

# Earliest Laurasian sauropod eggshells

GERALDINE GARCIA, LAURENT MARIVAUX, THIERRY PÉLISSIE,  
and MONIQUE VIANEY-LIAUD



Garcia, G., Marivaux, L., Péliissié, T., and Vianey-Liaud, M. 2006. Earliest Laurasian sauropod eggshells. *Acta Palaeontologica Polonica* 51 (1): 99–104.

Megaloolithid eggshells, known from many Cretaceous deposits since 19<sup>th</sup> 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.

Géraldine Garcia [geraldine.garcia@univ-poitiers.fr], Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Faculté des Sciences Fondamentales et Appliquées, Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers cedex, France;

Laurent Marivaux [marivaux@isem.univ-montp2.fr] and Monique Vianey-Liaud [movianey@isem.univ-montp2.fr], Laboratoire de Paléontologie, Institut des Sciences de l'Evolution, cc 064, Université Montpellier II, Place E. Bataillon, 34095 Montpellier cedex 05, France;

Thierry Péliissié [Thierry.PELISSIE@wanadoo.fr], Association "Les phosphatières du Quercy", La Caminade, 46230 Bach, France.

## 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).

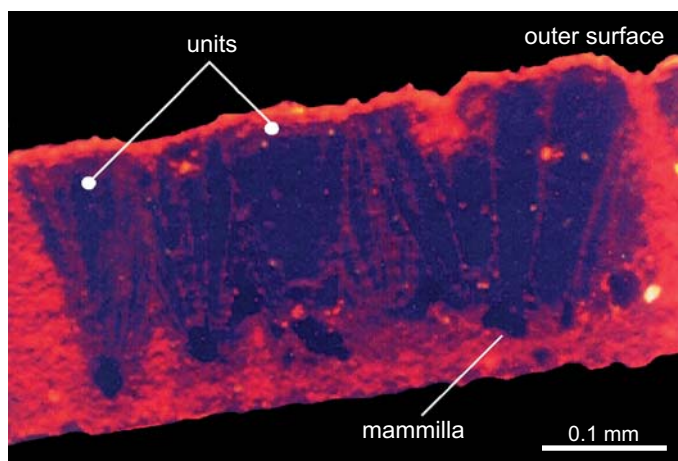


Fig. 1. UM2-LBA 1. Thin section of Bajocian eggshell analyzed with cathodoluminescence. La Balme, Cajarc Formation, Quercy Limestones, France.

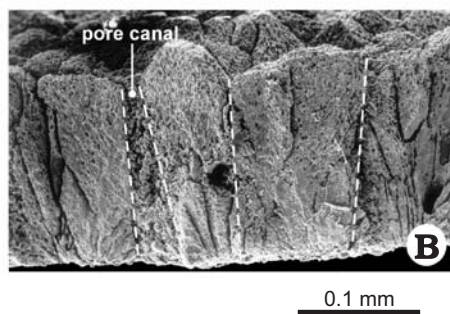
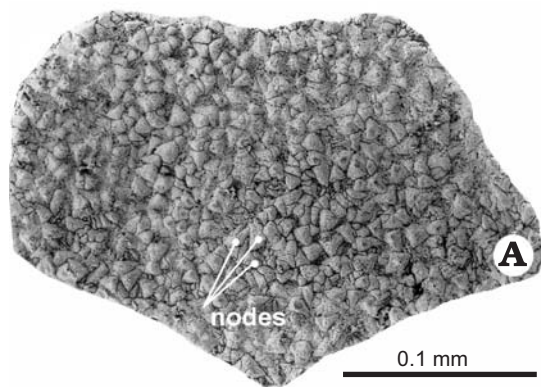


Fig. 2. UM2-LBA 2. Bajocian megaloolithid eggshells. A. SEM, outer ornamentation showing tightly packed nodes. B. SEM, radial view, note discretispherulitic shell units. La Balme, Cajarc Formation, Quercy Limestones, France.

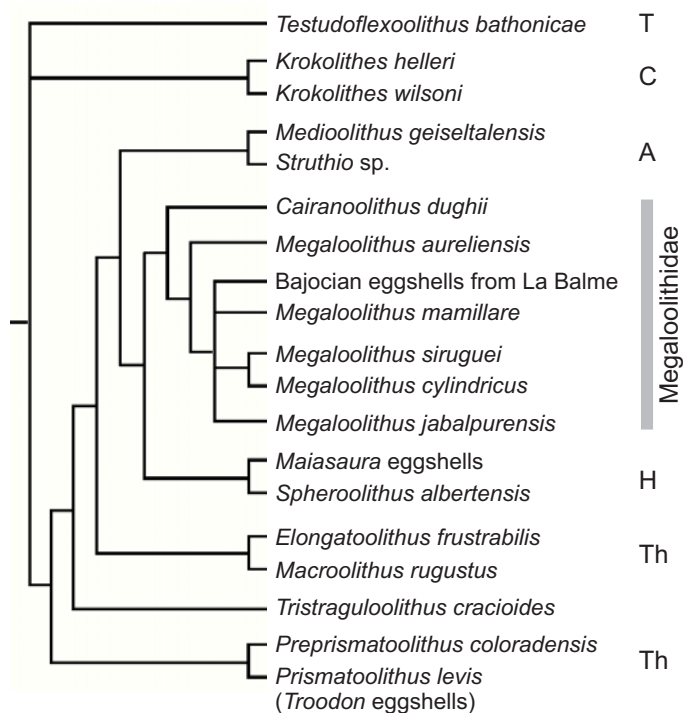


Fig. 3. Strict consensus of 10 equally most parsimonious trees, based on the analysis of 27 eggshell selected characters (see Appendix 1). *Testudoflexoolithus* and *Krokolithes* eggshells have been selected for an outgroup comparison. Each tree has a length of 60 steps, a Consistency Index (CI) of 0.583 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 tubo-canalliculate with canals of 60  $\mu$ 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>Tristraguloolithus 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.



## Acknowledgments

We thank Bernard Marandat and Jean-Jacques Jaeger (both from Institut des Sciences de l'Evolution, University of Montpellier II) for their field assistance, and Vincent Barbin (University of Reims) for his help in the eggshell cathodoluminescence analysis. Kenneth Carpenter (Denver Museum of Nature & Science, Denver) and Xabier Pereda-Suberbiola (University Del Pais Vasco, Bilbao) kindly reviewed the manuscript and made useful comments.

## References

- Bonaparte, J.F. and Vicente, M. 1979. El hallazgo del primer nido de dinosaurios Triasicos (Saurischia, Prosauropoda), Triasico Superior de Patagonia, Argentina. *Ameghiana* 16: 173–182.
- Bray, E. and Hirsch, K.F. 1998. Eggshell from the Upper Jurassic Morrison Formation. *Modern Geology* 23: 219–240.
- Carpenter, K. 1999. *Eggs, Nests and Baby Dinosaurs*. 336 pp. Indiana University Press, Bloomington.
- Chiappe, L.M., Coria, R.A., Dingus, L., Jackson, F., Chinsamy, A., and Fox, M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* 396: 258–261.
- Chiappe, L.M., Salgado, L., and Coria, R.A. 2001. Embryonic skulls of titanosaur sauropods dinosaurs. *Science* 293: 2444–2446.
- Cubaynes, R., Faure, P., Hantzpergue, P., Pélissié, P., and Rey, J. 1989. Le Jurassique du Quercy: unités lithostratigraphiques, stratigraphie et organisation séquentielle, évolution sédimentaire. *Géologie de la France* 3: 33–62.
- Day, J.J., Upchurch, P., Norman, D.B., Gale A.S., and Powell, H.P. 2002. Sauropod trackways, evolution and behaviour. *Science* 296: 1659.
- Garcia, G. and Vianey-Liaud, M. 2001a. Nouvelles données sur les coquilles d'œufs de dinosaures de Megaloolithidae du sud de la France: systématique et variabilité intraspécifique. *Comptes Rendus de l'Académie des Sciences de Paris* 332: 185–191.
- Garcia, G. and Vianey-Liaud, M. 2001b. Dinosaur eggshells as new bio-chronological markers in Late Cretaceous continental deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 169: 153–164.
- Grellet-Tinner, G., Chiappe, L.M., and Coria, R. 2004. Eggs of titanosaurid sauropods from the Upper Cretaceous of Auca Mahuevo (Argentina). *Canadian Journal of Earth Sciences* 41: 949–960.
- Hirsch, K.F. 1989. Interpretations of Cretaceous and pre-Cretaceous eggs and shell fragments. In: D.D. Gillette and M.G. Lockley (eds.), *Dinosaur Tracks and Traces*, 89–97. Cambridge University Press, Cambridge.
- Hirsch, K.F. 1994. Upper Jurassic eggshells from the Western Interior of North America. In: K. Carpenter, K.F. Hirsch, and J.R. Horner, (eds.), *Dinosaur Eggs and Babies*, 137–150. Cambridge University Press, Cambridge.
- Hirsch, K.F. 1996. Parataxonomic classification of fossil chelonian and gecko eggs. *Journal of Vertebrate Paleontology* 16: 752–762.
- Hirsch, K.F. and Quinn, B. 1990. Eggs and eggshell fragments from the Upper Cretaceous Two Medicine Formation of Montana. *Journal of Vertebrate Paleontology* 10: 491–511.
- Horner, J.R. and Weishampel, D.B. 1996. A comparative embryological study of two ornithischian dinosaurs. *Nature* 383: 103.
- Khosla, A. and Sahni, A. 1995. Parataxonomic classification of late Cretaceous dinosaur eggshells from India. *Journal of the Paleontological Society of India* 40: 87–102.
- Kohring, R. and Hirsch, K.F. 1996. Crocodylian and avian eggshells from the middle Eocene of the Geiseltal, Eastern Germany. *Journal of Vertebrate Paleontology* 16: 67–80.
- Maddison, W.P. and Maddison, D.R. 1992. *MacClade, Analysis of phylogeny and character evolution, version 3.04*. Sinauer Associates Inc. Sunderland Mass, Massachusetts.
- Mateus, I., Mateus, M., Mateus, O., Taquet, P., Ribeiro, V., and Manupella, G. 1997. Couvée, œufs et embryons d'un dinosaure théropode du Jurassique supérieur de Lourinha (Portugal). *Comptes Rendus de l'Académie des Sciences de Paris* 325: 71–78.
- McIntosh, J.S. 1990. Sauropoda. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 345–401. University of California Press, Berkeley.
- Mikhailov, K.E. 1994. Theropod and protoceratopsian dinosaur eggs from the Cretaceous of Mongolian and Kazakhstan. *Paleontological Journal* 28: 101–120.
- Mikhailov, K.E. 1997. Fossil and recent eggshells in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Palaeontology* 56: 5–80.
- Mikhailov, K.E., Bray, E.S., and Hirsch, K.F. 1996. Parataxonomy of egg remains (Veterovata): principles and applications. *Journal of Vertebrate Paleontology* 16: 763–769.
- Penner, M.M. 1985. The problem of dinosaur extinction: contribution of the study of terminal Cretaceous eggshells from southeast France. *Géobios* 18: 665–669.
- Salgado L. and Calvo J.O. 1997. Evolution of titanosaurid sauropods. II: The cranial evidence. *Ameghiniana* 34: 33–48.
- Salgado, L., Coria, R.A., and Chiappe, L.M. 2005. Osteology of the sauropod embryos from the Upper Cretaceous of Patagonia. *Acta Palaeontologica Polonica* 50: 79–92.
- Sereno, P.C. 1999. The evolution of dinosaurs. *Science* 284: 2137–2147.
- Slowinski, J.B. 1993. "Unordered" versus "ordered" characters. *Systematic Biology* 42: 155–165.
- Swofford, D.L. 1993. *PAUP—Phylogenetic Analysis Using Parsimony. Vers. 3.1.1*. Computer software and manual. Illinois Natural History Survey, Illinois.
- Turner, C.F. and Peterson, F. 2004. Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis. In: C.A. Turner, F. Peterson, and S.P. Dunagan (eds.), *Reconstruction of the Extinct Ecosystem of the Upper Jurassic Morrison Formation*. *Sedimentary Geology* 167: 309–335.
- Upchurch, P. and Martin, J. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology* 23: 208–231.
- Varrichio, D.J. and Jackson, F.D. 2004. A phylogenetic assessment of prismatic dinosaur eggs from the Cretaceous Two Medicine Formation of Montana. *Journal of Vertebrate Paleontology* 24: 931–937.
- Vianey-Liaud, M., Mallan, P., Buscaïl, O., and Montgelard, C. 1994. Review of French dinosaur eggshells: morphology, structure, mineral, and organic composition. In: K. Carpenter, K. Hirsch, and J.R. Horner (eds.), *Dinosaur Eggs and Babies*, 151–183. Cambridge University Press, Cambridge.
- Vianey-Liaud, M., Hirsch, K., Sahni, A., and Sigé, B. 1997. Late Cretaceous Peruvian eggshells and their relationships with Laurasian and eastern Gondwanan material. *Géobios* 30: 75–90.
- Watrous, L.E. and Wheeler, Q.D. 1981. The outgroup comparison method of character analysis. *Systematic Zoology* 30: 1–11.
- Wedel, M.J., Cifelli, R.L., and Sanders, R.K. 2000. Osteology, paleobiology and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica* 45: 343–388.
- Weishampel, D.B. 1990. Dinosaurian distribution. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 63–139. University of California Press, Berkeley.
- Wilson, J.A. 2002. Sauropod dinosaur phylogeny: Critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136: 217–276.
- Wilson, J.A. and Sereno, P.C. 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* 18: 1–68.
- Zeletnisky, D.K. 2004. A cladistic analysis of theropod ootaxa. Abstract, *Journal of Vertebrate Paleontology* 24 (Supplement to No. 3): 134A.
- Zeletnisky, D.K. and Hills, L.V. 1996. An egg clutch of *Prismatoolithus levis* oosp. nov. from the Oldman Formation (Upper Cretaceous),

- Devil's Coulee, Southern Alberta. *Canadian Journal of Earth Science* 33: 1127–1131.
- Zeletnisky, D.K., Hills, L.V., and Currie, P.J. 1996. Parataxonomic classification of ornithoid eggshell fragments from the Oldman Formation (Judith River Group, Upper Cretaceous), southern Alberta. *Canadian Journal of Earth Science* 33: 1655–1667.
- Zeletnisky, D.K. and Hirsch, K.F. 1997. Fossil eggs: identification and classification. In: D.L. Wolberg, E. Stump, and G. Rosenberg (eds.), *Dinofest International: A Symposium Held at Arizona State University*, 279–286. Academy of Natural Sciences, Philadelphia.
- Zeletnisky, D.K. and Hills, L.V. 1997. Normal and pathological eggshells of *Spheroolithus albertensis*, oosp. nov., from the Oldman Formation (Judith River group, Late Campanian), southern Alberta. *Journal of Vertebrate Paleontology* 17: 167–171.
- Zhao, Z. 1975. The microstructure of dinosaurian eggshells of Nanshiung Basin, Guangdong Province. *Vertebrata Palasiatica* 17: 131–136.
- Zhao, Z. 1979. The advancement of researches on the dinosaurian eggs [in China]. In: *Mesozoic and Cenozoic Red Beds of South China*, 329–340. Science Press, Beijing.

## 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.