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Earliest Laurasian sauropod eggshells

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Megaloolithid eggshells, known from many Cretaceous deposits since 19th century, are now recognized as remnants of sauropod dinosaurs. Our paper reports the discovery of megaloolithid egg remains from the Middle Jurassic (Bajocian) of the Quercy area (southwestern France). The new Jurassic ootaxon differs from related Cretaceous oospecies in having unusually thin shells. Even *Megaloolithus aureliensis*, the thinnest Cretaceous megaloolithid from France is three times thicker than the Jurassic eggshells. The cladistic analysis of ootaxa reveals a peculiar point in contradiction with the phylogenetic results based on skeletal remains: the Megaloolithidae belonged to sauropod dinosaurs, which appear to be the sister group of the hadrosaur eggs (Spheroolithidae oofamily). This result could indicate a significant amount of homoplasy in the evolution of eggshell structures, depending strongly on the incubation environment (particularly for some characters as ornamentation, pore openings and pore canals), the reproductive physiology and the oviduct function. The Bajocian eggshells might represent the earliest offshoot of the Megaloolithidae oofamily and represent the earliest sauropod eggshell record known from the deposits of Laurasia supercontinent.

Key words: Sauropoda, fossil eggs, megaloolithid eggshells, Bajocian, Quercy.

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Introduction

Most dinosaur eggs and eggshells have been found in Cretaceous deposits (Hirsch 1989; Mikhailov 1997). In Laurasia, the oldest egg material is Upper Jurassic in age: Kimmeridgian from the Morrison Formation, Colorado (USA) and also Kimmeridgian–Tithonian from Portugal (Hirsch 1994; Turner and Peterson 2004; Mateus et al. 1997). It represents a typical prismatic morphotype (Prismatoolithidae). The discoveries of embryos inside eggs have shed new light on prismatoolithid assignment, which are now regarded as laid by theropod dinosaurs, like *Troodon formosus* in North America (Horner and Weishampel 1996) and also allosaurids in Portugal (Mateus et al. 1997). In Gondwana, the earliest fossil eggshells, probably of crocodiles (Carpenter 1999), have been reported from the Upper Triassic of Argentina (Bonaparte and Vicente 1979).

During the Jurassic, more than 80% of dinosaur genera have been recorded in Laurasia, but only two basic types of dinosaur eggshells are known from the area. In order to explain the discrepancy between the egg and dinosaurian fossil records, some authors have speculated that Jurassic and older dinosaurian eggs were not rigid- but soft-shelled, as mainly the hard eggshells had chances to be fossilized (Penner 1985;

Bray and Hirsch 1998). In addition, environmental conditions might have contributed to the absence of dinosaur eggs in the Upper Triassic and Jurassic sediments. There are few exposures of continental deposits and even fewer floodplain deposits, being favorable paleoenvironments for nesting of some dinosaur groups, and for their fossilization.

Institutional abbreviation.—UM2-LBA, Laboratory of Paleontology, University of Montpellier II, France.

Material and methods

The Bajocian eggshells (about 170 Ma) described herein, have been obtained by screen-washing deposits from La Balme locality (Quercy area, southwestern France), composed of lignitic marls interbedded with marine limestones (Cajarc Formation; Cubaynes et al. 1989). The eggshells are calcitic and partially recrystallized (Fig. 1), and were found associated with numerous small fossil remains including crocodylians, turtles, squamates, fishes, charophytes (Porocharacea), and gastropods. We have used scanning electron microscope (SEM) and cathodoluminescence method for studying radial sections and outer surfaces.

In the cladistic analysis, all the selected characters are equally weighted. The multistate characters were considered as ordered if changes from one state to another required passing through intermediate states (Slowinski 1993). With such an *ad hoc* assumption, character state assignments do not convey *a priori* judgments about character polarity (unconstrained parsimony). Characters are polarized via the out-group comparison method (Watrous and Wheeler 1981).

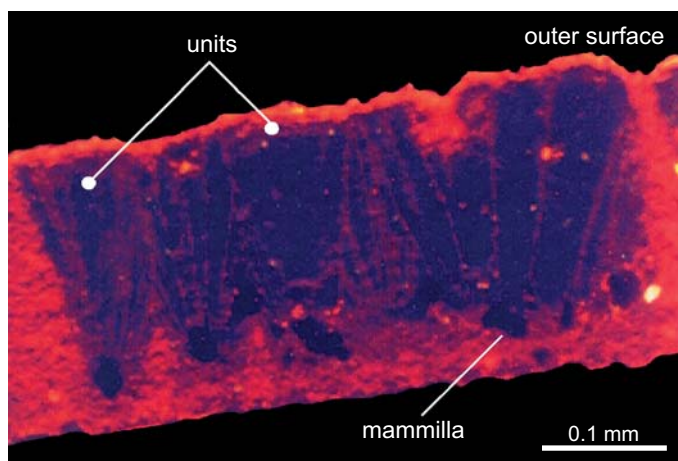


Fig. 1. UM2-LBA 1. Thin section of Bajocian eggshell analyzed with cathodoluminescence. La Balme, Cajarc Formation, Quercy Limestones, France.

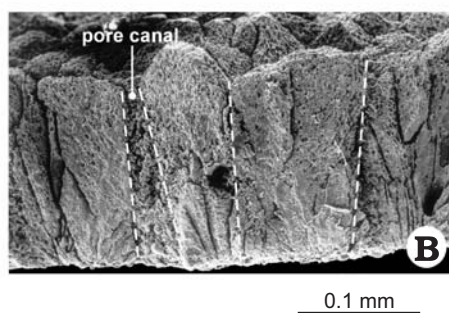
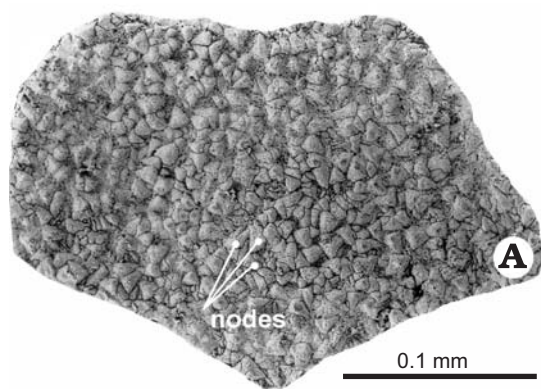


Fig. 2. UM2-LBA 2. Bajocian megaloolithid eggshells. A. SEM, outer ornamentation showing tightly packed nodes. B. SEM, radial view, note discretispherulitic shell units. La Balme, Cajarc Formation, Quercy Limestones, France.

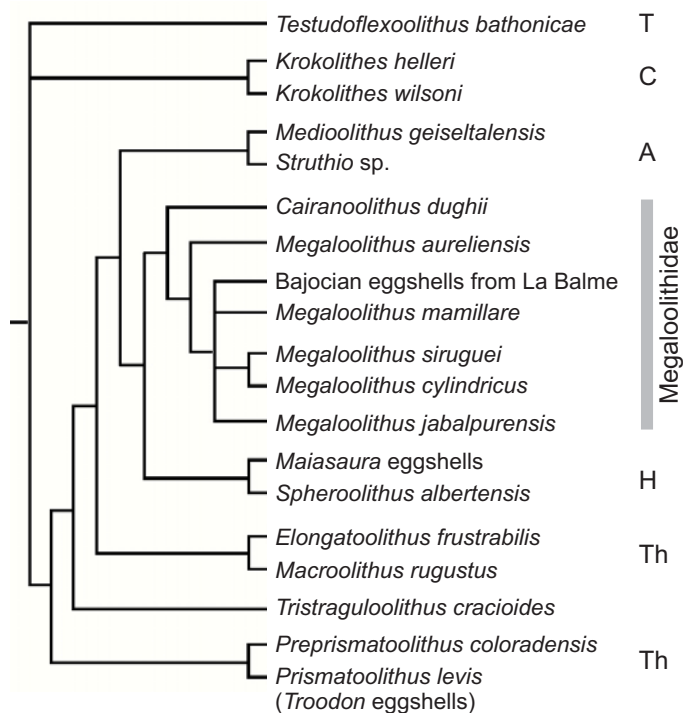


Fig. 3. Strict consensus of 10 equally most parsimonious trees, based on the analysis of 27 eggshell selected characters (see Appendix 1). *Testudoflexoolithus* and *Krokolithes* eggshells have been selected for an outgroup comparison. Each tree has a length of 60 steps, a Consistency Index (CI) of 0.583 and a Retention Index (RI) of 0.788. Phylogenetic reconstructions were performed by PAUP 3.1.1 (Swofford 1993). Heuristic searches using stepwise addition and a randomized input order of taxa (100 replications) have been executed. No differential character weights were used. Selected characters and data matrix are given in the Appendix 1. T, turtle; C, crocodile; A, avian; H, hadrosaur; Th, theropod. The cladistic analysis (see Table 2) is based on the analysis of 27 selected eggshell characters after Mikhailov (1997). This analysis supports a theropod dinosaur origin for birds, already demonstrated by Zeleznitsky (2004) and Varrichio and Jackson (2004).

Parataxonomy

Morphotype Discretispherulitic Mikhailov, Bray, and Hirsch, 1996

Oofamily Megaloolithidae Zhao, 1975 (emend. 1979)

Oogenus *Megaloolithus* Vianey-Liaud, Mallan, Buscail, and Montgelard, 1994

Megaloolithus sp.

Material examined.—About 10 eggshell fragments from the site of La Balme in the Quercy Limestones (central and southern France) (UM2-LBA 1–10).

Referred specimens.—UM2-LBA 1 and UM2-LBA 2.

Description.—The outer surface of eggshells is nodose with nodes tightly packed (Fig. 2A). The pore system is tubocanaliculate with canals of 60 μ m in average diameter. On the outer surface, the nodes are prominent like in *Megaloolithus siruguei*, a megaloolithid from southern Europe (Gar-

Table 1. Taxa used for the cladistic analysis.

Oofamilies	Age	Localization	References
Testudoflexoolithidae			
<i>Testudoflexoolithus bathonicae</i>	Upper Jurassic	Hare Bushea Quarry (England)	Hirsch 1996
Krokolithidae			
<i>Krokolithes helleri</i>	Middle-Upper Eocene	Geiseltal Quarry (Germany)	Kohring and Hirsch 1996
<i>Krokolithes wilsoni</i>	Middle-Upper Eocene	De Beque Formation (Colorado, USA)	Kohring and Hirsch 1996
Ostrich eggshell			
<i>Struthio</i> sp.	Recent	Chad	
Incertae sedis			
<i>Tristraguloolithus cracioides</i>	Upper Cretaceous	Oldman Formation (Alberta, Canada)	Zeletnisky et al. 1996
Palaeognathus eggshell			
<i>Medioolithus geiseltalensis</i>	Middle Eocene	Geiseltal Quarry (Germany)	Kohring and Hirsch 1996
Prismatoolithidae			
<i>Preprismatoolithus coloradensis</i>	Upper Jurassic	Morrison Formation (Colorado, USA)	Hirsch 1994
<i>Prismatoolithus levis</i>	Upper Cretaceous	Oldman Formation (Alberta, Canada)	Zeletnisky and Hills 1997
Elongatoolithidae			
<i>Elongatoolithus frustrabilis</i>	Upper Cretaceous	Djadokhta Formation (Mongolia)	Mikhailov 1994
<i>Macroolithus rugustus</i>	Upper Cretaceous	Guangdong Province (China)	Mikhailov 1994
Spheroolithidae			
<i>Maiasaura</i> eggshells	Upper Cretaceous	Two Medicine Formation (Montana, USA)	Hirsch and Quinn 1990
<i>Spheroolithus albertensis</i>	Upper Cretaceous	Oldman Formation (Alberta, Canada)	Zeletnisky and Hills 1996
Megaloolithidae			
<i>Cairanoolithus dughii</i>	Upper Cretaceous	Aix Basin (Bouches du Rhône, France)	Vianey-Liaud et al. 1994, emended Garcia and Vianey-Liaud 2001a
<i>Megaloolithus aureliensis</i>	Upper Cretaceous	Aix Basin (Bouches du Rhône, France)	Vianey-Liaud et al. 1994, emended Garcia and Vianey-Liaud 2001a
<i>Megaloolithus mamillare</i>	Upper Cretaceous	Aix Basin (Bouches du Rhône, France)	Vianey-Liaud et al. 1994, emended Garcia and Vianey-Liaud 2001a
<i>Megaloolithus siruguei</i>	Upper Cretaceous	Aix Basin (Bouches du Rhône, France)	Vianey-Liaud et al. 1994, emended Garcia and Vianey-Liaud 2001a
<i>Megaloolithus cylindricus</i>	Upper Cretaceous	Lameta Formation (India)	Khosla and Sahni 1995
<i>Megaloolithus jabalpurensis</i>	Upper Cretaceous	Lameta Formation (India)	Khosla and Sahni 1995
Bajocian eggshells from La Balme	Middle Jurassic	Cajarc Formation (Quercy, France)	This paper

cia and Vianey-Liaud 2001a). The inner surface displays some mammillae coalescing into ridges. The radial section shows sharply separated units with fan-like pattern of thin wedges (Fig. 2B). The accretion lines, mainly seen at the bottom of some units, are semi-concentric like in the genus *Megaloolithus*, a Gondwanan ootaxon (Vianey-Liaud et al. 1997). The shell thickness varies between 0.15 and 0.25 mm.

Discussion and conclusion

All these aforementioned characters are consistent with the discretispherulitic morphotype described as typical for the Megaloolithidae (Mikhailov 1997). The derived features described above set clearly the new ootaxa apart (Fig. 3) from

Spheroolithidae (hadrosaurs), Elongatoolithidae and Prismatoolithidae (theropods), avian eggshells (*Struthio* and *Palaeognathus*), Krokolithidae (crocodiles) and Testudoflexoolithidae (turtles) (Appendix 1), but consistently point toward megaloolithid affinities. Nevertheless, the cladistic analysis of ootaxa reveals a peculiar point in contradiction with the phylogenetic results based on skeletal remains (see, e.g., Sereno 1999): the Megaloolithidae belonging to sauropod dinosaurs appear to be the sister group of the hadrosaur eggs (oofamily Spheroolithidae). This result could indicate a significant amount of homoplasy in the evolution of these eggshell structures, depending strongly of the incubation environment (particularly for some characters such as ornamentation, pore openings and pore canals), the reproductive physiology and the oviduct function. Moreover, this analysis

Table 2. Taxon-character matrix. Scores of characters: 0, 1, 2, 3, ordered; ?, incomplete or unknown; –, absent.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Testudoflexoolithus bathonicae</i>	0	1	0	–	0	0	0	–	–	–	–	0	1	0	0	1	0	0	?	?	0	0	1	1	?	0	0
<i>Krokolithes helleri</i>	1	0	0	–	0	0	0	–	–	–	–	0	0	0	0	1	0	0	0	0	0	0	1	1	?	1	2
<i>Krokolithes wilsoni</i>	1	0	0	–	0	0	0	–	–	–	–	0	0	0	0	1	0	0	0	0	0	0	1	1	?	1	2
<i>Struthio</i> sp.	1	1	1	0	2	0	0	–	–	–	–	0	3	1	1	0	1	1	?	1	0	1	1	1	1	–	–
<i>Tristragaloolithus cracioides</i>	1	1	1	0	0	0	2	?	0	?	?	0	3	1	1	0	1	0	0	0	0	0	?	?	?	–	–
<i>Medioolithus geiseltalensis</i>	1	1	1	0	0	0	0	–	–	–	–	0	3	1	1	0	1	1	1	1	0	1	0	0	0	–	–
<i>Preprismatoolithus coloradensis</i>	1	1	0	1	0	0	1	0	1	–	?	0	3	0	0	1	1	0	1	0	1	0	1	2	1	0	2
<i>Prismatoolithus levis</i>	1	1	0	1	0	0	0	1	–	–	–	0	3	0	0	1	1	0	1	0	0	0	1	2	1	0	2
<i>Elongatoolithus frustrabilis</i>	1	1	0	0	1	1	2	1	2	0	0	0	3	1	1	1	1	0	0	0	0	0	1	2	0	0	2
<i>Macroolithus rugustus</i>	1	1	0	0	1	1	2	0	2	0	0	0	3	1	1	1	1	0	0	0	0	0	1	2	0	0	2
<i>Maiasaura</i> eggshells	1	1	0	–	1	0	2	0	2	?	1	1	2	1	0	1	1	1	1	1	0	1	1	1	?	0	1
<i>Spheroolithus albertensis</i>	1	1	0	–	1	0	2	0	2	1	1	1	2	1	0	1	1	1	1	1	0	1	?	?	?	0	1
<i>Cairanoolithus dughii</i>	1	1	0	–	1	0	1	0	0	?	0	2	2	1	0	1	0	0	1	0	0	?	0	0	0	0	1
<i>Megaloolithus aureliensis</i>	1	1	0	–	1	0	2	0	0	1	0	1	2	0	0	1	0	0	1	1	0	1	0	0	0	0	0
<i>Megaloolithus mamillare</i>	1	1	0	–	1	0	2	0	0	1	0	1	2	0	0	1	0	0	1	1	0	1	0	0	0	0	0
<i>Megaloolithus siruguei</i>	1	1	0	–	2	0	2	0	0	1	0	1	2	0	0	1	0	0	1	1	0	1	0	0	0	0	0
<i>Megaloolithus cylindricus</i>	1	1	0	–	1	0	2	0	0	1	0	1	2	0	0	1	1	0	1	1	0	1	0	0	0	0	0
<i>Megaloolithus jabalpurensis</i>	1	1	0	–	2	0	2	0	0	1	0	1	2	0	0	1	0	0	1	?	0	?	0	0	0	0	0
Bajocian eggshells from La Balme	1	1	0	–	0	?	2	?	0	0	?	1	2	0	0	1	0	0	1	1	0	1	?	?	?	1	0

based only on eggshell features, which has allowed to differentiate specific systematic level such as the clades of Crocodylia, Theropoda, Sauropoda, was limited to discern larger scale relationships, especially among hadrosaur and sauropod examples.

The Megaloolithidae comprise eight described oospecies from the Upper Cretaceous of Southern France. This important diversity, representing 58% of identified ootaxa, makes them the most abundant eggshell type occurring with a widespread distribution by the end of the Mesozoic era (Garcia and Vianey-Liaud 2001b). The new Jurassic material mainly differs from related Cretaceous oospecies in having an unusually thin shells. Even *Megaloolithus aureliensis*, the thinnest Cretaceous megaloolithid from France (Vianey-Liaud et al. 1994), is three times thicker than the Jurassic eggshells. It follows that the Megaloolithidae are the oldest Mesozoic oofamily known. The Bajocian eggshells might actually represent the earliest offshoot of this oofamily. Once initialized, the elaboration process of the discretispherulitic eggshells has been going on for more than 100 Ma, illustrating the close relationships between the Jurassic and Cretaceous egg producing animals. Taking into consideration the monophyly of Megaloolithidae, it might be expected that this oofamily testifies to close phylogenetic relationships between some related dinosaur families showing similar eggshell pattern. The same is true for some recent birds (Mikhailov 1997; Zeleznitsky and Hirsch 1997), in which several families lay eggs belonging to a single oofamily. The recent

discovery in Argentina of embryonic remains related to titanosaurs (sauropods) inside typical discretispherulitic eggs (Chiappe et al. 1998, 2001; Grellet-Tinner et al. 2004; Salgado et al. 2005) confirmed that megaloolithids are probably associated with sauropods. In that context, the Jurassic Laurasian neosauropods such as brachiosaurids, camarasaurids, and diplodocoids, could be the potential parental candidates for the newly found material from La Balme. After the prosauropod extinction (Hettangian/Sinemurian), neosauropods diversified rapidly to become the dominant large-bodied herbivores from the Middle to Late Jurassic ecosystems. However, sauropods North of the Tethys, contemporaneous with the La Balme vertebrates, are poorly documented in France. Only some indeterminate sauropod remains have been recovered from Bathonian to Kimmeridgian localities (Weishampel 1990; McIntosh 1990). If the parental research (association between the animals and their eggs) is extended to the Middle Jurassic sites paleogeographically close to the Quercy (such as Great Britain), several families might be looked for as candidates. In this area, numerous localities have yielded fossil bones of three sauropod taxa (Cetiosauridae, Diplodocidae, and Brachiosauridae, Weishampel 1990; Day et al. 2002; Upchurch and Martin 2003). Of these families, the Brachiosauridae, of still debatable monophyly (Salgado and Calvo 1997; Wedel et al. 2000) and which are basal Titanosauriformes (Wilson and Sereno 1998; Wilson 2002), could have laid the Bajocian megaloolithid eggs.

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Appendix 1

Character description

Data were processed with Mac Clade 3.04 (Maddison and Maddison 1992). Heuristic searches using stepwise addition and a randomized input order of taxa (100 replications) have been performed. No differential character weight was used; ord, ordered character states; unord, unordered character states.

1. Eggshell nature (unord): 0, aragonite; 1, calcite.
2. Organic core (ord): 0, present; 1, absent.
3. Outer layer (ord): 0, absent; 1, present.
4. Ratio between continuous or prismatic and mammillary layers (ord): 0, less of 4:1; 1, more of 4:1.
5. Eggshell thickness (ord): 0, $X < 1$ mm; 1, $1 < X < 2$ mm; 2, $X > 2$ mm.
6. Thickness according to the egg region (unord): 0, homogeneous; 1, variable.
7. Outer surface ornamentation (ord): 0, smooth; 1, irregular; 2, well sculptured.
8. Ornamentation according to the egg region (unord): 0, homogeneous; 1, variable.
9. Ornamentation type (unord): 0, nodes; 1, ridges; 2, both ridges and nodes like the linearituberculate and sagenotuberculate types.
10. Node size (unord): 0, > 0.3 mm; 1, < 0.3 mm.
11. Orientation of the ornamentation (unord): 0, absent; 1, along the long axis of the egg.
12. Mammillae (inner surface) (ord): 0, separated; 1, sometimes interlocking; 2, often interlocking.
13. Unit shape (unord): 0, in wedges; 1, testutoid; 2, spherulitic; 3, ornithoid.
14. Fusion of the units (ord): 0, absent; 1, present.
15. Layers (ord): 0, one; 1, two.
16. Accretion lines (ord): 0, absent; 1, present.
17. Oval/round pore openings (unord): 0, absent; 1, present.
18. Irregular shape of the pore openings/round pore openings (unord): 0, absent; 1, present.
19. Arrangement of the pore openings (unord): 0, isolated; 1, with organized pores (in chain or in circle or grouped).
20. Diameter of the pore canals (unord): 0, regular; 1, irregular.
21. Pore canals (unord): 0, straight; 1, oblique.
22. Pore ramification (ord): 0, absent; 1, present.
23. Section in the equatorial part of the egg (unord): 0, circular or sub-circular; 1, oval.
24. Elongation of the egg (unord): 0, length equal to the equatorial section; 1, longer than the equatorial section; 2, more than twice longer than the equatorial section.
25. Ends of the egg (unord): 0, equal in shape; 1, one end more pointed.
26. Presence of growth lines (ord): 0, throughout the eggshell thickness; 1, only in the part of the eggshell.
27. Shape of the growth lines (ord): 0, semi-concentric; 1, sinuous (undulating); 2, horizontal.