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Dinosaur fossil records from India and their palaeobiogeographic implications: an overview

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ABSTRACT

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The complex palaeogeographic history of India involving a gradual transition from Gondwana to Laurasia with an intervening phase of prolonged physical isolation, and the biotic signatures of this complex history as preserved in India's Mesozoic fossil record are of much current interest and continue to be debated. Seen in this context, the fossil record of dinosaurs from India provides a unique opportunity to study their diversity and palaeobiogeographic distribution in time and space. The Indian fossil record, as currently documented, is patchy and restricted mainly to three intervals of the Mesozoic era: Late Triassic, Early/Middle Jurassic and Late Cretaceous. The Late Triassic–Jurassic record, representing a Pangean setting, is known primarily from the Gondwana formations of Pranhita–Godavari (P–G) Valley in the southern Indian state of Andhra Pradesh, although sporadic Jurassic occurrences are also known from Kutch (Gujarat) and Rajasthan. The earliest Late Triassic dinosaur fauna of India comes from the rhynchosaur–dominated Lower Maleri Formation of Carnian age. Known from fragmentary and isolated specimens, the Late Triassic dinosaur fauna is currently represented by the sole species *Alwalkeria maleriensis*, which is possibly a basal saurischian with uncertain relationships. A slightly younger dinosaur fauna from the archosaur–dominated Upper Maleri Formation of late Norian–earliest Rhaetian age consists of a more diverse assemblage including the two named basal sauropodomorphs (*Nambalia roychowdhurii* and *Jaklapallisaurus asymmetrica*). In contrast to the Late Triassic, the Early Jurassic record of Indian dinosaurs described from the Upper Dharmaram and Lower Kota formations of P–G Valley, is far more abundant, diverse and based on more nearly complete material that is currently referred to four named taxa of stem sauropodomorphs or basal sauropods (*Lamplughsaura dharmaramensis*, *Pradhania gracilis*, *Kotasaurus yamanpalliensis*, *Barapasaurus tagorei*) plus an ornithischian (Ankylosauria). *Kotasaurus*, one of the earliest known sauropods, is more primitive than *Barapasaurus* and shared numerous plesiomorphic characteristics with prosauropods. Together, the Late Triassic and Early Jurassic sauropods dinosaurs of India document the early radiation of this group. Amongst the other important records of Jurassic dinosaurs in India is the oldest known camarasauromorph sauropod whose identification is based on a metacarpal, a first pedal paw and a fibula from the Middle Jurassic (Bajocian) strata of Khadir Island, Kutch. Fragmentary postcranial skeletal material of an unidentified Middle Jurassic dinosaurs is also known from Kuar Bet (Patcham Island) in the Rann of Kutch and the Jumara area of Kutch Mainland.

Post–Gondwana, the Late Cretaceous dinosaurs of India occur in a different geodynamic setting in which the Indian Plate, as traditionally considered, was a northward drifting island continent in the middle of the Indian Ocean. Apart from the solitary record of a Cenomanian–Turonian sauropod from Nimar Sandstone, Cretaceous dinosaurs from India are documented mainly by skeletal remains and eggs/eggshells from the Maastrichtian infratrappean (=Lameta Formation) and intertrappean deposits in the Deccan Volcanic Province of eastern, western and central peninsular India, and from broadly coeval Kallamedu Formation of Cauvery Basin, southern India. Skeletal remains of the Lameta dinosaurs belong to two major groups, titanosaur sauropods and abelisaurid theropods, plus a possible ankylosaur, whereas the Cauvery records include fragmentary titanosaur bones and a solitary tooth of a troodontid theropod. Apart from bones and teeth, a number of dinosaur egg–bearing nesting sites are also known to occur in the Lameta Formation of east–central and western India, extending for more than 1,000 km across the states of Madhya Pradesh, Gujarat and Maharashtra. Close phylogenetic relations of the Lameta titanosaurs and theropods with corresponding taxa from the Maastrichtian of Madagascar (*Vahiny*, *Majungasaurus*) and the rare occurrence of Laurasian elements such as a troodontid, pose interesting palaeobiogeographic problems in the context of India's supposed oceanic isolation, especially after its separation from Madagascar at ~ 88 Ma.

Key–words—Triassic, Jurassic, Cenomanian–Turonian, Cretaceous, Dinosaurs, India, Palaeobiogeography.

INTRODUCTION

DINOSAURS were one of the most important components of the Mesozoic terrestrial ecosystems and India's dinosaur fauna is of considerable importance in understanding the origin, evolution and dispersal patterns of some of the dinosaur clades. The fossil record of dinosaurs from India provides a unique opportunity to study their diversity in time and space, both in the Pangean setting and during India's northward drift following its separation from Gondwanaland. An overview of previous studies on dinosaur remains from the Gondwana and post–Gondwana sedimentary deposits of India is presented here with the objective of bringing out the current status of India's fossil records and highlighting their palaeobiogeographic significance.

FOSSIL RECORD

Late Triassic

Globally, dinosaurs make their first appearance in the late Triassic but their early evolutionary history is not well understood because of the global scarcity of fossiliferous continental strata of late Middle Triassic (Ladinian) and early Late Triassic (Carnian) age. This part of the dinosaur history includes the split between the two main clades of dinosaurs, Saurischia and Ornithischia, and the appearance of relatively large basal sauropodomorphs. Our knowledge of early dinosaurs is based mainly on fossils from a few upper Carnian–lowermost Norian (~232–225 Mya) localities situated in a palaeolatitudinal belt of approximately 40–50° S in Argentina, Brazil, Zimbabwe and India (Ezcurra, 2012). The best known Late Triassic dinosaur assemblages including genera such as *Eoraptor, Herrerasaurus* and *Saturnalia*, occur in South America. A majority of these early dinosaurs

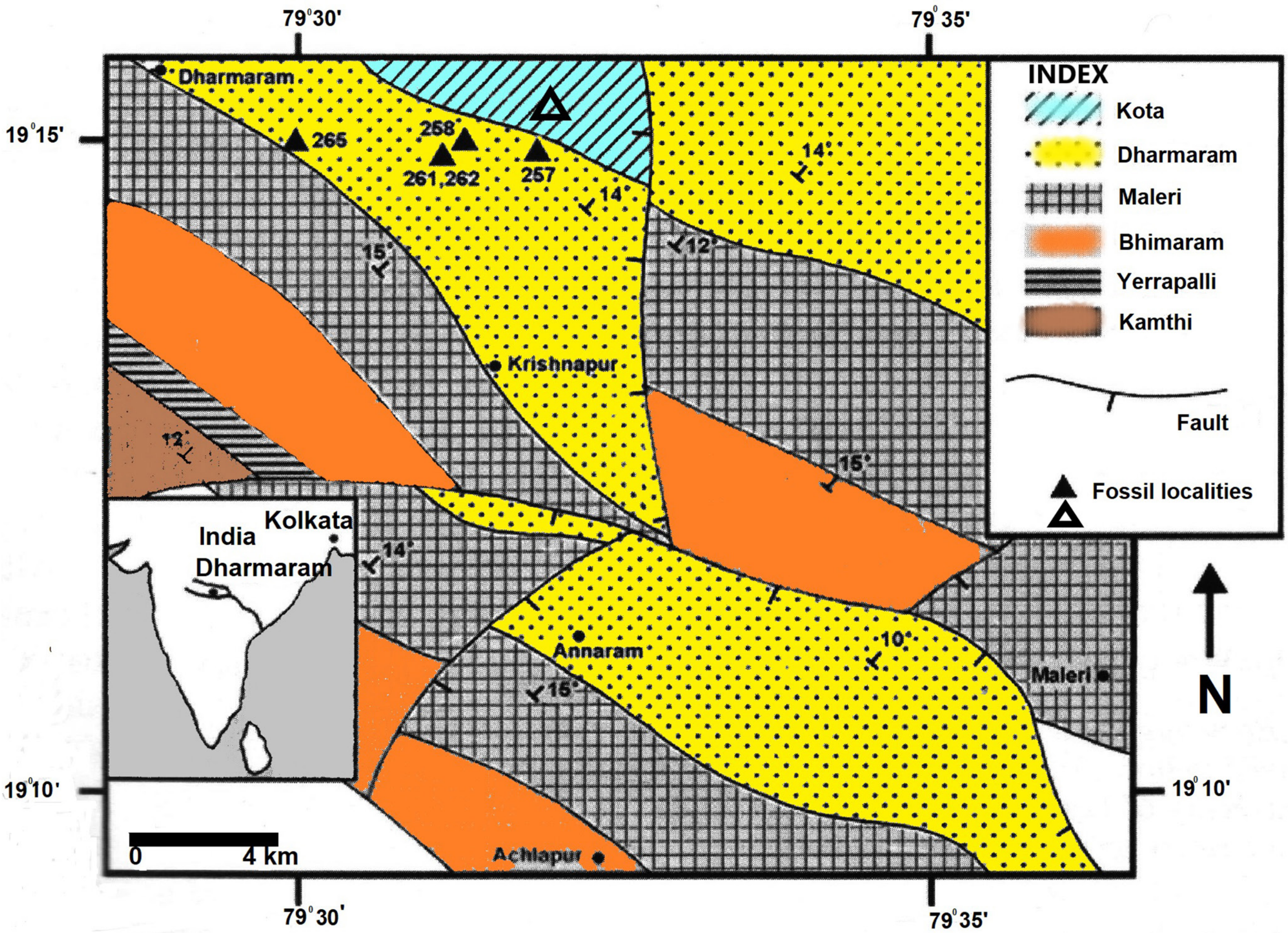

Fig. 1—Geological map showing the Late Triassic-Jurassic dinosaur-yielding horizons of Maleri, Dharmaram and Kota formations in the Pranhita-Godavari Valley, Andhra Pradesh. Basal sauropodomorphs ISI R257, 258, 261, 262, and 265 were found between the villages of Dharmaram and Krishnapur (map adapted from Kutty & Sengupta, 1989; Kutty *et al.*, 2007).

Table 1—Updated list of dinosaur taxa from Late Triassic–Late Cretaceous of India (KC= Kallamedu Formation, Cauvery Basin; KK= Kaladongar Formation, Kuar Bet, Kutch; L= Lameta Formation; LD= Lower Dharmaram Formation; LK= Lower Kota Formation; LM= Lower Maleri Formation; N= Nimar Sandstone; UD= Upper Dharmaram Formation; UK= Upper Kota Formation; UM= Upper Maleri Formation). (Source: Carrano & Sampson, 2008; Wilson *et al*., 2011; Chatterjee *et al*., 2017; Bandyopadhyay & Ray, 2020).

LATE TRIASSIC (Late Carnian):		
Saurischia	*Alwalkeria maleriensis*	(LM)
LATE TRIASSIC (Early Norian):		
Sauropodomorpha	*Nambalia roychowdhurii*	(UM)
	Jaklapallisaurus asymmetrica	(UM)
	Guibasauridae indet.	(UM)
	Dinosauriformes indet. (ISI R282)	(UM)
	Dinosauriformes indet. (ISI R284)	(UM)
LATE TRIASSIC (Rhaetian):		
Sauropodomorpha	*Jaklapallisaurus asymmetrica*	(LD)
	Sauropodomorpha indet.	(LD)
Neotheropoda	Indet.	(LD)
EARLY JURASSIC (Hettangian):		
Sauropodomorpha	*Lamplughsaura dharmaramensis*	(UD)
	Pradhania gracilis	(UD)
EARLY JURASSIC (Sinemurian–Toarcian):		
Sauropoda	*Barapasaurus tagorei*	(LK)
	Kotasaurus yamanpalliensis	(LK)
Ornithischia	Ankylosauria indet.	(LK)
MIDDLE JURASSIC		
Sauropoda	Camarasauromorpha gen et sp. indet.	(KK)
Theropoda	Dromaeosauridae indet.	(UK)
Ornithischia	Ankylosauria indet.	
	Ornithischia indet.	(UK)
CRETACEOUS (Cenomanian–Turonian):		
	Sauropoda indet.	(N)
CRETACEOUS (Maastrichtian):		
Sauropoda	*Jainosaurus septentrionalis*	(L)
	(=Antarctosaurus septentrionalis)	
	Isisaurus colberti	
	(=Titanosaurus colberti)	(L)
Theropoda	*?Lametasaurus indicus*	(L)
	?Indosaurus matleyi	(L)
	?Indosuchus raptorius	(L)
	Rahiolisaurus gujaratensis	(L)
	Rajasaurus narmadensis	(L)
	Laevisuchus indicus	(L)
	Troodontidae indet.	(KC)
Ornithischia	?Ankylosauria indet.	(L)

were small–sized with a 2–9 m body length, quadrupedal and facultatively bipedal, and essentially omnivorous and herbivorous.

In India, sporadic occurrences of late Triassic dinosaurs are known from Pranhita–Godavari (P–G) and Rewa basins of peninsular India.

P–G Basin (Fig. 1)—The P–G Basin contains a nearly continuous faunal succession from the Late Permian to the Early Jurassic, and potentially even into the Middle Jurassic (Bandyopadhyay & Sengupta, 2006). Huene (1940) reported the first dinosaur bones from the Maleri Formation of P–G Basin including a fragmentary femur, a tibia and three dorsal vertebrae attributed to two dinosaur taxa, an indeterminate coelurosaur theropod ("Podokesauridae") and a prosauropod (cf. *Massospondylus* sp.). However, Colbert (1958) reinterpreted the supposed podokesaurid fossils as belonging to a single species and also did not agree with Huene's (1940) identification of the two large vertebrae as dinosaurian, assigning them instead to phytosaurs. The most recent re–appraisal of this material by Ezcurra (2012) shows that only one of the specimens originally described by Huene (1940), a proximal tibia (33/621a), is referable to Dinosauria based on the presence of a distinct, laterally curved cnemial crest, a structure usually found in dinosaurs (Fig. 2). Another find from the Lower Maleri Formation (Carnian), originally described as a basal theropod based on the holotype material consisting of a partial skull, several vertebrae and hindlimb elements, was named *Walkeria maleriensis* (Chatterjee, 1987). This taxon, nearly contemporaneous with the oldest Argentinian dinosaurs, was renamed *Alwalkeria maleriensis* since the original generic name was preoccupied. *Alwalkeria* was later regarded as a dinosaur of uncertain or eusaurischian affinities but its holotype was considered to be a chimera (Novas, 1997; Langer, 2004). More recently, *A. maleriensis* was considered to be a valid saurischian species with uncertain relationships due to its unusual femoral morphology and a somewhat conservative astragalar structure (Remes & Rauhut, 2005; Novas *et al.*, 2011; Ezcurra, 2012; Fig. 3). In sum, the dinosaur fauna was a minor component of the Late Triassic rhynchosaur–dominated tetrapod assemblage of Lower Maleri Formation, and is correlated to the South American *Hyperodapedon* AZ (late Carnian–early Norian), is represented by the lone species *Alwalkeria maleriensis*.

Compared to the Lower Maleri Formation, the archosaur–dominated Upper Maleri Formation of late Norian–earliest Rhaetian age is known to have yielded an abundant and more diverse assemblage (Kutty *et al.*, 2007; Novas *et al.*, 2011), which includes several basal sauropodomorphs based on postcranial remains (*Nambalia roychowdhurii*, *Jaklapallisaurus asymmetrica*, an unnamed, small guaibasaurid represented by two cervical vertebrae (ISI R277), and two basal dinosauriform taxa (Table 1). A similar abundance of sauropodomorphs occurs in the coeval beds of South America and Europe.

The Lower Dharmaram Formation (Latest Norian–Rhaetian), which overlies the Upper Maleri Formation contains at least two dinosaur taxa based on isolated postcranial material including a femur assigned to a basal sauropodomorph (*Jaklapallisaurus asymmetrica*), and a second femur assigned to an indeterminate basal neotheropod based on the presence of a strongly inturned femoral head and a pyramidal anterior trochanter (Novas *et al.*, 2011).

Rewa Basin: Fragmentary remains including vertebrae and limb bones of a basal saurischian dinosaur have been reported (but not described) from the Late Triassic (Carnian)

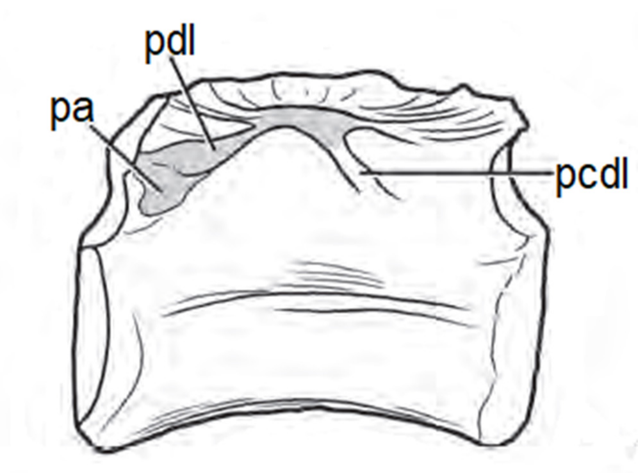

Fig. 2—Lateral view of Late Triassic dinosaur proximal right tibia described by Huene (1940) from Lower Maleri Formation (Abbreviations: pa= parapophysis; pcdl= posterior centrodiapophyseal lamina; pdl= paradiapophyseal lamina). Adapted from Ezcurra (2012).

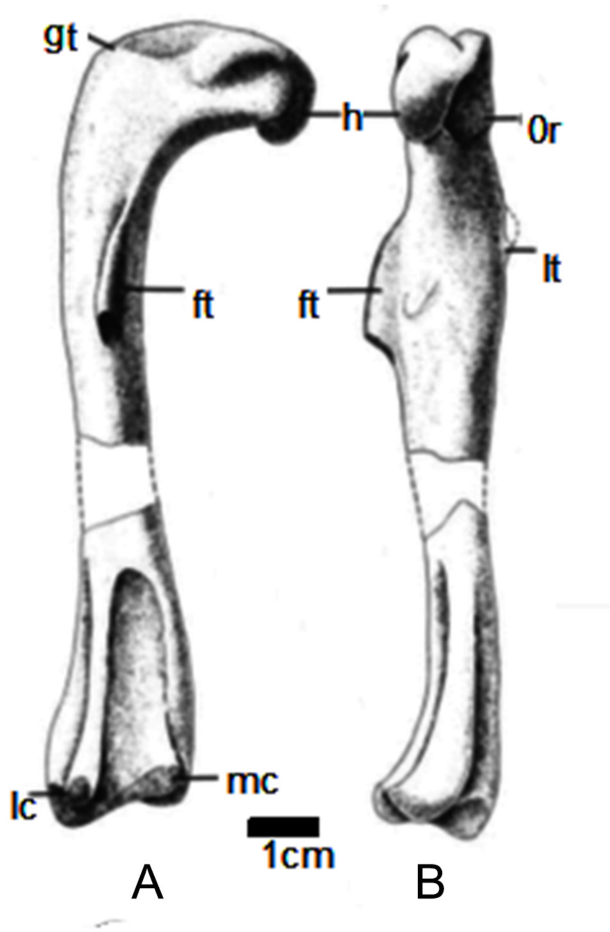

Fig. 3—Posterior (A) and medial (B) views of femur of Late Triassic *Alwalkeria maleriensis* from Lower Maleri Formation (Abbreviations: gt= greater trochanter, h= head, lc= lateral condyle, mc= medial condyle, ft= fourth trochanter, lt= lesser trochanter, or= obdurate ridge). Figure adapted from Chatterjee (1987).

Fig. 4—Skeletal restoration of *Lamplughsaura dharmaramensis* (adapted from Kutty *et al*., 2007).

Tiki Formation of Rewa Basin (Ray *et al*., 2016). Most recently, ungual phalanges (claws) attributed to a small theropod dinosaur have also been reported from the Tiki Formation (Rakshit *et al*., 2018).

Overall, as compared to their diverse South American counterparts, the Late Triassic dinosaurs of India formed a relatively small component of the tetrapod fauna, especially that known from the Lower Maleri Formation. In comparison, the Upper Maleri and Lower Dharmaram dinosaur assemblages were relatively rich in basal sauropodomorphs and resemble those from South America and Europe, but unlike North America where they are intriguingly absent, probably due to provincialism related to palaeolatitudinal differences (Nesbitt *et al*., 2009; Novas *et al*., 2011). It is also becoming increasingly apparent that there was significant diachroneity in the early radiation of dinosaurs within the Gondwana landmasses.

Early Jurassic

Significant global changes in plate configurations and ecosystems took place during the Jurassic Period when the Indian Plate was located in a warm temperate regime. Dinosaur remains from this period are known mainly from the Early Jurassic sequences of P–G Valley (Adilabad District, Andhra Pradesh), represented by the Upper Dharmaram Formation (Early Jurassic, Hettangian); Lower Kota Formation (Early Jurassic, Sinemurian–Pleinsbachian age); Upper Kota Formation (Middle Jurassic, Toarcian–?Aalenian) and the Bagra Formation of Late Jurassic age. It is to be noted that a younger age (Middle Jurassic) has been favoured by some workers for the dinosaur–yielding Lower Kota Formation based on the isolated teeth of ornithischians and theropods, and especially due the presence of dromaeosaurids (see below).

The Dharmaram Formation, which overlies the tetrapod rich Maleri Formation (Table 1), is characterized by basal thick coarse–grained gritty sandstone and clay beds (Loyal *et al*., 1996). Based on a number of bones recovered from the Dharmaram Formation, Kutty (1969) recognized two basal sauropodomorph taxa, a small thecodontosaurid and an enormous plateosaurid. Well–preserved sauropodomorph remains from the Upper Dharmaram Formation have been assigned to *Lamplughsaura dharmaramensis*, *Pradhania gracilis* and an indeterminate form (Kutty *et al*., 2007). *Lamplughsaura*, a stem sauropod about 10 m long, is possibly the earliest known sauropod from India and may be a sister taxon to *Vulcanodon* from the Early Jurassic of Zimbabwe (Novas *et al*., 2011). It was a heavily built quadrupedal creature with a small head, a long and adaptable neck, and a long tail (Kutty *et al*., 2007; Fig. 4). Diagnostic features of this species include teeth with coarse denticles on the distal edge. Compared to *Lamplughsaura*, *Pradhania* was smaller and lightly built, and it was possibly a facultative biped from which *Lamplughsaura* descended. *Lamplughsaura* appears to represent an intermediate stage between the bipedal plateosaurid *Pradhania* and quadrupedal, long–necked sauropods (Kutty *et al*., 2007). The sauropod remains from the Early Jurassic of India are of great significance in understanding the origin and early radiation of this group.

The next younger dinosaur–bearing interval (early Jurassic, Sinemurian–Toarcian) is the fluviatile Kota Formation which overlies the Dharmaram Formation and consists of 20–30–m–thick alternation of laminated and massive limestones with subordinate sandstone and mudstone. The Kota Formation is divisible into two units, a lower sandstone–mudstone dominated unit and an upper marl/limestone unit (Rudra, 1982). An age ranging from Sinemurian to Pliensbachian has been assigned to the lower unit, whereas the upper part is dated as Toarcian–?Aalenian (Bandyopadhyay & Sengupta, 2006). Sauropod remains occur abundantly in the lower unit of Kota Formation. Two well–known sauropod taxa named from the lower unit are *Barapasaurus tagorei* (Jain *et al*., 1975; Bandyopadhyay *et al*., 2010) and *Kotasaurus yamanpalliensis* (Yadagiri, 1988, 2001; Yadagiri *et al*., 1979; Wilson & Sereno, 1998).

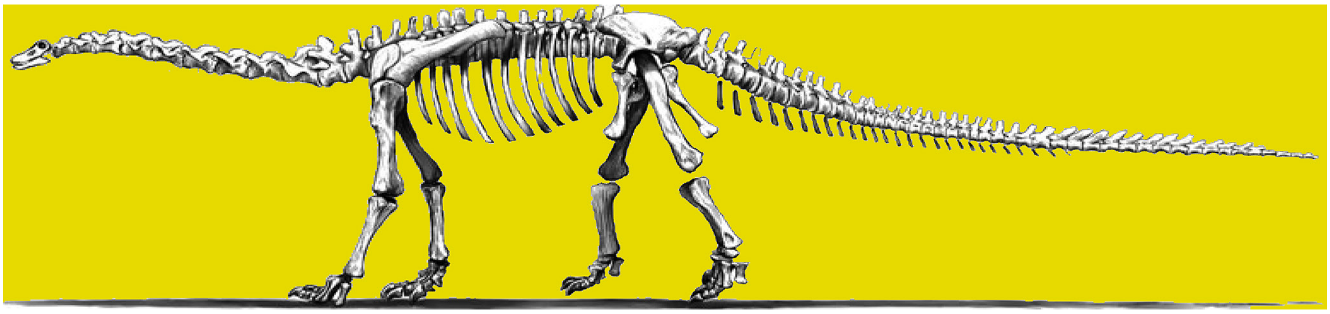

Fig. 5—Schematic drawing of the mounted skeleton of *Barapasaurus tagorei* (adapted from Bandyopadhyay *et al*., 2010).

Barapasaurus had a gigantic size of about 14 m body length with graviportal and columnar limbs (Fig. 5), and its teeth are spoon–shaped with bulbous bases and wrinkled enamel. *Barapasaurus* is known from nearly six complete skeletons. The initial bones were found in 1958, but the majority of specimens were discovered in 1960 and 1961 (Bandyopadhyay *et al.*, 2010). Jain and colleagues described the discoveries in 1975 (Jain *et al.*, 1975) and Bandyopadhyay and colleagues (2010) provided a more through osteological description. The skeletal material is catalogued at the Indian Statistical Institute (ISI), and the majority of bones are on display at the ISI's Geological Museum as part of a mount (Bandyopadhyay *et al.*, 2010; Fig. 5). More than 300 bones of *Barapasaurus* were collected along with associated huge fossilized tree trunks at the interface of mudstone and sandstone layers occupying an area of about 277 sqm (Bandyopadhyay *et al.*, 2010). One of the specimens was partially articulated, but the majority of the bones were found disarticulated. At least six individuals are represented as evident from six left femora (Bandyopadhyay *et al.*, 2010). Taphonomically, this assemblage was interpreted as a *Barapasaurus* herd that died as a result of a catastrophic flood (Bandyopadhyay *et al.*, 2002, 2010).

The connection of *Barapasaurus* to the Sauropoda has been a matter of some debate. It was not ascribed to any one group when first identified (Jain *et al.*, 1975), although the presence of several primitive, prosauropod–like characteristics was noted. Initially, *Barapasarus* was thought to be similar to *Shunosaurus* from China and *Patagosaurus* from Patagonia (Bandyopadhyay, 1999). *Barapasaurus* was also considered to be related to another early sauropod, *Vulcanodon*, though the family Vulcanodontidae, being polyphyletic, became obsolete in 1984 (Upchurch, 1995). Upchurch (1995) created the clade Eusauropoda, which comprises all recognized sauropods. *Vulcanodon* was placed outside the Eusauropoda, whereas *Barapasaurus* was placed within it, indicating that *Barapasaurus* is more derived than *Vulcanodon* (Bandyopadhyay *et al.*, 2010). *Barapasaurus* is considered to be a basal member of Eusauropoda, more derived than the Chinese *Shunosaurus* (Wilson & Sereno, 1998; Chatterjee *et al.*, 2017). *Barapasaurus* is strikingly dissimilar to *Spinophorosaurus nigerensis* from the Middle Jurassic of Niger, one of the most complete basal sauropods currently known (Remes *et al.*, 2009).

Kotasaurus yamanpalliensis is a basal sauropod that coexisted with *Barapasaurus* during the Early Jurassic (Yadagiri, 1988, 2001; Yadagiri *et al.*, 1979). Much of the skeleton is known for *Kotasaurus* although the skull is missing (Yadagiri, 2001; Fig. 6). With an estimated body length of 9 m and a weight of 2.5 tonnes, *Kotasaurus yamanpalliensis* was a huge, quadrupedal herbivore with a long neck and tail, although it is believed to be more modest in size and primitive relative to *Barapasaurus tagorei* and *Vulcanodon* (Chatterjee, 2020). *Kotasaurus* is comparable to later sauropods, but it is one of the most primitive sauropods yet discovered and resembled prosauropods in numerous basic (plesiomorphic) traits (Yadagiri, 2001).

As compared to a large number of well documented sauropod remains, there are hardly any theropod and ornithischian fossils known from the Early Jurassic Lower Kota Formation except for an ankylosaurian (Ornithischia) dermal armor (Galton, 2019). However, this record is based on the interpretations of previously published (Nath *et al.*, 2002) and unpublished photos. In some respects, the small lateral body scutes from Kota were considered by Galton (2019) to

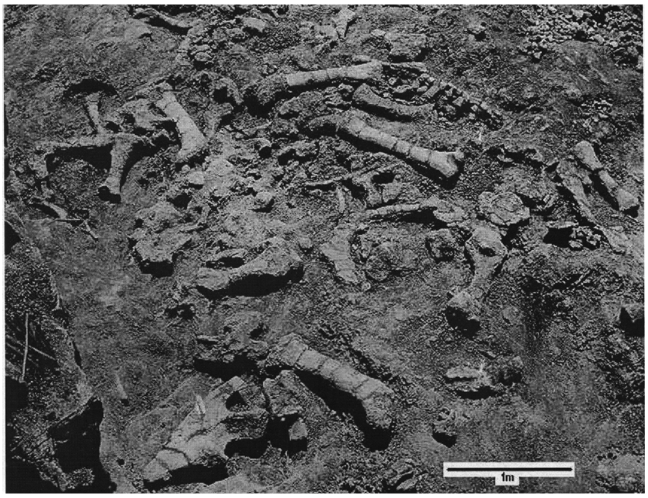

Fig. 6—*Kotasaurus* bones in the Yamanpalli excavation site. Scale bar = 1 m (after Yadagiri, 2001, reproduced with permission from *Journal of Vertebrate Palaeontology*).

Fig. 7—Late Triassic (Carnian, ~222 Ma) palaeogeographic map showing the global distribution of early dinosaurs (red stars) (map from CR Scotese, 2014).

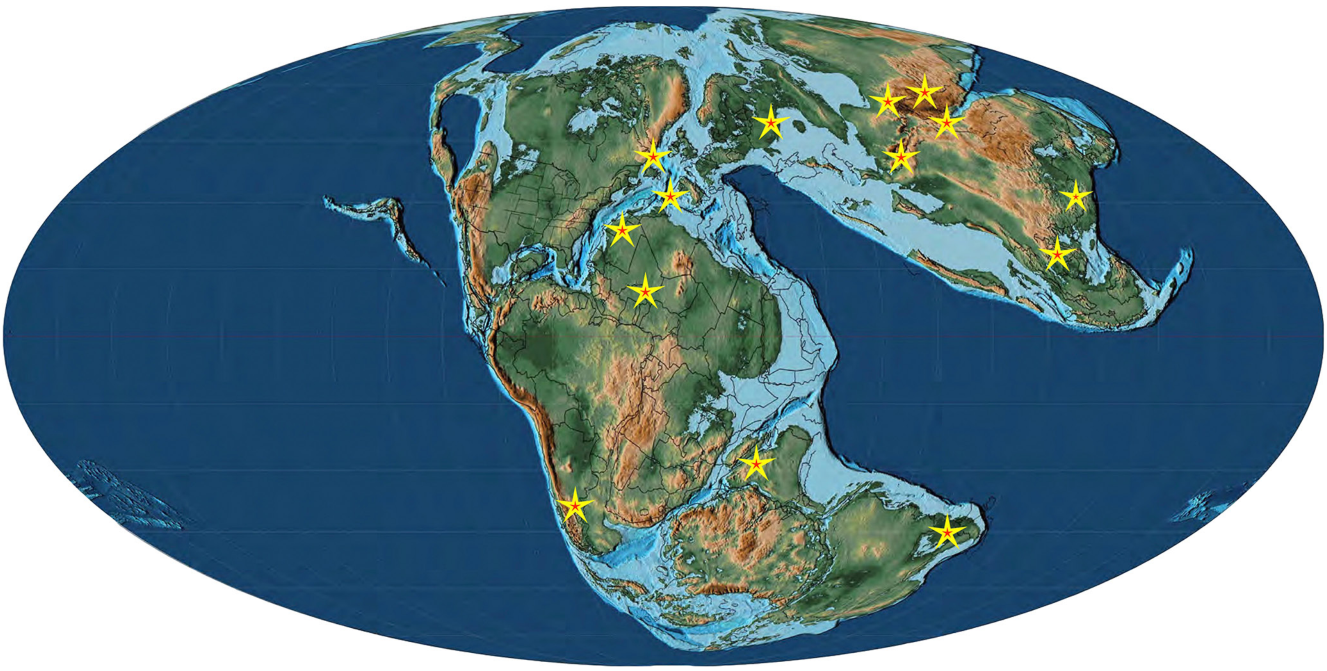

Fig. 8—Middle Jurassic (Bajocian & Bathonian, ~170 Ma) palaeogeographic map showing the global distribution of sauropod dinosaurs (yellow stars) (map from CR Scotese, 2014).

be similar to those of ankylosaurs. Nath *et al.*'s (2002) original collection is now untraceable.

Apart from the P–G Valley, a rare occurrence of dinosaur footprints has recently been described from the early Jurassic Thaiat Member of the Lathi Formation at the Thaiat ridge, near Jaisalmer in western Rajasthan, western India (Pieńkowski *et al.*, 2015). The two footprints, attributed to the theropods *Eubrontes* cf. *giganteus* and *Grallator tenuis*, were found in sediments of a tidal origin deposited in a seasonal to semi–arid climate.

Taken together, the Late Triassic and Early Jurassic dinosaurs of India are important in understanding the Pangean biogeography (Kutty *et al.*, 2007) as it was during this interval that sauropodomorphs evolved and began to radiate to regions that subsequently became separate continents (Fig. 7).

Gondwana is thus considered to be the centre of origin for the basal sauropodomorphs because of their presence in four of the southern landmasses. India's role as an important centre for early radiation of sauropods is evident from the discovery of a small massospondylid prosauropod *Pradhania* (Kutty *et al.*, 2007) closely related to the Early Jurassic *Massospondylus* from South Africa, and the basal sauropods such as *Lamplughsaura, Kotasaurus,* and *Barapasaurus* in the Early Jurassic (Novas *et al.*, 2011; Chatterjee *et al.*, 2017). The presence of large and basal sauropods suggests that India was the site of faunal immigrations and emigrations during the Jurassic. Although the worldwide distribution of basal sauropodomorphs suggests that there were no major geographic or climatic barriers to their movement, recent data on the Middle Jurassic sauropods of Niger does point to a separation of Laurasian and South Gondwanan Middle Jurassic sauropod faunas by a barrier created by the Central Gondwanan Desert (CGD), forming two different palaeobiogeographical domains (Remes *et al.*, 2009).

Middle Jurassic

Globally, the Middle Jurassic dinosaur fossil record is limited because of the paucity of continental fossil–bearing strata of this age, particularly in the Gondwana landmasses where the record is inadequate except in Argentina. Sauropods from the Early and Middle Jurassic periods were distributed across Pangaea (Fig. 8) with a low diversity but their early history is poorly understood.

The Middle Jurassic dinosaurs of India are also poorly known. Mathur *et al.* (1985) reported the presence of a few fragmentary bones including vertebrae and a large number of possible scutes from the Middle Jurassic of Jaisalmer Basin and attributed them to dinosaurs based on bone histology. Moser *et al.* (2006) suggested that these scutes could possibly belong to a thyreophoran or an armoured dinosaur, but alternatively also hinted at the possibility that they could pertain to a crocodylomorph. These authors also suggested that Mathur *et al.*'s (1985) collection was recovered from the Lathi Formation of Bajocian or pre–Bajocian age and not from the overlying Jaisalmer Formation.

The presence of Middle Jurassic dinosaurs in Kutch was noted by Ghevariya & Srikarni (1992) who reported vertebrae, pelvic elements, teeth and eggshells from the conglomeratic levels of Patcham Island of Kutch. Subsequently, in an important discovery, articulated dinosaurian remains were reported by Satyanarayana *et al.* (1999) from the Middle Jurassic (?Aalenian to Bajocian) Dingy Hill Member of Kaladongar Formation of Kuar Bet, Patcham Island, in the Rann of Kutch (Fig. 9). This collection included 12 vertebrae and limb elements currently deposited with the Border Security Forces Headquarter. The coarse–grained sandstone and conglomerate strata of Kuar Bet yielded fragmentary dinosaur skeletal remains, including vertebrae and limb parts, as well as huge petrified trees. The dinosaur–bearing Kaladongar Formation occurs in near–shore depositional setting (Satyanarayana *et al.*, 1999). This record was followed by another find of a Middle Jurassic (Callovian) dinosaur bone in Kutch by Jana and Das (2002) who reported a fragmentary tibia from the Chari Formation of the Mainland and attributed it to a sauropod.

Another important occurrence of dinosaur remains from Kutch was reported by Moser *et al.* (2006) who described fragmentary sauropod bones from the Bajocian of the

Fig. 9—Middle Jurassic articulated sauropod remains from Kuar Bet, Pachcham Island, Kutch, western India (adapted from Satyanarayana *et al.*, 1999).

Fig. 10—Incomplete distal end of the right femur (VPL/KH/3500) of Sauropoda indet. from Nimar Sandstone (Cenomanian-Turonian) of central India (after Khosla *et al*., 2003).

Khadir Island and assigned three of the recovered bones (a metacarpal, a first pedal claw and a fibula) to a macronian (= Camarasauromorpha). This find from Kutch constitutes the oldest representative of Camarasauromorpha, the group which also includes titanosaurs (e.g., Upchurch *et al.*, 2004). Middle/Late Jurassic camarasauromorph dinosaurs are also known from Madagascar, Morocco and China (Rimblot–Baly *et al.*, 1995; Monbaron *et al.*, 1999; Zhang & Chen, 1996), but the earliest record of camarasauromorphs in India may suggest their origin In India in the early Middle Jurassic and subsequent dispersal to Laurasia.

More recently, Prasad and Parmar (2020) reported isolated theropod and ornithischian teeth from the upper Kota Formation of Middle Jurassic age. The theropod teeth consist of several morphotypes described as belonging to Dromaeosauridae and a *Richardoestesia*–like form. According to these authors, the Kota dinosaur fauna suggests close biogeographic links between India and Laurasia during the Middle Jurassic.

The Bagra Formation of Satpura Basin of central India is a potential source of Late Jurassic dinosaur fauna of India and may provide important palaeobiogeographic information from an interval when the East Gondwana landmass started to separate from the West Gondwana. The presence of possible titanosaur material including vertebrae and limb elements has been noted in this formation (Chatterjee & Hotton, 1986; Chatterjee *et al.*, 2017) but the formation is still poorly sampled.

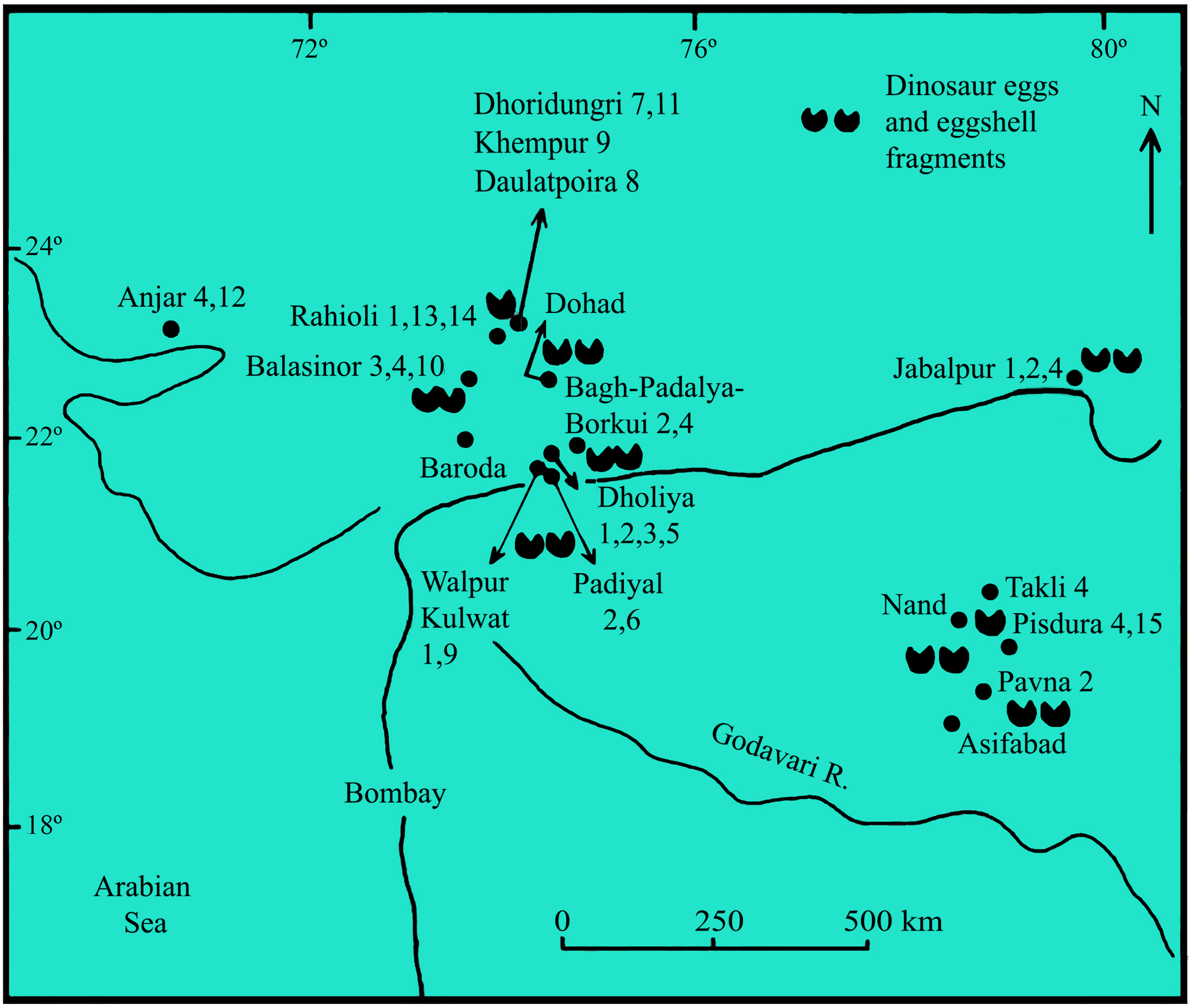

Fig. 11—Map showing the distribution of the Indian Late Cretaceous dinosaur eggs/nesting sites: 1, *M. cylindricus*; 2, *M. jabalpurensis*; 3, *Fusioolithus mohabeyi*; 4, *F. baghensis*; 5, *F. dholiyaensis*; 6, *F. padiyalensis*; 7, *Megaloolithus dhoridungriensis*; 8, *M. megadermus*; 9, *M. khempurensis*; 10, Problematica (? Megaloolithidae); 11, Incertae sedis; 12, *Subtiliolithus kachchhensis*; 13, *Ellipsoolithus khedaensis*; 14, cf. *Trachoolithus*; 15? *Spheroolithus* (map modified after Fernández & Khosla, 2015; Khosla, 2017; Khosla & Lucas, 2020 c-e).

Fig. 12—Two nearly complete sauropod eggs belonging to the oospecies *Megaloolithus cylindricus* (Khosla & Sahni, 1995) preserved in grey Lameta limestone at Salbardi- Ghorpend Village, Betul District, Madhya Pradesh and Amravati District, Maharashtra, India. Coin for scale (diameter 3 cm).

Cretaceous

The Indian Plate broke apart from the East Gondwana landmass during the early Cretaceous and continued drifting northwards until it collided with Asia sometime in the early Paleogene, around ~55 Ma. The only records of dinosaurs from the Indian Cretaceous are restricted to two intervals, the Late Cretaceous (Cenomanian–Turonian) and the end–Cretaceous (Maastrichtian). The early and mid–Cretaceous records of dinosaurs are virtually blank in India.

Cenomanian–Turonian: The only record of dinosaurs from this interval in India comes from the Narmada Valley of central India, where the Nimar Sandstone, conformably underlying the well–known marine strata of the Bagh Group, yielded several fragmentary bones including a large femur of a gigantic sauropod dinosaur (Khosla *et al.*, 2003, Fig. 10). Several other fragmentary bones such as humerus, radius, ulna, etc. have also been recorded from this unit (Khosla *et al.*, 2003). The topmost part (Green Sandstone) of the Bagh beds has also produced isolated theropod teeth (Prasad *et al.*, 2016).

Maastrichtian: The Maastrichtian dinosaurs of India come mainly from the Deccan volcano–sedimentary sequences of eastern, central and western peninsular India, and the Kallamedu Formation of Cauvery Basin, south India. The sedimentary deposits associated the Deccan Traps volcanic flows include those below the basaltic flows (i.e., Lameta Formation or infratrappean beds) and those sandwiched between the flows (i.e., intertrappean beds). Of these dinosaur–bearing horizons in the Deccan volcanic province, the best–known finds are known from the Lameta Formation which occurs mostly as a thin, discontinuous outcrops. The Lameta Formation has yielded one of the most abundant and diverse records of Cretaceous dinosaur bones and eggs from India (Mohabey, 1983; Srivastava *et al.*, 1986; Vianey–Liaud *et al.*, 1987, 2003; Bajpai *et al.*, 1993; Sahni & Khosla, 1994; Khosla & Sahni, 1995, 2003; Loyal *et al.*, 1996, 1998; Bajpai & Prasad, 2000; Khosla, 2001, 2014, 2017, 2019; Fernández & Khosla, 2015; Khosla & Verma, 2015; Kapur & Khosla, 2016, 2019; Khosla & Lucas, 2020 a–e; Khosla *et al.*, 2020). However, associated or articulated bones are rare, as are the associated bones and eggs, and this has led to much confusion about phylogenetic affinities and palaeobiogeographic relationships of the Indian Cretaceous dinosaurs.

Studies on Lameta dinosaurs date back to the Eighteenth Century when the British Army Captain Sleeman (1844) discovered titanosaur bones from the Lameta beds of

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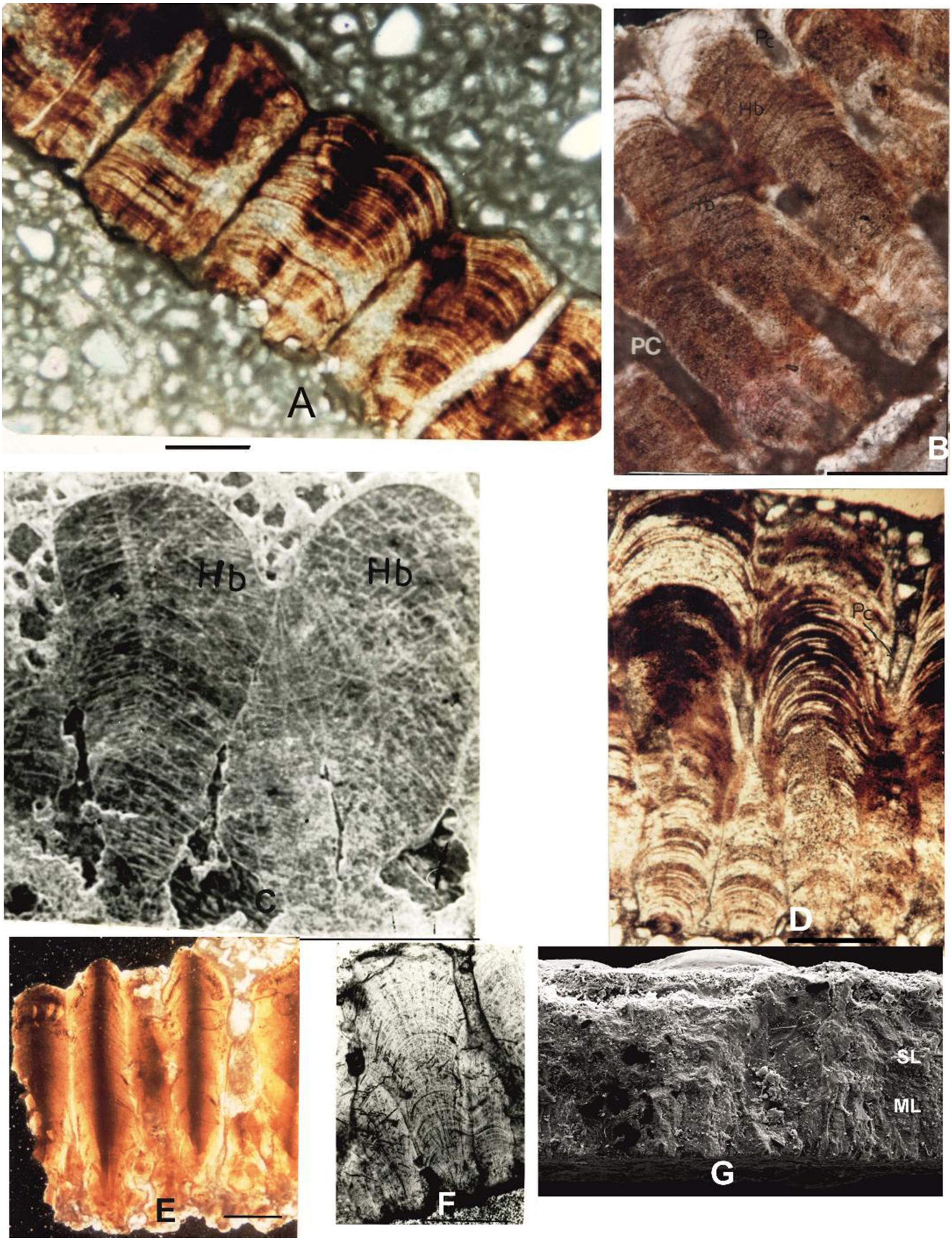
Fig. 13a—Late Creatceous dinosaur eggshells from India. **(A)** *Fusioolithus dholiyaensis* (Khosla & Sahni, 1995; Fernández & Khosla, 2015), Radial thin section, plane polarized light, Dholiya (VPL/KH/451), District Dhar, Madhya Pradesh. Note fusion between spheroliths displaying shallow curved growth lines; blending between three or four basal caps is also seen and ending into a single multinode (after Khosla & Lucas, 2020d). Bar length = 500 µm. (B) *Fusioolithus padiyalensis* (Khosla & Sahni, 1995; Fernández & Khosla, 2015), Radial thin section, under cross-nicols, Padiyal (VPL/KH/590), District Dhar, Madhya Pradesh. Note the thin, fused spheroliths with herringbone pattern, moderately curved accretion lines and irregularly spaced pore canals (after Khosla & Lucas, 2020d). Bar length = 500 µm. (C) *Fusioolithus baghensis* (Khosla & Sahni, 1995; Fernández & Khosla, 2015), Radial thin section, SEM, Bagh caves (VPL/KH/552), District Dhar, Madhya Pradesh. Note fan-shaped spheroliths and herringbone pattern (after Khosla & Lucas, 2020d). Bar length = 1 mm. (D). *Fusioolithus mohabeyi* (Khosla & Sahni, 1995; Fernández & Khosla, 2015). Radial thin section, PPL, Dholiya (VPL/KH/233), District Dhar, Madhya Pradesh; note extremely curved growth lines and a small pore canal filled with sparry calcite (after Khosla & Sahni, 1995). Bar length = 500 µm. (E). *Megaloolithus cylindricus* (Khosla & Sahni, 1995). Radial thin section, Pat Baba Mandir, Jabalpur (VPL/KH/214); note cylinder-shaped spheroliths and under cross-nicols showing sweeping extinction pattern. Bar length = 500 µm. (F). *Megaloolithus jabalpurensis* (Khosla & Sahni, 1995). Radial thin section, Bara Simla Hill (VPL/KH/270), Jabalpur, Madhya Pradesh; note small and large fan-shaped spheroliths and moderately arched growth lines. Bar length = 500 µm. (G). *Subtiliolithus kachchensis* (Khosla & Sahni, 1995). Radial, thin, fractured section, SEM, Anjar (VPL/KH/5701), District Kachchh, Gujarat; note double layered eggshell showing separate mammillary layer and dim spongy layer (Bar length 1.2 cm = 100 µm). Abbreviations: Hb, herringbone pattern; *ML* mammillary layer, *SL* spongy layer, Pc, pore canal; *SEM* scanning electron microscope.


A
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Jabalpur (in Matley, 1921), followed by Lydekker (1877) who described these bones systematically under the name *Titanosaurus indicus*. Subsequently, Huene and Matley (1933) described the Lameta dinosaurs in a monograph and also made additional collections. However, a number of dinosaur taxa were erected on the basis of fragmentary or isolated material (Huene & Matley, 1933) and many of them have now been shown to be invalid (Carrano *et al.*, 2010; Wilson *et al.*, 2011). Berman and Jain (1982) described a braincase and Jain and Bandyopadhyay (1997) described the articulated postcranial material as *Titanosaurus colberti*, a name that was later replaced with *Isisaurus colberti* because of certain unique characters possessed by the Indian species, such as a short, vertically directed neck and long forelimb (Wilson & Upchurch, 2003; Carrano *et al.*, 2010; Chatterjee, 2020). *Isisaurus* has been suggested to exhibit similarities to 'lognkosaurian' titanosaurs of South America (Wilson *et al.*, 2011). It was also shown that the fossils that originally formed the basis for erection of *Titanosaurus indicus* are not sufficiently diagnostic to defend its uniqueness at the generic or specific level, hence the name "*Titanosaurus*" and associated rank taxa such as "Titanosauridae" were considered invalid (Wilson & Upchurch, 2003). Current understanding based on cranial and post–cranial material shows that the Indian titanosaurs belong to two distinct taxa, *Jainosaurus septentrionalis* (Chatterjee & Rudra, 1996; Wilson *et al.*, 2005) and *Isisaurus colberti* (Jain & Bandyopadhyay, 1997; Wilson & Upchurch, 2003). These two taxa co–existed and were relatively large (~25 m). A large ellipsoid osteoderm of a titanosaur from the Bara Simla Hill of Jabalpur was also reported to occur in association with *Jainosaurus* material indicating that this titanosaur was possibly armoured (D'Emic *et al.*, 2009). The presence of titanosaur osteoderms in India extends the geographic distribution of armoured dinosaurs. *Isisaurus*, on the other hand, lacked an osteoderm. *Isisaurus* shows similarities to *Antarctosaurus* and *Argentinosaurus* of Argentina. It was possibly more derived than *Jainosaurus* and has been reported from the contemporary Pab Formation of Pakistan on the basis of a braincase (Wilson *et al.*, 2005). Significantly, the braincase of *Jainosaurus* resembles that of *Vahiny* of Madagascar, indicating their close phylogenetic relationships (Rogers & Wilson, 2014). Another interesting fact about the Indian Late Cretaceous titanosaurs is that their coprolites yielded the earliest fossil record of grasses (Poaceae) (Prasad *et al.*, 2005). Apparently, both titanosaurs and gondwanathere mammals in the Lameta ecosystem consumed these early grasses (Verma *et al.*, 2012, 2016).

The second major group represented in the Lameta dinosaur fauna are abelisaur theropods, comprising the relatively small–sized noasaurids and the large and more derived abelisaurids. A number of taxa named by Huene and Matley (1933) nearly 90 years ago come from the famous quarry called "Carnosaur Bed' at Bara Simla Hill of Jabalpur: *Indosaurus matleyi* Huene & Matley, 1933; *Indosuchus raptorius* Huene & Matley, 1933; *Jubbulpuria tenuis* Huene & Matley, 1933; *Laevisuchus indicus* Huene & Matley, 1933; *Lametasaurus indicus* Matley, 1924; *Ornithomimoides mobilis* Huene & Matley, 1933;-*Ornithomimoides? barasimlensis* Huene & Matley, 1933. However, most of the Lameta theropods have had a complex taxonomic history and their taxonomic status and validity of remained doubtful as these species were named on the basis of fragmentary remains (see reviews by Wilson *et al.*, 2003; Novas *et al.*, 2004, 2010; Carrano & Sampson, 2008; Wilson *et al.*, 2011). Novas *et al.* (2004) concluded that all of the theropod elements belong to a single theropod clade, the Abelisauroidea. Based on a re–evaluation and phylogenetic analysis, Carrano and Sampson (2008) concluded that several of the Lameta theropods, especially *Indosaurus*, *Rajasaurus* and *Lametasaurus* show close similarity and may be synonymised, with the last–named genus (*Lametasaurus*) getting nomenclatural preference (Carrano & Sampson, 2008). However, the validity of *Lametasaurus* is also doubtful and it may even be a chimera (Chatterjee & Rudra, 1996) since several elements in the original description, including the hindlimbs and pelvis, have been referred to *Rajasaurus* (Wilson *et al.*, 2003). Novas *et al.* (2010) also considered *Lametasaurus indicus, Indosuchus raptorius*, and *Indosaurus matleyi* as *nomina dubia*, and recognised only two valid large theropod species from the Lameta Formation: *Rajasaurus narmadensis* and *Rahiolisaurus gujaratensis*, both from the Rahioli Locality of Gujarat.

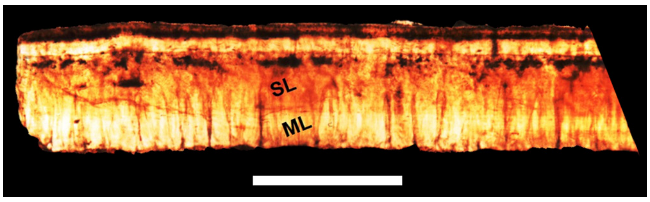

Fig. 13b—Ornithoid eggshell (*Subtiliolithus kachchhensis* Khosla & Sahni, 1995). Radial thin section under polarizing light microscope showing double layered eggshell with well-defined mammillary and spongy layers (VPL/KH/5719). Abbreviations: ML, mammillary layer; SL, spongy layer. Scale = 500 µm.

Chatterjee and Rudra (1996) reported the occurrence of a possible ankylosaur (? nodosaurid) from the Lameta Formation near Rahioli quarry, represented by several associated spines, limbs and girdle bones. More recently, Chatterjee (2020) reiterated the presence of new ankylosaur material including isolated vertebrae, humerus, femur and several armour fragments such as solid dorsal scutes and hollow lateral spikes.

Apart from the skeletal evidence, the shell structure of Indian dinosaur eggs provides another comparative framework for assessment of the biogeographic affinities of Indian dinosaurs (Bajpai *et al.*, 1993; Sahni *et al.*, 1994; Fernández & Khosla, 2015; Kapur & Khosla, 2016, 2019; Khosla, 2019; Khosla & Lucas, 2020e). Dinosaur eggs of both sauropod and theropod affinities are well known from the Maastrichtian Lameta Formation and Deccan Intertrappean beds of east–west and central peninsular India (Figs 11–12) (Mohabey, 1983; Bajpai *et al.*, 1993; Srivastava *et al.*, 1986; Sahni & Khosla, 1994; Sahni *et al.*, 1994; Khosla & Sahni, 1995, 2003; Loyal *et al.*, 1996, 1998; Bajpai & Prasad, 2000; Mohabey, 1998; Khosla, 2001, 2017; Sahni, 2003; Vianey–Liaud *et al.*, 2003; Fernández & Khosla, 2015; Khosla &Verma, 2015; Aglawe & Lakra, 2018; Kapur & Khosla, 2016, 2019; Khosla & Lucas 2020a–e; Khosla *et al.*, 2020).

Based on the eggshell structure, as many as five oofamilies (Fusioolithidae, Megaloolithidae, Elongatoolithidae, Spheroolithidae, Subtiliolithidae) and 15 oospecies have been identified from the Deccan volcano–sedimentary province (Fernández & Khosla, 2015; Khosla, 2019; Figs 13a, b).

In a review of parataxonomy of Late Cretaceous sauropod egg species of India and Argentina, it was noted that five oospecies, namely *Megaloolithus jabalpurensis, M. cylindricus, M. megadermus, Fusioolithus baghensi*s and *F. berthei*, are common to India, Argentina, Africa and southern Europe (Fernández & Khosla, 2015; Khosla, 2019; Khosla & Lucas, 2020e). The Indian dinosaur ootaxa show close resemblance to forms known from France, Spain, Africa and Argentina. According to these authors, a close phylogenetic relationship exists between the oospecies of India and southern Europe, and between Argentina, India and Africa.

Apart from the Lameta Formation, fragmentary dinosaur remains have long been known from the Kallamedu Formation (Ariyalur Group) of Cauvery Basin, in the Ariyalur District of Tamil Nadu, southern India (Blanford, 1862; Matley, 1929). The described fossils include a tooth referred to *Megalosaurus* (Lyddeker, 1879) and a tibia, a femur and vertebrae originally referred to a theropod (Yadagiri & Ayyasami, 1987) but later considered to be a possible sauropod (Krause *et al.*, 2006). Based on a single isolated tooth, a troodontid theropod was also recorded recently from the late Kallamudu Formation (Goswami *et al.*, 2013). A solitary egg was also recorded from Kallamedu Formation (Kohring *et al.*, 1996; Dhiman *et al.*, 2019).

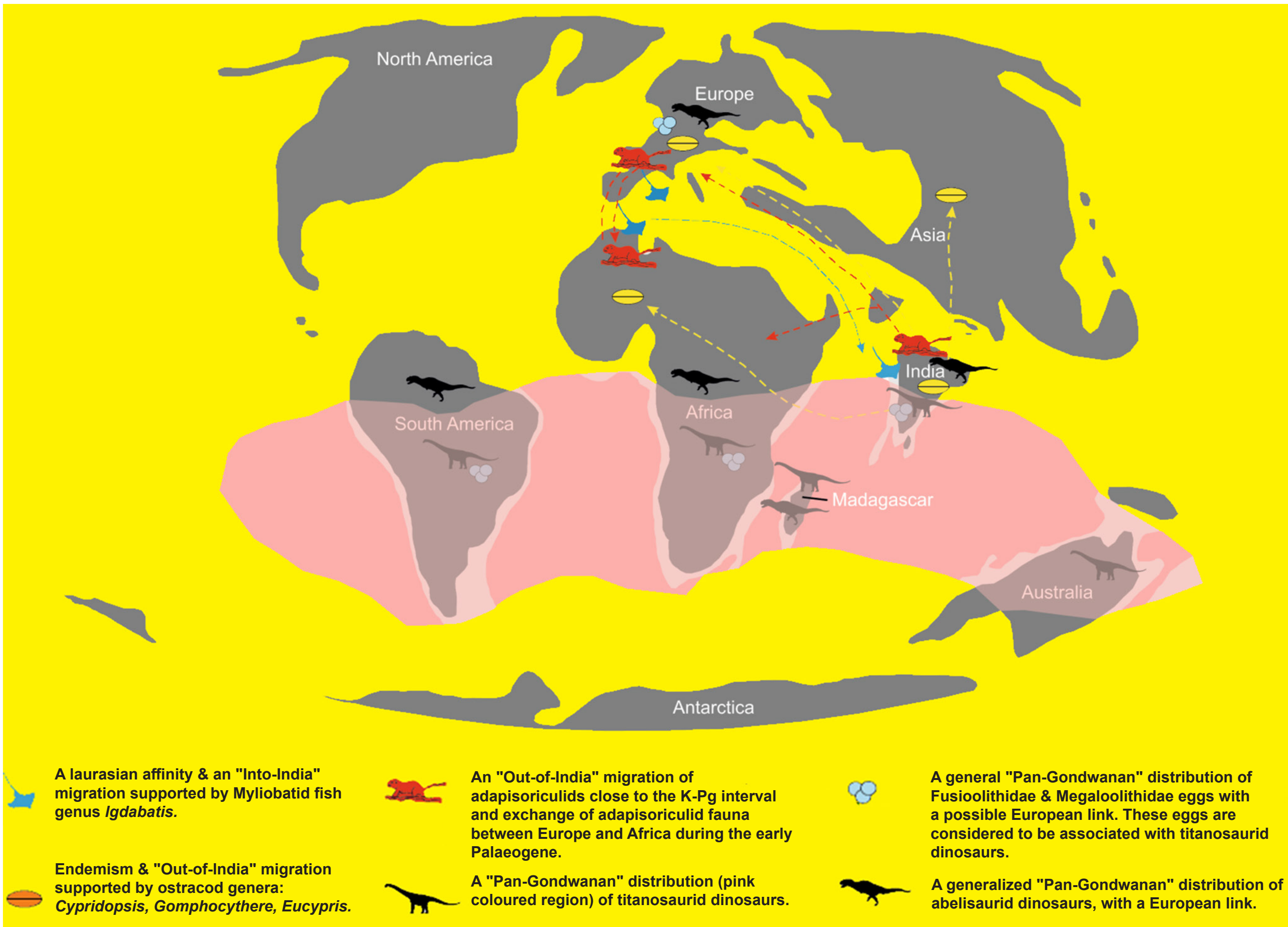

Fig. 14—Latest Cretaceous palaeogeographic map indicating the biogeographic affinities of the various faunal groups, with focus on dinosaurs (Map modified after Scotese, 2001; Khosla, 2019).

The Lameta dinosaur fauna has interesting palaeobiogeographic implications. Titanosaurs, dominantly Gondwanan sauropods, are widely known from the Late Cretaceous deposits of South America, Australia, North America, Mongolia and China. The Lameta titanosaurs do not show evidence of pronounced endemism as would be expected from their supposedly long isolation especially after India's separation from Madagascar at ~ 89 Ma. Recent studies have highlighted strong similarities between Indian and Madagascan titanosaurs (Wilson *et al.*, 2009). *Vahiny depereti* from the Late Cretaceous Maevarano Formation of Madagascar was found to be close to *Jainosaurus* from the Lameta Formation (Rogers & Wilson 2014). *Isisaurus* also shows similarities to *Antarctosaurus* and *Argentinosaurus* of Argentina (Chatterjee *et al.*, 2017). A more recent study of two dorsal vertebrae of a Lameta titanosaur also shows close similarity with *Mendozasaurus* from Argentina, highlighting close biogeographic links between India and South America (Wilson *et al.*, 2019).

Among the theropods, *I. raptorius* and *R. narmadensis* described from Jabalpur and Rahioli, respectively, are considered to be closely related (sister taxa) to *Majungasaurus crenatissimus* from Madagascar (Carrano & Sampson, 2008), supporting close biotic links between India and Madagascar during the Late Cretaceous. A smaller abelisaur from the Lameta Formation (*Laevisuchus indicus*) is closely allied to *Masiakasaurus knopfleri* from Madagascar (Sampson *et al.*, 2001; Carrano *et al.*, 2002).

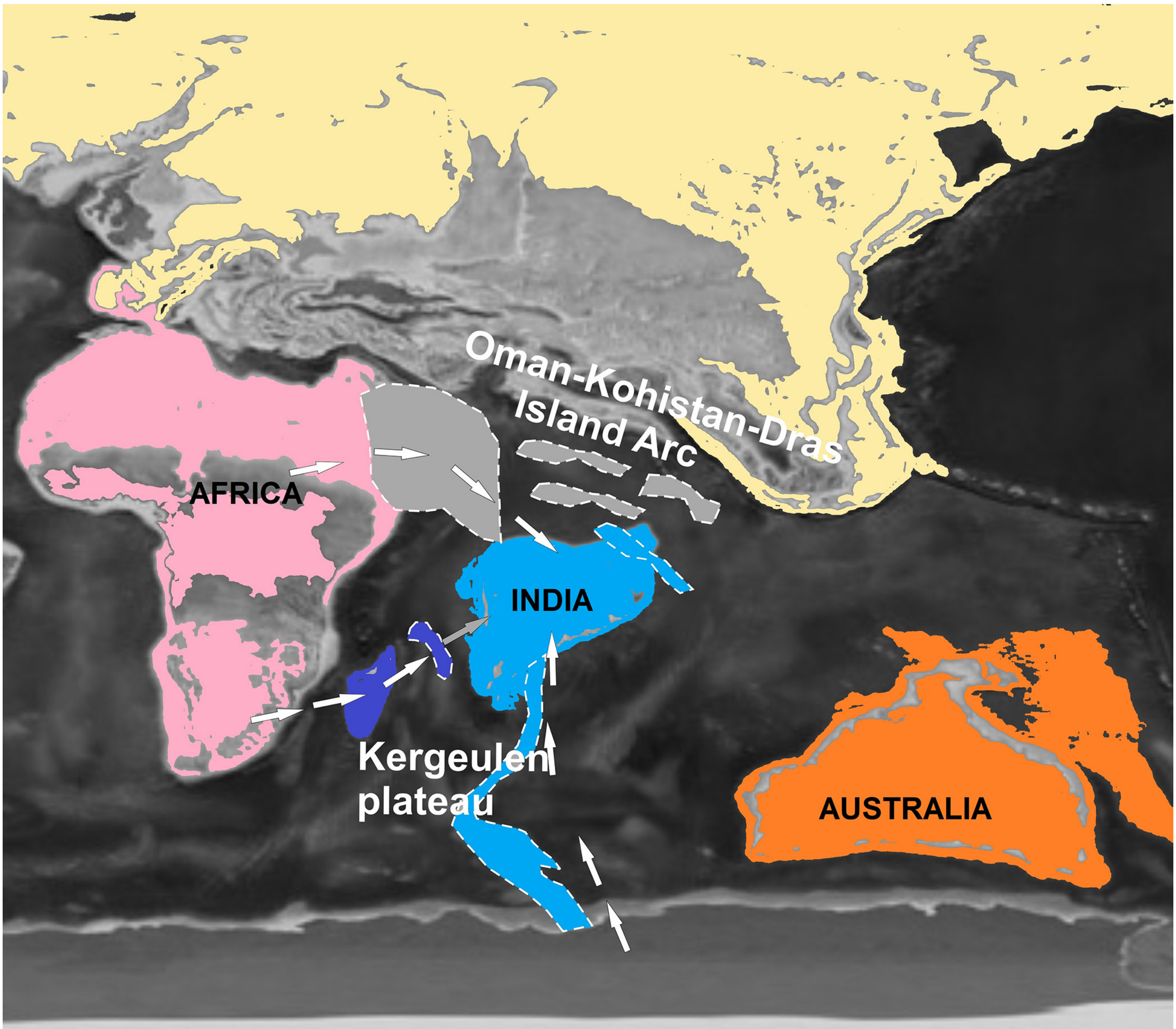

Fig. 15—Palaeobiogeographic reconstruction of the Indian subcontinent's presumed Gondwanan linkages. Map modified from reconstructions by Ron Blakey, NAU Geology (https://www2.nau.edu/rcb7/065Marect.jpg) (Map modified after Khosla, 2019).

The Gondwanan affinities of India's late Cretaceous fauna are also suggested by associated vertebrate groups such as gondwanathere mammmals and notosuchian crocodyliomorphs. These occurrences have led to hotly debated palaeobiogeographic scenarios (Fig. 14).

Major current hypotheses suggest the existence of a subareal route between Indo–Madagascar and South America via Antarctica and the Kerguelen Plateau/Gunnerus Ridge during the Late Cretaceous (Krause *et al.*, 1997; Sampson *et al.*, 1998; Case, 2002; Prasad *et al.*, 2013; Khosla, 2019, but see Ali & Aitchison, 2009 for an opposing viewpoint). An alternative dispersal route was hypothesized by Chatterjee and Scotese (2010) and Chatterjee *et al.* (2017) who proposed Late Cretaceous intermittent faunal exchanges between India and Africa via Oman–Kohistan–Dras Island Arc (Fig. 15).

An alternating scenario envisaging a more widespread (pan–Gondwanan) distribution of the ancestral taxa of dinosaurs including abelisaurids and other terrestrial faunal groups is favoured by other workers (e.g. Ali & Krause, 2011; Fig. 14). This model hypothesizes the presence of a common fauna distributed on all the Gondwanan landmasses during the early Cretaceous before the separation of Africa from other Gondwana continents at the beginning of Late Cretaceous (Sereno & Brusatte, 2008; Khosla, 2019). This was followed by the evolution of increasingly endemic faunal assemblages (Gondwanan relics) on each of the Gondwanan landmass. As regards the presence of a possible troodontid based on a single tooth in the late Cretaceous of the Cauvery Basin (Goswami *et al.*, 2013), it remains to be seen whether this record signifies a dispersal event from Laurasia to India or whether it reflects a poorly sampled Gondwanan record of troodontids. Future fossil discoveries from older intervals of Gondwanan landmasses, especially Africa, will allow a critical evaluation of pan–Gondwanan hypothesis.

In conclusion, the Lameta Formation has yielded the most diverse dinosaur fauna in India. Two major groups of saurischian dinosaurs, titanosaurid sauropods and abelisaurid theropods, occur in this formation (Huene & Matley, 1933; Chatterjee, 1978; Chatterjee & Hotton, 1986; Chatterjee & Rudra, 1996; Wilson *et al.*, 2003; Novas *et al.*, 2010). The assemblage is dominated by Gondwanan forms with closest phylogenetic relations to Madagascan and South American taxa, but Laurasian elements such as possible troodontid theropods and ankylosaurs may also be represented. These dinosaur taxa, together with other associated taxa such as adapisoriculid mammals and endemic non–marine ostracod faunas (Whatley & Bajpai, 2006) (Fig. 14) raise important palaeogeographic issues about India's physical connections with Gondwanan and/or Laurasian landmasses during the terminal phase of its northward drift, or a pan–Gondwanan distribution of ancestral taxa pertaining to the various clades.

Terminal Cretaceous: the last dinosaurs of India

The K–Pg boundary mass extinction was a global crisis, induced by both impact and Deccan volcanism, that marked the end of the dinosaur era. The role of the Deccan volcanic activity in K–Pg boundary extinctions is becoming increasingly evident with increasing precision of the age and duration of the Deccan eruptions. Recent data has precisely constrained the Deccan volcanism between 67 and 64 Ma, and the main pulse of the Deccan eruptions is believed to have taken place in a relatively short period of time during the magnetic polarity chron 29R (~750,000 years) around the K–Pg boundary (Chenet *et al.*, 2009; Keller *et al.*, 2009; Schoene *et al.*, 2015; Eddy *et al.*, 2020). Although both Lameta and Deccan Intertrappean beds are dated as

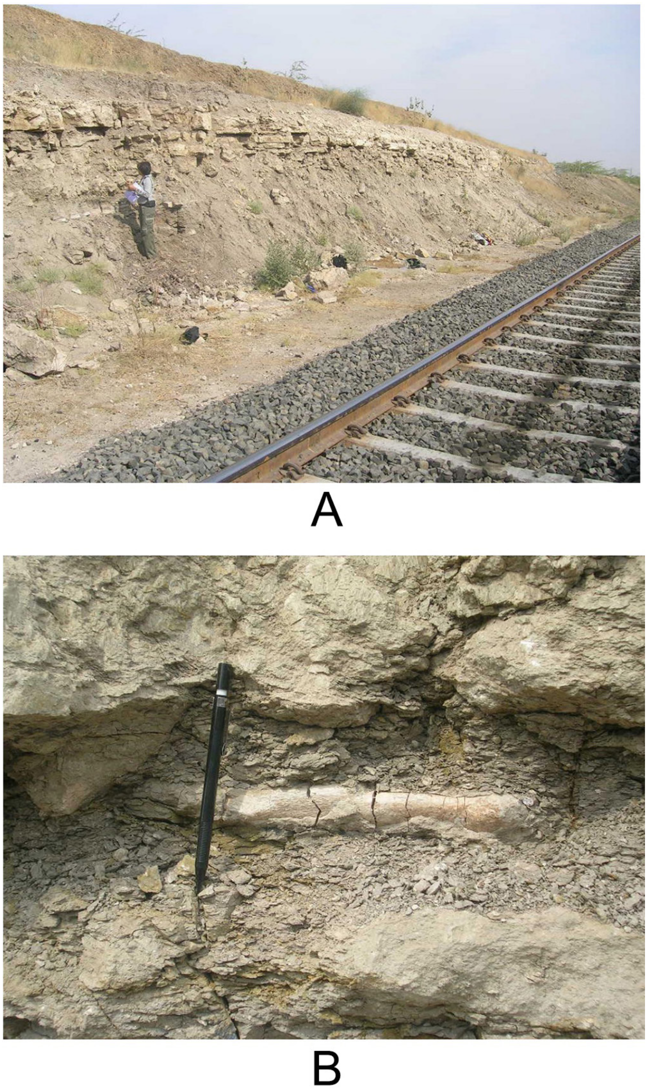

Fig. 16—A. Dinosaur-bearing intertrappean beds exposed near the railway track at Anjar, Kutch (Gujarat). B. Enlarged view of part of Fig. 16A showing an *in situ* dinosaur bone. Scale (pencil)= 14 cm.

Maastrichtian, the latter are generally slightly younger in age within Maastrichtian because of their stratigraphic position, and may even straddle the Cretaceous–Paleogene (K–Pg) boundary (Keller *et al.*, 2009; Khosla & Lucas, 2020a). The youngest stratigraphic record of dinosaurs of India occurs in these thin Maastrichtian intertrappean deposits sandwiched between the Deccan lave flows. Several non–marine Deccan Intertrappean localities in peninsular India are known to have yielded dinosaur remains, especially isolated teeth, rare fragmentary limb bones and eggshell fragments, but complete eggs are practically absent (Bajpai *et al.*, 1990; Khosla & Sahni, 1995, 2003; Khosla & Lucas, 2020c–e; Khosla *et al.*, 2020). The presence of fragmentary dinosaur remains in several intertrappean localities led to the general acceptance of a Maastrichtian age for these deposits (e.g., Sahni & Bajpai, 1988; Bajpai, 1996;; Bajpai & Prasad, 2000; Khosla & Sahni, 2003; Bajpai *et al.*, 2013; Kapur & Khosla, 2016, 2019; Khosla & Lucas 2020c–e), in contrast to a long held early Tertiary (Paleocene) age based mainly on plant fossils (Mehrotra, 1989). However, more recent investigations (e.g., Keller *et al.*, 2009; Khosla, 2015) provided definite evidence of an early Paleocene age for a section at Jhilmili (Madhya Pradesh) based on planktic foraminifers, indicating that intertrappeans can be exclusively Maastrichtian or Paleocene or may even straddle the K–Pg boundary in some localities in the Deccan volcanic province. No dinosaur remains have been found at Jhilmili or in any other intertrappean deposit dated as Paleocene. The most important dinosaur–yielding intertrappean localities include Anjar, Gujarat (Ghevariya, 1988; Bajpai *et al.*, 1993; Bajpai & Prasad, 2000); Asifabad, Andhra Pradesh (Rao & Yadagiri, 1981); Mohagaonkalan, District Chhindwara, Madhya Pradesh (Srinivasan, 1996); Ranipur, district Jabalpur, Madhya Pradesh (Mathur & Sharma, 1990). So far, the best evidence bearing on the question of the timing of dinosaur extinction in India has come from Anjar (Fig. 16) where a multidisciplinary approach involving data on dinosaur fossils, iridium anomalies, Ar–Ar ages and palaeomagnetic reversals was attempted (Bhandari *et al.*, 1996; Bajpai & Prasad, 2000). The origin of multiple Ir anomalies at Anjar is unclear but the apparently unreworked dinosaur remains and associated Maastrichtian fossils occurring above the Ir–enriched levels suggest that the Ir enrichment and dinosaur extinction in India may predate the K–Pg boundary and possibly occurred sometime in the early part of the magnetic chron 29R (Bajpai & Prasad, 2000).

SUMMARY AND CONCLUSIONS

The fossil record of dinosaurs from India includes several important taxa that bear significantly on our understanding of the dinosaur palaeobiogeography and evolutionary history, but this record is marked by significant temporal and spatial gaps, making it difficult to arrive at a comprehensive understanding of the Mesozoic vertebrate biogeography. The first dinosaur remains from India come from the late Triassic rhynchosaur–dominated Lower Maleri Formation (Pranhita Godavari Basin, Andhra Pradesh) which has yielded fragmentary bones including a tibia that is attributed to a basal saurischian (*Alwalkeria maleriensis*) of uncertain relationships. Abundant and relatively diverse Late Triassic basal sauropodomorphs occur in the overlying Upper Maleri and the Lower Dharmaram formations. However, well–preserved Early Jurassic dinosaurs have been reported from the two horizons, the Upper Dharmaram Formation and the Lower Kota Formation. The Upper Dharmaram fauna comprises three sauropodomorphs, *Pradhania gracilis*, *Lamplughsaura dharmaramensis* and an indeterminate one, whereas the overlying Kota Formation has yielded two sauropods (*Kotasaurus yamanpalliensis* and *Barapasaurus tagorei*) and an ankylosaur. Early Jurassic faunas of Upper Dharmaram Formation resemble those of coeval deposits of South Africa, America and China. Among the Middle Jurassic finds, fragmentary remains of camarasauromorph dinosaurs known from Kutch (Kuar Bet, Patcham Island, Gujarat) and the fragmentary bones from the Jaisalmer District of Rajasthan hold considerable potential for future studies.

The dinosaur fauna from India's post–Gondwanan drift phase since the Late Jurassic comprises not only the Gondwanan holdovers but possibly also migrants from the Laurasian landmasses. The Cretaceous records of Indian dinosaurs is largely limited to the Deccan volcano–sedimentary province of central and western India (Lameta Formation, intertrappean beds) and a few occurrences in the Maastrichtian Kallamedu Formation of Cauvery Basin, Tamil Nadu, southern India. Palaeobiogeographic considerations of the Indian dinosaur faunas present unresolved problems arising from close phylogenetic relations of the latest Cretaceous Indian dinosaurs with those from Madagascar and South America. Current explanations favour dispersal via southern (India–Madagascar–Antarctica South America via Kerguelen Plateau/Gunnerus Ridge) or a northern terrestrial route (Oman–Kohistan–Dras arc) or a pan–Gondwanan distribution of the ancestral taxa. A more complete fossil record, especially from the early/mid early Cretaceous of India, will help resolve such long standing issues.

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