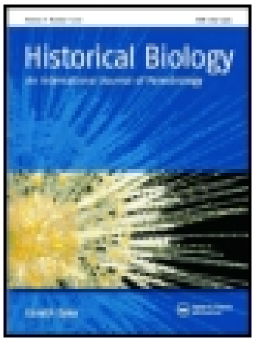

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Parataxonomy and palaeobiogeographic significance of dinosaur eggshell fragments from the Upper Cretaceous strata of the Cauvery Basin, South India

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Parataxonomy and palaeobiogeographic significance of dinosaur eggshell fragments from the Upper Cretaceous strata of the Cauvery Basin, South India

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ABSTRACT
In the past, fossilised dinosaur eggshells have been extensively documented from the Upper Cretaceous Lameta Formation of Central India and as many as nine oospecies are known at present from this formation. Compared to this, only one dinosaur oospecies has been described from the Cretaceous succession of the Cauvery Basin. However, the first fossil egg from India, identified as a chelonian egg, was documented from the Aptian – Albian Karai Formation of the Cauvery Basin in 1957. Following this, a solitary titanosaurid dinosaur egg was described from the Upper Cretaceous (Lower Maastrichtian) Kallankuruchhi Formation, Cauvery Basin in 1996. More recently, we have recovered isolated eggshell fragments from the marine part of the Upper Cretaceous (Late Maastrichtian) Kallamedu Formation. Based on eggshell morphology, microstructure and ultrastructure, these eggshell fragments are assigned to the oospecies *Fusioolithus baghensis*. The new find from the Cauvery Basin is important from palaeobiogeographic point of view as the oofamily Fusioolithidae is found in the Upper Cretaceous strata of India, France, Argentina and Morocco. Based on the common occurrence of similar oospecies in South America, Africa, Europe and India, a Late Cretaceous palaeobiogeographic connection between India and South America as well as Europe via Africa is suggested.

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Cretaceous; dinosaur; eggshells; palaeobiogeography; India

Introduction

Fossilised eggshell studies offer important information about the reproduction and nesting strategies of egg-laying animals (Horner and Makela 1979). Studies conducted on the micro- and ultra-structure of the fossilised eggshells help in comparing them with the modern analogues of reptilian and avian eggshells, which provide further insights into the habits of egg-laying organisms (Jackson et al. 2002). Additionally, effects of diagenesis after burial (Grellet-Tinner 2010), environmental and dietary effects on the egg-laying animal during the egg incubation period (Erben et al. 1979), palaeoenvironmental studies (Montanari et al. 2013), and information about taphonomical parameters (Hayward et al. 1997) can be gained from the study of eggs, nests, and eggshell fragments.

The study of fossil eggs and eggshells in the Indian subcontinent commenced with the discovery of fossilised turtle egg from the Aptian-Albian Karai Formation of the Cauvery Basin (Sahni 1957). The first published report on dinosaur eggshell fragments was by Sahni and Gupta (1982) from the Upper Cretaceous (Maastrichtian) Lameta Formation, Jabalpur. Since then, numerous other localities with dinosaur eggshells, eggs, and nesting sites have been discovered in the Lameta Formation of the Central and Western India and the intertrappean beds of the Deccan Volcanic Province (DVP) (Sahni et al. 1984; Srivastava et al. 1986; Vianey-Liaud et al. 1987, 2003; Sahni et al. 1994; Khosla and Sahni 1995; Srinivasan 1996; Mohabey 1998; Jain and Sahni 1985; Bajpai et al. 1993; Fernández and Khosla 2015; Srivastava and Mankar 2015). From the Deccan intertrappean beds, besides teeth and few fragmentary bones, eggshells are the only remains of dinosaurs documented (Sahni et al. 1984; Jain and Sahni 1985; Vianey-Liaud et al. 1987, 2003; Srinivasan 1996; Bajpai et al. 1993).

Dinosaur eggs described from India are predominantly represented by sauropods, while a few eggs with a probable theropod affinity have also been documented (Bajpai et al. 1993; Khosla and Sahni 1995; Loyal et al. 1998; Mohabey 1998). So far, no embryos have been documented from these sites. These eggs and eggshells were characterised as sauropod or theropod dinosaurs on the basis of co-occurrence of skeletal remains in the same horizon and by comparing the micro-structure and ultra-structure of the eggshells documented from other countries. Khosla and Sahni (1995) reported seven oospecies belonging to the oogenus *Megaloolithus* from the sandy carbonate horizon of the Lameta Formation of Jabalpur, Bagh and Jhabua regions (Madhya Pradesh), Balasinor and the intertrappean beds of Anjar (Gujarat). Subsequently, Mohabey (1998) described eight more oospeciesfrom a sandy carbonate horizon of the Lameta Formation exposed in Gujarat, Maharashtra, and

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Madhya Pradesh. However, Vianey-Liaud et al. (2003) observed that some of the oospecies described by Mohabey (1998) were junior synonyms to those described by Khosla and Sahni (1995). Hence from the combined list of Khosla and Sahni (1995) and Mohabey (1998), nine oospecies (*M. cylindricus*, *M. mohabeyi*, *M. padiyalensis*, *M. jabalpurensis*, *M. dholiyaensis*, *M. dhoridungriensis*, *M. khempurensis*, *M. megadermus*, *M. baghensis*) were considered as valid taxa (Vianey-Liaud et al. 2003).

More recently, Fernández and Khosla (2015) revisited the ootaxonomy of dinosaur eggshells from the Late Cretaceous of India and synonymised *M. matleyi* (Mohabey 1996) and *M. patagonicus* from the Late Cretaceous of Patagonia (Calvo et al. 1997) with *M. jabalpurensis* (Khosla and Sahni 1995). Additionally, *M. cylindricus* (Khosla and Sahni 1995) has been given priority over *M. rahioliensis* (Mohabey 1998). Fernández and Khosla (2015) also erected a new oogenus *Fusioolithus* which is characterised by the presence of partially fused shell units. Furthermore, *Megaloolithus baghensis* (Khosla and Sahni 1995) with fused spheroliths and merging growth lines of adjacent spheroliths has been made into a new combination *Fusioolithus baghensis* (Fernández and Khosla 2015) and *M. balasinorensis* (Mohabey 1998) has been synonymised with *F. baghensis* (Fernández and Khosla 2015).

Therefore at present, there are nine recognised megaloolithid oospecies: *Megaloolithus cylindricus* (Khosla and Sahni 1995), *M. jabalpurensis* (Khosla and Sahni 1995), *M. megadermus* (Mohabey 1998), *M. dhoridungriensis* (Mohabey 1998), *M. khempurensis* (Mohabey 1998), *Fusioolithus baghensis* (Khosla and Sahni 1995; Fernández and Khosla 2015), *F. padiyalensis* (Khosla and Sahni 1995; Fernández and Khosla 2015), *F. mohabeyi* (Khosla and Sahni 1995; Fernández and Khosla 2015), and *F. dholiyaensis* (Khosla and Sahni 1995; Fernández and Khosla 2015).

Recently, fossilised eggshells have been recovered from the basal part of the Upper Cretaceous (Upper Maastrichtian) Kallamedu Formation of Ariyalur Group, Cauvery Basin, South India. The objective of this paper is to systematically identify these eggshells in terms of their microstructural and ultrastructural features through parataxonomic classification and discuss their significance from palaeobiogeographic point of view. This represents the second Indian record of Cretaceous dinosaur eggshells from a marine depositional environment and outside the traditionally known Lameta Formation and Deccan intertrappean sequences. Previously, a solitary egg was described from the Upper Cretaceous (Lower Maastrichtian) Kallankuruchchi Formation exposed in the Tamil Nadu Cement Corporation Ltd. (TANCEM) mine under *Megaloolithus cylindricus.* The limited occurrence and low diversity of dinosaur eggshells from the Cretaceous rocks of the Cauvery Basin is apparently due to the marine depositional environments of majority of the lithostratigraphic units of this basin.

Materials and methods

The dinosaur eggshell fragments were collected from the basal part of the Kallamedu Formation close to the village of Ottakoil in the Cauvery Basin, India. The eggshell fragments were collected from the surface exposures through hand-picking. The isolated eggshell fragments were first cleaned in the ultrasonic vibrator. Some of the fragments were selected for Scanning Electron Microscope (SEM) imaging while a few were used for making petrographic thin sections (Leiggi and May 1994).

For SEM analysis, the cleaned samples were mounted on aluminium stubs and coated with gold-palladium. SEM images were taken using Zeiss EVOMA 10 model at the Indian Agricultural Research Institute, Pusa, New Delhi. For thin section analysis, standard histological techniques were applied (Chinsamy and Raath 1992). For the preparation of thin sections, three eggshell fragments were grinded on a glass plate using carborundum powder and the resultant flat surface was fixed on a glass slide using araldite. After drying for 1–2 days, the sample was then grinded on a lap wheel using 400 μm carborundum powder. Following this, the specimen was polished using 600 μm and then by 800 μm and 1000 μm carborundum powder until the thin section became30 μm thick. The thin sections were diamond-polished in the end. Axio Imager A1 m (Carl Zeiss) High Resolution Petrological Microscope in the Vertebrate Palaeontology Laboratory, Department of Geology, University of Delhi was used to study the thin sections.

The studied fossil material is deposited in the Vertebrate Palaeontology Laboratory, Department of Geology, University of Delhi under DUGF/564-574 catalogue numbers.

Geology of the Cauvery Basin

The Cauvery Basin is a pericratonic rift basin that occurs on the southeastern coast of India which formed during Late Jurassic-earliest Cretaceous rifting between India and Australia-Antarctica (Powell et al. 1988). This basin preserves one of the most complete shallow marine Cretaceous successions of India, ranging from Albian to Maastrichtian in age (Sundaram et al. 2001).

Blanford (1862) studied the Cretaceous sequence of the Cauvery Basin for the first time and classified it into the Uttatur Group, the Trichinopoly Group and the Ariyalur Group. Following Blanford's (1862) work, many lithostratigraphic classifications have been proposed for the Cretaceous succession of the Cauvery Basin. The most recent revision of these classifications was provided by Sundaram et al. (2001) which is followed in this paper (Figure 1). According to these authors, the basal Uttatur Group begins with the plant-bearing terrestrial to paralic facies of the Terani and Arogyapuram formations that overlie the Precambrian basement rocks with a nonconformity. This terrestrial sequence is overlain by the shallow marine Dalmiapuram and Karai formations. The latter yielded the vertebrate fossils consisting of shark and ichthyosaur remains besides a number of invertebrate fossils (Underwood et al. 2011; Verma et al. 2012; Ayyasami et al. 2016). The Trichinopoly Group is separated from the underlying Uttatur Group by a regional unconformity and is sub-divided into the Kulakkalnattam and Anaipadi formations of predominantly sandstone, mudstone and siltstone lithologies of shallow marine environment. Conformably overlying the Anaipadi Formation of the Trichinopoly Group is the Arilayur Group, which is further divided into the Sillakkudi, Kallankurichchi, and Kallamedu Formations. The Sillakkudi Formation comprising a sequence of sandstoneswith a locally developed limestone horizon was considered to have been deposited under littoral to subtidal shallow marine environment during

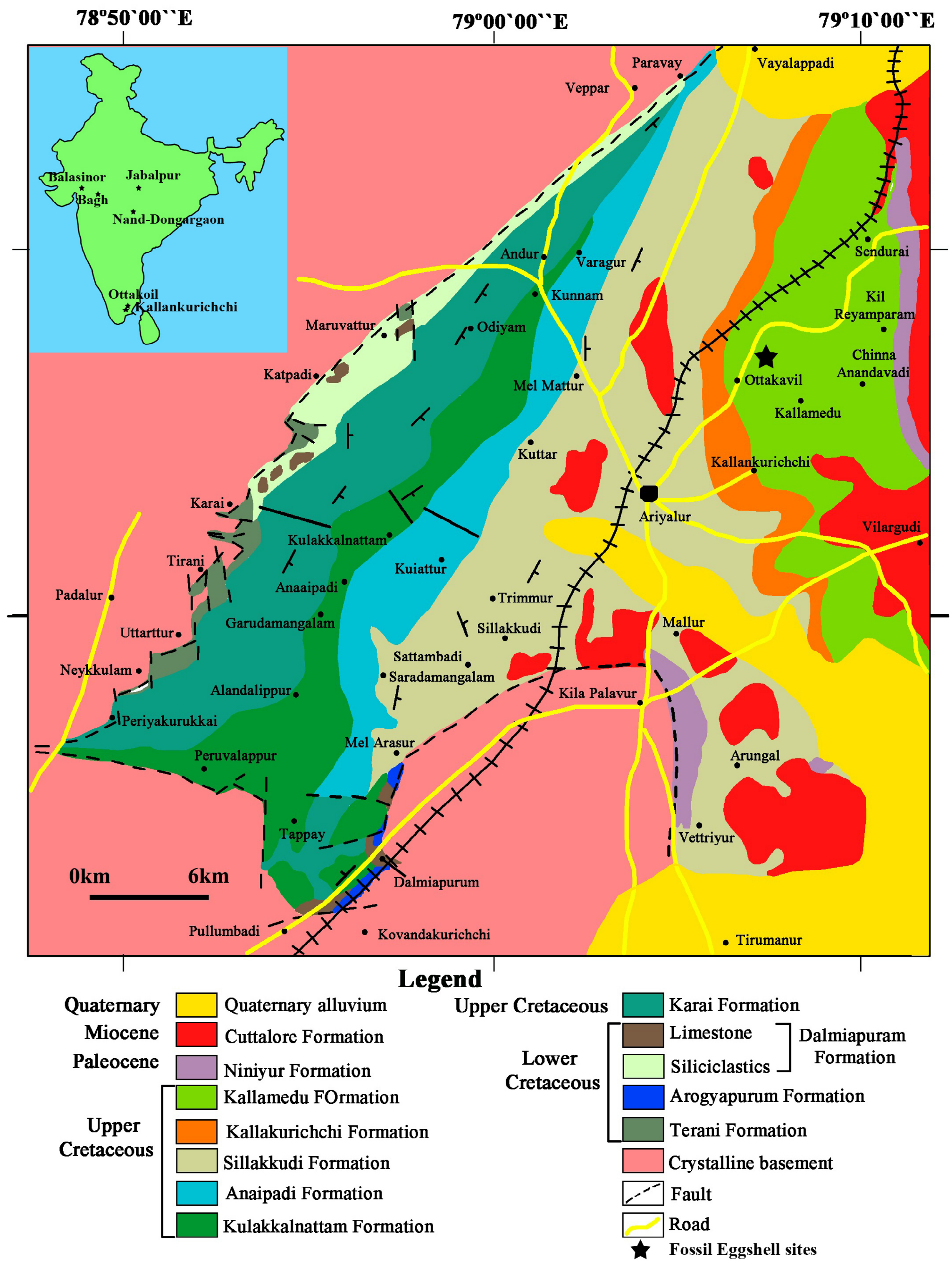

Figure 1. Geological map of Ariyalur district (After Sundaram et al.2001).

the Campanian (Ayyasami et al. 1992). The Kallankurichchi Formation essentially consists of bioclastic limestone and calcareous sandstone yielding *Pycnodonte*, *Inoceramus*, *Gryphaea* and *Alectryonia* of Early Maastrichtian age (Sundaram et al. 2001). It was interpreted to have been deposited in a shallow marine depositional environment under a transgressive regime (Sundaram et al. 2001). A solitary titanosaurid sauropod dinosaur egg is the only vertebrate documented from this formation (Kohring et al. 1996).

The Kallamedu Formation, the youngest Cretaceous formation of the basin, has a locally developed marine sandstone facies developed about 2 km north of Ottakovil village along a stream. The shallow marine sequence of Ottakkovil has a lithology of predominantly dirty yellow to off white, cross-bedded, medium to coarse grained sandstone overlying the Lower Maastrichtian Kallankurichchi Formation (Sundaram et al. 2001). The fossils recorded from this formation consist of *Stigmatophygus elatus*, *Durania mutabilis*, *Thalassinoides*, *Ophiomorpha*, *Dactyloidites*, *Nautilus* and fragments of *Gryphaea*, *Alectryonia* and fossilised wood (Ramkumar et al. 2004). Sastry et al. (1968, 1972), Radulović and Ramamoorthy (1992) and Mitrović-Petrović and Ramamoorthy (1993) have assigned a Middle Maastrichtian age to this formation. More recently, Rai et al. (2013) assigned a Late Cretaceous (Late Maastrichtian) age for lower marine levels of the Kallamedu Formation based on nannofossils. This marine unit at the base of the Kallamedu Formation was at one point of time considered as a separate formation (i.e. Ottakovil Formation) by Sastry et al. (1972) or a member of the Kallamedu Formation (Tewari et al. 1996) and is still regarded as an independent formation by some authors (Ramkumar et al. 2004). The upper part of the Kallamedu Formation, which marks the end of Cretaceous sedimentation, is a fluvial channel sandstone interspersed with overbank clays and silts. The continental upper part of the Kallamedu Formation has yielded fishes, amphibians, crocodiles, and turtles and fragmentary remains of dinosaurs (Blanford 1862; Matley 1929; Yadagiri et al. 1983; Yadagiri and Ayyasami 1987, 1989; Gaffney et al. 2001; Goswami et al. 2013; Prasad et al. 2013; Halliday et al. 2016).

Previous work

The predominantly marine Cretaceous rocks of the Cauvery Basin have been extensively studied in the past for their large invertebrate and microfossils and much of its biostratigraphy is based on these fossils (Banerji 1973; Sastri et al. 1977; Ayyasami 1990; Venkatachalapathy and Ragothaman 1995; Gale et al. 2002; Prasad and Pundeer 2002; Ayyasami 2006; Bragina and Bragin 2013; Rai et al. 2013). In comparison, the vertebrate fossil reports from these rocks are few and are known only from the marine Karai Formation and the continental upper part of the Kallamedu Formation. Until now, shark teeth representing *Cretalamna appendiculata*, *Dwardius sudindicus*, *Gladioserratus magnus*, *Protosqualus* sp., ?*Notidanodon* sp., ?*Eostriatolamia* sp., *Squalicorax* aff. *baharijensis* (Underwood et al. 2011), *Ptychodus decurrens* (Verma et al. 2012), ichthyosaur teeth belonging to Platypterygiinae indet. (Underwood et al. 2011) and vertebrae representing Ichthyosauria (Ayyasami et al. 2016) have been documented from the Aptian-Cenomanian Karai Formation. The continental upper part of the Upper Cretaceous (Middle Maastrichtian) Kallamedu Formation is known to yield vertebrate fossils ever since Blanford (1862) reported the occurrence of fragmentary dinosaur bones and teeth (Matley 1929; Yadagiri et al. 1983; Yadagiri and Ayyasami 1987, 1989). More recently, other vertebrate groups such as turtles (Gaffney et al. 2001), small vertebrates represented by fish, amphibians, crocodiles, dinosaurs and mammals (Goswami et al. 2012, 2013; Prasad et al. 2013; Halliday et al. 2016) have been described from the Kallamedu Formation.

As far as fossil eggs and eggshells are concerned, there have been only two published reports of fossilised eggs from the Cretaceous rocks of the Cauvery Basin. In fact, the first fossil egg reported from India came from the Uttatur Group of the Cauvery Basin (Sahni 1957). This egg is oval in shape and has a maximum length of 4.9 cm and maximum thickness of 2.7 cm. It was found in association with marine invertebrates such as ammonites and belemnites and was considered as a chelonian (*Notochelys*) egg (Sahni 1957). In 1996, a solitary sauropod dinosaur egg was described from the Upper Cretaceous (Lower Maastrichtian) Kallankuruchchhi Formation (Kohring et al. 1996). This egg was found in a quarry belonging to the TANCEM close to Kallankuruchchhi village in Ariyalur District, Tamil Nadu. Petrographic thin section and SEM study of the eggshell from the Kallankuruchchhi egg revealed nodose external ornamentation, cylindrical shell units with straight lateral margins and straight pore canals, and shell thickness and height/width ratio within the range of *M. cylindricus* known from the DVP (Kohring et al. 1996). This egg also showed the presence of additional nucleation sites on various levels within the shell which point to palaeopathological condition observed in modern turtle eggshells (Erben et al. 1979). The dinosaur egg from the Kallankuruchchhi Formation is twice as thick as eggshells documented from other localities of the DVP. This is the first dinosaur egg from India that was found in fully marine sediments indicating dislocation from its terrestrial environment and transportation to a shallow marine environment. Its thick eggshell layer possibly enabled it to withstand long distance transportation (Kohring et al. 1996).

Systematic description of fossil eggshells

Oofamily Fusioolithidae Fernández and Khosla 2015

Oogenus *Fusioolithus* **Fernández and Khosla 2015;** *Fusioolithus baghensis* **Khosla and Sahni 1995**

Megaloolithus baghensis **Khosla and Sahni 1995: 91–92**

M. balasinorensis **Mohabey 1998: 357–358**

Stratigraphic horizon and locality: Basal part of the Upper Cretaceous Kallamedu Formation (= Ottakovil Formation of Sastri et al. 1977)

Age: Late Maastrichtian

Material: Isolated eggshell fragments (DUGF/564-574) (Figures 2(a)–(f), 3(a)–(e), 4(a)–(d), 5(a)-(b))

Description: The external surface is characterised by circular to sub-circular nodes of varying sizes (Figures 2(a), (d), 3(e), 4(d)) which are both coalescing and partially discrete. These nodes are separated by a fair number of pore canals, showing compactituberculate orientation. The pores are visible as sub-circular to slightly elongate openings (Figures 2(a), (d), 3(e), 4(d)). The average node diameter ranges from 0.4 to 0.8 mm. The eggshell fragments have a thickness ranging from 0.89 to 1.6 mm.

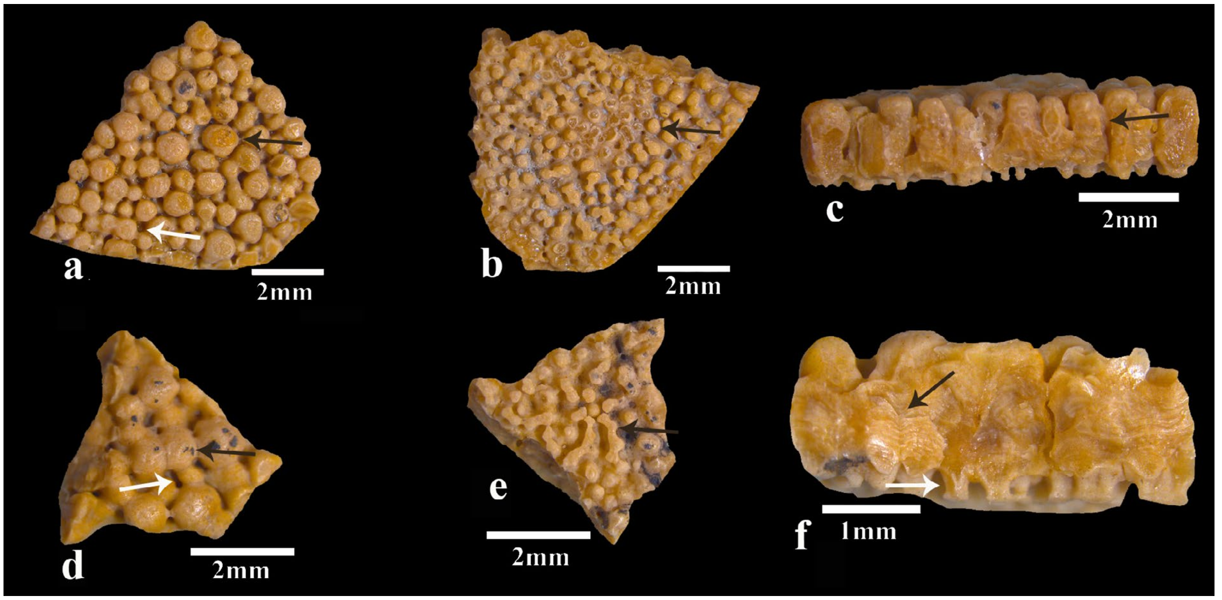

Figure 2. Stereoscope Binocular microscope images of the oospecies *Fusioolithus baghensis* from the Upper Cretaceous (Late Maastrichtian) basal part of the Kallamedu Formation, Cauvery Basin. (a), (d) External surface of the specimens DUGF/564–565, respectively, showing sub-circular nodes (black arrows) and pore spaces (white arrows) as the openings between them. (b), (e) Internal surface of DUGF/564–565, respectively, showing the basal cap units as discrete to partially coalescing protrusions (black arrows), with visible pore openings. (c), (f) Radial sections of DUGF/564–565, respectively, showing fan-shaped spheroliths, basal cap units (white arrow in 2(f)), vertical pore canals (black arrow in 2(c)) and arching growth lines (black arrows in 2(f)) fused with those of the adjacent spheroliths.

In some of the specimens, the internal surface can be seen as the basal cap unit protrusions which are partially discrete to coalescing (Figures 2(b), (e), 3(a), (b)). In other specimens, the internal surface has undergone weathering and swollen units are not present however, the openings between them are visible.

The individual spheroliths are fan-shaped, narrow at the base and become broad externally and coalesce with adjacent ones (Figures 2(c), (f), 3(c), 4(a), 5(a), (b)). The margin of spheroliths where they intersect with the adjacent spheroliths is vertical to subvertical in orientation. The height/width ratio of the spherolith is 2.8:1. The growth lines show arching beneath the nodes and merge with the growth lines of the adjacent spheroliths with a marked concavity (Figures 2(f), 5(a), (b)). Both concentric and radiating lines can be seen in the spheroliths (Figures 3(d), 4(a), (b)). The pore canals are narrow and somewhat straight showing tubocanaliculate pore system (Figures 2(c), 3(c)). A characteristic feature of the shell units is the swollen-ended basal cap unit at the base of the spheroliths (Figures 2(f), 3(c), 5(a), (b)). Its diameter ranges from 0.1 to 0.4 mm.

Remarks: Khosla and Sahni (1995) placed eggshells from the Upper Cretaceous Lameta Formation of Bagh area in Central India with shell architecture similar to that of Ottakovil eggshells in the oospecies *Megaloolithus baghensis* of the oofamily Megaloolithidae. Fernández and Khosla (2015) erected a new oofamily Fusioolithidae for the oospecies which shows fusion between the growth lines of the adjacent spheroliths. As the shell units show partial fusion in *M. baghensis*, Fernández and Khosla (2015) transferred this oospecies to their newly erected oofamily Fusioolithidae to distinguish it from the oofamily Megaloolithidae in which the spheroliths are distinctly separated from each other and the growth lines are restricted to the individual units. A new oogenus *Fusioolithus* within the oofamily Fusioolithidae was erected and a new combination *Fusioolithus baghensis* (Khosla and Sahni 1995; Fernández and Khosla 2015) was proposed for *M. baghensis*. *F. baghensis* was previously also described as (?) Titanosaurid Type-III by Sahni (1993) and Sahni et al. (1994) from the Lameta Formation of Jabalpur. Eggshells of this morphology have been documented from the Deccan intertrappean beds of Nagpur (Maharashtra), Anjar, Kachchh (Gujarat), and the Lameta Formation exposed in the Bagh Cave section and Lametaghat type section of the Lameta Formation at Jabalpur in Madhya Pradesh (Vianey-Liaud et al. 1987; Bajpai et al. 1990; Sahni 1993; Sahni et al. 1994; Khosla and Sahni 1995). The studied specimens from Ottakovil with compactituberculate ornamentation, coalesced and discrete nodes with an average diameter of 0.6 mm, short and broad fan-shaped, partially fused spheroliths, vertical to sub-vertical lateral margins of individual shell units, moderately arched growth lines entering into adjacent spheroliths, tubocanaliculate pore system with subcircular or elliptical pores and a height/width ration of 2.8:1, conform to the eggshell morphology of *F. baghensis*. Accordingly, the new eggshell specimens from Ottakovil are referred to *F. baghensis*. A comparative study of egg shell characteristics of various dinosaur oospecies known from India is presented in Table 1.The sandstones of Ottakovil with trough cross-bedding were considered to have been deposited in a relatively low energy, lower-upper shore face marginal marine environment (Tewari et al. 1996). The isolated eggshell fragments described here are considered to have undergone a short distance transportation into the marginal marine environment as they do not show rounding of edges as in those subjected to long distance transport.

Palaeobiogeographic significance of dinosaur oospecies

Previously, *F. baghensis* has been reported from the outcrops of the Lameta Formation near Bagh Budhist caves and Jabalpur in Madhya Pradesh, Pisdura in Maharashtra and Balasinor in

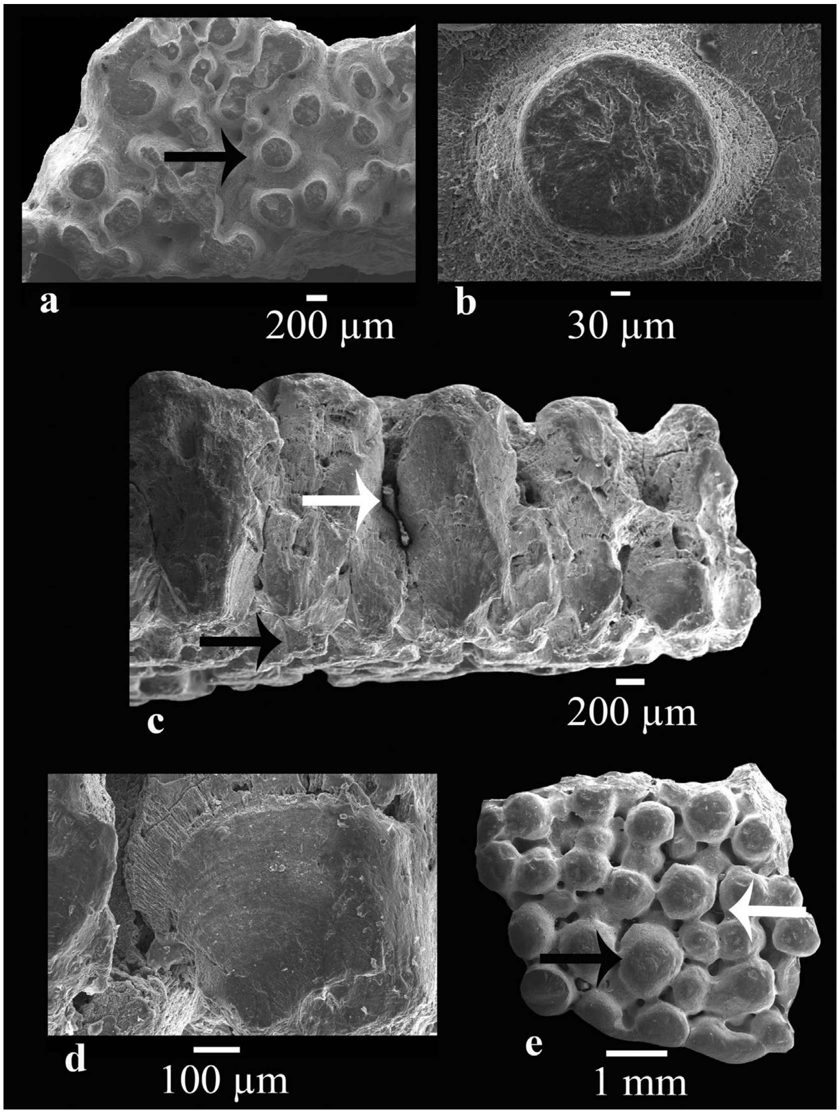

Figure 3. SEM images of the oospecies *Fusioolithus baghensis* from the Upper Cretaceous (Late Maastrichtian) basal part of the Kallamedu Formation, Cauvery Basin. (a) Internal surface of DUGF/570 with discrete to partially coalescing basal cap units as protrusions (black arrow), along with pore openings. (b) A magnified image of one of the basal units of DUGF/570. (c) Radial section of DUGF/570 showing fan-shaped spheroliths, pore canal (white arrow), and basal cap units (black arrow). (d) A magnified image of the lower section of one of the spheroliths (DUGF/570) showing concentric growth lines from the central core. (e) External surface of DUGF/570 showing circular to sub-circular nodes (black arrow) with pore openings in between (white arrow).

Gujarat, and the intertrappean beds of Nagpur in Maharashtra and Anjar in Gujarat (Jain and Sahni 1985; Srivastava et al. 1986; Vianey-Liaud et al. 1987; Sahni et al. 1994; Khosla and Sahni 1995; Mohabey 1998). Morphologically, similar species has been described as *Megaloolithus balasinorensis* from the Upper Cretaceous Lameta Formation (Mohabey 1998). Like-wise, eggs and eggshells having similar micro- and ultra-structural characters as that of *F. baghensis*, were also documented from the Upper Maastrichtian deposits of Aix-en-Provence Basin, France (Vianey-Liaud et al. 1997) and Suterranya locality, Tremp Basin, Spain (Vianey-Liaud and Lopez-Martinez 1997; Blas 2005) under *M. pseudomammilare*. *Patagoolithus salitralensis* from the Upper Cretaceous of Salitral Moreno, Argentina (Simón 2006) is also very similar morphologically to the presently studied eggshells. While describing the new combination *Fusioolithus baghensis*, Fernández and Khosla (2015) made *M. balasinorensis*, *M. pseudomammilare*, *Megaloolithus* cf. *baghensis* and *Patagoolithus salitralensis* as junior synonyms of *F. baghensis*.

The Indian subcontinent has undergone a long distance northward journey across Tethys sea following its break-up from the former Gondwanaland, particularly after its separation from Madagascar in the Late Cretaceous (88 Ma ago). Palaeontological studies of the Deccan infra- and inter-trappean beds, which record part of India's rapid northward journey have revealed that the fauna and flora represented is an admixture of endemic elements as well as those having Laurasian and Gondwanan affinities (Prasad and Sahni 2009). The ostracod fauna was shown to be predominantly endemic to India at species level (Whatley and Bajpai 2006). Leptodactlyid and hylid frogs, bothremydid turtles, nigerophiid and madtsoiid snakes, baurusuchian and notosuchian crocodiles, abelisaurid dinosaurs, and haramiyid and gondwanatherian mammals from the Upper Cretaceous infra- and inter-trappean beds demonstrateGondwanan affinities (Rage and Prasad 1992; Prasad and Rage 1995; Krause et al. 1997; Gaffney et al. 2001, 2003; Prasad and de Broin 2002; Wilson et al. 2003; Anantharaman et al. 2006; Prasad et al. 2007a, 2007b; Wilson

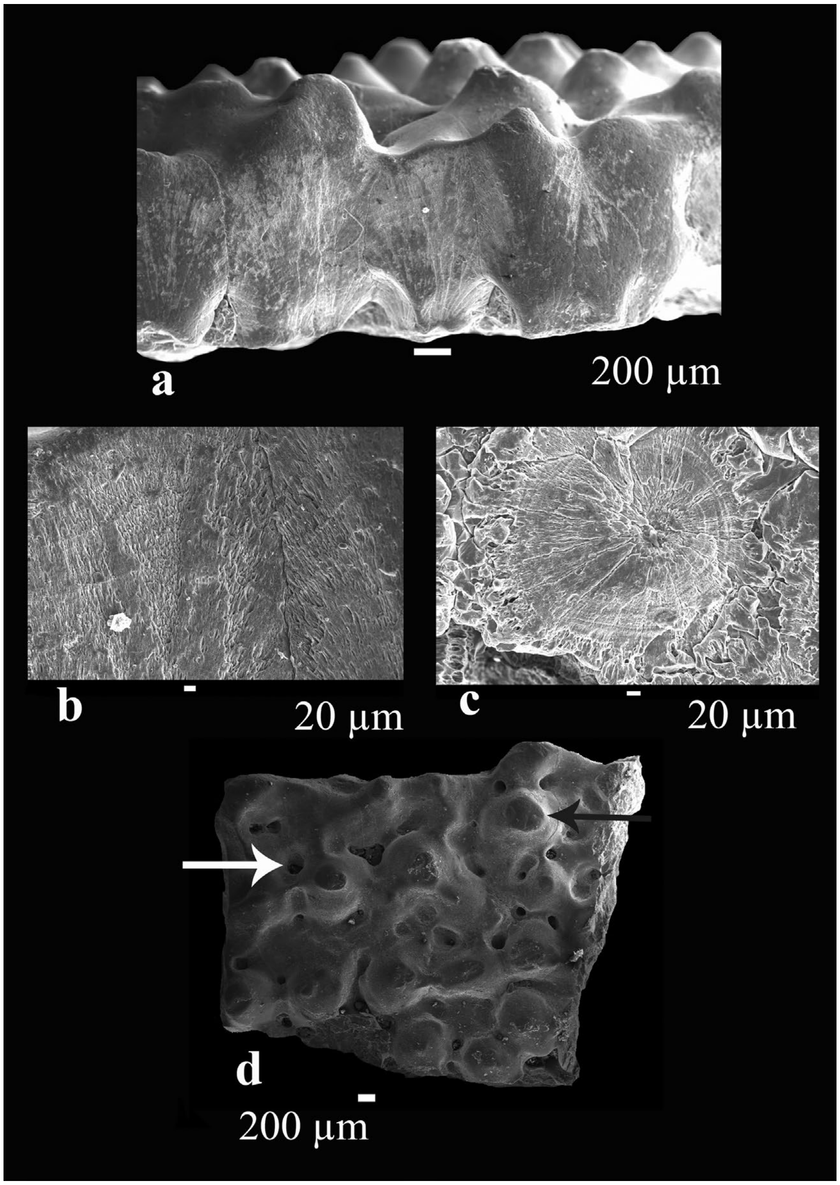

Figure 4. SEM images of the oospecies *Fusioolithus baghensis* from the Upper Cretaceous (Late Maastrichtian) basal part of the Kallamedu Formation, Cauvery Basin. (a) Radial surface of DUGF/571 with fan-shaped spheroliths and nodes seen as bulbous ends on the upper surface. (b) A magnified image of surface of spherolith (DUGF/571) showing the presence of both concentric and radiating lines. (c) A magnified image of basal unit of one of the spherolith (DUGF/571) from which both concentric and radiating lines can be seen. (d) External surface of DUGF/571 showing partially coalescing nodes (black arrow) and pore spaces in between them (white arrow).

et al. 2007; Rage et al. 2004; Novas et al. 2010; Wilson et al. 2010; Lapparent de Broin et al. 2009; Mohabey et al. 2011; Prasad et al. 2013). On the other hand, pelobatid and Gobiatinae frogs, anguimorph lizards, troodontid dinosaur, an ungulate mammal, charophytes and palms suggest Laurasian affinity (Sahni et al. 1982; Bhatia et al. 1990; Prasad and Rage 1991, 1995; Prasad et al. 2007b; Goswami et al. 2013; Srivastava et al. 2014).

The dinosaur oospecies from the Upper Cretaceous Lameta Formation belonging to the oofamilies Megaloolithidae and Fusioolithidae also exhibit close taxonomic relationships to those of Argentina and France. Among the Indian oospecies, *Megaloolithus jabalpurensis*, *M. cylindricus*, *M. megadermus*, *Fusioolithus baghensis* and *F. mohabeyi* have closely related forms in the Upper Cretaceous rocks of Argentina, France and Morocco. Eggshells with some similarities to that of *M. jabalpurensis* have previously been documented from the Upper Cretaceous (Maastrichtian) Rousset-Erben locality Aix-en-Provence Basin, France (Vianey-Liaud et al. 1994) and Upper Cretaceous Abella and Bastus localities of Tremp Basin, Spain (Vianey-Liaud and Lopez-Martinez 1997). In shape, size, external ornamentation, nodal diameter, shape of shell units, pattern of growth lines, pore system and eggshell thickness, *M. patagonicus* described from the Upper Cretaceous (Coniacian-Santonian) Baja de la Carpa Formation, Neuquen Province of Patagonia, Argentina (Calvo et al. 1997) compare very well with *M. jabalpurensis*. Because of these microstructural similarities between these two oospecies, Fernández and Khosla (2015) made *M. patagonicus* as a junior synonym of *M. jabalpurensis*.

Eggs and eggshells similar in morphology to *M. cylindricus* originally described from a number of Lameta nesting sites in central India and from the marine Upper Cretaceous Kallankuruchhi Formation of South India (Kohring et al. 1996)

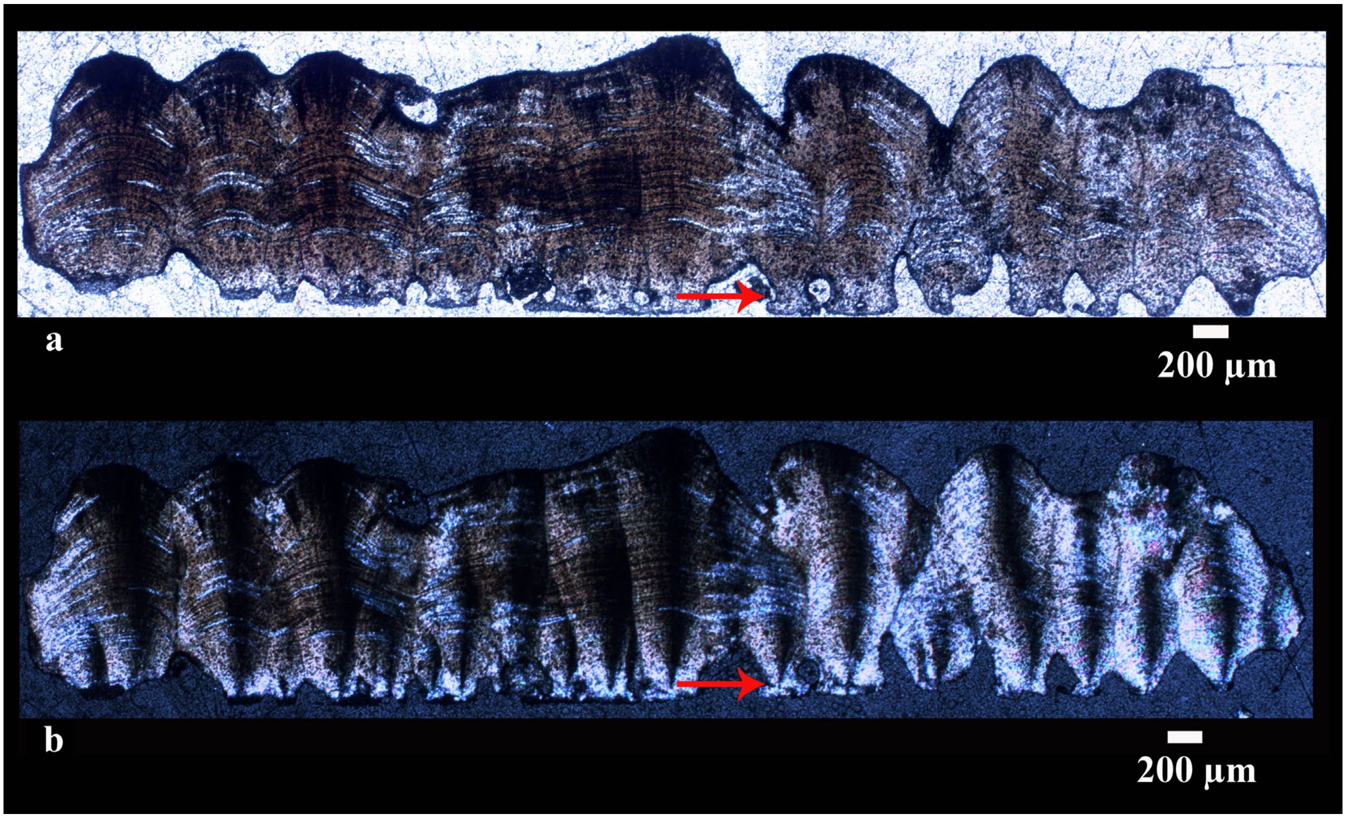

Figure 5. Thin section images of the oospecies *Fusioolithus baghensis* from the Upper Cretaceous (Late Maastrichtian) basal part of the Kallamedu Formation, Cauvery Basin. (a) Plane polarised light and (b) crossed polarised light images of the radial section (DUGF/572).
Note the fan-shaped spheroliths, basal cap units at the inner margin (see arrow) and growth lines that are arching upwards and showing coalescence with those of the adjacent spheroliths.

have also been recorded from the Upper Cretaceous rocks of France which include Penner Type I (Vianey-Liaud et al. 1987) from Aix-en-Provence Basin, Type 4 (Williams et al. 1984) from Maupague locality, and *M. microtuberculata* from La Cairanne locality (Garcia and Vianey-Liaud 2001). Though *M. siruguei* from the Upper Cretaceous of France resembled *M. cylindricus* (Vianey-Liaud et al. 2003) in its microstructure, it differs from the latter in having sub-circular nodes and pore system with transverse channels (Mohabey 1998; Sellés et al. 2013). Besides the similarity between *M. cylindricus* and the above cited French oospecies, egg and eggshells having microstructural characteristics and thickness similar to those of *M. cylindricus* were also reported from the Upper Cretaceous rocks of the Allen Formation, Rio Negro Province of Argentina (Type 1d of Fernández 2013). In fact, Fernández and Khosla (2015) have referred Type 1d from Argentina to *M. cylindricus*.

M. megadermus known from a site near Dholidhanti, Gujarat (India) in the Upper Cretaceous Lameta Formation is characterised by compactituberculate ornamentation of coarse densely packed nodes, and discrete, tall and narrow shell units with straight lateral margins (Mohabey 1998). Eggs and eggshells with similar morphology have been described by Kerourio (1987) under *Hypselosaurus* from the Upper Cretaceous rocks of Dansle Basin, France. More recently, similar eggshells have also been reported from the Upper Cretaceous rocks of Argentina as Tipo 1e (Fernández 2013).

As discussed above *F. baghensis* has been recorded from the Upper Cretaceous rocks of Aix-en-Provence, France (= *M. pseudomammilare*) and Salitral Moreno, Argentina (= *Patagoolithus salitralensis*).

Vianey-liaud and Garcia (2003) reported an oospecies *Megaloolithus maghrebiensis* from Upper Maastrichtian Achlouj 2, Middle Atlas, Morocco and found it similar to *F. mohabeyi* (Khosla and Sahni 1995; Fernández and Khosla 2015), however they have found the node diameter of *F. mohabeyi* to be smaller and the eggshell thickness to be less than that of *M. maghrebiensis*. Garcia et al. (2003) have compared *M. maghrebiensis* to *M. siruguei* (Garcia and Vianey-Liaud 2001) on the basis of similarity in some of the morphological features but have also mentioned differences in the form of node diameter, pore canals, and shape of the fan-units. Vianey-liaud and Garcia (2003) also reported a new oospecies *Pseudomegaloolithus atlasi* from Upper Maastrichtian, Achlouj 2, Middle Atlas, Morocco. On comparison of *Pseudomegaloolithus atlasi* with the oospecies *M. pseudomamillare* and *F. baghensis*, they have suggested that similar oospecies existed in the Upper Cretaceous formations of India, France and Peru. Chassagne-Manoukian et al. (2013) documented oospecies *Pseudomegaloolithus atlasi* from Maastrichtian, Douar Lgara, Tendrara High Plateaus, Morocco. On the basis of shape of growth lines they have compared it with *M. pseudomamillare* (Vianey-Liaud et al. 1997) from the Bagua Basin (Peru) and from Aix-en-Provence (France) and to *M. phensaniensis* (Mohabey 1998) from the Lameta Formation of Gujarat, India which is now synonymised with *Fusioolithus mohabeyi* (Fernández and Khosla 2015) by Vianey-Liaud et al. (2003). Chassagne-Manoukian et al. (2013) have also mentioned

Table 1. Summary of eggshell features of the Cretaceous dinosaur oospecies from India.

Eggshell Parameters	*M. jabalpurensis* (Khosla and Sahni 1995)	*M. cylindricus* (Khosla and Sahni 1995)	*M. megadermus* (Mohabey 1998)	*M. dhoridungriensis* (Mohabey 1998)	*M. khempurensis* (Mohabey 1998)	*F. padiyalensis* (Khosla and Sahni 1995)	*F. dholiyaensis* (Khosla and Sahni 1995)	*F. mohabeyi* (Khosla and Sahni 1995)	*F. baghensis* (Khosla and Sahni 1995)	*M. cylindricus* (Kohring et al. 1996)	*F. baghensis* (This paper)
Morphotype	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic	Discretispherulitic
Ornamentation	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate	Compactituberculate
Pore system	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate	Tubocanaliculate
Thickness (mm)	1.0–2.3	1.7–3.5	4.0–4.8	2.26–2.36	2.36–2.6	1.12–1.68	1.47–1.75	1.8–1.9	1.0–1.7	2.7–2.8	0.89–1.6
H/W	2.45:1	4:1	9.6:1	2.74:1	3.41:1	3.95:1	2.94:1	3.06:1	2.32:1	3.5:1	2.8:1
Average node diameter (mm)	0.47	0.8–1	–	–	0.6–0.8	–	–	–	0.6	–	0.4–0.8
Basal cap diameter (mm)	0.1–0.5	0.2–0.5	<0.4	0.37–0.39	0.23–0.26	0.07–0.21	0.15–0.3	0.14–0.21	0.2–0.3	–	0.1–0.4

the morphological differences between these two oospecies whilecomparing with *P. atlasi* from Tendrara High Plateaus, Morocco in terms of having higher node density, thickness and arched growth lines.

The oospecies *M. jabalpurensis*, *M. cylindricus*, *M. megadermus*, *F. baghensis*, *F. mohabeyi* provided additional evidence in support of close biogeographic linkages between India, South America, Africa and Europe in the Late Cretaceous (Figure 6).

A number of palaeobiogeographic models have been proposed to explain the presence of Gondwanan and Laurasian taxa in India at a time it was rapidly drifting towards the north in complete physical isolation (Sahni et al. 1982; Briggs 1989; Sahni and Bajpai 1991; Krause et al. 1997; Prasad and Sahni 1999; Briggs 2003; Rage 2003; Prasad and Sahni 2009; Jaeger et al. 1989; Chatterjee et al. 2013). The presence of Gondwanan elements in the drifting Indian plate has been explained through a migration route linking Africa to Greater India via Somalia (Briggs 1989, 2003; Chatterjee and Scotese 1999). Alternatively, a more widely preferred terrestrial route was from South America to Indo-Madagascar via Antarctica and Kerguelen Plateau/Gunnerus Ridge/Ninetyeast aseismic ridge (Krause et al. 1997; Case 2002; Chatterjee et al. 2013). However, Ali and Krause (2011) were of the opinion that the latter terrestrial faunal dispersal route was not operational in the Late Cretaceous as the intervening igneous provinces (e.g. Kerguelen Plateau) or Gunnerus Ridge were already submerged by 67.5 Ma.

As the existing palaeobiogeographic models are not well supported by geophysical evidence, here we seek to explain the common occurrence of at least five sauropod dinosaur oospecies (*M. jabalpurensis*, *M. cylindricus*, *M. megadermus*, *F. baghensis*, *F. mohabeyi*) in the Late Cretaceous of India, South America, Europe and Africa through an alternative dispersal route. In addition to these oospecies, adapisoriculid mammals were considered to have dispersed out of India into Europe and Africa close to the Cretaceous-Palaeogene boundary (Prasad et al. 2010). On the other hand, a coryphoid palm *Sabalites* was interpreted to have dispersed into India from Europe (Srivastava et al. 2014). Recent phylogenetic analysis of a large abelisaurid dinosaur *Arcovenator escotae* from the Late Campanian of Aix-en-Provence Basin of France has shown that *Arcovenator* is a sister taxon to *Majungasaurus* of Madagascar and *Rajasaurus*, *Rahiolisaurus* and *Indosaurus* of India and all of them nest in their own subfamily Majungasaurinae (Tortosa et al. 2014). These recent findings add to already known taxa of Laurasian affinities, such as pelobatid and discoglossid frogs, anguid lizards, a possible ungulate (*Kharmerungulatum*) and charophytes. All these fossil evidences point to the presence of a Late Cretaceous dispersal route between India and Europe via Africa. In the past, sweepstakes dispersals across the Neotethys using Kohistan and Dras island arcs, Transhimalayan magmatic arc and some oceanic islands as stepping stones were invoked to account for the presence of Laurasian elements in the Late Cretaceous of India (Prasad and Sahni 1999). In a modified version of this palaeobiogeographic scenario, Chatterjee and Scotese (2010) and Chatterjee et al. (2013) proposed that Kohistan-Ladakh-Oman island arc route may have played an important role in the dispersal of African and European taxa into and out of India. Assuming that the northeastern part of South America was close to the northwestern part of Africa in the Late Cretaceous (~90 Ma ago)

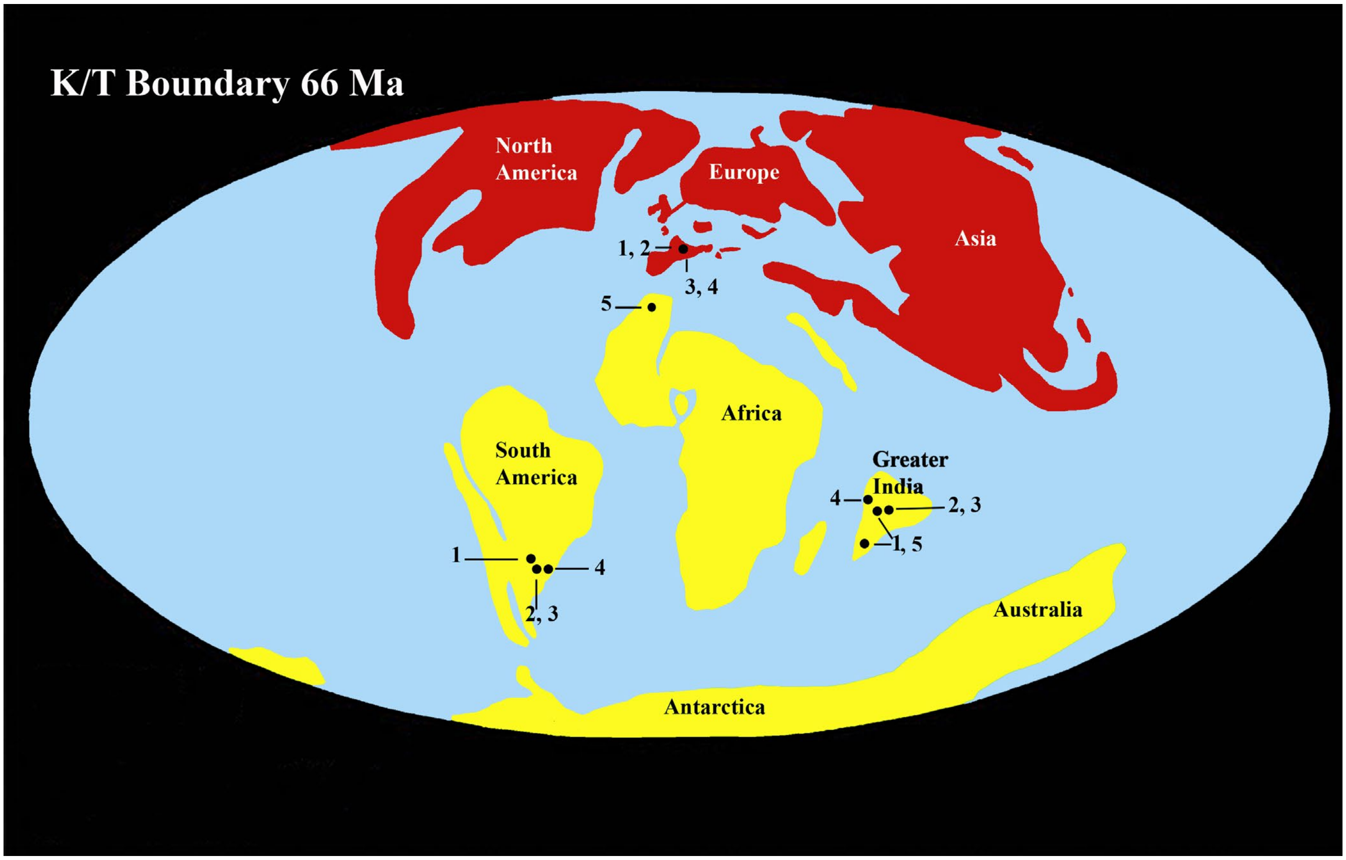

Figure 6. Late Cretaceous palaeobiogeographic map of the continents showing distribution of oospecies in India, France, Argentina, and Morocco (After Scotese 2001). 1, *F. baghensis* (Khosla and Sahni 1995); 2, *M. jabalpurensis* (Khosla and Sahni 1995); 3, *M. cylindricus* (Khosla and Sahni 1995); 4, *M. megadermus* (Mohabey 1998); 5. *F. mohabeyi* (Khosla and Sahni 1995).

as suggested by Sereno et al. (2004), dispersal of South American forms into India or vice versa via Kohistan-Ladakh-Oman island arc system is one plausible faunal dispersal scenario that we can visualize at present. As intermittent Late Cretaceous faunal dispersals between Africa and southern Europe were already suggested (Gheerbrant and Rage 2006), Africa may have played an important role in the Late Cretaceous faunal exchanges between India and Eurasia on one hand and India and South America on the other hand.

Conclusions

The new finding of fossilised dinosaur eggshell fragments from the Upper Cretaceous basal part of the Kallamedu Formation of the Ariyalur Group is important because it represents the second report of dinosaur egg and eggshells from the Cretaceous sedimentary succession of the Cauvery Basin in South India, the first being the solitary egg described from the Upper Cretaceous Kallankuruchhi Formation (Kohring et al. 1996). It also attests to the fact that at least two different titanosaurid sauropod dinosaur oospecies out of the nine oospecies documented from Central India inhabited the Cauvery Basin in the Late Cretaceous. The close taxonomic affinities of the eggshells with the oospecies of South America, Africa and Europe suggest that India was well connected biogeographically to South America and Europe via Africa in the Late Cretaceous.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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