STATUS AND PALAEOBIOLOGY OF THE LATE CRETACEOUS INDIAN THEROPODS WITH DESCRIPTION OF A NEW THEROPOD EGGSHELL OOGENUS AND OOSPECIES, ELLIPSOOLITHUS KHEDAENSIS, FROM THE LAMETA FORMATION, DISTRICT KHEDA, GUJARAT, WESTERN INDIA

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ABSTRACT: This paper highlights the Cretaceous theropod record in India along with its affinities, and palaeobiologic aspects including description of a new theropod eggshell from the Upper Cretaceous Lameta Formation of Gujarat, India. Recent discoveries and phylogenetic reassessment of various theropod families suggest the presence of the poorly known family Abelisauridae; recent reports confirm the presence of Majungasaurus crenatissimus (DEPRET, 1896), Indosuchus HUENE & MATLEY, 1933 possible Carnotaurus BONAPARTE, 1985 and ?Allosaurus MARSH, 1877. An updated list of various Cretaceous theropod genera includes abelisaurids (Indosuchus raptorius HUENE & MATLEY, 1932, Indosaurus matleyi HUENE & MATLEY, 1933, Majungasaurus crenatissimus (DEPRET, 1896) Carnotaurus sp., allosaurids (Compsosuchus solus HUENE, 1932, ?Allosaurus) and coelurosaurids (Jubbulpuria tenuis HUENE & MATLEY, 1933, Laevisuchus indicus HUENE & MATLEY, 1933). Other theropods, such as Ornithomimoides mobilis HUENE & MATLEY, 1933, O. (?)barasimlensis HUENE & MATLEY, 1933 and Dryptosauroides grandis HUENE, 1932 regarded as indeterminate, need further assessment for proper affiliation. In the ongoing discussion, we however, present significant new data on the first ever report of dinosaur eggshell material referable to a new oogenus and oospecies Ellipsooolithus khedaensis, (oofamily Elongatoolithidae) from near Rahioli, district Kheda, Gujarat. This material has been presently assigned to the Theropoda and can be easily differentiated from the other well known megaloolithid oospecies (broadly referable to Sauropoda due to associated titanosaurid bones; known from Madhya Pradesh, Gujarat, Maharashtra and Ariyalur in South India) on the basis of megascopic, microscopic and ultrastructural characteristics. Megascopically, the eggshell shape varies from elongated ellipsoid, having an elongation ratio range of 1.5 to 1.7. The eggshell thickness is 1.2-1.6 mm and the mammillary layer is 1/4-1/7 of the total thickness. At the microstructural level, an angusticanaliculate pore system is observed. As the present find constitutes the first record of elongatoolithid eggshells apart from well known Chinese and Mongolian localities, comments on possible sauropod-theropod palaeobiology are also discussed.
THEROPOD RECORD IN INDIA AND EGGSELL STATUS

Although Indian sauropod eggshell taxonomy and skeletal discoveries have made considerable advancements over the last few decades, the theropods unfortunately have received scant attention except for notable exceptions (HUENE & MATLEY, 1933; CHATTERJEE, 1978; CHATTERJEE & RUDRA, 1996). Except for the presence of a Triassic small theropod *Alwalkeria maleriensis* CHATTERJEE & CREISLER, 1994 from the Maleri Formation (Pranhita-Godawari Valley, district Adilabad, Andhra Pradesh), the dominant discoveries of theropod skeletal remains are associated with the Upper Cretaceous Lameta and Intertrappean sequences outcropping in central and southern parts of peninsular India. Although no Jurassic theropod record exists, the later theropods are stratigraphically associated with the Upper Cretaceous Lameta and Intertrappean sequences outcropping in central and southern parts of Peninsular India. We provide below a brief overview of theropod groups prevailing in the Indian subcontinent during the Cretaceous times.

The Indian Cretaceous theropods are broadly represented by skeletal remains of abelisaurids, allosaurids, coelurosaurids and some indeterminate forms (HUENE & MATLEY, 1933; BUFFETAUT, 1987; KRAUSE & HARTMAN, 1996; CHATTERJEE & RUDRA, 1996). Amongst these forms, the taxonomic affinities of larger theropods have remained in doubt, awaiting further assessment; in particular “megasaurids” from Kallamedu, south India (BLANFORD, 1862; LYDEKKER, 1879), Talil (Maharashtra, VIANEY-LIAUD, JAIN & SAHNI, 1987) and Rahioli (MATHUR & SRIVASTAVA, 1987). However, in comparison, the family Abelisaureae is a relatively better known group from the Carnosaur Bed of Lameta Formation, Jabalpur and is represented by *Indosuchus raptorius* HUENE & MATLEY, 1933, *Indosaurus matheyi* HUENE & MATLEY, 1933 and *Carnotaures BONAPARTE, 1985*. Of these, the first two forms, *Indosuchus HUENE & MATLEY, 1933* and *Indosaurus HUENE & MATLEY, 1933* and *Carnotaures BONAPARTE, 1985*. Of these, the first two forms, *Indosuchus HUENE & MATLEY, 1933* and *Indosaurus HUENE & MATLEY, 1933* originally referred to Allosauridae (HUENE & MATLEY, 1933), have been variously assigned, for instance *Indosuchus* as a tyranosaur and *Indosaurus* as a meglosaur (CHATTERJEE, 1978; BUFFETAUT, 1987); and more recently to abelisaurids (BONAPARTE & NOVAS, 1985; MOLNAR, 1990; MOLNAR, KURZANOV & DONG, 1990 and Sampson et al., 1996).

Recently, however, morphologic and phylogenetic comparison of various theropods including abelisaurids has been attempted by Sampson et al. (1996). In this work, it has been considered that premaxillary dentition of *Majungasaurus crenatissimus* (DEPRET, 1896) (from Upper Cretaceous of Madagas­cgar) including cross-sectional and serrational morphologies are strongly similar to that of the Indian theropod *Indosuchus raptorius* HUENE & MATLEY, 1933; for instance, both forms exhibit marked pattern of vertical ridges on the interdental plates. As such, the shared synapomorphies between these theropods have led Sampson et al. (1996) to consider them as sister taxa within the clade Abelisauridae. This viewpoint is also corroborated by Chatterjee & RUDRA (1996); in a detailed discourse on Gondwana theropod relationships, these workers associated a more primitive phylogenetic position to the abelisaurids in comparison to the allosaurids and tyrannosaurs. Further, the remains of *Majungasaurus crenatissimus* (Mahajanga Basin, Upper Cretaceous) represented by one premaxilla has been confirmed to belong to an abelisaurid with no "megasaurian" or tyrannosaurid characteristics (KRAUSE & DODSON, 1994; KRAUSE & HARTMAN, 1996). More recently, CHATTERJEE & RUDRA (1996: 517) believe that "Indosuchus is not a tyrannosaurid as was supposed earlier, but possibly an abelisaurid". These workers discovered a complete skeleton of *Indosuchus* from near Rahioli, Gujarat and referred it to allosaurids on the basis of similar lengths of forelimbs in these two taxa; however, hindlimb elements resemble those of *Camptosaurus*, a well-established abelisaurid.

Further, the other theropod known from Bara Simla Hill, *Indosaurus mateyi*, bears thickened frontals and elevated parietals; these features are also observed in *Carnotautes sastrei*, a well-established and a diagnostic abelisaurid known from Goro Frigio Formation (Albanian-Cenomanian) of Chubut, Argentina (BONAPARTE, 1985). Moreover, vertebral elements closely similar to that of *Camptosaurus* are also known from Rahioli, Gujarat (CHATTERJEE & RUDRA, 1996).

The remaining forms from Bara Simla Hill locality by HUENE & MATLEY (1933) were referred to coelurosaurs, which included *Compsosuchus solus* HUENE, 1932, *Laevissuchus indicus* HUENE & MATLEY, 1933, *Jubbulpuria tenuis* HUENE & MATLEY, 1933, *Coelurooides largus* HUENE, 1932, *Dryptosaures grandis* HUENE, 1932, *Ornithomimoides mobilis* HUENE & MATLEY, 1933 and O. (?)*barasimensis* HUENE & MATLEY, 1933. Of these forms, *Compsosuchus solus* was suggested by MOLNAR, KURZANOV & DONG (1990) and MOLNAR & FARLOW (1990) to be an allosaurid and particularly close to *Allosaurus fragilis*, on the basis of shared apomorphies.

From Bara Simla Hill locality, the only forms to have retained their assignment to coelurosaurs are *Jubbulpuria tenuis* and *Laevissuchus indicus*, but thought to be indeterminate (NORMAN, 1990). Other forms which remain unidentified and await assessment are *Coelurooides largus*, *Dryptosauroidea*
grandis, Ornithomimoides mobilis and O. (?) baramsimiensis. Further, D. grandis is considered by Molnar (1990) to possess no carnosaurian characters, while ornithomimosaurids are not present south of Mongolian localities (Barsbold & Osmolska, 1990).

PRESENT EGG SHELLS AND NESTS: LOCALITY, STRATIGRAPHY AND FIELD DISPOSITION

Recent palaeontological work near Rahioli (District Kheda, Gujarat) led to acquisition of a large number of ellipsoid eggs both in isolated form as well as in nests (Fig. 2-3). The present eggshell locality is situated west of Lavaria Muwada and south of Kevadiya at a distance of nearly 1.5 km NW of Rahioli (Fig. 1).

The egg-bearing horizon is confined to the uppermost calcitized sandstone. Stratigraphically, this bed lies 1 m below the level, that had earlier yielded spherical-shaped dinosaur eggshells belonging to the oofamily Megaloolithidae. However more recently elongatoolithid and megaloolithid egg nests have been recorded from the same stratigraphic level in this area. At least 60 eggs (ellipsoidal) have been located in more than half a dozen nests in addition to stray eggs and eggshell debris (Mohabey, 1996b.) A single nest has yielded thirteen eggs. In a single nest the eggs are disposed horizontally in a single layer (Fig. 2C).

SYSTEMATICS

Oofamily
Elongatoolithidae Zhao, 1975
Oogenus
Ellipsoidolithus n. oogen.

Diagnosis: Ornithoid basic type; ratite morphology; angusticanalulate pore system; outer sculpture is lineartuber culate and dispersituber culate; ellipsoid eggs (elongation ratio 2) varying in diame-
ter from 98-110 mm and 65-80 mm at polar and equatorial region respectively; eggshell thickness 1.2-1.6 mm; two-layered eggshell; mammillary layer comprises 1/4-1/7 of the total eggshell thickness.

**Etymology:** The oogenus *Ellipsoolithus* is named after the predominant ellipsoidal shape of the eggs.

*Ellipsoolithus khedaensis* n. oosp. (Fig. 5 A-E; Fig. 6)

**Holotype:** An almost complete egg (Reg. No. 1491/CRP/96, housed at GSI, Nagpur).

**Etymology:** The name *khedaensis* is derived after District Kheda, Gujarat.

**Type locality:** West of Lavaria Muwada and south of Kevadiya and at a distance of 1.5 km NW of Rahioli, district Kheda, Gujarat.

**Type horizon:** Lameta Formation; Upper Sandy Carbonate (calcretized paleosol); Upper Cretaceous.

**Referred material:** Many near complete to partial eggs and eggshell debris.

**Repository:** More than a dozen more or less complete and partial eggs are housed at Geological Survey of India, Nagpur with Dr. D. M. Mohabey; a few almost complete eggs are with Dr. Raminder S. Loyal, Centre of Advanced Study in Geology, Panjab University, Chandigarh.

**Diagnosis:** Ellipsoidal eggs assuming near oval shape, polar and equatorial diameter range 98-110 mm and 65-80 mm; elongation ratio ranging between 1.5-1.7 mm; thickness 1.2-1.6 mm; ornamentation variable along egg surface, dispersituberculate to ramotuberculate at the polar region, lineartuberculate on the equatorial portion; two-layered; mammillary layer ranges 1/4-1/7 of total eggshell thickness but more commonly 1/4; bulbous mammillae; spheroliths with curving domes.

**Description:** Eggs are predominantly ellipsoidal in shape and assuming a near oval-shape. Polar and equatorial diameters ranges between 98-110 mm and 65-80 mm respectively (Fig. 4). The eggshell thickness varies from 1.2-1.6 mm. Surface ornamentation comprises dispersituberculate to ramotuberculate patterns at the polar region, depicting irregularly dispersed and ramified ridges and nodes. At the equatorial region, lineartuberculate ornamentation is observed, with linear (and sometimes discontinuous) arrangement of tubercular nodes and lineations, which are elongated parallel to the longer axis of the eggshell (MOHABEY, 1996b).

The microstructure of the eggshell is double-layered with radiating structures and presence of thick wedges in the mammillary layer. The mammillary layer is about 1/6-1/7 but more commonly 1/4 of the total shell thickness. The spheroliths are broad having wide domal-shaped roofs. The spheroliths are fused and separated in the mammillary zone. Under SEM, thick wedge-shaped crystallites are seen in the mammillary layer. The upper spongy layer shows gently curving growth lines towards the upper part of the spheroliths. The pore system is anastigmaticalicate.

**Remarks:** The eggshells and nests assigned to the oofamily Elongatoolithidae are the most domi-
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Fig. 3 - Egg nest in plan and section; near Lavaria Muwada locality, district Kheda, Gujarat; Lameta Formation; Upper Sandy Carbonate (calcretized paleosol); Late Cretaceous.

nant components of Late Cretaceous assemblages of China (ZHAO, 1975, 1994) and central Asian regions of Mongolia and China (KURZANOV & MIKHAILOV, 1989; MIKHAILOV, 1991, 1995; MIKHAILOV, SABATH & KURZANOV, 1994).

In China, the oofamily Elongatoolithidae is stratigraphically associated with the Upper Cretaceous Yuanpu Formation and Pingling Formation exposed in the Nanxiong Basin, though the reports from lower part of the Cretaceous exist (ZHAO, 1994). From these Upper Cretaceous formations, ZHAO (1975, 1994) described eggshells and nests of Macroolithus yaotunensis ZHAO, 1975, M. rugustus YOUNG, 1965, Macroolithus sp., Elongatoolithus andrewsi ZHAO, 1975, E. elongatus YOUNG, 1954, Elongatoolithus sp., and Nanhsiungoolithus chuheitenensis ZHAO, 1975. Of these, Elongatoolithus and Macroolithus were reassigned to Oolithes elongatus, discovered by YOUNG (1965) based on material from Shantung Province, Guandung and Jiangxi Province in China (MIKHAILOV, SABATH & KURZANOV, 1994).

As far as the Central Asian material is concerned, elongatoolithid eggshells are known from the Upper Cretaceous Mongolian Barun Goyot, Djadokhta and Nemegt formations; only one locality is Lower Cretaceous in age (MIKHAILOV, SABATH & KURZANOV, 1994). This Mongolian eggshell material is categorized into groups E1 (including Elongatoolithus and Macroolithus) and E2 (comprising an unnamed genus).

The present eggshell material differs from the ootaxa Elongatoolithus andrewsi ZHAO, 1975, Macroolithus rugustus YOUNG, 1965 and Nanhsiungoolithus chuheitenensis ZHAO, 1975 in megascopic and microstructural characteristics. The overall shape in these three oospecies is obtuse at one end and pointed at the other with subcircular nodes and deep channeling (ZHAO, 1993); elongation ratios are also higher, i.e. 2-2.2 in Elongatoolithus and 2-2.4 in Macroolithus. The microstructure of Elongatoolithus andrewsi shows small mammillae with circular cross sections and growth lines in upper spongy layer are almost straight. The other oospecies Macroolithus yaotunensis bears polar diameter 170 mm and shows tiny, parallel walled mammillae with indistinct margins.

In comparison, in Ellipsoolithus a nearly oval shape is diagnostic and elongation ratio is 1.5-1.7 with polar diameter varying from 98-110 mm and equatorial diameter ranging from 65-80 mm. The ornamentation comprises dispersituberulate to ramotuberculate pattern at the polar end and lineartuberculate on the equatorial portion.

Further the microstructure shows bulbous and fused mammillae with undulating growth line pattern in spongy layer; the spheroliths are characteristically dome-shaped.

PALAEOBIOLOGY

Further, it is quite interesting to observe that both kind of eggshell materials (comprising those of titanosaurids and the present eggshells) are re-

Fig. 4 - Plot of polar and equatorial diameter of ellipsoid eggs, near Lavaria Muwada; district Kheda, Gujarat; Lameta Formation, Upper sandy Carbonate (calcretized paleosol); Late Cretaceous.
Fig. 5 - Egg nests from near Lavaria Muwada; district Kheda, Gujarat; Lameta Formation, Upper Sandy Carbonate (calcretized paleosol); Upper Cretaceous. A - A nest showing seven ellipsoid shaped eggs (136/GSI/PAL/CR/NG/94). B - A nest showing seven ellipsoid shaped eggs (137/GSI/PAL/CR/NG/94). C - A nest showing three ellipsoid shaped eggs (138/GSI/PAL/CR/NG/94). D - Lineartuberculate ornamentation in equatorial region. E - Radial thin section showing two layered eggshell microstructure showing dome-shaped spheroliths and tightly packed mammillary layer (149/GSI/PAL/CR/NG/94). Bar (scale) represents A: 5cm; B: 5 cm; C: 5 cm; D: 1 cm; E: 250 μm.
Fig. 6 - Radial polished section of *E lipsoolithus khedaensis* showing a single spherolith with a well developed mam­millae (VPL/R/101); isolated eggshell at approximately 1.5 km NW of Rahioli, district Kheda, Gujarat; Lameta Formation; Upper Sandy Carbonate (calcretized paleosol); Upper Cretaceous. Bar (scale) represents 50 μm.
restricted to the same lithology and also lie at the same stratigraphic level, suggesting important implications on the community behaviour and dynamics of these reptiles i.e. a possible prey-predator relationship. In this complex community scenario, though it would be a bit premature to speculate on building a structured ichnoecoenoses (DODSON et al., 1990) the present data points to abundant titanosaurid populations providing a great predatory delight for the rarer abelisaurid and other theropods.

CONCLUSIONS

The Late Cretaceous dinosaur fauna was dominated by the titanosaurids, abelisaurids and other theropods. Though the megaloolithid eggs (broadly assignable to titanosaurids) occur in plenty along the east, west and central Narmada River region in the Lameta Formation and Intertrappean beds (MOHABEY, 1983, 1984a, 1984b, 1986, 1990a, 1990b, 1991, 1996a, 1996b; MOHABEY & MATHUR, 1989; MOHABEY, UDHOJ & VERMA, 1993; KHOSLA, 1996; KHOSLA & SAHNI, 1995; SRIVASTAVA et al., 1986; VJANEY-LIAUD, JAIN & SAHNI, 1987; SAHNI, 1990, 1993; SAHNI et al., 1994) and seven to eight of its species are known (SAHNI & KHOSLA, 1994; KHO­SLA, 1996; KHOSLA & SAHNI, 1995; MOHABEY, 1996a; LOYAL, KHOSLA & SAHNI, 1996), the elongatooolithid eggs (assignable to theropods) are scarcely known excepting the present find of Ellip­soolithus (MOHABEY, 1996b) from a nesting site at Lawaria Muwada and Kevadiya (near Rajhili). Further, the present fossil collection comprises only eggshells, nests, isolated eggs and shell debris; unfortunately no associated skeletal/embryonic material was found, which could warrant proper affiliations of these eggshells to the generic level. In this context, we are of the opinion that the abelisaurs could have been a dominant Indian Late Cretaceous dinosaur group; similar view on abelisaurid distribution is expressed by CHATTERJEE & RUDRA (1996). We, henceforth, urgently require more field discoveries of elongatooolithid eggshells with associated skeletal material as also the trackway evidences, not only from the Indian landmass but also from biogeographically contiguous Madagascar region.

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ABBREVIATIONS

CR = Catalogue Register Number; GSI = Geological Survey of India; NG = Nagpur; PAL = Palaeontology Division + VPL = Vertebrate Palaeontology Laboratory; R=Rahioli

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