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RELATIONSHIPS BETWEEN EUROPEAN AND INDIAN DINOSAUR EGGS AND EGGSHELLS OF THE OOFAMILY MEGALOOLITHIDAE

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ABSTRACT—Indian and French dinosaur eggshell oospecies belonging to the oofamily Megaloolithidae are compared and, of the fourteen Megaloolithidae oospecies previously described from the Late Cretaceous of India, seven are considered junior synonyms. Comparisons between nine oospecies from India and France reveal four groupings which show similarities between megaloolithids of these countries: (1) *Megaloolithus microtuberculata*, *M. cylindricus*, and *M. padiyalensis*; (2) *M. mamillare* and *M. jabalpurensis*; (3) *M. siruguei* and *M. khempurensis*; and (4) *M. pseudomamillare* and *M. baghensis*. Five oospecies from India have no French equivalents, whereas the oogenus *Cairanoolithus* is endemic to France. Updated synonymy *Megaloolithus* oospecies shows a total of nine distinct oospecies from India: *Megaloolithus cylindricus*, *M. mohabeyi*, *M. padiyalensis*, *M. jabalpurensis*, *M. dholiyaensis*, *M. dhoridungriensis*, *M. khempurensis*, *M. megadermus*, and *M. baghensis*. One oospecies, *M. jabalpurensis*, is common to India and South America and is considered here to be possibly a senior synonym of *M. patagonicus*. The similarities in egg taxa suggest close phyletic relationships, as well as the probable existence of a terrestrial connection of dinosaur fauna between India and Europe during the Cretaceous, and between the two gondwanan areas Patagonia and India.

INTRODUCTION

Eggshells assignable to the oofamily Megaloolithidae were initially found in Europe (e.g., Dughi and Sirugue, 1957), then subsequently in India (Mohabey, 1984; Jain and Sahni, 1985) and South America (Kerourio and Sigé, 1984; Vianey-Liaud et al., 1987, 1997; Chiappe et al., 1998). Megaloolithid eggs have often been attributed to sauropods (Vianey-Liaud et al., 1987; Sahni and Khosla, 1994; Sahni et al., 1994; Khosla and Sahni, 1995; Loyal et al., 1996); however, this correlation was based on circumstantial evidence. Because both sauropods and megaloolithids are common in Upper Cretaceous deposits of Gondwana, it previously had been assumed that the latter were laid by the former. The recent discovery of sauropod embryos in megaloolithid eggs from Argentina confirms that at least some megaloolithid oospecies were laid by sauropod dinosaurs (Chiappe et al., 1998).

To date, fourteen oospecies from India (Khosla and Sahni, 1995; Mohabey, 1998) and eight from Europe (Vianey-Liaud et al., 1994; Garcia and Vianey-Liaud, 2001a) have been assigned to the oofamily Megaloolithidae. These oospecies usually have spheroidal eggs (with the exception of some oval eggs from France) and are characterized by eggshell of the tubospherulitic (discretispherulitic) morphotype. Comparisons are made between the Indian oospecies previously described by Khosla and Sahni (1995) with those described by Mohabey (1998). In addition, a comparison between Gondwanian (mainly India, and Patagonia) and European megaloolithid oospecies will enable us to establish similarities in the oofauna between these regions.

MATERIAL AND METHODS

The rich Upper Cretaceous dinosaur localities in India and France have produced hundreds of eggs and eggshell fragments. The specimens are housed at Vertebrate Paleontology Laboratory, Panjab University, Chandigarh; Paleontology Division, Geological Survey of India, Nagpur, Maharashtra; Geological Survey of India, Gandhinagar, Gujarat, India; Laboratoire de Paléontologie, ISEM, cc 064, Université Montpellier II, Place Eugène Bataillon, 34095 Montpellier, France; Muséum d'Histoire Naturelle d'Aix-en-Provence, rue Espariat, 13100 Aix-en-Provence, France; Muséum d'Histoire Naturelle du Havre, Place du Vieux Marché, 76600—Le Havre.

Specimens from India include: a nearly complete silicified egg and more than 150 eggshell fragments of *Megaloolithus cylindricus*; 30 eggshell fragments of *M. mohabeyi*; 8 eggshell fragments of *M. padiyalensis*; nest containing 4 eggs and more than 500 eggshell fragments of *M. jabalpurensis*; 30 eggshell fragments of *M. dholiyaensis*; a nearly complete egg, broken eggs, and eggshell fragments of *M. dhoridungriensis*; two complete eggs and numerous eggshell fragments of *M. megadermus*; a nearly complete egg and more than 50 eggshell fragments of *M. baghensis*.

Specimens from France include: five more or less crushed eggs and several hundreds of eggshell fragments of *M. microtuberculata* from La Cairanne (Provence); about 50 eggs of *M. siruguei* from several localities from Provence to Pyrénées (Vitrolles Le Porry, Ventabren, Puyloubier, Maupague-Saint Ser, Roquefumade, Rennes-le-Château, Saint-André-de-Roquelongue, etc.) and thousands of eggshell fragments from this and other localities; about 30 eggs from several localities of *M. mamillare* from Provence to Pyrénées (Rousset Erben, Vitrolles-La Plaine, Vitrolles Eurocopter), Bastus (Spain) and thousands of eggshell fragments from this and other localities; 6 eggs of *M. baghensis = M. pseudomamillare* from Les Bréguières and Maupague-Saint Ser (Provence), hundreds of fragments from this and other localities.

Pertinent information on each oospecies has been displayed in tabular form (Figs. 1 and 2) and includes characters such as egg shape, size, eggshell thickness and type locality. Microstructural features are displayed by camera lucida drawings of thin sections from material described by Khosla and Sahni (1995), or are redrawn from illustrations by Mohabey (1998). Thus, features such as shell thickness and morphologies of the

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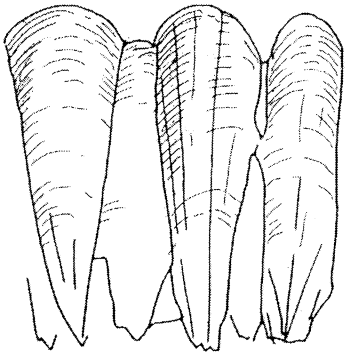
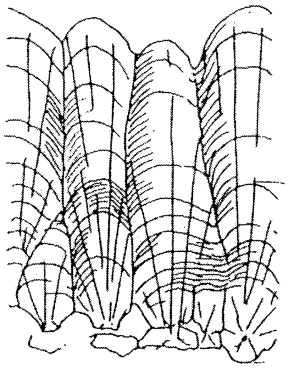
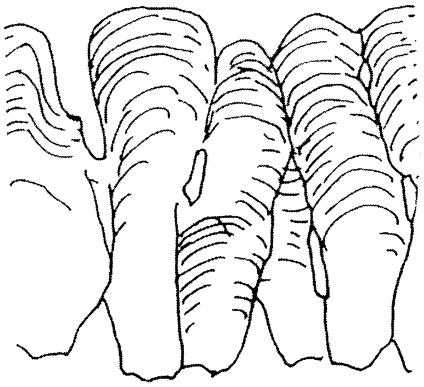
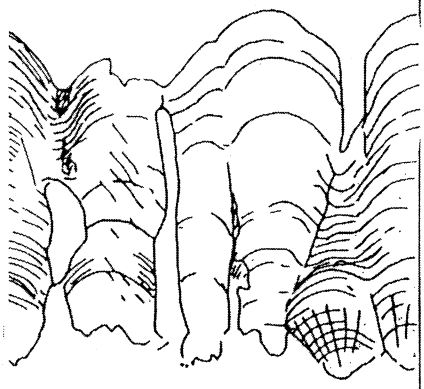
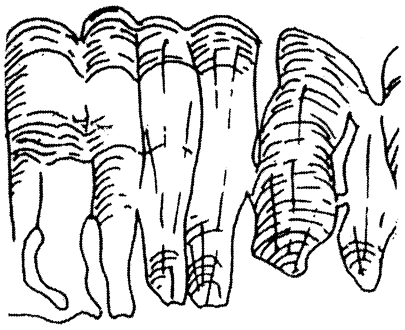
Khosla and Sahni 1995	Mohabey 1998	Short comments
Megaloolithus cylindricus Spherical eggs :∅ 120-200mm Thickness 1.7-3.5mm Type from : Chui Hill 	***Megaloolithus rahiolensis*** Spherical eggs :∅ 125-160mm Thickness 2.8-3.5mm Type from : Rahioli 	In Mohabey (1998) there is a problem of scale for the figure 4E-F. The represented thin section appears to be thinner (less than 2mm) than the given dimensions (2,8→3,5mm) ***(scale = 1mm)***
Megaloolithus mohabeyi Spherical eggs :∅ 160-190mm Thickness 1.8-1.9mm (only 3 fragments measured) Type from : Dholyia 	***Megaloolithus phensaniensis*** Spherical eggs :∅ 160-190mm Thickness 1.65-1.90mm Type from : Phenasani 	In their discussion, Khosla and Sahni (1995) already indicate that the microstructure of eggs from Phenasani Lake is similar to *M.mohabeyi*. The material figured by Mohabey (1998, fig.5A-F) show sometimes strong thickness and microstructural variations (fig.5A and E) The inner part of the thin section (fig 5D) is strongly weathered and recrystallized. (see fig.3)
Megaloolithus padiyalensis Fragments only Thickness 1.12-1.68mm Type from : Padiyal 		The microstructure is close to that of *M. mohabeyi*, but the units are slender and thinner

FIGURE 1. Comparisons between Indian oospecies. Figures redrawn from photographs in cited papers or directly from thin sections. Column 1, Khosla and Sahni, 1995, Column 2: Mohabey, 1998. The oospecies in the same row are possibly synonymous. The drawings are at the same scale. Scale equals 1 mm.

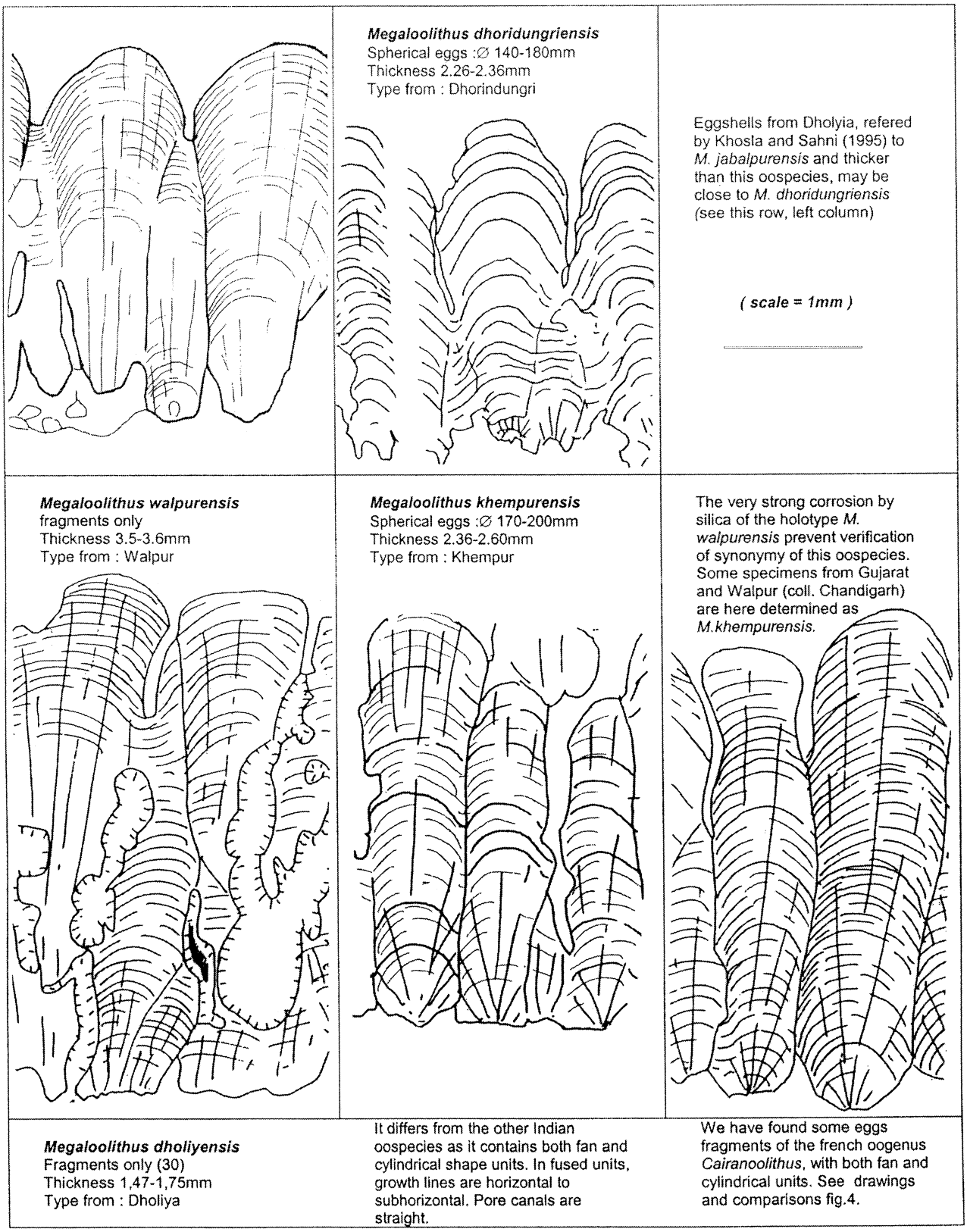
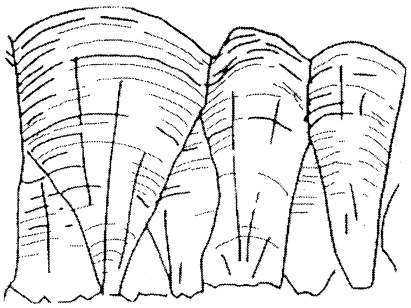
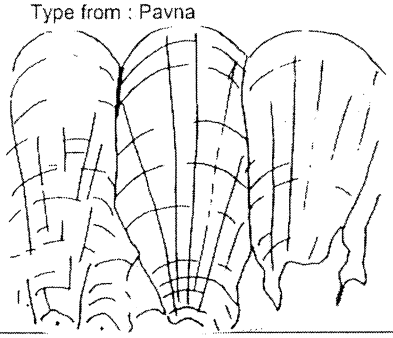


FIGURE 1. Continued.

Megaloolithus jabalpurensis
Spherical eggs :∅ 140-160mm
Thickness 1.00-2.30mm
Type from : Bara Simla Hill, Jabalpur



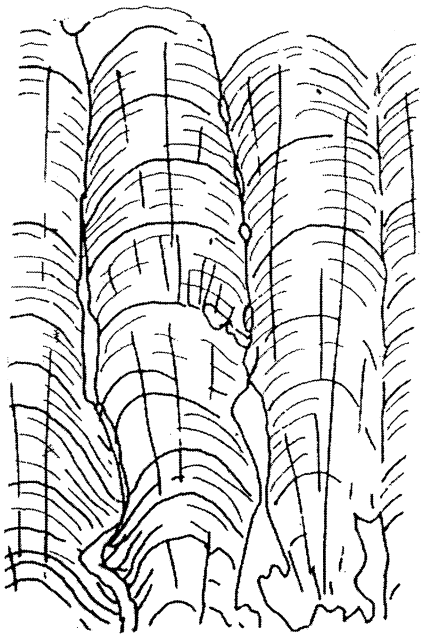
Megaloolithus matleyi
Spherical eggs :∅ 160-180mm
Thickness 1.50-2.00mm (and may be more : Mohabey 1996)
Type from : Pavna



The two types are very similar, with their discrete fan shaped units. It is probably the same oospecies.

There is a problem of scale in the fig. 6 E-G given by Mohabey (1998) . Scale bar is indicated to be 1mm, but it must be 0.5mm. If not, the measurements do not fit.

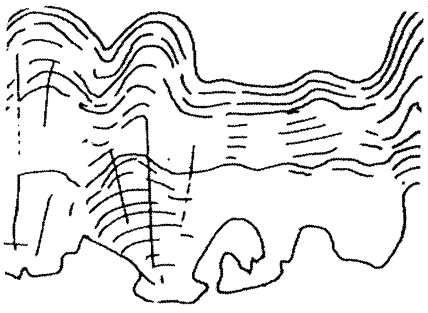
Megaloolithus megadermus
Spherical eggs :∅ 130-180mm
Thickness 4,0-4,80mm to more than 5mm
Type from : Dholidanti



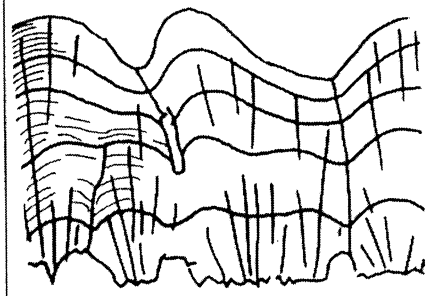
The thin section, redrawn here in the central column, seems to be incompletely figured (Mohabey, 1998: fig. 7C).
The main character of the oospecies is the strong shell thickness, with much elongated units (W/h ratio = 9).

Mohabey errered in his discussion (p.355) about the French locality named by him « Dans le Basin ». It is probably Aix or Arc Basin in Provence.
The paper he has cited (Kerourio, 1987) has been published in a scientific popular article. The thin section he compares *M. megadermus* is *M. siruguei*.
This french oospecies has a W/h ratio 4 to 5.

Megaloolithus baghensis
Spherical eggs :∅ 140-200mm
Thickness 1.00-1.70mm
Type from : Bagh Caves



Megaloolithus balasinorensis
Spherical eggs :∅ 140-180mm
Thickness 1.45-1.65mm
Type from : Balasinor



These two oospecies have fused units, short and broad, with arched growth lines. They are synonymous.

FIGURE 1. Continued.

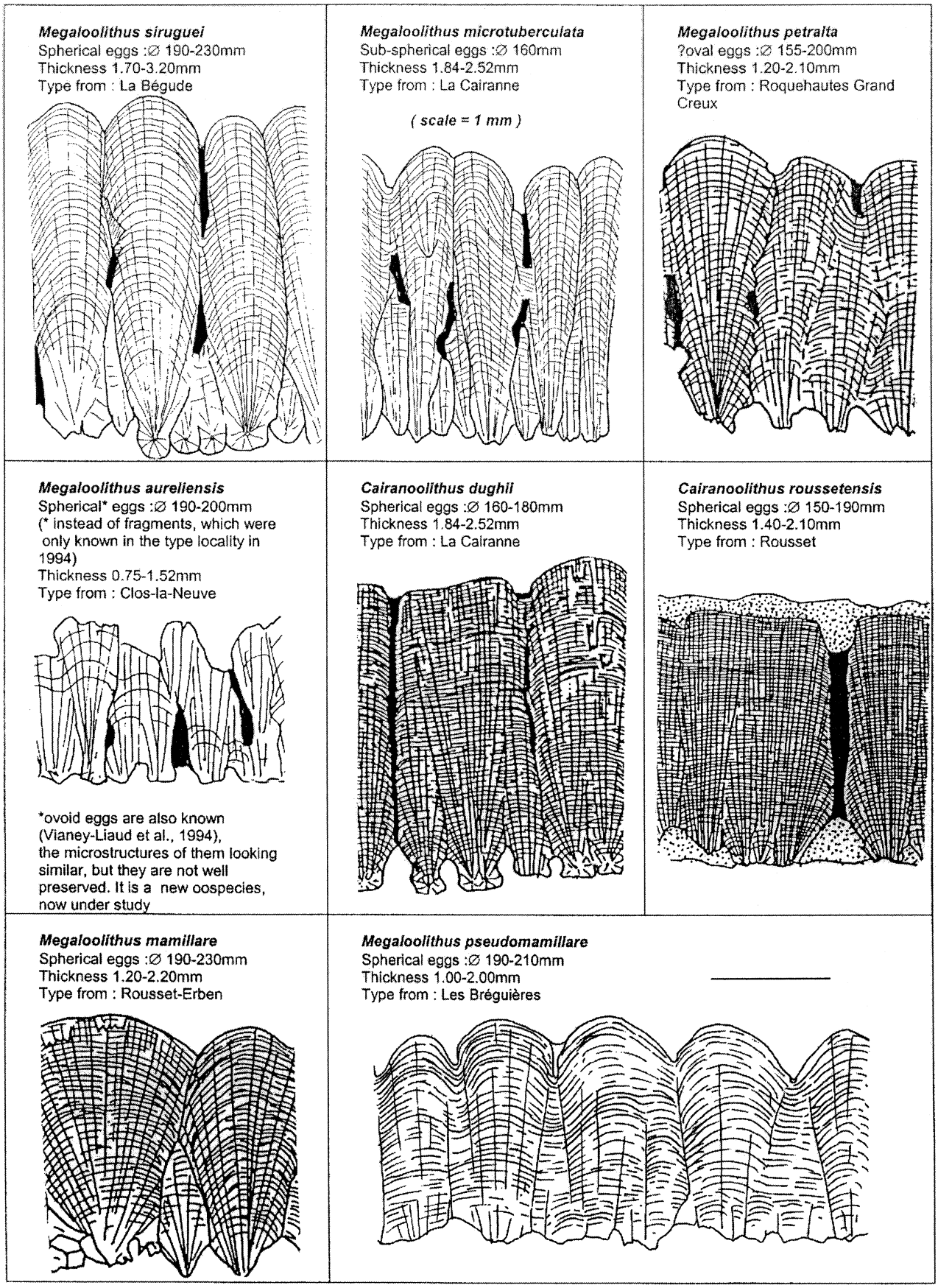


FIGURE 2. The French megaloolithid oospecies. Drawn from thin sections. The drawings are at the same scale. Scale equals 1 mm.

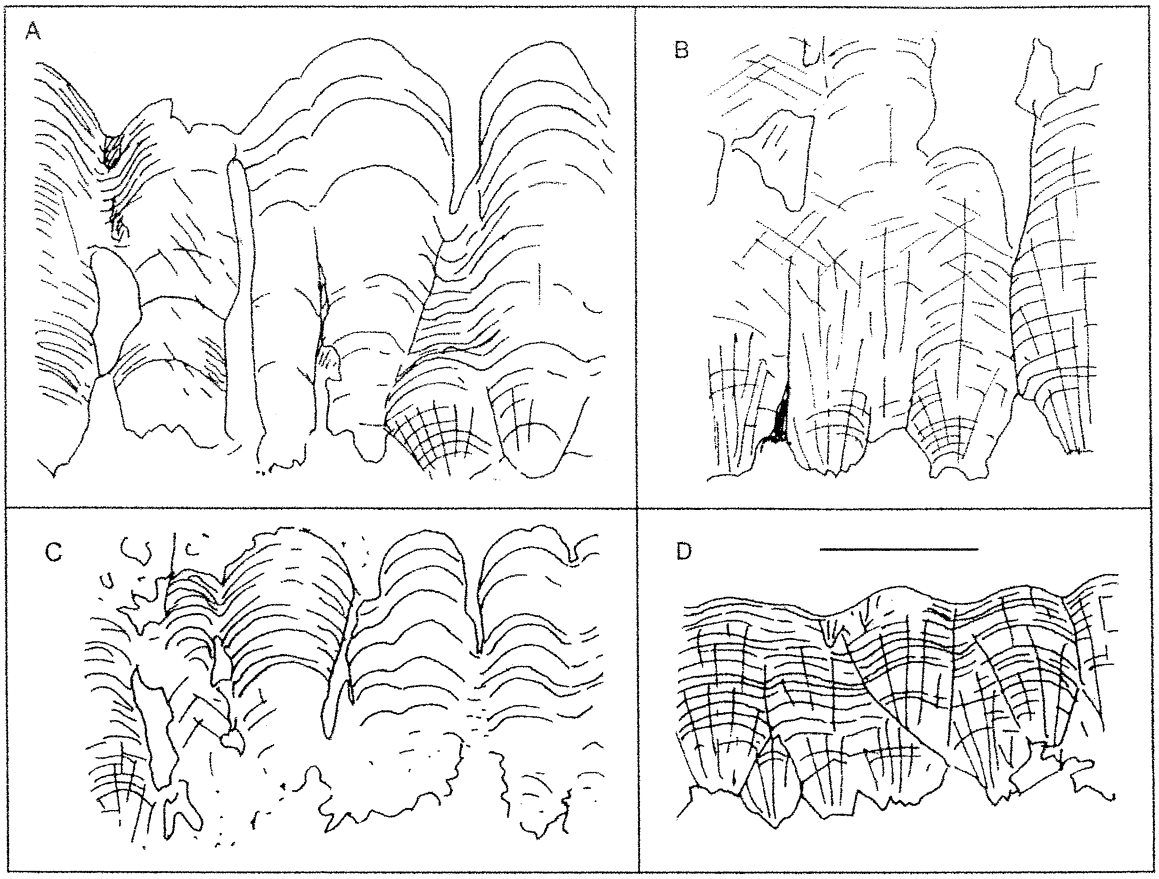


FIGURE 3. Drawings of the four thin sections figured by Mohabey (1998:fig. 5A–E), for his new oospecies *Megaloolithus phensaniensis*. The microstructure **D** seems clearly different of **A**. The inner part of **C** is badly weathered. Scale equals 1 mm.

shell units could be used to compare oospecies and determine their validity, in addition to the available information on size and shape of the eggs.

REVIEW AND COMPARISON OF *MEGALOOLITHUS* OOSPECIES FROM INDIA AND FRANCE

Megaloolithus eggs from India resemble those from France in having a nodular outer surface ornamentation and clearly arched growth lines of the shell units. None of the Indian oospecies have flattened nodes or a smooth surface, which is characteristic of the French oogenus *Cairanoolithus*. For this reason, all are referred to the oogenus *Megaloolithus*.

Morphotype DISCRETISPHERULITIC
Oofamily MEGALOOLITHIDAE Zhao, 1975 (emend. 1979)

Megaloolithus cylindricus Khosla and Sahni, 1995:89–90, pl. 1, figs. 1–6, fig. 5.

Megaloolithus rahioliensis Mohabey, 1998:349, figs. 3A, 4A–F (Type locality: Rahioli, Gujarat, India).

Type Locality—Chui Hill (Madhya Pradesh, India).

Among the Indian oospecies described, *M. cylindricus* Khosla and Sahni, 1995 and *M. rahioliensis* Mohabey, 1998, do not show significant macro- or microstructural differences (see Fig. 3). The units are slender, often cylindrical, sometimes slightly enlarged at their top, and delimited by well defined boundaries. The growth lines are clearly arched. The material used to establish *M. cylindricus* was described previously by Sahni (1993) and Sahni et al. (1994) as (?)Titanosaurid Type I. Although Mohabey (1998) states that *M. rahioliensis* is similar to (?)Titanosaurid Type I, it is our interpretation that this material represents the same oospecies. Therefore, *M. cylindricus* Khosla and Sahni, 1995, has publication priority over *M. rahioliensis* Mohabey, 1998, and the latter is considered the junior synonym of *M. cylindricus*. Khosla and Sahni (1995) indicate that the arching of the growth lines of *M. cylindricus* increases in the upper part of the shell units, but it is not a general feature.

A single, complete spheroidal egg (200 mm in diameter) with similar macro- and microstructural features to those of *M. cylindricus* has been described from marine Maastrichtian deposits of Ariyalur area (Kohring et al., 1996). The specimen is not given a parataxonomic name, but features including nodose ornamentation, cylindrical-shaped shell units, and straight pore canals make it remarkably similar to *M. cylindricus*. The shell thickness of this specimen (2.7–2.8 mm) is also within the range of thickness for *M. cylindricus* (1.7–3.5 mm).

Mohabey (1998) stated that *M. cylindricus* (as *M. rahioliensis*, see above) closely resembled *M. siruguei* from the Upper Cretaceous of France, but differed in having a ''perfectly spherical shape, more discrete nodes on the outer surface, polygonal to subcircular outlines and narrower pore canals.'' These characters are also found in *M. siruguei*. Indeed, *M. siruguei* has spherical eggs, the diameter of which is between 190 to 230 mm. The actual differences between the two oospecies are the larger size of *M. siruguei* eggs and the generally smaller diameter of the nodes in *M. cylindricus* (about 0.60 mm at Chui Hill, 0.40 to 0.70 at Rahioli, and 0.40 to 1.10, with average around 0.65–0.70 in *M. siruguei* from la Bégude).

Khosla and Sahni (1995) have noted the similarities between

M. cylindricus and *M. siruguei*, although the Indian oospecies is sometimes thicker. *M. cylindricus* is recorded from five localities, and the eggshell thickness varies considerably from one locality to another: the thinnest eggshells are from Chui Hill (1.70–2.10 mm; Jabalpur, Madhya Pradesh), the thickest from Patbaba ridge (2.10–2.52 mm; Jabalpur, Madhya Pradesh); Dholiya (2.10–2.45 mm; District Dhar, Madhya Pradesh); Walpur (2.24–3.50 mm; District Jhabua, Madhya Pradesh); Balasinor (2.87–3.50 mm; Gujarat, Western India; Sahni et al., 1994; Khosla and Sahni, 1995; Khosla, 1996; Loyal et al., 1996). Thin sections of this oospecies from the different Indian localities, and comparisons with several thin sections of *M. siruguei*, allow detection of the microstructural variability, and show that there are at least two different oospecies among the material referred to *M. cylindricus*. Samples from the type locality, and from Patbaba ridge, Dholiya, Walpur and Rahioli (Gujarat) have the same nodal diameters. These nodes are smaller than in the samples from that of the other sites of Gujarat, particularly from Balasinor that belong to another oospecies, *M. khempurensis*.

M. cylindricus shows similarities with *M. siruguei* as seen above, and also with *M. microtuberculata* (Garcia, 1998; Garcia and Vianey-Liaud, 2001a). The last is found in La Cairanne, in levels underlying those with *M. siruguei*. Both show the same shape of elongated and slender fan-shaped units and the same ''reticulate'' pattern of the pore canals (straight canals, not always crossing the whole eggshell thickness, linked by oblique or tranverse bridges). They differ by the smaller size of *M. microtuberculata* eggs (up to 160 mm only), and the smaller diameters of shell units (0.19 to 0.6, average 0.3 mm).

So, owing to the size of eggs and for the width of units, *M. cylindricus* is intermediate between *microtuberculata* and *siruguei*. The reticulate pattern of the pore canals is not observed in *M. cylindricus*. For these reasons, we cannot synonymize *cylindricus* with one of these two French oospecies, even if their microstructural patterns display similarities.

Megaloolithus mohabeyi Khosla and Sahni, 1995:91, pl. I, fig. 8, fig. 5.

Megaloolithus phensaniensis Mohabey, 1998:349–351, figs. 3B, 5A–F (Type locality: Phensani, Gujarat, India).

Type Locality—Dholiya (Madhya Pradesh, India).

Megaloolithus phensaniensis is considered as a junior synonym of *M. mohabeyi* because both oospecies have the same egg diameters, the same eggshell thickness and show similar macro- and microstructural. These characteristics include single nodes of variable sizes on the outer surface and fan-shaped units (i.e., the units widen from the basal cap to the top), with highly arched growth lines Fig. 1. Thirty eggshell fragments of *M. mohabeyi* from Dholiya (District Dhar, Madhya Pradesh) are characterized by shell units with arched roofs and growth lines that show remarkable variability in the degree of convexity. The node diameters are variable, ranging from 0.28–0.76 mm (n = 33; average = 0.5 mm).

Better preserved eggs and eggshell fragments of *M. mohabeyi* have been collected from Balasinor, Rojhav, Phenasani Lake and Waniawao Quarry in Gujarat (Mohabey, 1991). The eggshell of these crushed, spherical eggs (160–190 mm in diameter) is comparable in thickness (1.65–1.90 mm) to those eggshells from Dholiya (1.80–1.90 mm). Eggshells of *M. mohabeyi* were found in the same place with those of *M. cylindricus*, indicating that at least two dinosaurs were laying eggs in the same area.

Megaloolithus padiyalensis Khosla and Sahni, 1995:93–94, pl. IV, figs. 5–6, fig. 5.

Type Locality—Padiyal (Madhya Pradesh, India).

This oospecies has been reported from the Lameta Formation of Padiyal (District Dhar, Madhya Pradesh) and is represented by few eggshell specimens. The eggshells display microstructural characteristics similar to those of *M. mohabeyi*, but the shell units are thinner, generally more slender, and are often fused together in *M. padiyalensis*. The shell units diplay various lengths and widths and are often fused laterally. The basal caps are generally eroded, and the pore canals somewhat enlarged by recrystallizations. Pore canals sometimes appear interrupted, and some are oblique, that let us suppose a possible ''reticulate'' pattern as in *M. siruguei* and *M. microtuberculata* (Vianey-Liaud and Garcia, 2000).

In comparison to French eggshell oospecies *M. microtuberculata*, *M. padiyalensis* has thinner shell units (Fig. 3). So far, *M. padiyalensis* is known only by fragmentary eggshells, whereas *M. microtuberculata* by complete, spherical eggs (160 mm in diameter).

Megaloolithus jabalpurensis Khosla and Sahni, 1995:90–91, pl. I, fig. 7; pl. II, figs. 1–4, fig. 5.

Megaloolithus matleyi Mohabey, 1996:188–191, figs. 4–7. (Type locality: Pavna, Chandrapur District).

? *Megaloolithus patagonicus* Calvo et al., 1997:27–30, figs. 5–8 (Type locality Neuquen Group, Patagonia, Argentina).

Megaloolithus matleyi, Mohabey, 1998:352–353, figs. 3E, 6D–G. (Type locality: Pavna, Chandrapur District).

Type Locality—Bara Simla Hill, Jabalpur (Madhya Pradesh, India).

M. matleyi, and less likely *M. patagonicus*, are considered junior synonyms of *M. jabalpurensis*, because all three oospecies show similar microstructural characteristics, such as short fan-shaped shell units. The eggshell thickness is 1.00–2.00 mm and the nodal diameter is up to 1 mm.

M. jabalpurensis was described from Bara Simla Hill (Jabalpur, Madhya Pradesh). Additional specimens were previously described by Tripathi (1986) and Vianey-Liaud et al. (1987), and also under the name Titanosaurid Type-II(?) by Sahni (1993), Sahni et al. (1994), and Tandon et al. (1995) from the Lameta Formation (Maastrichtian) of Jabalpur. Recently, three crushed, fragmented, but nearly complete, silicified eggs (140–160 mm in diameter) have been found at Padalya, District Dhar in Madhya Pradesh. Previously, complete eggs (140–160 mm in diameter; eggshell 1.0–1.5 mm thick) were also collected from the Waniawao near Dohad in Panchmahal District, Gujarat (Mohabey and Mathur, 1989).

The mega- and microstructural characteristics (Fig. 4) of this oospecies is nearly identical to those described as *M. matleyi* (Mohabey, 1996, 1998) found in Pavna (Chandrapur District, Maharashtra) and Pat baba Ridge (Jabalpur). *M. jabalpurensis* (1.00–2.38 mm) from Jabalpur (Madhya Pradesh), Dholiya, Padiyal and Borkul (District Dhar, Madhya Pradesh), is thinner than *M. cylindricus* (1.70–3.50 mm), and displays fan-shaped units of variable shapes and width. As noted by Mohabey (1998), the generally wide fan-shaped units of *M. jabalpurensis* are similar to those of *M. mamillare* from southern France and northern Spain. Their node diameters are up to 1 mm, whereas in European oospecies they can reach 1.4 mm. The main difference between these oospecies is the diameter of the eggs, clearly smaller in *M. jabalpurensis* (140–160 mm) than in french *M. mamillare* (190–230 mm).

More recently, Calvo et al. (1997) described parataxon *M. patagonicus* known from Upper Cretaceous (Coniacian–Santonian) Neuquen Group (Patagonia, Argentina). *M. jabalpurensis* is similar to the oospecies *M. patagonicus* in egg shape and size, eggshell thickness, external ornamentation, nodal diameter, pattern of growth lines, pore system etc. We tentatively synonymize them.

Megaloolithus dholiyaensis Khosla and Sahni, 1995:92–93, pl. III, figs. 2–3, fig. 5.

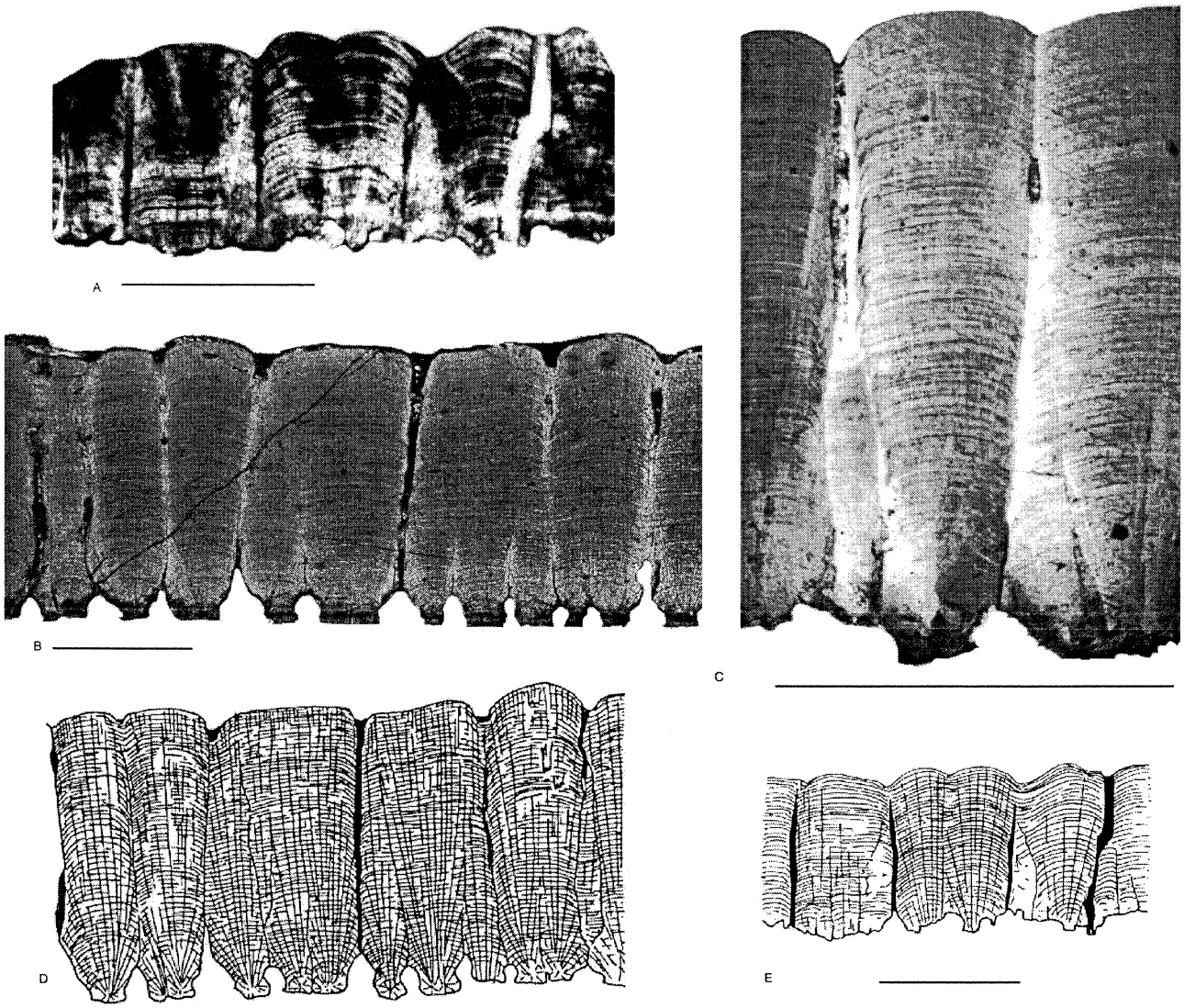


FIGURE 4. Comparisons between *Megaloolithus dholiyensis* (Dholiya, India) (**A**, **E**) and *Cairanoolithus dughii* (La Cairanne, France) (**B**, **C**, **D**). Same enlargement for D and E only. Scale equals 1 mm.

Type Locality—Dholyia (Madhya Pradesh, India).

M. dholiyaensis has been reported from the Lameta Formation of Dholiya (District Dhar, Madhya Pradesh) and is represented by a few eggshell specimens. The shell thickness lies within the range of *M. jabalpurensis*, the microstructure, however, differs in having both cylindrical and fan-shaped units that are mostly multinodose and fused together. The growth lines are horizontal, subhorizontal or slightly arched. The pore canals are straight. All these characters are similar to French oogenus *Cairanoolithus* (Fig. 4). But they differ by the arched growth lines under the well developed nodes. In *Cairanoolithus*, when the nodes exist, they are generally flattened, and the growth lines horizontal. A few nodes may be rounded.

Megaloolithus dhoridungriensis Mohabey, 1998:352, fig. 6A–C.

Type Locality—Dhoridungri (Madhya Pradesh, India).

This oospecies differs from the other oospecies described by Khosla and Sahni (1995), in their fan-shaped units with highly arched growth lines. The shape of the units, called ''conical'' by Mohabey (1998) (i.e., fan-shaped) is not significantly different of that of *M. jabalpurensis* in this respect. The primary differences are the larger size of the units (but keeping the same ratio H/W), and the more highly arched growth lines. Some specimens from Dholiya, determined first by Khosla and Sahni (1995) as *M. jabalpurensis*, may be *M. dhoridungriensis*. (Khosla and Sahni, 1995:plate I, fig. 7, p. 99) because they display these differences.

Megaloolithus khempurensis Mohabey, 1998:351–352, fig. 5G–K.
Megaloolithus walpurensis Khosla and Sahni, 1995:93, pl. IV, figs. 1–4, fig. 5 (Type locality: Walpur).

Type Locality—Khempur (Gujarat, India).

Megaloolithus khempurensis, discovered in Khempur and Werasa (Kheda district, Gujarat), shows similar microstructural characteristics with *M. siruguei*. Both are represented by large, spherical eggs (diameter 170–200 mm for *M. khempurensis* and 190–210 mm for *M. siruguei*). Eggshell fragments collected from La Bégude and Rousset-Village (France) by Vianey-Liaud et al. (1994) are 2.33–2.68 mm, similar to the thickness of eggshell fragments of the Indian oospecies *M. khempurensis* (2.36–2.60 mm). The average nodal diameter of *M. siruguei* is 0.65–0.70 mm, which is more or less similar to that of the Indian oospecies *M. khempurensis* (0.60–0.80 mm). The pore diameter in *M. siruguei* is 50–80 μm whereas in *M. khempurensis* it is

50–90 μm. Despite these similarities, one microstructural difference can be noticed. In *M. khempurensis*, the basal part of the units show a unique and big basal cap, when they are not damaged, whereas in *M. siruguei* they are clearly smaller, and sometimes twin-spherulitic. Thus, the unit shape is elongated fan-shaped in *M. siruguei* and nearly cylindrical in *M. khempurensis*.

Microstructurally, the Indian oospecies closest to the French *M. siruguei* is probably *M. khempurensis* (Mohabey, 1998). But, we choose to keep the validity of both oospecies because of the clear size difference of the basal caps and shape of the shell units.

M. khempurensis resembles *M. megadermus* having thick shell and cylindrical shell units with broad basal caps and regularly arched growth lines. Measurements indicate that *M. khempurensis* is thinner than *M. megadermus* (2.36–2.60 mm) compared to 4.0–4.5 mm, although based on Mohabey's illustration (1998:fig. 5), the eggshell is more than 3 mm thick. Moreover, Mohabey gives a H/W ratio of 9.6 for *M. megadermus*, whereas it is 3.4 for *M. khempurensis*. Well-preserved specimens from Balasinor and Walpur, named *M. cylindricus* by Khosla and Sahni (1995), probably belong to *M. khempurensis*. Eggshells referred to *Megaloolithus walpurensis* are thick (3.50–3.60 mm), with shell units similar to those of *M. khempurensis* (H/W ratio about 3) (Fig. 3) but *M. walpurensis* was described from three fragments that are deeply corroded by silica, and whose inner surfaces are very badly preserved. Nethertheless, we tentatively suggest synonymy with *M. khempurensis*.

Megaloolithus megadermus Mohabey, 1998:353–357, figs. 3F, 7A–G.

Type Locality—Dholidanti (Gujarat, India).

The specimens of *Megaloolithus megadermus* are numerous, complete and well preserved. They are clearly recognizable by their thickness (4–5 mm) and greatly slender units (H/W = 9).

Recently, Khosla (work in progress) has recovered more than 30 eggshell fragments from Dholiya (District Dhar, Madhya Pradesh), that are more than 4.5 mm in thickness, closely resembling the specimens named *M. megadermus* by Mohabey. No French oospecies is as thick as *M. megadermus*.

Megaloolithus baghensis Khosla and Sahni, 1995:91–92, pl. II, figs. 5–8; pl. III, figs. 1, 5.

Type Locality—Bagh Caves (Madhya Pradesh, India).

?*Megaloolithus pseudomamillare* Vianey-Liaud et al., 1997:78–81, figs. 2–3 (Type locality: Les Bréguières).

Megaloolithus balasinorensis Mohabey, 1998:357–358, figs. 3G, 7H–K, 8A, B (Type locality: Balasinor).

Eggshells belonging to this oospecies are widely distributed in the intertrappean sequences including those of Anjar (District Kachchh, Bajpai et al., 1990; Khosla and Sahni, 1995); Nagpur (Vianey-Liaud et al., 1987; Sahni, 1993, (?)Titanosaurid Type-III; Sahni et al., 1984, 1994), and also in the Lameta Formation at Pisdura (Jain and Sahni, 1985). Complete spherical eggs (140–200 mm in diameter) have been recorded from the Lameta Formation at Balasinor Quarry in Kheda (Srivastava et al., 1986, Kheda Type-A; Mohabey, 1998, as *M. balasinorensis*). The eggshells described as ?Titanosaurid Type-III have also been recorded by Sahni et al. (1994) from these localities as well. The eggshells are characterized by short and broad fan-shaped units that are discrete, fused, mostly multinodose and exhibiting slight arched and near horizontal growth lines that follow the contour of the outer shell surface. *Megaloolithus baghensis* named by Khosla and Sahni (1995) and *M. balasinorensis* named by Mohabey (1998) have an identical microstructure and should be synonymized.

M. baghensis, from Bagh Caves (Khosla and Sahni, 1995) (=*M. balasinorensis* from Balasinor, Mohabey, 1998), shows many micro- and ultrastructural similarities with *M. pseudomamillare* (Vianey-Liaud et al., 1997), but the French egg is generally larger (190–210 mm), although some eggs from Balasinor reach 200 mm. The growth lines are prominent in the shell units, and are horizontal to subhorizontal in the multinodal shell units. The arch of the growth lines increases in the upper part of the shell units. The eggshell thickness varies from 1 to 2 mm. This peculiar microstructure led Vianey-Liaud et al. (1997) to identify eggshell fragments from Peru, Bolivia, and India (Takli and Pisdura) as *M. pseudomamillare* previously known from the Aix Basin, France. Therefore, *M. baghensis* Khosla and Sahni (1995) has publication prioty over *M. pseudomamillare* Vianey-Liaud et al., 1997. *M. balasinorensis* Mohabey, 1998 and, tentatively, *M. pseudomamillare* are considered junior synonyms of *M. baghensis*.

DISCUSSION

Comparisons between *Megaloolithus* oospecies described by Khosla and Sahni (1995), Mohabey (1998), with those described by Vianey-Liaud et al. (1994, 1997) and Garcia and Vianey-Liaud (2001a), demonstrate close similarities between four French and five Indian oospecies. The French oospecies *M. microtuberculata*, *M. mamillare*, *M. siruguei*, and *M. pseudomamillare* resemble the Indian oospecies, *M. cylindricus*, *M. padiyalensis*, *M. jabalpurensis*, *M. khempurensis*, and *M. baghensis* (Fig. 5). Some of the Indian and French megaloolithid oospecies are unique and have no equivalent in either country. This includes *M. mohabeyi*, *M. dholiyaensis*, *M. dhoridungriensis* and *M. megadermus* from India, and *M. aureliensis*, *M. petralta* and the oogenus *Cairanoolithus* from France.

Nine oospecies of the oogenus *Megaloolithus* are here recognized from the Cretaceous of India. These oospecies occur in discontinuous outcrops throughout the Narmada River region in India. They are restricted to a pedogenized sandy calcrete (Sahni and Khosla, 1994) that is believed to be synchronous, even if it remains uncertain, along more than 250 km of discontinuous exposures. In southern France, the diachronism of some continental Upper Cretaceous continental deposits has been demonstrated (Cojan, 1989; Bessière et al., 1980; Bilotte et al., 1983; Lepicard et al., 1985; Garcia and Vianey-Liaud, 2001b).

Eight megaloolithid oospecies have been described in France and Spain, six belonging to *Megaloolithus* and two to *Cairanoolithus*. The stratigraphical occurrence of these oospecies is well known (Fig. 5). If we compare the diversity of megaloolithid eggs in the upper Campanian/lower Maastrichtian of France (one oospecies of *Cairanoolithus* and at least three of *Megaloolithus*) with that of the contemporaneous dinosaur taxa (one species of Tyreophora; one or two species of Titanosauridae; one or two Ornithopoda including *Rhabdodon*—Buffetaut, 1989; Buffetaut and Loeuff, 1991; Pereda-Suberbiola, 1993; Garcia et al., 1999), it seems that the various megaloolithid oospecies cannot be all referred to the same taxon. Mikhailov (1994, 1997) has demonstrated that specific egg genera can be correlated with specific dinosaur families or suborders, therefore all *Megaloolithus* eggs would have been laid by the same family or suborder. Because the Argentinian megaloolithid egg (*M. Jabalpurensis*? = *M. patagonicus*) is known to have been laid by a titanosaurid, possibly *Saltosaurus* (Chiappe et al., 1998), similar Indian eggs, and closely related French eggs must have been laid by sauropods as well. However we consider it possible that the two different European oogenera *Megaloolithus* and *Cairanoolithus*, or even the different oospecies of *Megaloolithus*, may have been laid by different dinosaur taxa, both saurischians and ornithischians.

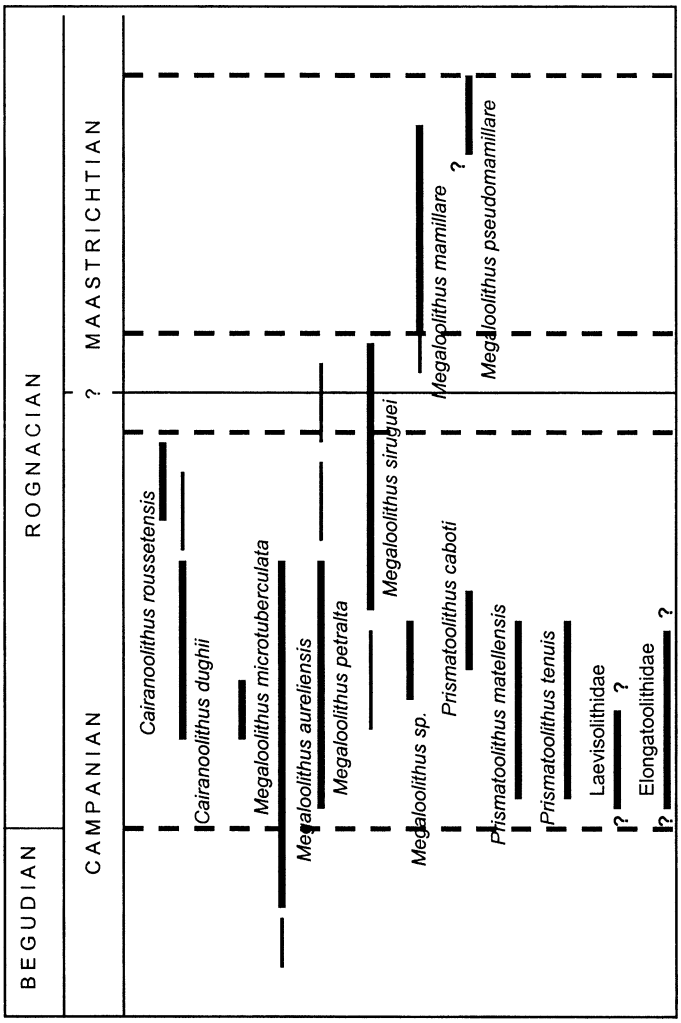


FIGURE 5. Stratigraphic distribution of oospecies in French localities.

As seen previously, the great number of *Megaloolithus* oospecies (nine or more) on the Indian subcontinent should imply a large diversity of dinosaur taxa. Presently, only three sauropod species and one thyreophoran appear to be valid (Hunt et al., 1994).

Only a few localities in India have yielded both eggs and eggshells, including Bara Simla Hill and PatBaba Ridge (Jabalpur, Madhya Pradesh). In the Lower Limestone, three *Megaloolithus* oospecies have been recorded (*M. baghensis*, *M. cylindricus*, and *M. jabalpurensis*) and only two or three sauropods (*Titanosaurus indicus*, *Titanosaurus* sp., and *Jainosaurus septentrionalis*) and one thyreophoran (*Lametasaurus indicus*). This record also supports the possibility that the oofamily Megaloolithidae may correspond to different types of dinosaur taxa.

In Africa, which may have formed a bridge between Europe and India during the Cretaceous, megaloolithid eggs are currently unknown, despite the presence of sauropod bones remains (Lapparent, 1960; Powell, 1986; Jacobs et al., 1993).

CONCLUSIONS

(1) Comparisons between the parataxonomic classifications proposed by different group of workers (i.e., Khosla and Sahni, 1995; Mohabey, 1998; Vianey-Liaud et al., 1994, 1997) on the Indian and French Cretaceous dinosaur eggshell show that there are close similarities between four groups of French and Indian *Megaloolithus* oospecies (*Megaloolithus microtuberculata*/*M. cylindricus*/*M. padiyalensis*; *M. mamillare*/*M. jabalpurensis*; *M. siruguei*/*M. khempurensis*; *M. pseudomamillare*/*M. baghensis*). Presently, Indian Late Cretaceous dinosaur eggshell oospecies are represented by nine distinct eggshell oospecies belonging to the oofamily Megaloolithidae (i.e., *Megaloolithus cylindricus* Khosla and Sahni, 1995, *M. mohabeyi* Khosla and Sahni, 1995, *M. padiyalensis* Khosla and Sahni, 1995, *M. jabalpurensis* Khosla and Sahni, 1995, *M. dholiyaensis* Khosla and Sahni, 1995, *M. dhoridungriensis* Mohabey, 1998, *M. khempurensis* Mohabey, 1998, *M. megadermus* Mohabey, 1998 and *M. baghensis* Khosla and Sahni, 1995).

(2) The co-occurrence of the oogenus *Megaloolithus* (Megaloolithidae) in southern Europe, India and South America, highlights the Gondwanian component of the Late Cretaceous European dinosaur faunas. Moreover, the close relationships of some of the French and Indian oospecies demonstrates a possible terrestrial connection between the southern European islands with Gondwanian lands, such as India in the Late Cretaceous.

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