# GONDWANAN DINOSAURS OF INDIA: AFFINITIES AND PALAEOBIOGEOGRAPHY

# RAMINDER S. LOYAL, ASHU KHOSLA & ASHOK SAHNI

Loyal, R.S., Khosla, A. & Sahni, A. 1996 12 20: Gondwanan dinosaurs of India: affinities and palaeobiogeography. *Memoirs of the Queensland Museum* **39**(3) 627-638. Brisbane. ISSN 0079-8835.

The record of Indian dinosaurs is now well known and extends from Late Triassic to the terminal Cretaceous. The Indian dinosaurs are based on fragmentary cranial, skeletal and egg material which is a cause of some uncertainty in the analysis of their taxonomic affinities, age and palaeobiogeography. The Indian dinosaurian record starts with the Triassic Maleri Formation, which yields Alwalkeria maleriensis, a coelurosaur. The overlying Dharmaram Formation contains phytosaurs, aetosaurs, plateosaurids and a sphenosuchid. The early Jurassic Kota Formation has yielded numerous bones (cranial and postcranial) of Barapasaurus tagorei, besides semionotid fishes, coelacanths, pleurosaurs, crocodiles and mammals. The Cretaceous dinosaurian record is from sedimentary sequences associated with the Deccan volcanics and is dominated by skeletal remains of titanosaurid sauropods and theropods, such as Indosuchus raptorius and Indosaurus matleyi. The Kallamedu Bone Bed (Ariyalur Formation) has yielded bones and a tooth of Megalosaurus. The cranial and postcranial skeleton of a stegosaur Dravidosaurus blanfordi is known from the Trichinopoly Group. Khosla & Sahni (1995) have classified Indian dinosaur eggs and eggshell fragments into eight new oospecies (in the oofamilies Megaloolithidae and Subtiliolithidae): Megaloolithus cylindricus, M. jabalpurensis, M. mohabeyi, M. baghensis, M. dholiyaensis, M. walpurensis, M. padiyalensis and Subtiliolithus kachchhensis. Besides these Late Cretaceous eggshells, footprints are known from the Bhuj Formation of Early Cretaceous age (Ghevariya & Srikarni, 1990). Coprolites of dinosaurs and (probable) chelonians are known from the Late Cretaceous of Pisdura, and include four categories of ribbed and non-ribbed forms. The palaeobiogeographic analysis of the Indian dinosaurs implies they are part of a cosmopolitan distribution. However, migrations through an earlier Madagascan connection and through island arcs in the Cretaceous (represented by Dras volcanics) and earlier collision arcs and microplates in Late Permian to Cretaceous (represented by northernmost Gondwana fragments of Tibet, Iran, Iraq and Afghanistan) led to an influx of some taxa. These paths of migration are significant in explaining the cosmopolitan character of the Indian biotas and their similarities to Laurasian faunas during the drift of the Indian Plate. India, dinosaurs, Mesozoic, tracks, dinosaur nests, eggs.

R.S. Loyal, A. Khosla & A. Sahni, Centre of Advanced Study in Geology, Panjab University, Chandigarh, 160 014, India; 1 July 1996.

Dinosaur remains in India are found in the Triassic-Cretaceous sequence of peninsular India (Table 1), however Middle Jurassic-Middle Cretaceous gaps are quite significant. In this context, the Pranhita-Godavari valley, where a thick continental vertebrate-rich sequence of Late Permian-Cretaceous age is exposed, has assumed considerable significance as a site for Gondwanan dinosaurs.

While the Pranhita-Godavari Valley (Fig. 1) represents a repository of dinosaurs of Triassic-Jurassic age, the younger terminal Cretaceous dinosaur fauna is most diverse. It occurs along the Narmada Valley of central India, associated with the Lameta Formation and is spread over more than 10,000 sq. km., below the Deccan volcanosedimentary sequence (Sahni et al., 1994, Fig. 2). In addition, Cretaceous dinosaurs also

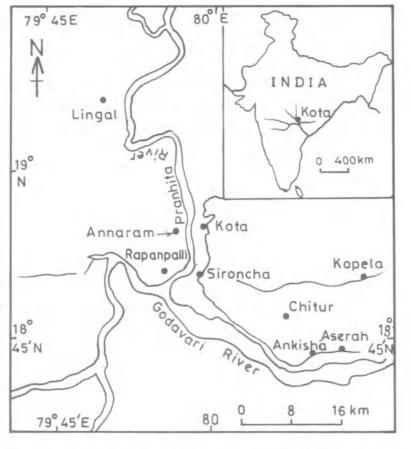
occur towards the south, associated with the Ariyalur Formation.

# TRIASSIC

The oldest record of Indian dinosaurs comes from the Late Triassic Maleri Formation, which is exposed near the village Maleri (near Tandur) in the district Adilabad, Andhra Pradesh. Lithologically, red clays are abundant, along with lime-pellet rocks (calcirudites, calcarenites) and quartzose sandstones (Kutty & Sengupta, 1989).

The biotic elements of Maleri Formation include vertebrates, coprolites, invertebrates and plants. Dominant in the Lower Maleri, is *Alwalkeria maleriensis*, which constitutes the earliest Indian dinosaur (Chatterjee, 1987) and is based on imperfectly known fragmentary material, a partial skull, vertebrae, a femur and astragali. It is referred to the basal theropods, belonging to a group of slightly built predaceous dinosaurs.

The overlying Dharmaram Formation is composed of a basal thick sandstone followed by more sandstones and clay beds. The sandstones resemble the Maleri sandstones, but are more coarsegrained and gritty (Kutty et al., 1987). The lower part of the Dharmaram Formation - besides the occurrence of the fish Xenacanthus and Ceratodus - is characterised by the presence of a phytosaur (Nicrosaurus), dominant aetosaurs and a small prosauropod (Kutty & Sengupta, 1989). The Upper Dharmaram Formation, on the other hand, is far richer and contains a large plateosaurid, an ornithischian and a sphenosuchid (Kutty, 1969; Kutty et al., 1987). Although as the fauna remains undescribed as yet, a Late Norian-Rhaetian age is preferred by most workers for this fauna.



# JURASSIC

The continental Kota Formation, of Early Jurassic age, lies conformably above the Dharmaram Formation and in turn is overlain by Gangapur Formation of Early Jurassic age (Kutty et al., 1987). The stratotype of this formation is named after Kota village, on the eastern bank of the Pranhita River. This formation has provided a vast amount of information about its exceedingly rich continental fauna, comprising fishes, reptiles, mammals, freshwater ostracodes, conchostrachans and land insects (Kutty et al., 1987).

The lithic units of the Kota Formation are characterised by sandstones (ferruginous arkoses), with cross-bedding, and limestones with desiccation polygons and worm-bored layers (Robinson, 1970; Jain, 1980; Yadagiri & Rao, 1987).

Field work conducted by palaeontologists of the Indian Statistical Institute in the Kota Formation during 1960-61 led to the recovery of about 300 sauropod bones from a bone bed occurring between a sandstone-clay lens. This vertebrate material was assiduously studied by Dr S.L. Jain and his colleagues, who established a new

FIG. 1. Map of Pranhita-Godavari Valley with fossil- bearing localities (after Jain et al., 1975).

sauropod, *Barapasaurus tagorei*, one of the best known Early Jurassic dinosaurs in the world (Jain, 1975, 1979). A complete mounted skeleton of this dinosaur is displayed at the Geology Museum, Indian Statistical Institute, Calcutta.

Barapasaurus tagorei was a large sauropod with slender limbs, spoon-shaped teeth with coarse denticles, opisthocoelous cervical and anterior dorsal centra, with the other centra platycoelous. Neural spines are not bifurcate and the centra are not cavernous, but have oval depressions in the lateral surface. The ilium possesses a welldeveloped anterior process, the ischium is relatively slender and rod-like distally and the pubis has a well-developed terminal expansion.

Jain et al. (1979) commented on the level of development of *Barapasaurus*, stating that it is intermediate between the prosauropod stage and that of known sauropods (e.g., the limbs, though graviportal, are slender). The anterior caudals have not developed procoelous centra. The sacrum is narrow, with the pelvic depression small in comparison to length of the pubis. Mc-Intosh (1990) tentatively assigned *Barapasaurus* 

LITHO-UNIT, AGE	CONTAINED FOSSILS	LITHOLOGY
Deccan volcano-sedimentary sequences Late Cretaceous	mammals, dinosaurs (titanosaurids), frogs, fishes, charophytes, ostracodes	sandstones, shales, marls, associated with Deccan basalts
Chikiala		ferruginous sandstones conglomerates
Gangapur Early Cretaceous	Gleichenia, Pagiophyllum Ptilophyllum	gritty sandstones, pink mudstones, ferruginous sandstones
Kota Early Jurassic	holostean fishes, sauropods, pterosaurs, early mammals	sandstones, siltstones, clays and a limestone band
Dharmaram late Late Triassic	prosauropods	sandstones, red clays
Maleri early Late Triassic	metoposaurs, aetosaurs, phytosaurs, rhynchosaurs	red clays, sandstones, lime-pellet rocks
Bhimaram Sandstone late Middle Triassic	labyrinthodont, dicynodont	sandstones (ferruginous in lower part), red clays
Yerrapalli early Middle Triassic	stahleckeriid, kannemeyeriid dicynodonts	red violet clays, sandstones, pellet rocks
Kamthi Late Permian-Early Triassic	dicynodonts from basal beds	ferruginous, non-felspathic sandstones, purple siltstones

TABLE 1. Gondwana stratigraphy of Pranhita-Godavari Valley (modified after Kutty et al., 1987).

to the Vulcanodontidae (Cooper, 1984) on the basis of the narrow sacrum, deeply furrowed caudals, long forelimbs, apron-like pubis, elongate metatarsals and teeth with coarse denticles.

The associated fauna of the Kota dinosaurs includes semionotid fishes (*Tetragonolepis*, *Lepidotes*, *Parapedium*), a coelacanth (*Indocoelacanthus robustus*), a pholidophorid fish (*Pholidophorus*), a pterosaur (*Campylognathoides*) and teleosaurid crocodiles (Kutty et al., 1987; Jain & Roy Chowdhury, 1987). Early Jurassic mammals from the Kota Formation are represented by *Kotatherium*, *Trishulotherium* and *Indotherium* (Datta, 1981; Yadagiri, 1984; 1985).

# CRETACEOUS

SKELETAL MATERIAL. The Indian Cretaceous dinosaur record is associated with the non-marine post-Gondwana sequence of central and western India. This sequence is represented by Lameta Formation, which has received considerable attention for the last 70 years for its fairly extensive dinosaurian fauna. Stratigraphically, the dinosaur-rich vertebrate beds underlie the Deccan Traps, with an aerial extent of more than 10,000 sq. kms. As such, this vertebrate sequence is crucial to the dating and duration of the traps, more so as the Late Cretaceous extinction mechanisms might be related to the eruptions (Courtillot et al., 1986; Buffetaut, 1987).

The stratotype of the Lameta Formation is situated at Lametaghat, near Jabalpur on the banks of Narmada river. The classic dinosaur areas here are Bara Simla Hill and Chui Hill, in addition to Pisdura in Maharashtra. The first detailed account of the geology of the Jabapur area was given by Matley (1921), who prepared an excellent map of the area on a scale measuring 8 inches to a mile, along with a description of various lithic units.

Huene & Matley (1933) described postcranial elements of the titanosaurid sauropods, viz. *Titanosaurus indicus* and *Antarctosaurus septentrionalis* from Bara Simla Hill, and a third sauropod *Laplatasaurus madgascariensis* from Pisdura. From the same locality carnosaurs were also described: *Indosuchus raptorius* and *Indosaurus matleyi*, along with coelurosaurs, such as *Compsosuchus solus*, *Laevisuchus indicus*, *Jubbulpuria tenuis*, *Coeluroides largus*, *Dryptosauroides grandis*, *Ornithomimoides mobilis* and O.(?) barasimlensis.

Of the aforementioned forms Antarctosaurus septentrionalis has been given a new generic name Jainosaurus by Hunt et al. (1994) because of its distinctness from the Argentinian form, the genotypic A. wichmannianus. The main differences are in braincase of the Indian and Argentinian forms. Earlier Indian braincase studies on 'Antarctosaurus' septentrionalis were by Berman & Jain (1982) however the specimens were recovered from Dongargaon near Pisdura. Further, Indosaurus and Indosuchus regarded by Chatterjee (1978) as a megalosaur and tyrannosaurid (respectively), are now considered as abelisaurids (see Chatterjee, this volume).

As compared to the saurischian fauna, the information and taxonomic assignment of ornithischians have remained largely in doubt.

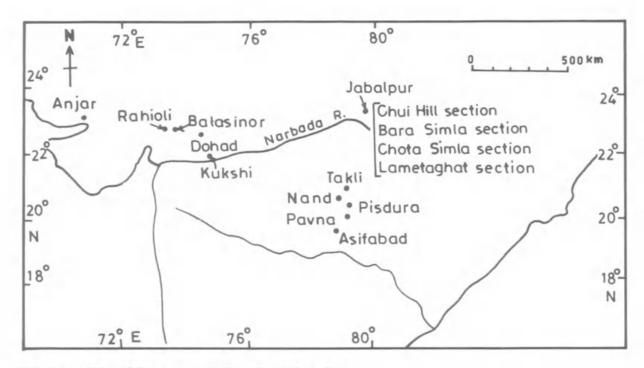


FIG. 2. Localities of dinosaur eggshells and nests in India.

Lametasaurus indicus described from Bara Simla Hill by Matley (1933) was at that time considered to be a stegosaurian. Later Chakarvarti (1934) and Walker (1964) opined that this genus could not be an ankylosaurian. Recently, works by Berman & Jain (1982), Buffetaut (1987) and Molnar & Frey (1987) opined that Lametasaurus could well have been a titanosaurid. Molnar (pers. comm., 1996) believes it to be a chimaera (based on bones and skeletons of saurischians and crocodilians). However a new ankylosaurian specimen is reported by Chattergee & Rudra (this volume).

From South India, the dinosaur studies were first conducted by Blanford (1862), who reported bones and a tooth of *Megalosaurus* from the same horizon in the Kallamedu Bone Bed (Ariyalur Formation, Late Cretaceous). Matley (1929) reported fragmentary bones of *Titanosaurus* along with teeth of a megalosaur and bones of a stegosaurian. Much later, Yadagiri & Ayyasami (1979) described cranial and postcranial skeleton of stegosaur *Dravidosaurus blanfordi* from the Trichinopoly Group (Turonian-Santonian). In this work, a brief mention is also made of the presence of bones of a sauropod, theropod and stegosaur from the Kallamedu Bone Bed.

EGGSHELLS. The Late Cretaceous eggshell material and nesting sites have been most abundant and have assumed considerable significance

over the last decade, providing evidence of a large dinosaur hatchery (Figs 2, 3). The eggshells and nesting sites underlie the Deccan Trap flows and are uniformly found in a hard sandy carbonate with strong development of a calcretised palaeosol towards the top (Tandon et al., 1990; Jolly et al., 1990; Sahni et al., 1994, Fig. 3). In addition, Late Cretaceous eggshells are also known from the sandy limestones of the Kallankurichi Formation of the Ariyalur sequence (Kohring et al., 1996).

Up to now, considerable work has been done to categorise main eggshell morphotypes (discussed later) based on megascopic and microscopic characters (Mohabey, 1982; 1984; Srivastava et al., 1986; Vianey-Liaud et al., 1987; Jain 1989; Sahni, 1989; Mohabey & Mathur, 1989; Jolly et al., 1990; Sahni, 1993; Sahni et al., 1994 and many others). This research and the present work, have established five eggshell morphotypes, three of which have been assigned to titanosaurid sauropods (parataxonomic oofamily Megaloolithidae, Zhao, 1979) and the fourth to the ornithoid type. In a recent work, Khosla & Sahni (1995) established eight oospecies including seven of the oogenus Megaloolithus referable to sauropods and one, Subtiliolithus, an ornithoid. These oospecies are:

Megaloolithus cylindricus Khosla & Sahni (1995)(Pl. 1, Fig. A): spherical eggs 12-20cm in diameter; eggshell thickess varying from 1.7-

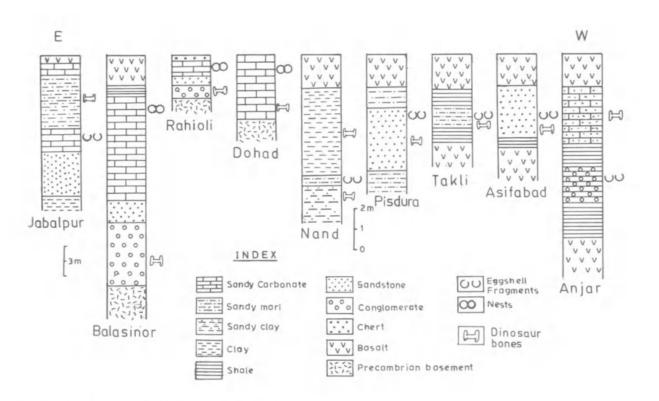


FIG. 3. Stratigraphic sections with associated eggshells and nests.

3.5mm; spheroliths cylindrical; pores subcircular; pore canals long and narrow; tightly packed subcircular basal caps, 0.2-0.5mm in diameter.

Megaloolithus jabalpurensis Khosla & Sahni (1995)(Pl. 1, Figs B, C): spherical eggs 14-16cm in diameter; eggshell thickness 1-2.3mm; nodose external surface; spheroliths with varying width and shapes; elongate to circular pores; tightly packed basal caps (more so than in *M. cylindricus*) 0.1-0.5mm in diameter.

Megaloolithus mohabeyi Khosla & Sahni (1995): spherical eggs 16-19cm in diameter; eggshell thickness 1.8-1.9mm; nodose external surface; spheroliths long and fused to adjacent ones; growth lines convex to undulating; pores elliptical; broad and semicircular basal caps, 0.14-0.21mm in diameter.

Megaloolithus baghensis Khosla & Sahni (1995)(Pl. 1, Fig. D): spherical eggs 14-20cm in diameter; eggshell thickness 1.0-1.7mm; nodes discrete to fused; spheroliths fan-shaped, distinct or partially fused and look more compressed when ending in multiple nodes; pores subcircular to elliptical; basal caps swollen-ended, 0.2-0.3mm in diameter.

Megaloolithus dholiyaensis Khosla & Sahni (1995): eggshell thickness 1.47-1.75mm; nodose outer surface; spheroliths cylindrical and fan-shaped; pore canals straight; basal caps subcir-

cular to conical, isolated to fused, 0.15-0.30mm in diameter. So far found only as fragments.

Megaloolithus walpurensis Khosla & Sahni (1995): eggshell 3.5-3.6mm thick; spheroliths irregularly fan-shaped and showing fusion towards the outer surface; pore canals short, thin, slender, with slit-like openings; basal caps conical to subcircular, 0.25-0.30mm in diameter. So far found only as fragments.

Megaloolithus padiyalensis Khosla & Sahni (1995): eggshells 1.12-1.68mm thick; nodose external surface; small irregular, slender spheroliths; small and large pore canals; basal caps circular to semicircular, 0.07-0.21mm in diameter. So far found only as fragments.

Subtiliolithus kachchhensis Khosla & Sahni (1995)(Pl. 1, Fig. E): eggshells extremely thin, 0.35-0.45mm; external surface exhibits irregularly spaced microtubercles; double layered; spongy layer poorly defined; mammillary layer 1/2-1/3 of the total eggshell thickness; mammillae tightly packed, 0.03-0.05mm in diameter. So far found only as fragments.

The eggshells referred to a new morphotype (Elongatoolithidae) were recovered from near Rahioli (district Kheda, Gujarat) and work on them is in progress. This morphotype is currently being described in detail with Dr D.M. Mohabey, GSI, who has also recovered the same type of

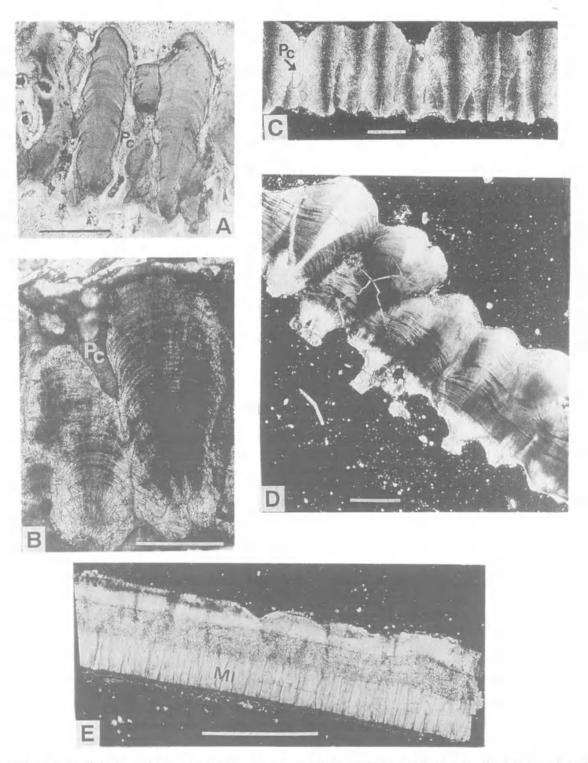


PLATE 1. A, Radial view of *Megaloolithus cylindricus* (VPL/AK 220), Pat Baba Mandir, Jabalpur (Madhya Pradesh). Note cylindrically shaped spheroliths. B, Radial view of *Megaloolithus jabapurensis* (VPL/AK 275), Bara Simla Hill, Jabalpur (Madhya Pradesh), showing small and large fan-shaped spheroliths. C, Radial view of *Megaloolithus jabalpurensis* (VPL/AK 276), Bara Simla Hill, Jabalpur (Madhya Pradesh). Note sweeping extinction pattern of spheroliths. D, Radial view of *Megaloolithus baghensis* (VPL/AK 556), Pisdura, Chandrapur district, Maharashtra. Note small and large fused spheroliths with moderately arched growth lines. E, Radial view of *Subtiliolithus kachchhensis* (VPL/AK 580), Anjar, District Kachchh, Gujarat. Note two-layered eggshell. Mammillary layer is well defined while spongy layer is faintly developed. ML=mammillary layer, Pc=pore canal; scale = 500µm. (VPL/AK=Vertebrate Palaeontology Lab./Ashu Khosla).

eggs. These eggshells are ellipsoid in shape, with a thickness of 1.2-1.6mm, and ornamentation varying from sagenotuberculate (at poles) to lineartuberculate in the equatorial region. The microstructure shows a double layer with radiating structures in the mammillary zone —the latter being about half of the total thickness. Gently curving growth striations are observed in the outer spongy layer. The spheroliths are slender and fused towards the upper part.

TRACKS. As well as the skeletal and eggshell material, dinosaur pedal tracks are also known from the Early Cretaceous Bhuj Formation exposed in the Pakhera and Fatehgarh areas of Kachchh (Ghevariya & Srikarni, 1990). From the Pakhera area, tracks belonging to a juvenile and an adult individual were reported. These types were interpreted as ornithopod, as claws were absent. From the Fatehgarh area, diversely shaped (rectangular, oval and diamond shaped) tracks were described from hard sandstone; the associated grey shale bears an Upper Gondwanan plant, *Ptilophyllum*.

#### PALAEOENVIRONMENTS

The Triassic Maleri Formation, has long been thought to have been deposited in a river valley system, the sandstones representing the channel deposits and clays suggesting an interchannel floodplain (Jain, 1990). The cross-bedded and lenticular sandstones represent cut-off meanders of the mainstream, with clays deposited on waterlogged floodplains (Sengupta, 1970). Jain (1990) described the general environment of the Maleris as indicative of well-aerated country, inhabited by aquatic vertebrates, in a forest habitat. The waterholes and their environs were dominated by amphibians and arboreal vertebrates. The eosuchian *Malerisaurus* probably lived on floodplains or marshy land close to lakes.

The environment for the overlying Dharmaram Formation, from its base to the top of the lower Kota Formation is similar to that of an upwardlyfining sequence deposited under a laterally shifting meandering stream (Rudra, 1982).

As mentioned earlier, the overlying Kota Formation is a typical continental deposit. There were two kinds of depositional environment: sandstones and clays representing fluviatile conditions (river deltas), and thin limestones suggesting deposition in inland lakes (Robinson, 1970). Further, two different climatic conditions also prevailed; one with moderately high relief and rainfall and the other low relief and rainfall. Tasch et al. (1975), on the basis of conchostracans, and Govindan (1975), on the presence of ostracodes, supported a fresh water environment for the deposition of the limestone within small basinal ponds. According to Rudra (1982) the Kota Limestone suggests periodic precipitation of impure lime muds in freshwater playa-type lakes. The presence of inclined and vertical burrows indicates quiet sedimentary episodes, and pelletoidbearing laminations indicate a very slow rate of sedimentation (Maulik & Rudra, 1986). Periods of drought are also suggested by the presence of semionotid fish in cracked limestone — this circumstance has been explained by Jain (1980; 1983) as owing to the mortality of semionotids in the oxygen-deficient evaporating water of the Kota lakes. The large sauropods, such as Barapasaurus, inhabited land close to the Kota lake and fed upon the aquatic vegetation, while the crocodiles fed on fishes and lived on the banks (Jain & Roychowdhury, 1987). Broadly, the Kota lake environment is pictured as a shallow water body, with pholidophorids and coelacanths inhabiting its deeper parts.

The Late Cretaceous Lameta Formation has provided a fairly extensive record of terrestrial dinosaurs, ostracodes, charophytes and invertebrates; the environmental interpretation has therefore been of much fascination.

The marine interpretation of the Lameta Formation is based on the presence of algal-like structures, glauconite beds and thalassinoid burrows (Chanda, 1963; Chanda & Bhattacharya, 1966). Singh (1981) opined that both the Bagh and Lameta Formations are the product of a Turonian-Senonian marine transgression; wherein an estuarine tidal flat complex was indicated by crab burrows, bioturbated carbonate and marl facies.

The marine interpretation was first challenged by Brookfield & Sahni (1987) who believed that the evidence favouring a marine environment may have been misinterpreted, for instance the algal structures in the limestones are pedogenic carbonate structures of palaeosols. Further, on the basis of the dinosaur eggs, bones and associated freshwater biota (charophytes, ostracodes and other invertebrates), it was concluded that the entire Lameta sequence consists of pedogenically-modified piedmont calcrete deposited in a semi-arid environment dominated by a large river.

Subsequently, on the basis of Matley's (1921) map of the Jabalpur area, Tandon et al. (1990) studied the sedimentology and facies of sections

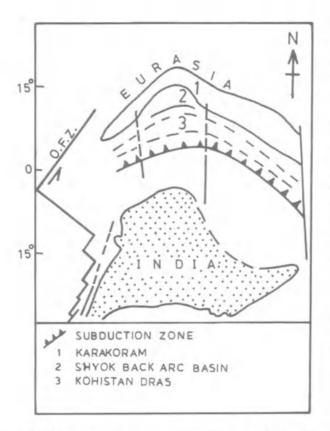


FIG. 4. Late Cretaceous palaeoposition of the Indian plate and Kohistan-Dras Island Arc (after Sharma, 1987; Sahni & Bajpai, 1991).

at Lametaghat, Chui Hill and Bara Simla Hill in detail. At Bara Simla Hill they identified several undulations associated with 'relief highs' and 'relief lows' — these were interpreted (through computer studies) to represent shoulders and ramps on an ancient geomorphic surface. The relief high characterises dinosaur nest-bearing nodular carbonates, while the relief lows are associated with a marly dinosaur bone-bearing horizon. Both these palaeo-relief surfaces form part of fanpalustrine flat system with repeated sheetwash activity, wherein the upper sandy carbonate represents emergent areas with high pedogenic modification, while the lower marly facies has low pedogenic modification (Tandon et al., 1990; Sahni et al., 1994).

Further, the nesting sites, in as much as they are associated with pedogenic calcrete, fringed small lakes. Desiccation and subsequent sheetwash activity occurred leading to rapid matrix cementation and preservation of large dinosaur nests (Jolly et al., 1990). In this context extensive field work at Bara Simla Hill, Chui Hill and Lametaghat suggest a single stratigraphic level of sauropod nests associated with pedogenic calcretes in the Lower Limestone layer (Sahni & Khosla, 1994). Evidence of multiple layers of nesting is absent; the different topographic levels can be explained by the undulatory character of the palaeogeomorphic surface (Tandon et al., 1990). As such there is a strong evidence for 'site selectivity' on the part of the dinosaurs, rather than site fidelity. Moreover, the pedomorphic surface along the entire stretch of terrain from Jabalpur in the east towards Gujarat in west was selected by the sauropods for nesting sites (Jolly et al., 1990).

An alluvial-limnic environment under semiarid conditions was suggested for various subenvironments of the Lametas exposed in Dongargaon Hill and Dhamni-Pavna sections by Mohabey et al. (1993). The eggshell-bearing horizons, especially near Pavna, are associated with overbank facies. Pink and red clays suggest the leaching action of reducing waters with occasional ponding of water, as shown by freshwater charophytes and ostracodes. However, at Pisdura and Dongargaon, a channel facies with immature pebbly and gritty sandstones with calcrete layers was delineated, with crossstratification, convoluted bedding and channel fill structures. The lacustrine facies is characterised by finely laminated silty clays and contains Lepisosteus, Lepidotes and ostracodes (Candionella and Mongolianella).

The palaeophysiologic conditions of the Indian Cretaceous eggshells have been characterised mainly on shell thickness, pore distribution, density, pathologic thickening or thinning and resorption of mammillae (Sahni et al., 1994). The porosity values, which reflect nest humidity, for the eggshells are substantially less; these values are measured by water vapour conductance which vary from 2.65mg/(day.tor) to 3.49mg/(day.tor); such low values are probably due to the semi-arid environment. The O<sup>I8</sup> and C<sup>13</sup> values of the Lameta eggshells

The O<sup>18</sup> and C<sup>13</sup> values of the Lameta eggshells indicate that dinosaurs drank water from rivers and evaporating pools and consumed C-3 type plants, such as palms, dicot shrubs and conifers (Sarker et al., 1991).

#### PALAEOBIOGEOGRAPHY

Until recently, the main arguments supporting the hypothesis of Gondwanaland were derived from glaciation and distinctive floras. In recent years geophysics and oceanography have contributed suggestive new data, but it is the information from Gondwanan vertebrates that has proved to be of inestimable value in providing a clearer palaeobiogeographic analysis in the scenario of drifting plates.

A look into the affinities of the Indian Gondwana tetrapods clearly provides sufficient evidence of Laurasian influence in these palaeocommunities, with no endemism. The Triassic Maleri dinosaur Alwalkeria is more or less similar to Coelophysis of North America and Procompsognathus of Germany. The lower Jurassic Kota dinosaur, Barapasaurus tagorei bears affinities to the European Ohmdenosaurus liasicus, Patagonian Patagosaurus fariasi and Chinese Shunosaurus lii.

Significant evidence, however, is the discovery of Maastrichtian mammal *Deccanolestes hislopi* in the Intertrappeans of Naskal, Andhra Pradesh (Prasad & Sahni, 1988). This genus shows morphological similarity to the North American *Cimolestes* and Mongolian *Kennalestes*.

Palaeorycted mammals are also known from the Paleocene of Morocco (Cappetta et al., 1978). In addition to palaeoryctids, molar teeth belonging to Docodontidae are known from the Late Jurassic of India (Prasad & Khajuria, 1990). Besides, pelobatid frogs, lizards and turtles, known from the Intertrappean beds of Nagpur, are also known from North American and Russian localities.

Amongst the invertebrates, the Intertrappean of Nagpur has yielded Cypris, Candona, Altanicypris, which are similar to Mongolian-Chinese form. Charophytes, such as Platychara perlata known from the Intertrappeans, are closely similar to P. compressa of North America. The aforementioned picture of lack of endemism and the cosmopolitan distribution of Indian dinosaurs, has been utilised and interpreted by some stabilists, who have invoked static models of Indian-Eurasian plates and their contiguity in the past (Chatterjee, 1984; 1987; Chatterjee & Hotton, 1986). These workers are of the view that India was never an island continent during its convergence towards Eurasia, and believed in a narrower Tethys with India occupying a position between Somalia and Eurasia in its pre-drift position (Chatterjee & Hotton, 1986). Also, the presence of Laurasian biotas in India and migrations, may be a consequence of land corridors between India and Eurasia that were maintained during Cretaceous (Chatterjee, 1992).

However the work of ardent mobilists, notably Sahni (1984), Sahni & Bajpai (1991) and Loyal (1984, 1985), have seriously questioned the validity of Chatterjee's (1984, 1987) conclusions. Sahni (1984), while analyzing and admitting the Eurasiatic faunal presence in the Indian Gondwanas, concluded that migration of land faunas took place during the Cretaceous-Palaeocene from the eastern part of Africa, as India was then close to Madagascar. Later, Sahni et al. (1987) and Sahni & Bajpai (1991) suggested that the necessary land passage might have been provided by the island arcs of Dras Volcanics (Fig. 4); this activity might have been initiated earlier, in Late Jurassic (Sharma, 1987). In this context, an early Cretaceous India-Eurasia collision was suggested by Jaeger et al. (1989).

Further, to account for the cosmopolitan distribution, one of us (RSL) is of the opinion that two dispersal corridor routes existed for Gondwanaland-Laurasia intermigrations, viz. India-South Tibet-Afghanistan-Iran-Turkey and India-Africa-Siberia (Loyal, 1985). The fragmented portion of northernmost Gondwanaland (Tibet, Iran, Iraq, Afghanistan) formed a migrating festoon of island arcs, establishing links with Eurasia throughout Late Permian-Cretaceous. Therefore, these paths of migration (in Laurasia and Gondwanaland) were extremely significant in as much as they help explain the lack of faunal endemism of the Indian biotas during its time of geographic isolation and rapid northward journey.

Finally, though there exists now (as aforementioned) a growing body of vertebrate and invertebrate faunal data from the Indian Plate, pointing to strong India-Laurasia links similar palaeobiogeographic data from other Gondwanic areas (Africa, S. America, Antarctica, Australia) is almost meagre. Therefore, in this context, Laurasia-Gondwanaland faunal comparisons remain poorly understood: hence urgent and extensive fieldwork in the Mesozoic terrain of Gondwanic regions is necessary.

#### ACKNOWLEDGEMENTS

The authors are grateful to Dr R.E. Molnar for review and valuable comments on various aspects of Gondwanan dinosaurs. One of us (AK) is thankful to the Council of Scientific and Industrial Research (CSIR, New Delhi) for financial assistance in the form of a Senior Research Fellowship.

#### LITERATURE CITED

BERMAN, D.S. & JAIN, S.L., 1982. The braincase of a small sauropod dinosaur (Reptilia: Saurischia) from upper Cretaceous Lameta Group, Central India, with review of Lameta Group localities. Annals of Carnegie Museum 51: 405-422.

- BROOKFIELD, M.E. & SAHNI, A., 1987. Palaeoenvironments of the Lameta Beds (Late Cretaceous) at Jabalpur, Madhya Pradesh, India: Soils and biotas of a semi-arid alluvial plain. Cretaceous Research 8: 1-14.
- BUFFETAUT, E., 1987. On the age of dinosaur fauna from the Lameta Formation (Upper Cretaceous of Central India). Newsletters in Stratigraphy 18: 1-6.
- CAPPETTA, H., JAEGER, J.J., SEBATIER, M., SUDRE, J. & VIANEY-LIAUD, M. 1978. Decouverté dans le Paleocene du Maroc des plus anciens mammiferes eutheriens d'Afrique. Geobios 11: 257-263.
- CHAKRAVARTI, D.J. 1934. On a stegosaurian humerus from the Lameta Beds of Jubbulpore. Quarterly Journal of the Geological, Mining and Metallurgical Society of India 6(3): 75-79.
- CHANDA, S.K., 1967. Petrogenesis of the calcareous constituents of the Lameta Group around Jabalpur, M.P., India. Journal of Sedimentary Petrology 37: 425-437.
- CHANDA, S.K. & BHATTACHARYA, A. 1966. A re-evaluation of the stratigraphy of the Lameta — Jabalpur contact around Jabalpur, M.P. Journal of the Geological Society of India 7: 91-99.
- CHATTERJEE, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. Palaeontology 21: 83-127.
  - 1984. The drift of India: A conflict in plate tectonics. Mémoires de la Société géologique de France 147: 43-48.
  - 1987. The new theropod dinosaur from India with remarks on the Gondwana-Lauriasia connection in the Late Triassic. Pp. 183-189. In McKenzie, G.D. (ed.) 'Gondwana six: Stratigraphy, Sedimentology and Paleontology'. Geophysical Monographs 41.
- CHATTERJEE, S. & HOTTON, N. 1986. The paleoposition of India. Journal of Southeast Asian Earth Science 1: 145-189.
- CHATTERJEE, S. & RUDRA, D.K. 1996. KT events in India: impact, rifting, volcanism and dinosaur exticntion. Memoirs of the Queensland Museum, this volume 489-532.
- COOMBS, W.P. & MARYANSKA, T. 1992. Ankylosauria. Pp. 456-483. In Weishampel, D.B., Dodson, P. & Osmólska, H. (eds) 'The Dinosauria'. (University of California Press: Berkeley).
- COURTILLOT, V., BESSE, J. VANDAMME, D., MONTIGNY, R., JAEGER, J.J. & CAPPETTA, H. 1986. Deccan flood basalts at the Cretaceous/Tertiary Boundary. Earth and Planetary Science Letters 80: 361-374.
- DATTA, P.M. 1981. The first Jurassic mammal from India. Zoological Journal of Linnean Society, London 73: 307-312.

- GALTON, P.M. 1981. Craterosaurus pottonensis Seeley, a stegosaurian dinosaur from the Lower Cretaceous of England and a review of Cretaceous stegosaurs. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 161: 28-46
- GHEVARIYA, Z.G. & SRIKARNI, C. 1990. Anjar Formation, its fossils and their bearing on the extinction of dinosaurs. Pp. 106-109. In Sahni, A. & Jolly, A. (eds) 'Cretaceous Event Stratigraphy and the Correlation of Indian Nonmarine Strata'. (Panjab University: Chandigarh).
- HUENE, F. von & MATLEY, C.A. 1933. The Cretaceous Saurischia and Ornithischia of the Central Provinces of India. Memoir of Geological Survey of India, Palaeontologia Indica ns 21: 1-72.
- JAEGER, J.J., COURTILLOT, V. & TAPPONIER, P. 1989. Paleontological view of the ages of the Deccan Traps, the Cretaceous Tertiary Boundary and the India-Asia Collisions. Geology 17: 316-319.
- JAIN, S.L., 1980. The continental Lower Jurassic Fauna from the Kota Formation, India. Pp. 99-123, In Jacobs, L.L. (ed.) 'Aspects of Vertebrate History'. (Museum of Arizona Press: Flagstaff).
  - 1983. Spirally coiled coprolites from the Upper Triassic Maleri Formation, India. Palaeontology 26: 813-829.
  - 1990. An Upper Triassic vertebrate assemblage from Central India. Bulletin of the Indian Geologists Association, 67-84.
- JAIN, S.L., KUTTY, T.S., ROY CHOWDHURY, T. & CHATTERJEE, S., 1975. The sauropod dinosaur from the Lower Jurassic Kota Formation of India. Proceedings of the Royal Society, London Ser. A. 188: 221-228.
  - 1979. Some characteristics of *Barapasaurus tagorei*, a sauropod dinosaur from the Lower Jurassic of Deccan, India. Pp. 204-261, In Laskar, B. & Raja Rao, C.S. (eds) 'Fourth International Gondwana Symposium'. (Geological Survey of India: Calcutta).
- JAIN, S.L. & ROY CHOWDHURY, T. 1987. Fossil vertebrates from the Pranhita-Godavari valley (India) and their stratigraphic correlation. Pp. 219-228, In McKenzie, G.D. (ed.) 'Gondwana Six: Stratigraphy, Sedimentology and Palaeontology'. Geophysical monograph 41.
- JOLLY, A., BAJPAI, S. & SRINIVASAN, S. 1990. Indian sauropod nesting sites (Maastrichtian, Lameta Formation): a preliminary assessment of the taphonomic factors at Jabapur, India. Pp. 78-81. In Sahni, A. & Jolly, A. (eds) 'Cretaceous Event Stratigraphy and the Correlation of the Indian Nonmarine Strata'. (Panjab University: Chandigarh).
- KHOSLA, A. & SAHNI, A. 1995. Parataxonomic classification of Late Cretaceous dinosaur eggshells from India. Journal of the Palaeontological Society of India. 40: 87-102.

- KOHRING, R., BANDEL, K., KORTUM, D. & PAR-THASARTHY, S. 1996. Shell structure of a dinosaur egg from the Maastrichtian of Ariyalur (Southern India). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1996: 48-64.
- KUTTY, T.S. 1969. Some contribution to the stratigraphy of the Upper Gondwana Formation of the Pranhita Godavari Valley, Central India. Journal Geological Society of India 10: 33-48.
- KUTTY, T.S., JAIN, S.L. & ROY CHOWDHURY, T. 1987. Gondwana sequences of the northern Pranhita-Godavari Valley: its stratigraphy and vertebrate faunas. Palaeobotanist 36: 214-229.
- KUTTY, T.S. & SENGUPTA, D.P. 1989. The Late Triassic Formations of the Pranhita-Godavari Valley and their vertebrate succession – a reappraisal. Indian Journal of Earth Science 16: 189-206.
- LOYAL, R.S., 1984. Bearing of paleontological data on the collision models of the Indian plate. Pp. 284-285. 27th International Geological Congress', Moscow.
  - 1985. Migration routes of Gondwana vertebrates and drift models of the Indian Plate. 6th International Gondwana Symposium, Ohio, 64 (abstract).
- MATLEY, C.A. 1921. The coprolites of Pisdura, Central Provinces. Records of the Geological Survey of India 74: 535-547.
  - 1929. The Cretaceous dinosaurs of the Trichinopoly district and the associated rocks with them. Records of the Geological Survery of India 61: 337-349.
- MAULIK, P.K. & RUDRA, D.K. 1986. Trace fossils from the freshwater Kota Limestone of the Pranhita – Godavari Valley, South Central India. Bulletin of Geological, Mining and Metallurgical Society of India 54: 114-123.
- McINTOSH, J.S. 1990. Sauropoda. Pp. 345-401. In Weishampel, D.B., Dodson, P. & Osmólska, H (eds) 'The Dinosauria'. (University of California Press: Berkeley).
- MOHABEY, D.M. 1982. On the occurrence of dinosaurian fossil eggs from Infratrappean Limestones, Kheda, Dist. Gujarat. Current Science 52: 1194.
  - 1984. The study of dinosaurian eggs from Infratrappean limestones in Kheda district, Gujarat. Journal of Geological Society of India 25: 329-337.
- MOHABEY, D.M. & MATHUR, U.B., 1989. Upper Cretaceous dinosaur eggs from new localties of Gujarat. Journal of Geological Society of India 33: 32-37.
- MOHABEY, D.M., UDHOJI, S.J. & VERMA, K.K. 1993. Palaeontological and sedimentological observations on non-marine Lameta Formation (Upper Cretaceous) of Maharashtra, India: their palaeoecological and palaeoenvironmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 105: 83-94.

- MOLNAR, R.E. 1980. Australian Late Mesozoic terrestrial tetrapods: some implications. Mémoire de la Société géologique de France 139: 131-143.
- MOLNAR, R.E. & FREY, E., 1987. The paravertebral elements of the Australian ankylosaur *Minmi* (Reptilia: Ornithischia, Cretaceous). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 175: 19-37.
- PRASAD, G.V.R. & KHAJURIA, C.K. 1990. Late Mesozoic mammals from India and their significance. Pp. 50-51. In Sahni, A. & Jolly, A. (eds) 'Cretaceous Event Stratigraphy and the Correlation of the Indian Nonmarine Strata', (Panjab University: Chandigarh).
- PRASAD, G.V.R. & SAHNI, A. 1988. First Cretaceous mammal from India. Nature 332: 638-640.
- SAHNI, A. 1984. Cretaceous-Paleocene terrestrial faunas of India: Lack of endemism during drifting of the Indian Plate. Science 226: 441-443.
  - 1989. Paleoecology of the Late Cretaceous dinosaur eggshell sites from peninsular India. Pp. 179-185. In Gillette, D.D. & Lockley, M.G. (eds) 'Dinosaur Tracks and Traces' (Cambridge University Press: Cambridge).
  - 1993. Eggshell ultrastructure of Late Cretaceous Indian dinosaurs. Pp. 187-193 In Kobayashi, J., Mutevei, H. & Sahni, A. (eds) 'Structures, formation and evolution of fossil hard-tissues'. (Tokai University Press: Tokyo).
- SAHNI, A. & BAJPAI, S. 1991. Eurasiatic elements in the Upper Cretaceous non marine biotas of peninsular India. Cretaceous Research 12: 177-183.
- SAHNI, A. & KHOSLA, A. 1994. Paleobiological, taphonomical and paleoenvironmental aspects of Indian Cretaceous nesting sites. Pp. 215-224. In Lockley, M.G., dos Santos, V.F., Meyer, C.A. & Hunt, A. (eds) 'Aspects of Sauropod Paleobiology', Gaia 10: 215-224.
- SAHNI, A., RANA, R.S. & PRASAD, G.V.R., 1987. New evidence for paleobiogeographic intercontinental Gondwana relationships based on late Cretaceous-earliest Paleocene coastal faunas from Peninsular India. Pp. 207-218. In McKenzie, G.D. (ed.) 'Gondwana Six: Stratigraphy, Sedimentology and Palaeontology'. Geophysical monograph 41.
- SAHNI, A., TANDON, S.K., JOLLY, A., BAJPAI, S., SOOD, A. & SRINIVASAN, S. 1994. Upper Cretaceous dinosaur eggs and the nesting sites from the Deccan volcano-sedimentary province of peninsular India. Pp. 204-226. In Carpenter, K., Hirsch, K. & Horner, J. (eds) 'Dinosaur eggs and babies'. (Cambridge University Press: Cambridge).
- SARKAR, A., BHATTACHARYA, S.K. & MOHABEY, D.M. 1991. Stable isotope analysis of dinosaur eggshells, paleoenvironmental implications. Geology 19: 1068-1071.
- SENGUPTA, S. 1970. Gondwanan sedimentation around Bheemaram (Bhimaram), Pranhita-Godavari Valley, India. Journal of Sedimentary Petrology 40: 140-170.

- SHARMA, K.K. 1987. Crustal growth and two stage India-Eurasia collision in Ladakh. Tectonophysics 134: 17-28.
- SINGH, I.B. 1981. Palaeoenvironment and palaeogeography of the Lameta Group sediments (Late Cretaceous) in Jabalpur area, India. Journal of the Palaeontological Society of India 26: 38-53.
- SRIVASTAVA, S., MOHABEY, D.M., SAHNI, A. & PANT, S.C. 1986. Upper Cretaceous dinosaur egg clutches from Kheda district Gujarat, India: their distribution, shell ultrastructure and palaeoecology. Palaeontographica Ser. A 193: 219-233.
- TANDON, S.K., VERMA, V.K., JHINGRAN, V., SOOD, A., KUMAR, S., KOHLI, R.P. & MIT-TAL, S. 1990. The Lameta beds of Jabalpur, Central India: Deposits of fluvial and pedogenically modified semi-arid fan-palustrine flat system. Pp. 27-30 In Shani, A. & Jolly, A. (eds) 'Cretaceous Event Stratigraphy and Correlation of Indian Nonmarine Strata'. (Panjab University: Chandigarh).
- TASCH, P., SASTRY, M.V.A., SHAH, S.C., RAO, B.R.J., RAO, C.N. & GHOSH, S.C., 1973. Esthirids of the Indian Gondwanas: Significance for continental rift. Pp. 445-452. In Campbell, K.S.W.

(ed.) 'Gondwana Geology.' (Australian National University Press: Canberra).

- VIANEY-LIAUD, M., JAIN, S.L. & SAHNI, A. 1987. Dinosaur eggshells (Saurischia) from the Late Cretaceous Intertrappean and Lameta Formation (Deccan, India). Journal of Vertebrate Paleontology 7: 408-424.
- WALKER, A.D. 1964. Triassic reptiles from the Elgin area: Ornithosuchus and origin of carnosaurs. Philosophical Transactions of Royal Society of London Ser. B 248: 53-134.
- YADAGIRI, P. 1984. New symmetrodonts from the Kota Formation (Early Jurassic), India. Journal of Geological Society of India 25: 514-521.
  - 1985. An amphidontid symmetrodont from the Early Jurassic Kota Formation, India. Zoological Journal of Linnean Society 85: 411-417.
- YADAGIRI, P. & AYYASAMI, K., 1979. A new stegosaurian dinosaur from Upper Cretaceous sediments of South India. Journal of Geological Society of India 20: 521-530.
- YADAGIRI, P. & RAO, B.R.J., 1987. Contribution to the stratigraphy and vertebrate fauna of Lower Jurassic Kota Formation, Pranhita-Godavari Valley, India. Palaeobotanist 36: 230-244.



Loyal, Raminder S, Khosla, Ashu, and Sahni, Ashok. 1996. "Gondwanan dinosaurs of India: affinities and palaeobiogeography." *Memoirs of the Queensland Museum* 39, 627–638.

View This Item Online: <u>https://www.biodiversitylibrary.org/item/123909</u> Permalink: <u>https://www.biodiversitylibrary.org/partpdf/303871</u>

Holding Institution Queensland Museum

**Sponsored by** Atlas of Living Australia

**Copyright & Reuse** Copyright Status: Permissions to digitize granted by rights holder.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.