargaon areas (Chandrapur district, Maharashtra; Text-fig. 7). The Lameta Formation is overlain by the Deccan traps in east, west, central and southern peninsular India (Khosla and Lucas 2020c).



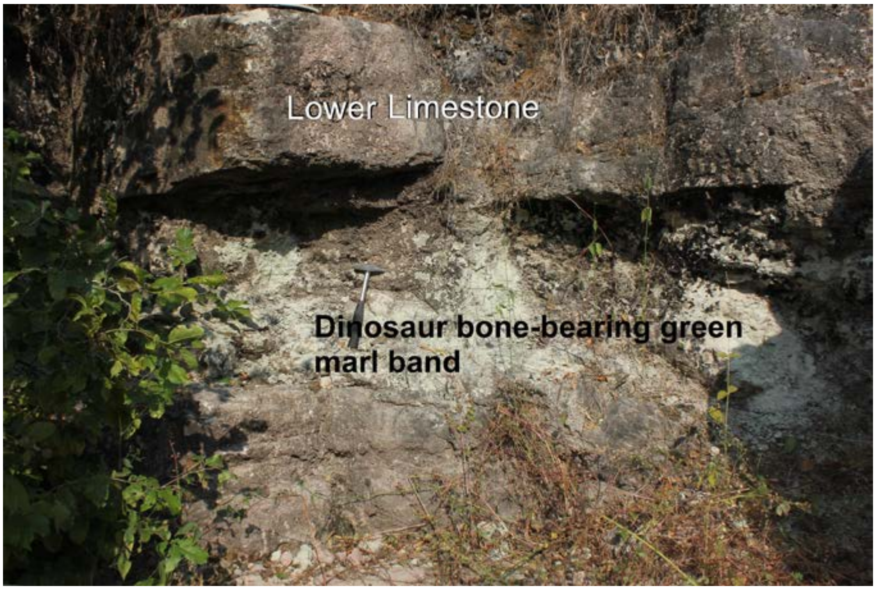
Text-fig. 7. Dinosaur skeletal-bearing sections (arrowed) of the Maastrichtian Lameta Formation at Pisdura, Chandrapur district, Maharashtra (A) and Dongargaon, Chandrapur district, Maharashtra (B) (modified after Khosla and Lucas 2020c).

Initial workers such as Lydekker (1877) recorded two caudal vertebrae, a chevron and incomplete femur of a sauropod (named by him as *Titanosaurus indicus*) from the Lower Limestone horizon at Bara Simla Hill (Jabalpur district). The slope yielded separate bones and teeth over the course of the following 50 years, including an initial theropod tooth designated as '*Orthogoniosaurus matleyi*' (Das-Gupta 1930; Wilson *et al*. 2003). Lydekker (1879) recorded also some titanosaur caudal vertebrae from the Lameta Formation of Pisdura (Chandrapur district, Maharashtra), which he assigned to a new species, *Titanosaurus blanfordi*. In addition to the sauropod material, Lydekker (1877) identified *Megalosaurus* sp., from Ariyalur beds at Tiruchirappalli, based on a solitary tooth.

British army personnel and the famous geologist Charles Matley excavated dinosaur skeletal material from the western slope of Bara Simla Hill at Jabalpur between 1917–1919. From the very beginning, Matley (1921a) thought that his assortment of bones from the 'Carnosaur bed' just below the Lower Limestone represented a single individual of another theropod, although just the sacrum and ilia were found in close proximity (Wilson *et al*. 2003). Matley (1921a) uncovered countless fragmentary sauropod bones, including a left ischium, fibula, radius, ulna (?), left scapula, right humerus, three caudal vertebrae, parts of a sacrum, broken ribs and a few chevron bones from the conglomeratic top of the Lower Limestone. Matley (1921a) also collected fragmentary sauropod bones (5000 osteoderms, several vertebrae, pelvic bones, a number of limb bones, two sacra, ribs, 20 chevron bones, more than 50 phalanges, numerous carpals, metacarpals and metatarsals), and various teeth of a predatory dinosaur from the Green Sandstone, which is overlain by the dinosaur eggshell-rich Lower Limestone. More recently, one of us (AK in 2016–2018 and 2020) re-examined the original site of the sauropod-bearing green marl band (Text-figs 8 and 9), which lies just above the Green Sandstone, and found a few fragmentary bones. At Chhota Simla Hill (Text-fig. 10), a huge vertebra, likely of a theropod, and a worn bone were recovered (Matley 1921a, b) from the Green Sandstone and conglomeratic band (Text-fig. 11), which lies about 60 cm beneath the Lower Limestone (Khosla and Lucas 2020c; Text-fig. 9).

Text-fig. 8. The original site of Matley (1921a) and Huene and Matley (1933) as it appears today, with the green marl band intercalated between the Green Sandstone and Lower Limestone horizon at Bara Simla Hill, Jabalpur, Madhya Pradesh.

The postcranial remains (sacrum, ilia, left tibia, dermal scutes, etc.) of a ?'stegosaurian' dinosaur (*Lametasaurus indicus* Matley, 1923) were recovered from the Lameta Formation of Jabalpur (Matley 1923). The fossil was later re-identified as an ankylosaur by



Text-fig. 9. Fragment of quarry wall at Chhota Simla Hill section (Jabalpur, Madhya Pradesh), with the Green Sandstone, dinosaur bone-bearing sandy pebbly marl band and dinosaur eggshell-bearing Lower Limestone (Khosla in preparation). Dinosaur bones were first excavated from the Green Sandstone horizon by Huene and Matley (1933). Hammer length = 29 cm.

Text-fig. 10. Panoramic view of the Chhota Simla Hill, Jabalpur, Madhya Pradesh, from where dinosaur bones were excavated.

Text-fig. 11. Fragmentary bone recovered from the conglomerate band at Chhota Simla Hill, Jabalpur, Madhya Pradesh. Coin diameter = 3 cm.

Huene and Matley (1933), and more recently identified as an abelisaurid (Wilson *et al*. 2003; Novas *et al*. 2004). Berman and Jain (1982) and Buffetaut (1987) commented that the dermal osteoderms of *L. indicus* may have belonged to *Titanosaurus indicus*. In spite of a few reports of stegosaur bones (*Brachypodosaurus gravis* Chakravarti, 1934) from the Lameta Formation of Central India (Huene and Matley 1933; Chakravarti 1934), and of *Dravidosaurus blanfordi* Yadagiri and Ayyasami 1979 from the Ariyalur Formation of South India (Yadagiri and Ayyasami 1979), none of the supposed stegosaur bones offer definite characters of that clade (Wilson *et al*. 2003). The sacrum and ilia collected by Matley (1921a), which are now lost (Chakravarti 1934), probably belong to a theropod. The osteoderms recovered from the 'Carnosaur bed' show close affinities to titanosaurian sauropods (*Saltasaurus* Bonaparte and Powell, 1980; *Ampelosaurus* Le Loeuff, 1995; Malagasy titanosaur in Dodson *et al*. 1998; *Magyarosaurus* Csiki, 1999) and theropods ('*Nuthetes*' Owen, 1854; *Ceratosaurus* Marsh, 1884; see Madsen and Welles 2000).

Huene and Matley (1933) excavated abundant dinosaur skeletal material from Bara Simla Hill (Jabalpur district) from three fossiliferous horizons (Text-fig. 12):

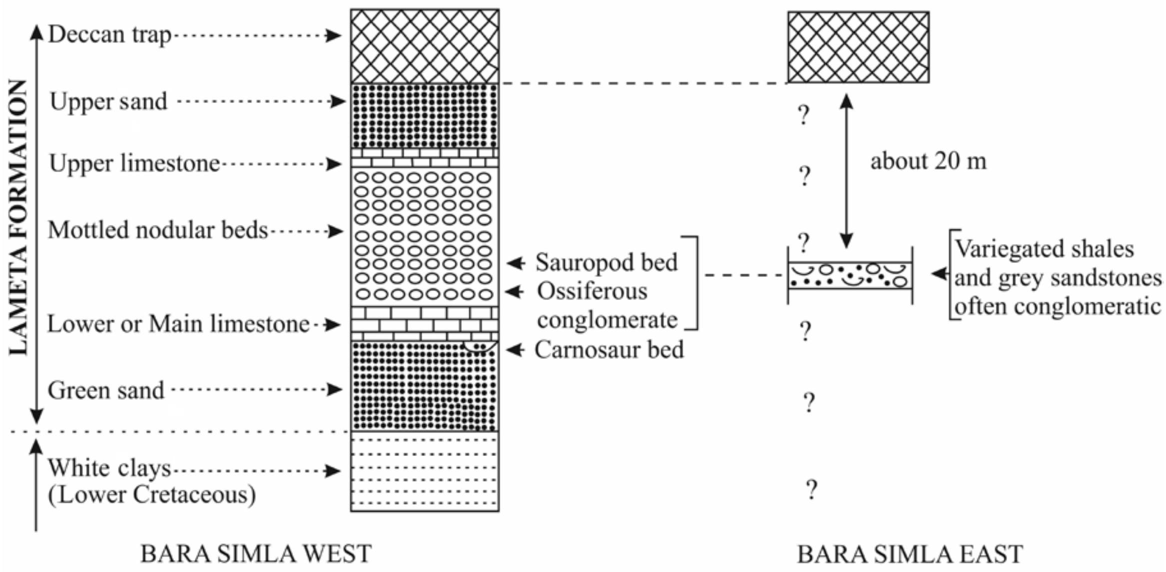
1. Sauropod bed: upper part of the Lower Limestone; with two different types of sauropods (*Antarctosaurus septentrionalis* Huene and Matley, 1933 and *Titanosaurus indicus*).
2. Ossiferous conglomerate: in the topmost part of the Lower Limestone; with fragmentary bones of a large sauropod.
3. Carnosaur bed: with diverse dinosaurs, e.g., scarce remains of sauropods and carnosaurs.

Barnum Brown recorded theropod dentaries and three caudal vertebrae from Bara Simla Hill in 1922 that could have belonged to a single individual, but no field notes with regard to their original configuration are known (Wilson *et al*. 2003). These dentaries were later assigned to *Indosuchus* Huene and Matley, 1933, but Walker (1964) distinguished them as tyrannosaurid (Chatterjee 1978). More recently, they have been re-evaluated and assigned to an abelisaurid theropod (Bonaparte *et al*. 1990; Molnar 1990; Chatterjee and Rudra 1996). Chatterjee and Rudra (1996) recovered lacrimal, jugal and angular bones of a theropod from Bara Simla Hill, whose detailed description is still awaited, and reconstructed a composite skull of *Indosuchus raptorius* Huene and Matley, 1933.

Abelisaurids are perhaps the most unusual predatory dinosaurs from disjunct Gondwanan continents during the Cretaceous. During the last 80 years, their remains have been recovered from the Upper Cretaceous Lameta Formation of the central and western parts of peninsular India, immediately underneath the Deccan basalts (Novas *et al*. 2010).

Dissociated parts of several predatory dinosaurs were found in the Lameta Formation, with the majority of them from a horizon known as the Carnosaur bed. Approximately 90 years ago, Huene and Matley (1933) described these fossils and recognized nine theropod species, which they sub-divided into the Carnosauria and Coelurosauria subgroups. In addition, they described a sizeable number of theropod hind limb bones (such as femora, tibia, metatarsals, and pedal phalanges) that they were unable to associate with any known species, but proposed to associate with coelurosaurid or allosaurid theropods (Novas *et al*. 2004).

The accessible collection of Cretaceous theropods from Bara Simla Hill housed at the Geological Survey of India at Kolkata was evaluated by Novas *et al*. (2004). According to Novas *et al*. (2004), previ-



Text-fig. 12. Lithostratigraphic scheme of two dinosaur localities, Bara Simla west and east (after Huene and Matley 1933 and Vianey-Liaud *et al*. 1987; scale about 1:1000; Khosla and Lucas 2020b).

ous researchers have acknowledged that *Indosaurus* Huene and Matley, 1933 and *Indosuchus* are abelisaurids. Based on cervical vertebrae, Novas *et al*. (2004) suggested that *Lametasaurus indicus* is a tiny abelisauroid that shares a cranial structure with *Masiakasaurus* Sampson, Carrano and Foster, 2001 and *Noasaurus* Bonaparte and Powell, 1980. Isolated vertebrae belonging to various parts of the neck and tail are used to represent the contentious taxa ‘*Ornithomimoides*’ Huene, 1932, ‘*Jubbulpuria*’ Huene and Matley, 1933, ‘*Dryptosauroides*’ Huene, 1932 and ‘*Compsosuchus*’ Huene and Matley, 1933, which also have abelisauroid characteristics. Novas *et al*. (2004) further considered that there are two distinct forms of abelisaurid feet: one with robust phalanges on digits III and IV, the other with transversely narrow, dorsoventrally thick phalanges on digit IV. The bones of the hind limbs that were previously referred to as ‘allosaurid’ and ‘coelurosaurian’ also exhibit abelisauroid characters. Allosaurid and coelurosaurian hind limb bones are now tentatively referred to as matching to *Indosaurus* or *Indosuchus*, while some pedal bones of lower size may belong to *Laevisuchus* Huene and Matley, 1933. Large size hind limb bones are tentatively referred to as corresponding to *Indosaurus* or *Indosuchus*. This review reveals that all of the theropods found in the Carnosaur bed are members of the Abelisauroidea, a single theropod clade. The Indian abelisaurids, e.g., *Lametasaurus* Matley, 1923, *Rajasaurus* Wilson, Sereno, Srivastava, Bhatt, Khosla and Sahni, 2003, *Indosaurus*, and *Indosuchus* (except for specimen ISIR 11, known as *I. raptorius*, now awaiting a comprehensive description), are fragmentary in nature, making it difficult to recognize the taxonomic validity of each of these taxa (Novas *et al*. 2004). Direct comparisons between each specimen and their respective taxonomic validity will eventually be resolved. Novas *et al*. (2004) commented that they continue to use the names *Indosaurus*, *Indosuchus*, *Lametasaurus*, and *Rajasaurus* until further research or discoveries may determine whether these taxa can be identified solely by their autapomorphies.

Based on Matley’s collection from Bara Simla Hill (Green Marl band) at Jabalpur and the Lameta Formation at Pisdura (Maharashtra) and Gujarat (western India), various authors, e.g., Huene and Matley (1933), Wilson *et al*. (2003), Novas *et al*. (2010), Khosla and Lucas (2020a–e) and Khosla (2021), worked on the problems of Lameta theropod taxonomy based on skeletal and fragmentary cranial elements. According to these authors, there are 11 named species of theropods (coelurosaurs most likely vastly overspilt), i.e., 3 smaller-bodied species [*Compsosuchus solus* (Huene, 1932), *Jubbulpuria tenuis* Huene and Matley, 1933 and *Laevisuchus indicus* Huene and Matley, 1933] and 8 medium-to-large sized theropods [*Rajasaurus narmadensis* Wilson, Sereno, Srivastava, Bhatt, Khosla and Sahni, 2003, *Rahiolisaurus gujaratensis* Novas, Chatterjee, Rudra and

Datta, 2010, *Indosaurus matleyi* (Huene and Matley, 1933), *Indosuchus raptorius*, *Dryptosauroides grandis* (Huene, 1932), *Coeluroides largus* (Huene, 1932), *Ornithomimoides mobilis* (Huene and Matley, 1933) and *O. barasimlensis* (Huene and Matley, 1933)].

However, many of these theropod taxa are based on bones of questionable affinity, and much of the holotypic material is presently damaged or lost. Nevertheless, their anatomy, phylogenetic associations and connections are beginning to clarify with the description of new material and survey of earlier collections. Re-assessment of these collections will help to better determine their systematic position (e.g., Novas and Bandyopadhyay 1999; Wilson *et al.* 2003; Novas *et al.* 2004; Carrano and Sampson 2008).

Overall, Late Cretaceous dinosaur skeletal material from peninsular India is characterized as follows (based on Vianey-Liaud *et al.* 1987; Hunt *et al.* 1994; Jain and Bandyopadhyay 1997; Wilson and Upchurch 2003; Wilson *et al.* 2003, 2011; Novas *et al.* 2004, 2010; Khosla and Lucas 2020c; Khosla 2021):

SAURISCHIA

1. Sauropoda:
Family **Titanosauridae**:
Titanosaurus indicus Lydekker, 1877; *T. blanfordi* Lydekker, 1879; *Jainosaurus* (= *Antarctosaurus*) *septentrionalis* (Huene and Matley, 1933); *Jainosaurus* cf. *septentrionalis* (Huene and Matley, 1933); *Isisaurus colberti* (Jain and Bandyopadhyay, 1997); indeterminate titanosaurid remains.

2. Carnosauria:
Family **Allosauridae**:
Indosaurus matleyi (Huene and Matley 1933); *Indosuchus raptorius* Huene and Matley, 1933
Family **Abelisauridae**:
Rajasaurus narmadensis Wilson, Sereno, Srivastava, Bhatt, Khosla and Sahni, 2003; *Rahiolisaurus gujaratensis* Novas, Chatterjee, Rudra and Datta, 2010; *Lametasaurus indicus* Matley, 1923

3. Coelurosauria:
Family **Compsognathidae**:
Compsosuchus solus (Huene, 1932)

4. Thyranoraptora:
Family **Coeluridae**:
Coeluroides largus (Huene, 1932); *Jubbulpuria tenuis* Huene and Matley, 1933; *Laevisuchus indicus* Huene and Matley, 1933; *Dryptosauroides grandis* (Huene, 1932)

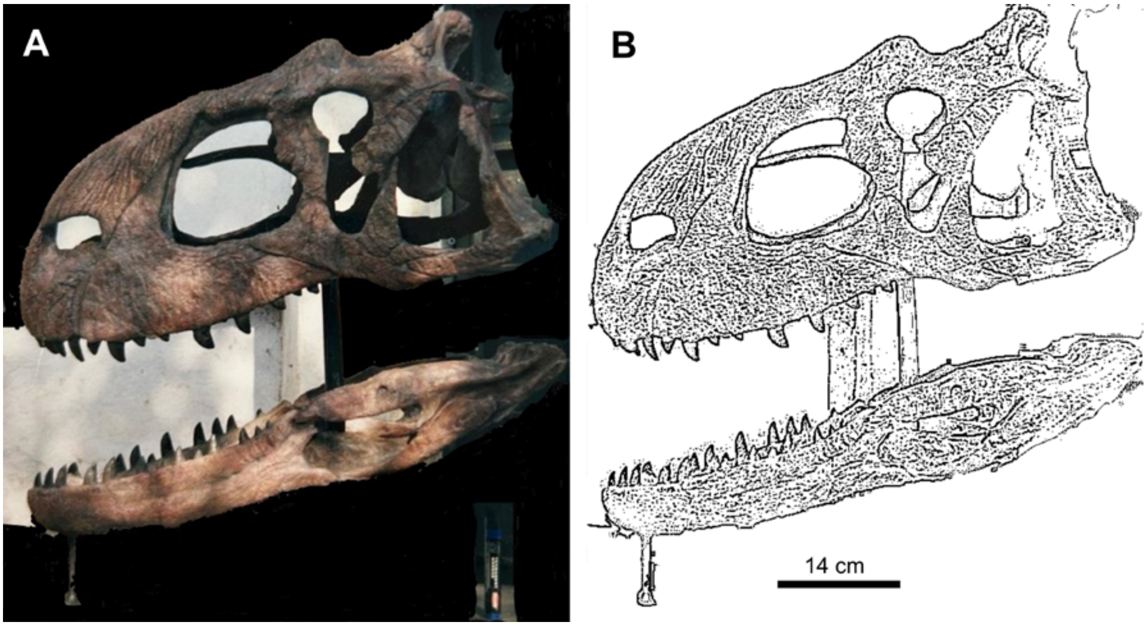
5. Ornithomimosauria:
Family **Ornithomimidae**:
Ornithomimoides mobilis (Huene and Matley, 1933); *O.* (?) *barasimlensis* (Huene and Matley, 1933)

Dinosaurs

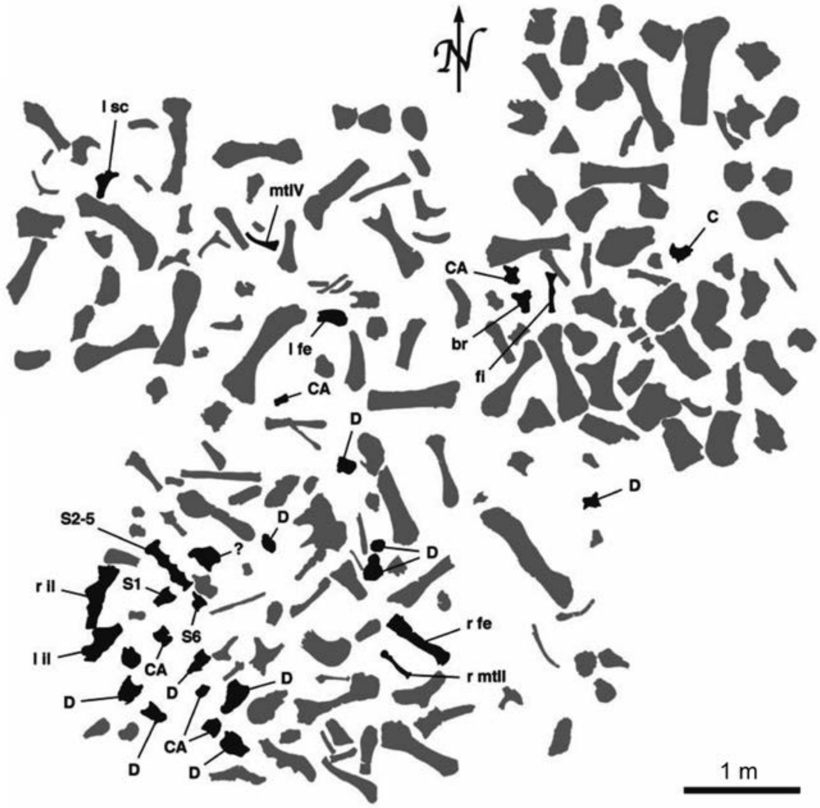
The cranial and postcranial remains of an abelisaurid theropod (*Rajasaurus narmadensis*, Text-fig. 13) were reported from the Maastrichtian rocks close to the town of Rahioli, Kheda district (Gujarat). The bones were recovered in a quarry where several paired bones, and a sacrum, ilia, and posterior dorsal and anterior caudal vertebrae were recovered (Text-fig. 14). GSI Type No. 21141/1-33, the holotype specimen, is a partial skeleton that includes the maxillae, premaxillae, braincase, quadrate bone, vertebrae, a femur and other hind limb bones, and tail. These post-cranial fossils are the first theropod postcrania to have been discovered from India.

Rajasaurus narmadensis was described from an incomplete skeleton consisting of a braincase (Text-fig. 15), supratemporal fenestrae and a unique middle nasofrontal projection, with the frontals shaping just the back edge of the eminence. Postcranial components include vertebrae and segments of the pelvic girdle and rear appendages. The axial skeleton consists of a cervical centrum, partial dorsal vertebrae, a sacrum with 6 sacral centra, and 7 partial caudal vertebrae. The appendicular skeleton includes partial ilia. The ilium, specifically, is powerfully developed with an edge that isolates the brevis fossa from the acetabulum. The wide and short pubic peduncle is shortened distally at around 50º from level as seen in horizontal view. The shaft of the femur is flattened anteroposteriorly and widens near the distal condyles. The tibial and fibular condyles are separated by a shallow intercondylar groove that is apparent in both distal and posterior views. Other preserved elements include the right distal tibia, right proximal fibula, right and left metatarsal II, and right metatarsal IV (Wilson *et al.* 2003).

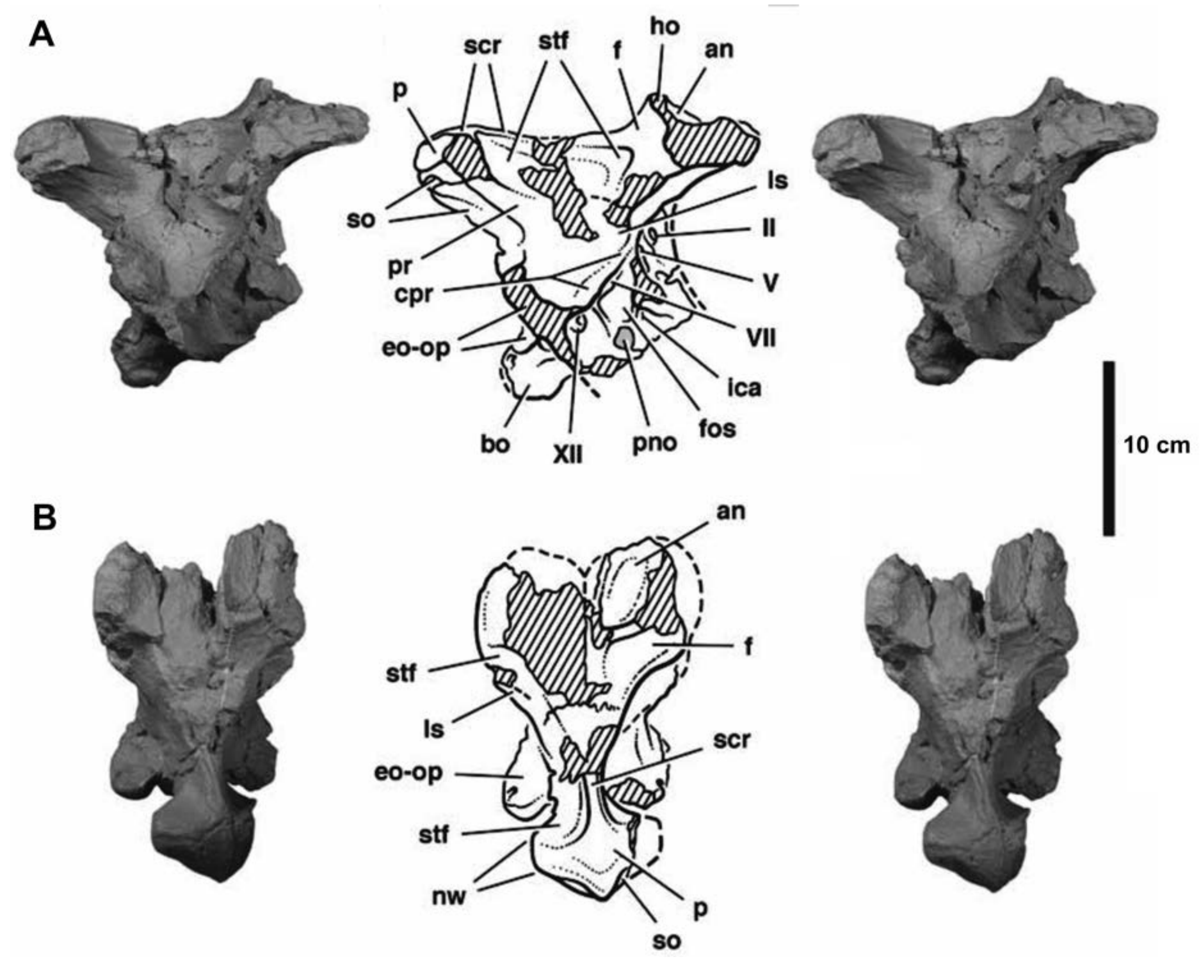
Anatomically, *Rahiolisaurus gujaratensis* is a thin limbed abelisaurid theropod based on material that includes a well-preserved right premaxilla with four partial teeth (Novas *et al.* 2010). The teeth are conical and somewhat flattened labiolingually. They have a piercing mesial carina but a rounded distal edge, and the long axis is oriented in the mesiodistal direction. The premaxillary interdental plates are combined and lack vertical edges, and the dental foramina are missing (see fig. 3.1 in Novas *et al.* 2010). The postaxial cervical vertebrae have a noticeable



Text-fig. 13. Abelisaurid *Rajasaurus narmadensis* (Wilson *et al*. 2003). A – reconstructed skull, which is on display at the Department of Geology, Panjab University Museum, Chandigarh, India; marker length = 14 cm. B – line drawing of the skull.



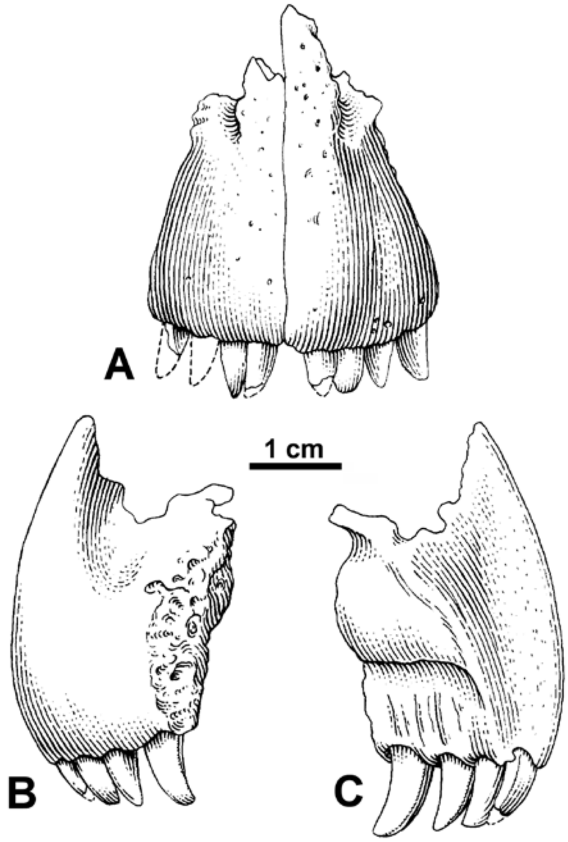
Text-fig. 14. Bones of the holotype of *Rajasaurus narmadensis* Wilson, Sereno, Srivastava, Bhatt, Khosla and Sahni, 2003 (GSI Type No. 21141) marked in black and titanosaurian sauropods marked in gray depicted on a quarry map of Temple Hill locality near Rahioli in Gujarat (after original quarry maps drafted in 1982–84 by S. Srivastava). Abbreviations: br – braincase; C – cervical vertebra; CA – caudal vertebra; D – dorsal vertebra; fe – femur; fi – fibula; il – ilium; l – left; mt – metatarsal; r – right; S – sacral vertebra; sc – scapula. Roman numerals indicate digit number; Arabic numerals indicate vertebral number (after Wilson *et al*. 2003).



Text-fig. 15. Stereopairs and line drawings of the braincase (cast) of *Rajasaurus narmadensis* Wilson, Sereno, Srivastava, Bhatt, Khosla and Sahni, 2003 (GSI Type No. 21141/1) in right lateral (A) and dorsal views (B). Cross-hatching indicates broken bone. Abbreviations: an – articular surface for nasal; bo – basioccipital; cpr – crista prootica; eo-op – exoccipital-opisthotic; f – frontal; fos – fossa; ho – horn; ica – internal carotid artery; ls – laterosphenoid; nw – nuchal wedge; p – parietal; pno – pneumatic opening; pr – prootic; scr – sagittal crest; so – supraoccipital; stf – supratemporal fenestra. Roman numerals denote openings for cranial nerves (after Wilson *et al*. 2003).

edge that interfaces with two zygapophyses. The pubis and ilium are firmly sutured. The ilium is moderately low with the postacetabular portion bearing a sharp caudodorsal eminence. The proximal half of the left pubis is well-preserved. The ischia are large and somewhat joined at the symphysis. The metatarsal I is rod like, and metatarsal II is constricted proximally. It should be remembered, though, that in 1933 no one had ever heard of an abelisaurid. *Abelisaurus* Bonaparte and Novas, 1985 was described for the first time from Argentina, and the family gained recognition when its representatives were recognized in Madagascar (*Majungasaurus* Lavocat, 1955) and, later, also in India. *Rajasaurus narmadensis* is clearly related to *Carnotaurus* Bonaparte, 1985 from South America and *Majungatholus* Sues and Taquet, 1979 from Madagascar, and also to the abelisaurids from Africa (Wilson *et al*. 2003).

Indosuchus raptorius is a medium-sized tyrannosaur described from a partial skull. The bones of *Indosuchus* demonstrate that it was a small, compact tyrannosauroid that was similar to the derived allosaurs from which it evolved (Walker 1964; Chatterjee 1978). The skull contains 4 premaxillary teeth, 14 maxillary teeth, and low tooth crowns (Text-fig. 16). The maxilla lacks a preantorbital fenestrae. There are premaxillary teeth with D cross-sections in the tip of the upper jaw, a tall, broad tipped nose, a large, dorsally raised maxilla, tyrannosaurian-type supratemporal fenestrae, and a narrowing of the skull bones over the orbits, which suggests binocular vision. The lingual portion of the maxilla over the fused interdental



Text-fig. 16. *Indosuchus raptorius* Huene and Matley, 1933, specimen AMNH 1753. A – anterior view of the conjoined premaxillae; B, C – lateral and medial views of the premaxilla (modified after Chatterjee 1978).

plate is smooth and vertical with a small overhanging shelf (Chatterjee 1978).

A virtually complete skeleton of *Indosuchus* from Rahioli (Kheda district, Gujarat) was described by Chatterjee and Rudra (1996) and Wilson *et al.* (2003). Characteristics of this taxon include the lack of pleurocoels in the presacral vertebrae, the small forelimb length relative to the hind limb, the footed pubis, and sturdy hind limb bones. However, a skeletal reconstruction that accompanies the description appears to run counter to several portions of the description (Chatterjee and Rudra 1996, fig. 13). Thus, the long bones in the reconstruction, like most abelisaurid long bones from Jabalpur, are not very robust (Matley 1923, pl. 11; Huene and Matley 1933, pl. 18; Wilson *et al.* 2003).

Indosaurus matleyi is a theropod dinosaur characterized by an incomplete skull (partial braincase) of unusual thickness. The cranium indicates that *Indosaurus* may have had horns over its eyes, although there is no direct fossil evidence of this. *Indosaurus matleyi* bears thickened frontals and raised parietals; these features are likewise seen in the South American dinosaur *Carnotaurus sastrei* Bonaparte, 1985, and indicated in an abelisaurid known from the Goro Frigio Formation of Albian–Cenomanian age in Argentina (Bonaparte 1985). In addition, vertebral components similar to those of *Carnotaurus* are known from the Upper Cretaceous Lameta Formation at Rahioli (Chatterjee and Rudra 1996; Loyal *et al.* 1998).

Other theropods that were recovered by Huene and Matley (1933) from the Bara Simla Hill were assigned to medium-to-large sized theropods that include *Compsosuchus solus*, *Ornithomimoides mobilis* and *O.* (?) *barasimlensis*, *Laevisuchus indicus*, *Jubbulpuria tenuis*, *Coeluroides largus* and *Oryptosauroides grandis*. Based on shared apomorphies, *C. solus* was considered an allosaurid (Molnar *et al.* 1990; Molnar and Farlow 1990). More recently, Wilson *et al.* (2011) questioned the validity of these theropod taxa.

Hunt *et al.* (1994) erected *Jainosaurus* for the Indian titanosaurid taxon and described *Jainosaurus* (= *Antarctosaurus*) *septentrionalis* from the Indian Infratrappean localities (Huene and Matley 1933; Hunt *et al.* 1994). Further, Wilson (2002, 2005) described *J. septentrionalis* as a titanosaur based on the contact between the quadrate and basal tubera and a pendant, non-articular ventral spine on the paroccipital process (Wilson *et al.* 2011). Other diagnostic characters of *J. septentrionalis* include an extended spur of the prootic that broadens onto the basipterygoid process and a diagonally arranged humeral deltopectoral process. Other important characters include the presence of anteroposteriorly thin bone covering part of the humerus, and an anteriorly protracted spiral condyle on the distal part of the humerus (Wilson *et al.* 2009). Other diagnostic characters displayed by the specimen of *J.* cf. *septentrionalis* from Chhota Simla Hill (very close to the Bara Simla Hill locality) include the proximally arranged fourth trochanter on the femur, a close mutual articulation of the tibia and fibula, and an anterior crest set off by a ridge on the fibula (Wilson *et al.* 2011).

Another titanosaur (sauropod) was discovered from the Upper Cretaceous Lameta Formation of Dongargaon (Chandrapur district, Maharashtra; Jain and Bandyopadhyay 1997). Their *Titanosaurus colberti* was later reassigned by Wilson and Upchurch (2003) to a new genus, *Isisaurus*. It is distinguished from other sauropods by its short, vertically oriented neck and long forelimbs. The humerus has a length of 148 cm (Jain and Bandyopadhyay 1997). According to Montague (2006), *Isisaurus* might have reached a length of about 18 m and a weight of about 14,000 kg based on that specimen.

Isisaurus is known from substantially better remains than the majority of the other Indian titanosaurs. Most of its postcranial skeleton has been discovered. Between 1984 and 1986, Jain and Bandyopadhyay discovered skeletal material in a mostly articulated condition; it includes dorsal, caudal, cervical, and sacral vertebrae, ribs, pelvis, scapula, coracoid, left forelimb, and other bones, though the skull, hind limb, and foot bones were not in articulation (Jain and Bandyopadhyay 1997). The skull of *Isisaurus* is robust and small. The angle at which the occipital condyle projects in the braincases of *Isisaurus* and *Jainosaurus* is a notable distinction. The *Isisaurus*-like braincase from Dongargaon (ISI R199) has the occipital condyle displaced off the plane of the occiput at an angle of around 120º according to Berman and Jain (1982), who considered this trait to be analogous to that of *Apatosaurus* Marsh, 1877 and *Diplodocus* Marsh, 1878. Wilson *et al.* (2009) also considered that the *Isisaurus* cranium is similar to that of *Apatosaurus* and *Diplodocus* (Family Diplodocidae). Other diagnostic characters include: 6 co-ossified vertebrae and ribs that compose the sacrum; chevron facets in the distal caudals on relatively low ridges; a large scapula; the preacetabular process of the ilium prominently pointed outwards; a robust pubis and ulna; and a flat and blade-like ischium (Jain and Bandyopadhyay 1997).

Various authors (e.g., Wilson 2002; Upchurch *et al.* 2004; Curry Rogers 2005; Wilson *et al.* 2011) included *Isisaurus* in their phylogenetic analysis. While its sister-group relationship to other titanosaurs remains disputed, its position as an outgroup to the Saltasauridae has been repeatedly verified. According to Wilson *et al.* (2011), an initial analysis indicates that *Isisaurus* is firmly linked with the South American 'lognkosaurian' titanosaurs, which include *Futalognkosaurus* Calvo, Porfiri, González-Riga and Kellner, 2007, *Mendozasaurus* González-Riga, 2003, and all species more closely related to them than to different sauropods, as per Calvo *et al.* (2007). Titanosaurs such as *Ligabuesaurus* Bonaparte, González-Riga and Apesteguía, 2006, *Bonitasaura* Apesteguía, 2004 and *Puertasaurus* Novas, Salgado, Calvo and Angolin, 2005, and different titanosaurs are among the 'lonkgosaurian' titanosaurs. González-Riga (2005) recognized resemblances between *Isisaurus* and *Mendozasaurus*, and Wilson *et al.* (2011) added to that with new evidence.

Critical review and current status of the *Titanosaurus* fauna in India

Three genera, i.e., '*Titanosaurus*' Lydekker, 1877, '*Antarctosaurus*' Huene, 1929, and '*Laplatasaurus*' Huene, 1929, were first documented as representing the diversity of sauropods in the Late Cretaceous of India. It was believed that each of these genera is closely comparable to taxa on other southern continents. The validity of '*Titanosaurus*' and the alleged close relationships between its constituent species, notably those from the Cretaceous of Madagascar and South America, have been contested by the recent systematic studies of Wilson *et al.* (2009). '*Laplatasaurus*' is also presently thought to be limited to South America, making the Indian species unreliable. In order to assess the validity, composition, and phylogenetic affinity of the Indian sauropod species '*Antarctosaurus*' (now known as *Jainosaurus*), Wilson *et al.* (2009) redescribed its anatomy in a detailed manner. They stated that the braincase, skull roof, and several postcranial elements that made up the type series of *J. septentrionalis* were all distinguished by their size in comparison to the other taxon from the same quarry, '*Titanosaurus indicus*'. Until recently, all postcranial bones were not known. In the collections of the Indian Museum in Kolkata, the type series humerus and a cast of the scapula were rediscovered. Wilson *et al.* (2009) examined the potential relationships between the components of the type series, revealing inferred evidence that supports the idea of classifying some of them as a single species. The cranium and a few postcranial bones are diagnostic, allowing *J. septentrionalis* to be identified from further material found in the same location and other parts of Indo-Pakistan (Wilson *et al.* 2009).

Six Indian Late Cretaceous titanosaurid (sauropod) dinosaurs have been found so far from the Lameta Formation, including *Jainosaurus* (= *Antarctosaurus*) *septentrionalis*, *J.* cf. *septentrionalis*, *Isisaurus colberti*, *Titanosaurus blanfordi*, *T. indicus*, and unidentified titanosaurid fragments (Huene and Matley 1933; Hunt *et al.* 1994; Wilson and Upchurch 2003; Wilson and Mohabey 2006; Wilson *et al.* 2011).

Diagnostic cranial and postcranial evidence collected from many Infra- and Intertrappean beds of India allowed Hunt *et al.* (1994) and Wilson *et al.* (2009) to identify *Isisaurus* and *Jainosaurus*. Apart from the central and western parts of peninsular India, *Isisaurus* has lately been recorded from western Pakistan and India (Wilson *et al.* 2009). Diagnostic features such as the alignment of the occipital condyle, the shape of the basal tubera, and proportional variations in the humerus and scapula are just a few of the features that distinguish the cranial and postcranial remains of *Jainosaurus* from those of the other Indian Cretaceous sauropod, *Isisaurus colberti* (Wilson *et al*. 2009). *Jainosaurus* appears to be more closely related to the 'Malagasy Taxon B' and the South American titanosaurs *Antarctosaurus wichmannianus* Huene, 1929, *Muyelensaurus* Calvo, Porfiri, González-Riga and Kellner, 2007, and *Pitekunsaurus* Filippi and Garrido, 2008, and then to *Isisaurus* or the Malagasy titanosaur *Rapetosaurus krausei* Curry Rogers and Forster, 2001 (Wilson *et al*. 2009). A sister-taxon connection between *Jainosaurus* and *Isisaurus* within the Titanosauria is not yet established, although it cannot be ruled out. Based on the available information, *Jainosaurus* thus could have near cousins in Madagascar and South America.

In the light of this, projections of faunal endemism following a prolonged time of isolation as India moved northward do not correspond with our present understanding of the Indo-Pakistani Cretaceous sauropods. Instead, cranial and postcranial traits show close evolutionary relationships between the titanosaurs from South America and Madagascar and *Jainosaurus*. There is currently no evidence that an indigenous sauropod fauna existed in present-day India during the Late Cretaceous (Wilson *et al*. 2009). These and other titanosaur phylogenetic connections will be the subject of future research and need to be verified further by a thorough cladistic examination of the Titanosauria (Wilson *et al*. 2009).

PALEOBIOGEOGRAPHICAL IMPLICATIONS OF INDIAN LATE CRETACEOUS DINOSAURS

Paleontological data from the Indian Subcontinent's Upper Cretaceous Deccan volcanic-sedimentary strata are critical for testing the geophysical hypotheses that argue for an isolated India during this time interval. During the Mesozoic, the paleobiogeographic setting of the Gondwana supercontinent had a significant impact on the dispersal of terrestrial vertebrates on adjacent continental areas such as India and Madagascar. The supercontinent was divided into a series of extensive landmasses (South America, New Zealand, Australia, Africa-Arabia, Antarctica, Madagascar, and the Indian subcontinent), that were becoming increasingly fragmented. Its land animals were separated, evolving into distinctive faunas, especially during the Late Jurassic and Cretaceous (Krause *et al*. 2019; Langer *et al*. 2019; Khosla 2021). Following its fragmentation, India moved northward as a distinct landmass, becoming isolated from Madagascar at around 88 Ma and traversing across the Neotethys to finally collide with Asia in the Early Eocene (Chatterjee and Scotese 2010; Khosla 2021).

The Late Cretaceous fossil fauna and flora found in the Deccan Infra- and Intertrappean sedimentary deposits of east, west, central and southern peninsular India comprise a mixture of Gondwanan and Laurasian elements (Khosla 2014, 2015; Kapur and Khosla 2016, 2019), as well as endemic ones, seemingly contradicting the geophysical model that depicts India as an island continent during the Late Cretaceous. The faunal similarities (predominantly dinosaurs) between the Indian Subcontinent's Upper Cretaceous and parts of Gondwana, such as Madagascar, Africa and Antarctica, provide intriguing hints about the degree of biogeographic connectedness between those areas (Kapur and Khosla 2016). As now understood, *Rajasaurus narmadensis*, *Rahiolisaurus gujaratensis* and *Indosaurus matleyi* are perceived as abelisaurid skeletal remains from peninsular India (Kapur and Khosla 2016, 2019; Khosla 2021).

Abelisaurid dinosaurs are mainly recognized as indigenous to Gondwana and are thought to play a key role in understanding Gondwana's Cretaceous biogeography (Sampson *et al*. 1998; Sereno *et al*. 2004). Two competing hypotheses have been presented to explain the absence or presence of abelisaurids in the African Cretaceous, 'Africa-first' and 'pan-Gondwana' (e.g., Sereno *et al*. 2004; Verma *et al*. 2016). According to the 'Africa-first' hypothesis, the absence of abelisaurids in Africa and their presence in India, Madagascar and South America implies that the group first appeared in Gondwana during the Early Cretaceous, after Africa's physical isolation (Sampson *et al*. 1998; Verma *et al*. 2016). Kapur and Khosla (2016) noted that abelisaurids have not been considered as widespread in the Laurasian mainlands because of their fragmentary record from Europe. Sereno *et al.* (2004), on the other hand, discovered abelisaurids in the Aptian–Albian and Cenomanian of Africa, leading them to conclude that the group had a pan-Gondwanan distribution. Therefore, the presence of abelisaurids in India, Madagascar, Africa and Europe can now better be explained and largely clarified by the 'Pan Gondwana' model, which identifies a common fauna on the Gondwanan territories before the separation of the African landmass during the Early Cretaceous (e.g., Sereno *et al*. 2004; Sereno and Brusatte 2008; Kapur and Khosla 2016, 2019; Khosla 2021). The 'pan-Gondwana' scenario thus postulates that abelisaurid dinosaurs originated in Gondwana before the Late Cretaceous, and three narrow and sporadic routes existed between the major Gondwana continents: (i) between South America and Africa, via the Walvis Ridge and Rio Grande Rise; (ii) during the Late Cretaceous, c. 97 Ma, via the Palmer Land Block and South Georgia island terrane between Antarctica and South America; and (iii) via the Kerguelan Plateau and Gunnerus Ridge flanked by Indo-Madagascar and Antarctica (Sereno *et al.* 2004; Sereno and Brusatte 2008; Verma *et al.* 2016).

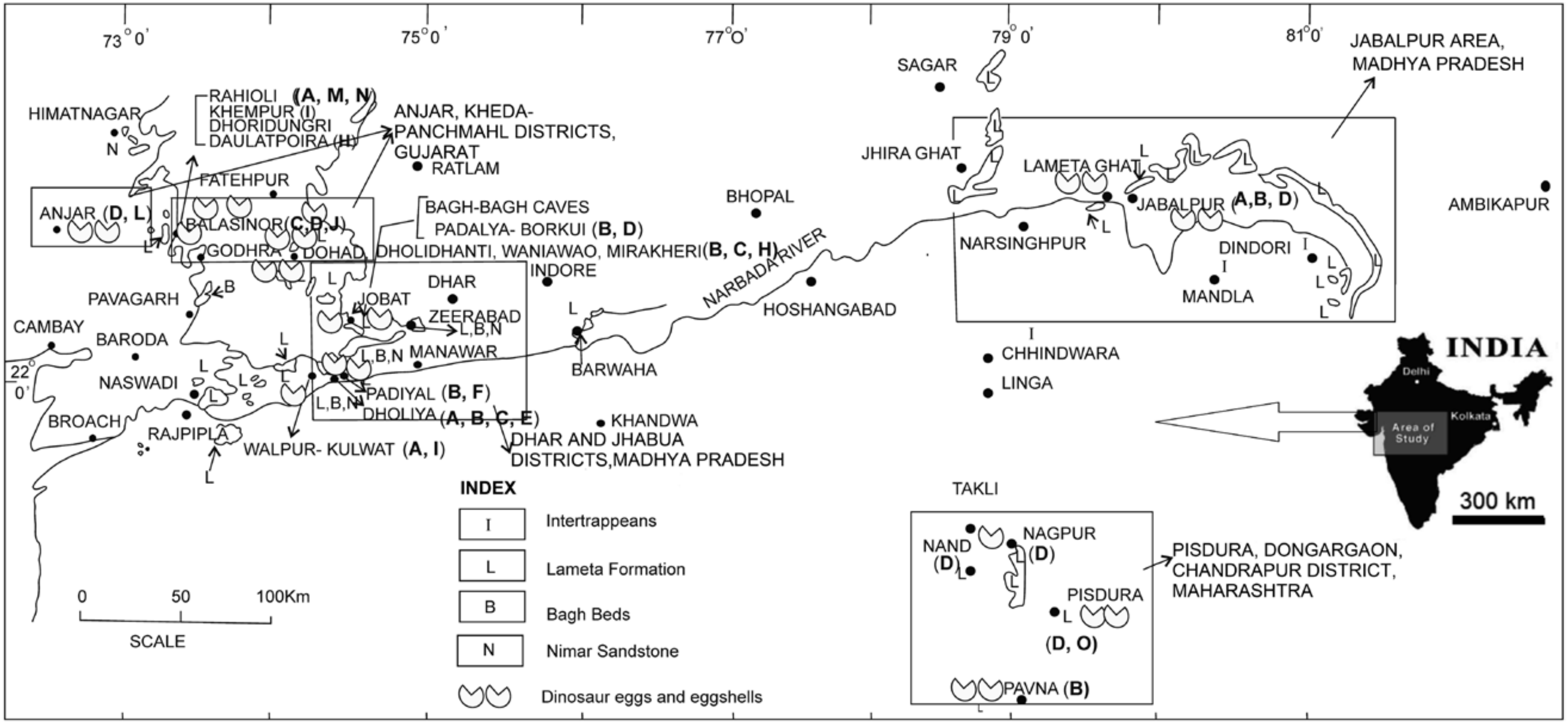
The primary difference between these two models is the time of the separation between Africa and South America, which Krause *et al.* (2006) comprehensively addressed. Abelisaurids had a Gondwanan distribution and reached an amalgamated Indo-Madagascar block from South America through Antarctica, the Kerguelan Plateau, and the Gunnerus Ridge before c. 97 Ma, and this is relevant to these hypotheses in the Indian setting (Verma *et al.* 2016). This is in line with Ali and Aitchison's (2008, 2009) paleogeographic reconstructions.

The European abelisaurid *Arcovenator escotae* Tortosa, Buffetaut, Vialle, Doutur, Turini and Cheylan, 2014 was discovered in the Upper Campanian of France. This clearly shows that abelisaurids were present in Europe prior to the time when the Gondwanan landmasses were totally disconnected (Kapur and Khosla 2016). Moreover, the definite phylogenetic investigation by Tortosa *et al.* (2014) shows that *Arcovenator* forms a clade with the Indo-Madagascar abelisaurids *Rajasaurus*, *Rahiolisaurus*, *Indosaurus* and *Mahajungasaurus* Lavocat, 1955, and that this clade is remotely related to the South American abelisaurids, suggesting a geologically closer predecessor for European *Arcovenator* and the Indo-Madagascar abelisaurids (Kapur and Khosla 2016, 2019; Khosla 2021).

In view of the phylogenetic hypotheses, various workers (Tortosa *et al.* 2014; Kapur and Khosla 2016, 2019; Khosla 2021) have additionally proposed a trans-maritime dispersal of abelisaurids between Europe and Africa toward the start of the Late Cretaceous and between India, Madagascar and Africa at the end of the Late Cretaceous. Ali and Aitchison (2008) and Kapur and Khosla (2016) contend that a close land association between Africa and Indo-Madagascar is unlikely in light of the geophysical evidence that shows a confined Indian Subcontinent surrounded by deep seas during the terminal period of its northward movement. An extensive marine barrier may thus have prevented dispersal of the large abelisaurids. The proximity of Africa with the Indian landmass or an unusual land association among India and Asia through the Kohistan-Dras Island may have shaped conceivable dispersal routes, as proposed by Chatterjee *et al.* (2013), yet this is in contrast to the most substantiated geophysical evidence (Kapur and Khosla 2016).

Based on cranial and postcranial remains, 6 titanosaurid dinosaur taxa are known from the Lameta Formation of peninsular India: *Jainosaurus* (= *Antarctosaurus*) *septentrionalis* (Huene and Matley 1933; Hunt *et al.* 1994); *Jainosaurus* cf. *septentrionalis*, (Wilson *et al.* 2011); *Isisaurus colberti* (Jain and Bandyopadhyay 1997; Wilson and Upchurch 2003); *Titanosaurus blanfordi* and *T. indicus* (Wilson and Upchurch 2003; Kapur and Khosla 2016); as well as indeterminate titanosaurid remains (Wilson and Mohabey 2006). Wilson and Upchurch (2003) and Wilson *et al.* (2011) re-examined the taxonomic status of the widely distributed '*Titanosaurus*' species in India and found that only *T. colberti*, which they renamed *Isisaurus colberti*, is valid. Wilson *et al.* (2009, 2011) reexamined the type series of '*Antarctosaurus*' *septentrionalis* and found that it does not belong to the South American genus *Antarctosaurus*. It has been renamed *Jainosaurus septentrionalis* and is still a recognized species (Hunt *et al.* 1994). Another Indian species, *Laplatasaurus madagascariensis* (Huene and Matley 1933; Wilson *et al.* 2011), has not yet been re-evaluated, partly because the type material is not, at this point, accessible, and it has been regarded as an invalid species by a number of workers (e.g., McIntosh 1990; Upchurch *et al.* 2004; Wilson *et al.* 2011). Thus, ongoing work considers just *Jainosaurus* and *Isisaurus* to be valid taxa (Wilson *et al.* 2011; Kapur and Khosla 2016).

The only sauropods bearing osteoderms were titanosaurs, although the evolutionary distribution of this characteristic within the Titanosauria has yet to be determined. While the bulk of titanosaur osteoderms were discovered in South American rocks, some have been discovered in European, Madagascan, and African Cretaceous strata. A titanosaur osteoderm from the Lameta Formation of Bara Simla Hill was described by D'Emic *et al.* (2009), extending the geographic range of these armored sauropods, though titanosaur distribution is reported to be wider than titanosaur osteoderm distribution. According to D'Emic *et al.* (2009), one or more of the following factors could account for the disparity: (i) only a few titanosaur taxa have osteoderms; (ii) titanosaurs were not well-armored; or (iii) these elements are subject to substantial collecting and/or (iv) taphonomic biases. To date, nearly 90 discrete titanosaur osteoderms have been described, and they can be assigned to 10 of the 40+ titanosaur genera that are currently documented (D'Emic *et al.* 2009).



Text-fig. 17. Map showing the distribution of Indian Late Cretaceous dinosaur nesting sites exposed in four areas: Jabalpur; Dhar and Jhabua Districts, Madhya Pradesh; Kheda-Panchmahal district, Gujarat; and Pisdura, Nand-Dongargaon, Chandrapur district, Maharashtra (modified after Khosla and Lucas 2020d). Abbreviations: **A** – *Megaoolithus cylindricus*; **B** – *Megaoolithus jabalpurensis*; **C** – *Fusioolithus mohabeyi*; **D** – *Fusioolithus baghensis*; **E** – *Fusioolithus dholiyaensis*; **F** – *Fusioolithus padiyalensis;* **G** – *Megaoolithus dhoridungriensis*; **H** – *Megaoolithus megadermus*; **I** – *Megaoolithus khempurensis*; **J** – Problematica (?Megaoolithidae); **K** – Incertae sedis; **L** – *Subtiliolithus kachchhensis*; **M** – *Elipsoolithus khedaensis*; **N** – cf. *Trachoolithus* sp.; **O** – ?*Sphaeroolithus* sp.

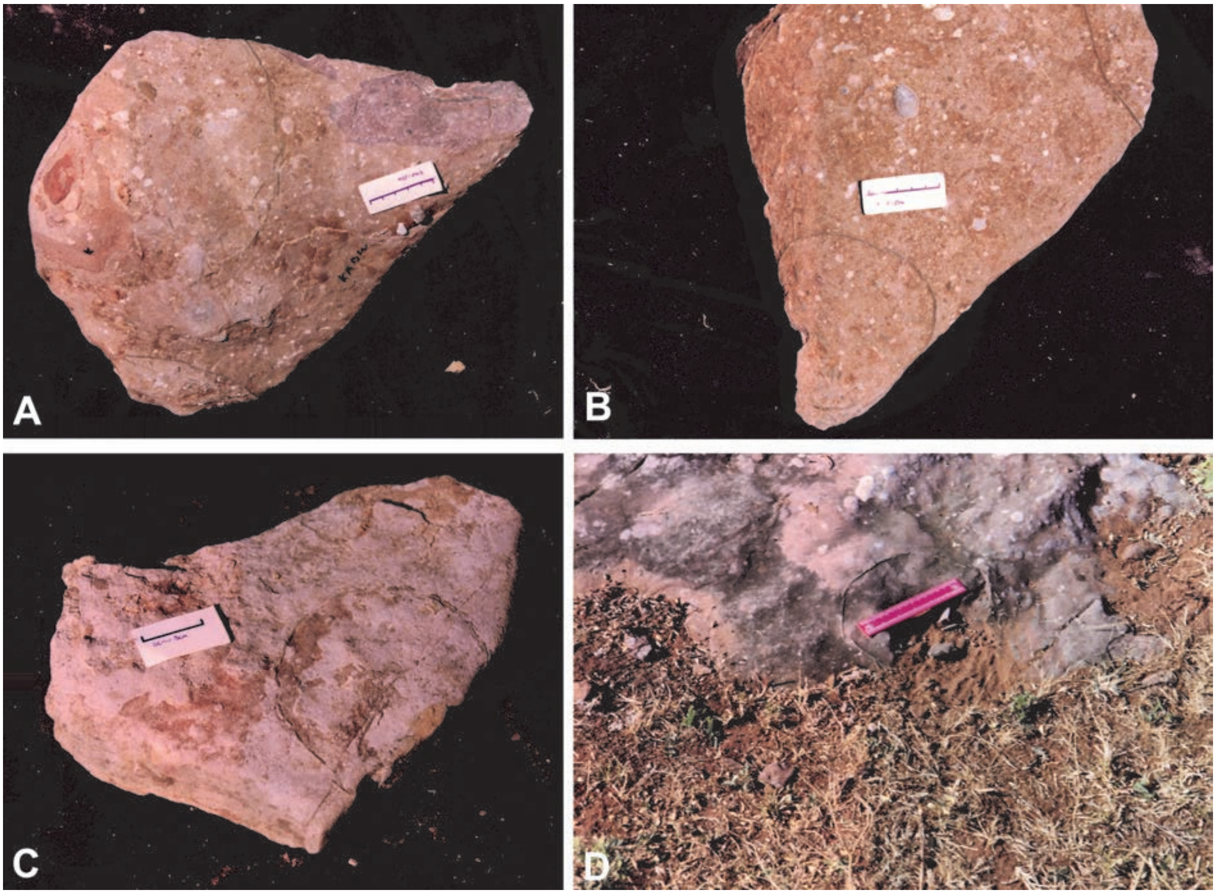
Isisaurus has been discovered in the Lameta Formation of western India (Chatterjee and Rudra 1996), central India (Jain and Bandyopadhyay 1997) and Pakistan (Wilson *et al.* 2005). *Jainosaurus* is only found in Central India (Chatterjee and Rudra 1996; Huene and Matley 1933). The holotype of *Isisaurus* has no osteoderms, and the majority of the skeleton was discovered in a small area (D'Emic *et al.* 2009). Malkani (2008) also recorded titanosaurids from the Upper Cretaceous (Pab Sandstone) of Pakistan and highlighted a greater diversity of these enormous vertebrates (five titanosaurid species of questionable validity) in the Indo-Pakistan area during the Late Cretaceous. To date, the Pab Formation has not yielded articulated remains of titanosaurs, nevertheless, abundant isolated elements have been discovered, few of which are well preserved and diagnostic (Wilson *et al.* 2011). From Pakistan, *Isisaurus colberti* (Wilson *et al.* 2005) is known from a largely complete, rather undeformed braincase, together with an *Isisaurus*-like ulna (Malkani 2006) and a humerus resembling that of *Jainosaurus* (Wilson *et al.* 2009, 2011). Malkani (2004, 2006, 2008) divided the 5 titanosaurid species known from the Pab Formation into two lineages, the Balochisauridae and Pakisauridae, which are hypothesized to vary in the sturdiness of their limb components and the form of the caudal centra, among other traits (Wilson *et al.* 2011).

The two-genera division of Indian titanosaurs is reflected in the bipartite categorization of Pakistani titanosaurs, and the likely occurrence of both Indian genera in Pakistan. It is likely that the sauropod faunas of the Upper Cretaceous Pab and Lameta formations overlap extensively (Wilson *et al.* 2011), though a detailed comparison of the titanosaurids from India and Pakistan has not been undertaken (Wilson *et al.* 2011; Kapur and Khosla 2016). There is still a chance that more titanosaur bones from the Pab Sandstone will be discovered, and be possibly assignable to *Jainosaurus* and *Isisaurus* (Wilson *et al.* 2011). Wilson *et al.* (2011) further reviewed the plates published by Malkani (2006) and his collection, which indicates that none of the 5 Pakistani titanosaur taxa named by Malkani appear to be valid. Wilson *et al.* (2011) concluded that while more titanosaur species may have existed in the Indo-Pakistan area, presently it is known to have only two valid taxa, *Isisaurus colberti* and *Jainosaurus septentrionalis*.

Curry Rogers and Wilson (2014) discovered another sauropod dinosaur, *Vahiny depereti*, from the Upper Cretaceous Maevarano Formation of Madagascar, with cranial morphology very comparable to that of the Indian titanosaurid *Jainosaurus* (Kapur and Khosla 2016). Thus, Curry Rogers and Wilson (2014) have precluded a separation between Madagascar and India during the Late Cretaceous because of the morphological comparability of the two genera *Jainosaurus* and *Vahiny* Curry Rogers and Wilson, 2014. Curiously, titanosaurid taxa from South America likewise share similarities with *Isisaurus* from India (Wilson *et al.* 2011; Kapur and Khosla 2016). Kapur and Khosla (2016) opined that our current understanding of the biogeographic evidence to identify such a terrestrial connection is limited by the lack of complete sauropod (titanosaurid) skeletal material and a detailed phylogenetic analysis. An uninterrupted terrestrial connection is the bare minimum for huge vertebrate migrations.

Notwithstanding, huge sauropods have been considered to have occupied shallow waters and to have been equipped for swimming (Taylor 2010; Kapur and Khosla 2016, 2019; Khosla 2021). The largest living vertebrates occupying land, such as elephants, are perceived as capable swimmers fit for swimming across large (around 50 km) marine expanses

Text-fig. 18. The oospecies *Fusioolithus baghensis* Fernández and Khosla, 2015 from the Lameta Limestone at Borkui (Dhar district, Madhya Pradesh). A – single sauropod egg (diameter 180 mm) embedded in the grey sandy Lameta Limestone; pen cover length = 5 cm. B – two broken eggs; pen length = 15 cm.



Text-fig. 19. *Megaloolithus* spp. from the Maastrichtian Lameta Limestone at Kadwal (Jhabua district, Madhya Pradesh). A, B – broken eggshell fragments embedded in the red sandy Lameta Limestone; scale = 5 cm. C – single broken egg embedded in the red sandy Lameta Limestone; scale = 5 cm. D – single broken egg (diameter 180 mm) embedded in the grey sandy Lameta Limestone belonging to the oospecies *M. jabalpurensis*; scale = 15 cm.

(Johnson 1980). Similarly, large sauropod dinosaurs have been considered to be flexible swimmers and probably had the ability to overcome the large marine borders adjacent to the Indian subcontinent during the Maastrichtian (Kapur and Khosla 2016; Khosla 2021). It is notable that Late Cretaceous dinosaur skeletal material has been generally recorded from the Lameta Formation and Intertrappean beds of east-west, central and southern part peninsular India, yet separated from these areas, Late Cretaceous dinosaurs are similarly known from the Kallamedu Formation of the Cauvery Basin (Kapur and Khosla 2016; Khosla 2021).

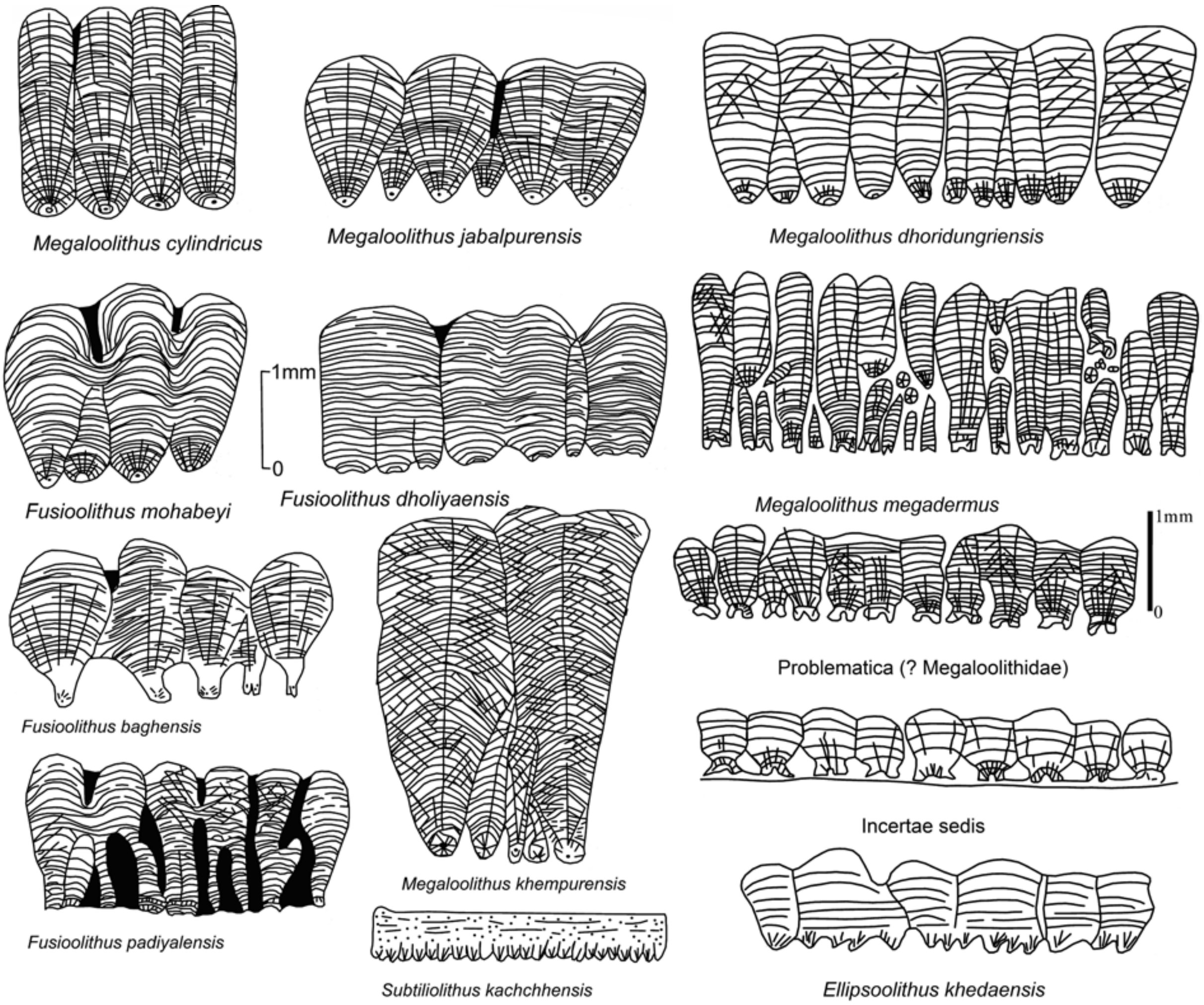
For the last three decades, the Infra- and Intertrappean beds of peninsular India have yielded hundreds of dinosaur nests, isolated eggs and eggshell fragments (Srivastava *et al*. 1986; Mohabey *et al*. 1993; Sahni *et al*. 1994; Sahni and Khosla 1994a, b; Khosla and Sahni 1995, 2003; Loyal *et al*. 1996, 1998; Mohabey 1998; Khosla 2001, 2017, 2021; Vianey-Liaud *et al*. 2003; Fernández and Khosla 2015; Khosla *et al*. 2015; Srivastava and Mankar 2015; Kapur and Khosla 2016, 2019; Aglawe and Lakra 2018; Text-figs 17–19) kindly mark the bracket in black color belonging to five oofamilies (Fusioolithidae, Megaloolithidae, Spheroolithidae, Elongatoolithidae and Subtiliolithidae) and 15 oospecies (Khosla and Sahni 1995; Fernández and Khosla 2015; Khosla 2021; Khosla *et al*. 2021).

Radial sections of the Indian parataxa (Text-fig. 20) and their micro and ultrastructural characters are given in Table 3. It is well known that most of the Indian Upper Cretaceous localities are dominated by two oofamilies (Megaloolithidae and Fusioolithidae).

The parataxonomic study of eggs and eggshells belonging to the oofamily Megaloolithidae from

Indian oospecies	Egg shape and diameter	Eggshell thickness [in mm]	Ornamentation	Shape of shell units	Growth lines	Pore canals and pores	Basal caps
Megaloolithus cylindricus (in Khosla and Sahni 1995)	spherical; 120–200 mm	1.70–3.50	compactituberculate; mostly discrete nodes	tall, slender, elongated, straight, compressed and cylindrical in shape; H/W = 4:1	highly arched	tubocanaliculate, pores subcircular, pore canals long, narrow and straight	medium-sized, subcircular in shape (0.2–0.5 mm in diameter)
Megaloolithus jabalpurensis (in Khosla and Sahni 1995)	spherical; 140–160 mm	1.00–1.75	compactituberculate; subcircular nodes	compressed, fan shaped and of variable width and shape; average H/W = 2.45:1	moderately arched upwards and following the contour of external profile	tubocanaliculate, pores circular to elongate, pore canals subvertical and inclined	subcircular in shape (0.1–0.5 mm in diameter)
Megaloolithus megadermus (in Mohabey 1998)	spherical; 130–180 mm	4.0–4.80	compactituberculate; tightly packed nodes	discrete, tall and narrow, lateral margins are straight; average H/W = 9.6:1	arched and acutely arched with extra growth centres	tubocanaliculate, pore canals long, straight and broad	short basal caps (less than 1/10 of shell unit)
Megaloolithus khempurensis (in Mohabey 1998)	spherical; 170–200 mm	2.36–3.60	compactituberculate; subcircular nodes	moderately long, discrete, fan-shaped, irregular and mostly cylindrical in shape; average H/W = 2.9: 1	shallow arched	tubocanaliculate, broad and narrow pore canals (80–90 µm in diameter)	subcircular (0.25–0.30 mm in diameter).
Megaloolithus dhoridungriensis (in Mohabey 1998)	spherical; 140–180 mm	1.12–1.68	compactituberculate; uneven pattern of fine tubercles (nodose)	discrete, tall and conical; average H/W = 2.74:1	highly arched in lower part and shallow arched upwards	tubocanaliculate, pore canals broad	subcircular
Problematica (?Megaloolithidae) (in Mohabey 1998)	spheroidal with variable diameters: 175×140 to 150×120 mm	1.35–1.65	ramotuberculate; small ridges and nodes.	broad, conical and fused; average H/W = 2:1	shallow to moderately arched	prolatocanaliculate	coalesced, forming a network of ridges
Incertae sedis (in Mohabey 1998)	oval; 180×140 mm	0.90	smooth to lineartuberculate	short, broad, discrete and distinct; average H/W = 1.40:1	growth lines not visible, diagenetically altered by silica	tubocanaliculate, pore canals straight	well separated
Fusioolithus baghensis (in Khosla and Sahni 1995; Fernández and Khosla 2015)	spherical; 140–200 mm	1.0–1.70	compactituberculate; discrete and coalesced nodes	short, broad and fan-shaped shell units, distinct or even partially fused; H/W = 2.32:1	moderately arched in discrete and horizontal to subhorizontal in multinodal shell units	tubocanaliculate, pores subcircular to elliptical, pore canals short, curved and narrow	swollen-ended variably spaced (0.2–0.30 mm in diameter).
Fusioolithus dholiyaensis (in Khosla and Sahni 1995; Fernández and Khosla 2015)	fragmentary eggshells	1.47–1.75	compactituberculate; no distinct nodes which are faintly developed, discrete and fused nodes	admixture of much common cylindrical and fan-shaped shell units; average H/W = 2.94:1	shallow moderately arched in discrete and horizontal to subhorizontal in fused shell units	tubocanaliculate, pore canals vertical and straight	subcircular, conical and coalesced (0.15–0.30 mm in diameter)
Fusioolithus mohabeyi (in Khosla and Sahni 1995; Fernández and Khosla 2015)	spherical; 160–190 mm	1.80–1.90	compactituberculate; circular and distinct nodes	long and fused to adjacent ones and exhibit highly arched nodal roofs; H/W = 3.06:1	highly arched crescent-shaped growth lines, sometimes exhibiting multi-convexed to wavering type	tubocanaliculate, elliptical, pore canals short, inclined and of irregular type	basal cap broad or semicircular in shape (0.14–0.21 mm in diameter)
Fusioolithus padiyalensis (in Khosla and Sahni 1995; Fernández and Khosla 2015)	fragmentary eggshells	1.12–1.68	compactituberculate	small, slender, irregular of various lengths and widths and are frequently fused laterally; average H/W = 3.95:1	shallow moderately arched	tubocanaliculate, pores subcircular to elliptical, pore canals small and large	tightly packed basal caps, circular to semicircular in shape (0.07–0.21 mm in diameter)
Subtiliolithus kachchhensis (in Khosla and Sahni 1995; Khosla et al. 2021)	fragmentary eggshells	0.46–0.49	subcircular microtubercles	two-layered, outer spongy layer (274.58 µm, CL:ML, 1.3:1) borders a squamatic zone; mammillary layer thick (1/2–1/3 of total shell thickness, 196.1 µm), comprising conical, crystalline aggregates with petaloid wedges.	faintly developed columnar prisms	angusticanaliculate, straight pore canals	mammillae tightly packed (0.03–0.05 mm in diameter), circular to polygonal in shape
Ellipsoolithus khedaensis (in Loyal *et al.* 1998; Mohabey 1998)	ellipsoidal, a near oval shape; variable diameter (98–110 × 65–80 mm)	1.20–1.64	lineartuberculate in equatorial region and dispersituberculate in polar region	two-layered, ratio of mammillary to spongy layer = 1:4	horizontal in lower part of shell units	angusticanaliculate, straight and narrow pore canals	mammillary layer 1/4–1/7 of total eggshell thickness
?*Sphaeroolithus* sp. (in Mohabey 1996a)	fragmentary eggshells	1.0–1.5	sagenotuberculate and dispersituberculate	well-defined margins	moderately arched and fused in upper shell unit margins	prolatocanaliculate, pores rounded	coalesced

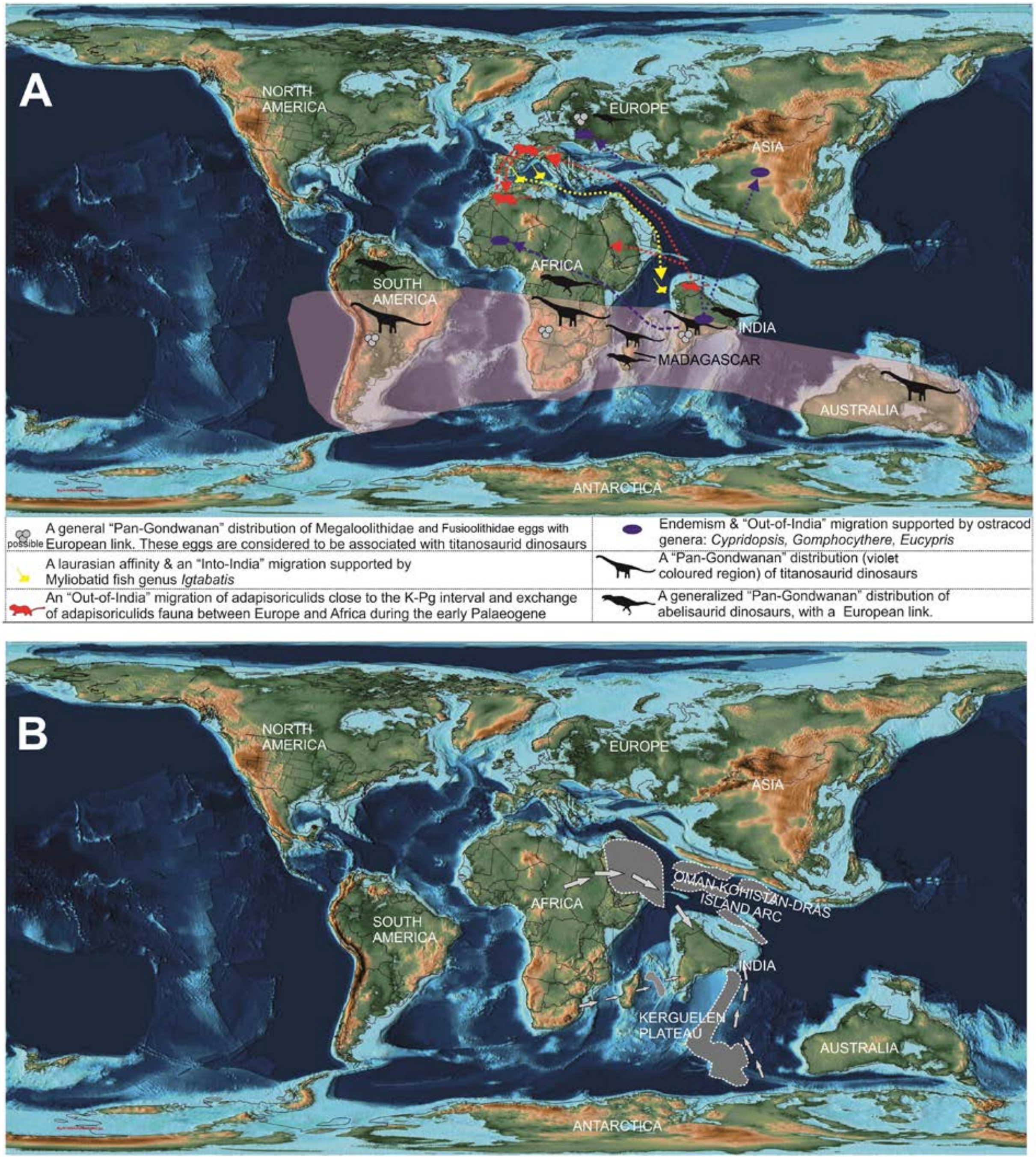
Table 3. Diagnostic characteristics of the Indian Late Cretaceous dinosaur eggshell oospecies (after Khosla and Lucas 2020d).



Text-fig. 20. Drawings of radial sections of Late Cretaceous dinosaur eggshell oospecies; modified from Khosla and Sahni (1995), Mohabey (1998), Khosla and Lucas (2020d).

France and Spain were started by Dughi and Sirugue (1957), and the eggshells from India show great similarity with them in micro- and megascopic characters (Fernández and Khosla 2015; Khosla and Lucas 2020a–e). Paleobiogeographically, the oofamilies Megaloolithidae and Fusioolithidae show particular affinities with eggshell oospecies of South America (Argentina), Africa (Morocco) and Europe (France and Spain; Khosla 2021). Detailed studies by, e.g., Khosla and Sahni (2003), Fernández and Khosla (2015), Khosla and Verma (2015), Kapur and Khosla (2016, 2019), Aglawe and Lakra (2018), and Khosla (2021), have concluded that 5 of the Indian eggshell oospecies, i.e., *Fusioolithus mohabeyi* Fernández and Khosla, 2015; *F. baghensis* Fernández and Khosla, 2015; *M. jabalpurensis* Khosla and Sahni, 1995; *M. megadermus* Mohabey, 1998 and *M. cylindricus* Khosla and Sahni, 1995, have also been observed from the Upper Cretaceous deposits of three mainland regions (Argentina, Morocco and Spain-France; Fernández and Khosla 2015; Dhiman *et al*. 2019; Khosla 2021).

The oospecies *Megaloolithus jabalpurensis* (Khosla and Sahni 1995) shows distinct affinities with *M. patagonicus* Calvo, Engelland, Heredia and Salgado, 1997 from the Upper Cretaceous (Coniacian–Santonian) of Nequèn Province, Patagonia, Argentina. In micro- and ultrastructural characteristics, *M. jabalpurensis* also shows close resemblance with eggshells known from France and the Abella and Bastus localities of Spain (e.g., Vianey-Liaud and Lopez-Martinez 1997; Vianey-Liaud *et al*. 2003; Fernández and Khosla 2015; Khosla and Lucas 2020a–e; Khosla 2021). As a result, *M. jabalpurensis* has been con-



Text-fig. 21. Paleobiogeographic maps for the Cretaceous–Paleogene boundary interval. A – Map highlighting the varied kinship of the faunal elements with special reference to dinosaurs (modified after Scotese 2001; reproduced from Kapur and Khosla 2019). B – Supposed Gondwanan connections with the Indian subcontinent (modified after Scotese 2001).

sidered as a senior synonym of *M. patagonicus* (Fernández and Khosla 2015; Khosla 2021). The micro- and ultrastructural characteristics of the Moroccan eggshell oospecies *Pseudomegaloolithus atlasi* (Megaloolithidae), which was erected by Chassagne-Manoukian *et al.* (2013), displays close similarities to Indian and South American eggshells. The comprehensive distribution of fusioolithid and megaloolithid eggs and eggshells in the Gondwanan and European continents additionally indicates that there was a likely terrestrial passage-way for dinosaur dispersal among the three Gondwanan zones, namely India, Africa and Patagonia, and between India and Europe, during the Late Cretaceous (Vianey-Liaud *et al.* 2003; Chassagne-Manoukian *et al.* 2013; Khosla 2014, 2021; Fernández and Khosla 2015; Khosla and Verma 2015; Kapur and Khosla 2016, 2019; Khosla and Luca 2020a–e; Text-fig. 21A).

In order to explain the presence of diverse Late Cretaceous Gondwanan biota in India, several dispersal routes have been proposed by various workers (Text-fig. 21B): a connection between India and Madagascar by means of the Chagos Laccadive ridge and the Mascarene Plateau (Sahni 1984); a land connection with Indo-Madagascar through the Seychelles plateau (Averianov *et al.* 2003; Rage 2003); a land connection between South America, Indo-Madagascar, and Africa through the Kerguelen Plateau and Antarctica (Krause *et al.* 1997; Prasad *et al.* 2010; Krause *et al.* 2019; Khosla 2021); a passage flanked by India and South America through the Ninetyeast Ridge-Kerguelen-Antarctica (Chatterjee and Scotese 2010); or terrestrial links between India, South America, Africa and Europe (Fernández and Khosla 2015; Khosla and Lucas 2020e; Khosla 2021).

Paleontologists thus continue to be perplexed by the occurrence of both Gondwanan and Laurasian biotic components in the Indian Upper Cretaceous deposits (Kapur and Khosla 2016, 2019; Khosla 2021). The Kohistan-Dras Volcanic Island Arc System, according to Prasad and Sahni (1999), may have allowed for faunal interchange if only the smaller-sized faunal components are included. A biotic interchange between Madagascar and India during the Late Cretaceous can be imagined in a similar way, with island jumping and putative dispersers, such as extremely small animals (Kapur and Khosla 2016). Despite this, models that assume direct linkages, particularly in India's north, should be reconsidered in the light of solid geophysical evidence (Kapur and Khosla 2016; Khosla 2021). The fossil data on large vertebrates, e.g., abelisaurid dinosaurs, according to Kapur and Khosla (2016), can be considered to indicate a pandemic Gondwanan distribution, arguing for the vicariance scenario. Some researchers (Ali and Krause 2011; Verma *et al.* 2012) hypothesized that the widespread distribution of abelisaurid dinosaurs could reflect a vicariant event of Gondwana separation prior to the end of the Early Cretaceous. Diverse lines of evidence, such as fossil, molecular, and geophysical data, etc., must all come together in the ideal situation to draw any firm conclusions. Regrettably, this is not the case with the fossil biota found in the Upper Cretaceous Indian strata (Khosla 2021). In the near future, additional vertebrate fossils from all Indian Cretaceous horizons and previous Gondwanan continents, primarily Africa and Madagascar, would be obligatory in order to clearly understand the level of biogeographic connection or separation of the Indian Subcontinent during the Late Cretaceous (Kapur and Khosla 2016; Khosla 2021).

INDIA'S LAST DINOSAURS

The end of the age of dinosaurs was the K-Pg boundary mass extinction, a global calamity brought on by both an impact and Deccan volcanism. The date and duration of the Deccan eruptions are being determined with greater accuracy, making it clearer how this volcanic activity contributed to the K-Pg boundary extinctions. The main pulse of the Deccan eruptions is now thought to have occurred in a relatively brief period of time during the magnetic polarity chron 29R (750,000 years) around the K-Pg boundary (Chenet *et al.* 2009; Keller *et al.* 2009a, b; Schoene *et al.* 2015; Eddy *et al.* 2020; Khosla and Bajpai 2021; Khosla and Lucas 2021). Recent radioisotopic data have precisely constrained the Deccan volcanism between 67 and 64 Ma (e.g., Chenet *et al.* 2009; Keller *et al.* 2009a, b; Schoene *et al.* 2015; Eddy *et al.* 2020). Despite the fact that the Deccan Intertrappean Beds and the Lameta Formation are both classified as Maastrichtian (uppermost Cretaceous), the latter is a bit younger in age within the Maastrichtian due to its stratigraphic position, and may even cross the Cretaceous/Paleogene (K-Pg) boundary (Keller *et al.* 2009a, b; Khosla and Lucas 2020a). These thin Maastrichtian Intertrappean Beds wedged between the Deccan lava flows include the latest stratigraphic record of Cretaceous dinosaurs in India. It is known that a number of freshwater Deccan Intertrappean localities in the east-west, central and southern parts of peninsular India have produced dinosaur remains, particularly solitary teeth, uncommon fragmentary limb bones, and eggshell fragments, although whole eggs are essentially nonexistent (e.g., Bajpai *et al.* 1990; Khosla and Sahni 1995, 2003; Khosla and Lucas 2020c–e; Khosla *et al.* 2021; Khosla and Bajpai 2021). The general consensus is that these deposits are Maastrichtian in age, as opposed to the long-held early Cenozoic (Paleocene) age based primarily on fossil evidence. This is because there are fragmentary dinosaur remains in several Intertrappean localities (e.g., Sahni and Bajpai 1988; Bajpai 1996; Bajpai and Prasad 2000; Khosla and Sahni 2003; Bajpai *et al.* 2013; Kapur and Khosla

Text-fig. 22. Dinosaur-bearing Intertrappean beds at Anjar, Kutch district, Gujarat. A – general view of the beds exposed near the railway track. B – enlarged view of A showing an *in situ* dinosaur bone. Pencil length = 14 cm (after Khosla and Bajpai 2021).

2016, 2019; Khosla and Lucas 2020c–e; Khosla and Bajpai 2021). On the basis of planktic foraminiferans, more recent investigations have revealed that the various Intertrappeans can be solely Maastrichtian or Paleocene, or even cross the K-Pg boundary in several places in the Deccan volcanic region (e.g., Keller *et al.* 2009a, b; Khosla 2015; Kania *et al.* 2022; Khosla *et al.* 2022). There have never been any dinosaur remains found in Jhilmili or in any other Intertrapppean deposits dated as Paleocene, but these studies based their conclusion on foraminiferans from a section at Jhilmili (Madhya Pradesh; Khosla 2015; Khosla and Bajpai 2021; Khosla *et al.* 2022, 2023).

The Intertrappean localities that contain significant dinosaur remains (broken skeletal material and eggshells) are known in the following states: Asifabad, Andhra Pradesh (Rao and Yadagiri 1981); Ranipur, Jabalpur district, Madhya Pradesh (Mathur and Sharma 1990), Mohagaonkalan, District Chhindwara, Madhya Pradesh (Srinivasan 1996); and Anjar, Gujarat (Ghevariya 1988; Bajpai *et al.* 1993; Bajpai and Prasad 2000). Thus far, Anjar (Text-fig. 22), where a multidisciplinary approach incorporating data on dinosaur fossils, iridium anomalies, Ar-Ar ages, and paleomagnetic reversals has commenced, has produced the best evidence relevant to the time of dinosaur extinction in India (Bhandari *et al.* 1996; Bajpai and Prasad 2000). Kutch in Gujarat is the only known Intertrapppean horizon that might contain the Cretaceous/Paleogene boundary. A record of an iridium anomaly in the Intertrappean Beds at Anjar (Kutch district, Gujarat) suggests that the Cretaceous/Paleogene boundary may have been there (Bajpai 1996). The (?) third Intertrappean sequence, which lies between basaltic Flows III and IV in the Anjar Intertrappean section, contains three layers of iridium-rich sediments (Bajpai 1996; Bhandari *et al.* 1996). There is an extensive collection of fossils, including bones and eggshell fragments of sauropods and the titanosaur oospecies *Fusioolithus baghensis* (Khosla and Sahni 1995; Fernández and Khosla 2015), ornithoid eggshells (*Subtiliolithus kachchhensis* Khosla and Sahni 1995; Khosla *et al.* 2021), and ostracods (*Mongolianella palmosa* Mandelstam, 1955; *Paracypretta jonesi* Bhatia and Rana, 1984 etc.) from the Anjar section. In this area, all of these forms have been discovered wedged between the middle and upper iridium layers (Bajpai 1996; Khosla and Sahni 2003). Ir-enrichment and extinction of the dinosaurs in India may have occurred before the K-Pg boundary and could have happened as early as magnetic chron 29R, according to the seemingly undisturbed dinosaur remains and accompanying Maastrichtian fossils found above the Ir-enriched strata at Anjar (Bajpai and Prasad 2000; Khosla and Bajpai 2021). Furthermore, the K-Pg boundary in the Anjar section was previously assigned a magnetostratigraphy-based age of 65.4 Ma; however, the absolute age of the K-Pg boundary is designated now at 66.04 Ma within the reverse magnetochron C29R (Renne *et al.* 2013; Kapur and Khosla 2019) using the most recent chronological data. This fact, along with the existing paleontological evidence, strongly suggests that the Ir-rich levels existed before the K-Pg boundary (Kapur and Khosla 2019).

CONCLUSIONS

Incomplete and indeterminate sauropod skeletal remains are known from the Cenomanian–Turonian deposits of the Nimar Sandstone (Dhar district, Madhya Pradesh) of the Lower Narmada region.

Indian Late Cretaceous (Maastrichtian) dinosaur skeletal, eggs and eggshell localities are confined to the Infra- and Intertrappean Beds of peninsular India and spread out extensively over an extensive area spanning 10,000 km^2 along the Narmada River region. Indian dinosaur eggs belong to 5 oofamilies and 15 parataxa and show close relationships with three continental areas (Argentina, Morocco and Spain-France), indicating terrestrial routes for dispersal. The idea of biotic exchanges between India and Madagascar during the Late Cretaceous has been highlighted by phylogenetic evidence in a paleogeographic context. Due to the strong evolutionary relationships between the last Cretaceous Indian dinosaurs, and those from Madagascar and South America, paleobiogeographic studies of the Indian dinosaur faunas present unresolved issues. According to current theories, the ancestral taxa were dispersed by southern (India-Madagascar-Antarctica-South America via the Kerguelen Plateau/Gunnerus Ridge) or pan-Gondwanan routes. While animal size should have been a limiting factor so that only small animals could disperse during trans-oceanic exchange, the exchange of fauna between India and Asia via the Kohistan-Dras Volcanic Arc System was not assumed previously. Except possibly for the large-sized vertebrates, crossing massive sea barriers was not possible. As a result, a straight terrestrial path, especially in India's north, is less likely, and the distribution of these massive vertebrates should be examined through the lens of a 'Pan-Gondwanan' paradigm (Kapur and Khosla 2016; Khosla 2021). Nevertheless, persistent problems with the paleobiogeographic history of India's Cretaceous dinosaurs will be solved with a more thorough fossil record, especially from the Lower/mid Cretaceous of India.

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