A PHYLOGENETIC APPROACH TO UNDERSTANDING DINOSAUR EGG DIVERSITY AND THE EVOLUTION OF REPRODUCTIVE TRAITS WITHIN DINOSAURIA

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Earth Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2014

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ACKNOWLEDGEMENTS

I thank my advisor, Dr. David Varricchio, committee members Drs. Frankie Jackson and Matt Lavin, my fellow Earth Sciences students, Earth Sciences faculty and staff, and my family for their constant support at all stages of this project. Funding was provided by NSF Grant # 0847777 (EAR) to D. Varricchio; NSF IRES Grant # 0854412 to F. Jackson and D. Varricchio; National Geographic Grant No. 8752-10 to D. Varricchio, X. Jin, and F. Jackson; and two MSU Undergraduate Scholars Program Grants to D. Barta, and to D. Barta, C. Bury, J. Croghan, and J. Drost. I am especially grateful to K. Chin and T. Culver (UCM), A. Halamski, C. Kulicki (ZPAL), J. Horner and E.-T. Lamm (MOR), R. Hunt-Foster (Museum of Western Colorado), X. Jin and W. Zheng (ZMNH), M. Kundrát (Uppsala University), W. D. Maxwell (University of the Pacific), K. Mikhailov (PIN), and M. Norell (AMNH) for access to and loans of specimens in their care, and for their hospitality during collections visits. This study was only possible because of them. K. Chin and T. Culver additionally provided access to the notes of the late K. Hirsch. I also thank M. Lavin, C. Organ, and M. Ivie for cladistics expertise, R. Avci for access to the MSU Imaging and Chemical Analysis Laboratory, and J. Horner for use of the Gabriel Lab for Cellular and Molecular Paleontology at Museum of the Rockies. R. Araújo, T. Carr, N. Carroll, R. Castanhinha, S. Chapman, T. Imai, D. Lawver, J. Liston, K. Mikhailov, M. Norell, S. Oser, A. Poust, M. Sander, J. Scannella, D. J. Simon, K. Stein, K.Tanaka, and S. Zhang contributed invaluable discussions and, in some cases, unpublished data.

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ABSTRACT

Fossil eggs provide a unique source of information about the reproductive biology of extinct vertebrates. Dinosaur eggshell, eggs, and clutches are of particular interest because of their great diversity in size, shape, microstructure, and clutch configurations relative to extant egg-laying taxa. In order to provide an explicity phylogenetic framework within which to investigate this diversity and to form more rigorous hypotheses about the identities of egg types that lack associations with adult or embryonic remains, cladistic analyses of 36 oological characters were peformed for 48 egg types. This study aimed to achieve a broader ootaxonomic coverage than previous studies, including pterosaur eggs for the first time in an outgroup with crocodilians and turtles in order to better polarize character states. The first set of analyses did not restrict the positions of ingroup eggs; however, the second utilized a backbone constraint to restrict the positions of taxonomically identified eggs on the tree, allowing unidentified ootaxa to fall out freely relative to a stable framework of relationships based on consensus osteological phylogenies. The results of all analyses reveal Chinese spheroolithids and Mongolian dendroolithids grouping together to the exclusion of other members of those oofamilies (and alongside therizinosauroid eggs) suggesting that Spheroolithidae and Dendroolithidae are polyphyletic. The constrained analysis additionally reveals *Ovaloolithus* and *Cairanoolithus* as the only egg types unresolved at the base of Dinosauria on an Adams consensus tree, suggesting that they could belong to either saurischians or ornithischians. All other taxonomically unidentified ootaxa fall out as saurischians, suggesting that the lack of ornithischian eggs in the fossil record is the result of real biases acting against their preservation, and is not simply an artifact of a lack of preserved embryos whereby they might be identified. Major transitions in dinosaur eggshell evolution include the evolution of a second structural layer of calcite within Avetheropoda, and a reversal to a single-layered condition within Therizinosauroidea. As in previous studies, a stepwise accumulation of avian-like character states within theropods precedes the appearance of extant avian clades. This study highlights the need for ongoing application of cladistic and related principles to the study of fossil eggs.

A PHYLOGENETIC APPROACH TO UNDERSTANDING DINOSAUR EGG DIVERSITY AND THE EVOLUTION OF REPRODUCTIVE TRAITS WITHIN DINOSAURIA

Introduction

Fossil eggshell, eggs, and clutches provide a unique source of data regarding the reproductive anatomy (Varricchio et al. 1997), physiology (Seymour 1979, Deeming 2006, Jackson et al. 2008), behavior (Horner and Makela 1979, Norell et al. 1995, Varricchio et al. 1999), and life history strategies (Janis and Carrano 1992, Werner and Griebeler 2013) of extinct vertebrates. Despite a long history of discoveries (Buffetaut and Le Loeuff 1994), fossil eggs have only comparatively recently merited consideration as body fossils that contain phylogenetic information (Mikhailov 1992). Non-avian dinosaur eggs are of particular interest to this and previous studies because of their relative abundance in the fossil record compared to the eggs of other clades (Lawver and Jackson In press, Varricchio et al. In prep.), greater range of variation in eggshell structure than among extant egg types (Carpenter 1999), importance for understanding the origins of avian reproduction, and the insights into dinosaur paleobiology that they provide (Varricchio and Jackson 2004a).

In order to document the sequence of evolution of reproductive characters throughout Sauropsida, particularly non-avian dinosaurs, previous authors drew schematic tree diagrams of eggshell structure using pre-cladistic ideas of overall similarity (Zhao 1979a, 1993) or mapped reproductive characters (including egg characters) onto existing phylogenetic trees derived from osteological data (Mikhailov 1992, Varricchio et al. 1999, Zelenitsky et al. 2002, Chiappe and Vargas 2003, Varricchio and Jackson 2004, Grellet-Tinner 2006, Grellet-Tinner et al. 2006, Reisz et al.

2012, Araújo et al. 2013). Another approach, the one presented herein, is the use of parsimony-based cladistic analysis to generate hypotheses about the evolution of reproductive characters. Parsimony and maximum likelihood analyses have the advantage of transparency and repeatability, lessen subjectivity in character weighting, and allow for an expansion of the taxonomic scope of a study to include eggs that cannot be mapped on an osteological cladogram because they lack embryos *in ovo* or a close association with adult skeletal material. Such eggs are important to include in an analysis because they may contain apomorphies or unique suites of characters not observed in taxonomically assigned eggs, thus providing a more complete picture of egg evolution. These 'unidentified' eggs may also extend the temporal range (first and last appearance) of a given character state beyond that inferred solely from eggs of known parentage. Also, as eggs that lack embryonic remains or adult associations can be the most abundant vertebrate fossils at some localities (Sellés et al. 2014, Varricchio et al. 2014), organizing this abundance and diversity of eggs within a cladistic framework can assist reconstruction and comparison of the faunal compositions of localities with scarce skeletal remains.

Previous cladistic studies (see Table 1 and following section) include representatives from only a few of the known dinosaur egg parataxa (ootaxa), largely focusing on saurischian eggs that contain identified embryos, particularly those of maniraptoran theropods, in order to better understand the acquisition of avian reproductive traits within Dinosauria (Grellet-Tinner and Chiappe 2004, Varricchio and Jackson 2004, Grellet-Tinner and Makovicky 2006, Zelenitsky and Therrien 2008a,b). Though these and other studies present crucial evidence that supports the hypothesis that most features of avian reproduction first evolved in dinosaurian ancestors, the utility of previous cladistic analyses for examining reproduction across the whole of Dinosauria is

hampered by two main factors. The first of these is the limited inclusion of taxonomically unassigned but potentially informative eggs (Grellet-Tinner and Chiappe 2004, Varricchio and Jackson 2004, Grellet-Tinner 2006, Zelenitsky and Therrien 2008a,b); the second is a lack of appropriate non-dinosaurian outgroups used to polarize character states (Zelenitsky 2004, Zelenitsky and Therrien 2008a,b, Tanaka et al. 2011). These and other issues are reviewed in the Previous Work section below.

The comprehensive cladistic analysis central to this study aims to achieve a broader coverage of dinosaur oofamilies for which no embryonic remains are known, and place these within a phylogenetic framework relative to both taxonomically identified dinosaur eggs, crocodilian eggs, and turtle eggs as an outgroup. Additionally, this study includes, for the first time, pterosaur and prosauropod (*Lufengosaurus* and *Massospondylus*) eggs, which may assist in identifying ancestral character states during parsimony analyses.

Questions investigated herein include: 1) Can taxonomically unassigned eggs be tentatively assigned to a parent dinosaur clade? What might these assignments reveal about the evolution of eggshell structure and biases in the fossil record of eggs? 2) What are the major homoplasies in dinosaur egg evolution, and what might account for them? 3) Can greater resolution of the 'mosaic evolution' of eggshell characters along the theropod-avian lineage be obtained? 4) How congruent are the topologies of phylogenetic trees derived from reproductive characters with those derived from traditional osteological datasets? What may account for disagreements between the two data sources? and 5) Are oofamilies monophyletic? Can the ootaxonomic system of classification be made explicitly phylogenetic for use in future studies? These questions draw attention to the nature of eggs as body fossils that represent primarily genetically controlled, evolving products of cellular secretion.

I investigate these questions through an unconstrained cladistic analysis solely of dinosaur eggshell, egg, and clutch characters. I then run the same analysis with the positions of taxonomically identified eggs on the resulting tree constrained to those positions recovered by current consensus phylogenies of skeletal material. The unconstrained and constrained trees are compared, and differences possibly resulting from homoplasy and weak character support are discussed. The topologies of both unconstrained and constrained trees are examined to assess their degree of congruence with the current system of ootaxonomic classification. Finally, this study provides an illustrated guide to egg and other reproductive characters in an attempt to aid interpretation by future workers, promote discussion of eggshell structures, and standardize terminology utilized in cladistic analyses of oological material.

Previous Work

This section relates, for the first time, a comprehensive history of parsimony analyses of eggs, eggshell, and reproductive characters, highlights some of the important accomplishments of past authors, and provides critical commentary on previous studies. Table 1 summarizes these analyses.

Zelenitsky's (1995) unpublished thesis pioneered the use of parsimony analysis to reconstruct an oological phylogeny, testing the eggshell character state distributions mapped onto an existing sauropsid phylogeny by Mikhailov (1992). Surprisingly, Zelenitsky's (1995) study was the only one before or since to use eggshell basic types as the operational taxonomic units (OTUs). In recent years, eggshell basic types and morphotypes have largely been disregarded as unnatural groupings (Zelenitsky et al. 2002) that are often redundant with oofamilies (Zelenitsky and Therrien 2008a) and will

not be treated further in the current study [but see Mikhailov (2014) for a defense of the usefulness of these categories].

No further cladistic analyses of eggshell were attempted until Grellet-Tinner's (2000) examination of extant and fossil paleognath eggshell. This work did not incorporate non-avian dinosaur eggs into the data matrix. Subsequent analyses of paleognath eggshell phylogeny (Grellet-Tinner 2001, Zelenitsky and Modesto 2003, Zelenitsky 2004, Grellet-Tinner 2005, 2006) sometimes included dinosaur outgroups. These studies also reexamined Grellet-Tinner's (2000) character coding, the usefulness of his continuous characters, and the incorporation of eggshell characters into an osteological data matrix to examine the interrelationships of Paleognathae. This research collectively demonstrates the usefulness of eggshell characters as a supplemental source of character data that can help to reveal relationships among clades otherwise resolved solely on the basis of osteological or molecular data.

Grellet-Tinner and Chiappe (2004) conducted the first study following Zelenitsky (1995) to focus primarily on non-avian dinosaur eggshell as the ingroup. This work formed an important first attempt to include a relatively small sampling of taxonomically identified dinosaur eggs in an analysis with extant turtle, crocodilian, and avian eggs. Additionally, it provides the first explicit character descriptions and published data matrix for non-avian dinosaur eggs.

Later that same year, Zelenitsky (2004) presented a comprehensive (27 taxa and 16 characters) cladistic analysis that was the first to include taxonomically unassigned oological material, setting a precedent for subsequent studies. Finally, Varricchio and Jackson (2004) published an analysis of dinosaur eggshell (both non-avian and avian) with turtle and crocodilian outgroups to determine the affinities of a taxonomically unassigned egg, the 'Two Medicine egg' [now named *Triprismatoolithus stephensi*

Jackson and Varricchio (2010)]. Importantly, this data matrix includes non-dinosaurian outgroups and recognizes the multi-layered nature of crocodilian eggshell (Ferguson 1982). These three seminal works in 2004 convincingly established that many traditionally 'avian' reproductive traits (e.g., multi-layered eggshell and asymmetric eggs) first evolved within Theropoda. Though Zelenitsky's (2004) unpublished Ph.D. thesis is the most comprehensive of the three in terms of both the number of included taxa and characters, it does not incorporate turtle or crocodilian outgroups to aid in polarizing character states for the ingroup. Though *Maiasaura* eggs and other spheroolithids were designated an outgroup by Zelenitsky (2004), the relatively late temporal occurrence and derived placement of hadrosaurids within Ornithischia and the lack of any identified eggs from more basal ornithischians suggest that hadrosaurid eggshell structure may not be a good exemplar of basal character states relative to the remainder of Dinosauria. For similar reasons, titanosaurian eggshell may not represent a reliable outgroup relative to other saurischian eggshell, as used by Zelenitsky and Therrien (2008a,b).

The next attempts to resolve dinosaur eggshell phylogeny were those of Grellet-Tinner (2005) and Grellet-Tinner and Makovicky (2006). Both included crocodilian eggs as an outgroup [though these are coded as possessing a single structural layer *contra* Ferguson (1982) and Varricchio and Jackson (2004)]. Grellet-Tinner and Makovicky (2006) included hadrosaurid eggs in addition to the saurischian taxa coded in Grellet-Tinner (2005). No taxonomically unassigned eggs were examined by either study, though the Phu Phock eggs included in both studies have since been found to contain lizard embryos (Fernandez et al. In review), and thus do not belong to a non-avian theropod or bird as originally hypothesized (Buffetaut et al. 2005).

Grellet-Tinner (2005) additionally made an important first attempt to create a total-evidence phylogeny of dinosaurs that incorporates oological and other reproductive characters into a traditional osteologically based data matrix. This attempt was limited to four taxa with identified eggshell, *Citipati osmolskae*, *Deinonychus antirrhopus*, *Byronosaurus jaffei*, and *Troodon formosus*. No change in tree topology was evident between the osteological phylogeny and the total-evidence phylogeny.

The analysis of Garcia et al. (2006) incorporated both taxonomically assigned and unassigned eggs, with fossil turtle and crocodilian eggs as an outgroup. This study focused primarily on relationships within the dinosaur oofamily Megaloolithidae. An unusual tree topology was recovered, in which a clade that contains both megaloolithid (probable sauropod) and spheroolithid (hadrosaur) eggs forms the sister group to the clade containing bird eggs, to the exclusion of non-avian theropod eggs. This topology is not congruent with previously published osteological cladistic analyses of Dinosauria (Sereno 1999, Pisani et al. 2002). A potential explanation may lie in Garcia et al.'s (2006) coding of *Preprismatoolithus coloradensis* and *Prismatoolithus levis* eggshell as possessing a single layer, whereas previous studies (Hirsch 1994, Jackson et al. 2010) demonstrate that these egg types have at least two structural layers [likely three for *Prismatoolithus levis*, see Jackson et al. (2010)], homologous with those of birds. The inclusion of highly taphonomically variable characters (e.g. Character 5, eggshell thickness; and Character 23, shape of section in the equatorial part of the egg), and the coding of crocodilian eggshell as possessing a single layer are additionally problematic.

Winkler (2006) presented the first analysis solely dedicated to examining chelonian eggshell characters. However, she failed to include any non-turtle taxa as an outgroup. Though a high degree of homoplasy exists in the eggshell characters, Winkler (2006) nevertheless found two characters whose states unambiguously support an *Elseya*-

Emydura clade and one that unambiguously supports a clade of South American chelids plus *Hydromedusa*. Additional ambiguous character support was found for the latter clade and an additional clade of Australasian chelids.

The cladistic analysis of Moreno-Azanza et al. (2008) used the data matrix of Garcia et al. (2006) to examine the phylogenetic affinities of Early Cretaceous megaloolithid eggshells. The authors recovered both the oofamily Megaloolithidae and the oogenus *Megaloolithus* as monophyletic, with an additional clade of Late Cretaceous *Megaloolithus* retained in their strict consensus tree. Thus, this is perhaps the best-resolved analysis of a single oofamily, though the inclusion of some of Garcia et al.'s (2006) more problematic characters (see above) raises questions about the accuracy of the results.

Zelenitsky and Therrien (2008a,b) focused mostly on resolving the evolution of reproductive traits within theropods with a relatively small sample of characters and taxa and fail to include any non-dinosaurian outgroups. Though the results are largely congruent with topologies from osteological cladistic analyses, the utility of these data matrices for examining oological character evolution throughout the whole of Dinosauria is limited.

The phylogenetic analysis of Jin et al. (2010) is an expansion, both in characters and taxa, of the data matrix of Varricchio and Jackson (2004). It was performed to examine the affinities of *Dictyoolithus hongpoensis*, recovering this unassigned egg as possibly belonging to a theropod.

Sellés (2012), in an attempt to reveal interrelationships among 10 *Megaloolithus* oospecies, modified the data matrix of Jin et al. (2010) to include three new characters related to shell unit morphology and shell thickness. He also changed character states and codings for some characters, and incorporated additional taxonomically unassigned

ootaxa. Sellés (2012) performed a second cladistic analysis in the same unpublished dissertation, with the same altered character states and codings, but with only one of the new characters. This second analysis, attempting to resolve the affinities of *Cairanoolithus*, also included a number of unassigned ootaxa not previously incorporated into the data matrix of Jin et al. (2010).

Finally Tanaka et al. (2011), López-Martínez and Vicens (2012), Ribeiro et al. (2014), and Moreno-Azanza et al. (In press) have all used one or more of the existing data matrices reviewed above to assess the phylogenetic affinities of specimens of particular interest to their studies. This is a positive development for the field of palaeoology, as explicitly phylogenetic ootaxon definitions will help to supplant the use of redundant or paraphyletic categories used to classify fossil eggs (basic types, morphotypes, and some oofamilies), aid in comparing ootaxa to one another, and perhaps reduce the amount of subjectivity involved in identifying new ootaxa. Beyond such systematic considerations, the growing examination of amniote eggshell characters within a cladistic framework will help to identify major trends, reversals, and homoplasies in the evolution of eggshell structures, allow for comparison with datasets derived from other types of characters (e.g. skeletal or molecular), and recognize taxonomically unassigned fossil eggs as a potentially useful source of character data.

Table 1. Previous cladistic analyses of amniote eggs. Entries with multiple numbers for taxa and characters in corresponding order indicate that multiple analyses were performed in the thesis or paper.

Author(s)	Year	Taxa	Number of Taxa	Number of Characters
Zelenitsky	1995	Squamates, turtles, crocodilians, non-avian dinosaurs, birds	7	8
Grellet-Tinner	2000	Paleognath birds	12	22
Grellet-Tinner	2001, unpublished master's thesis	Non-avian dinosaurs, paleognath birds	14	15
Zelenitsky and Modesto	2003	Ratites	7	9
Grellet-Tinner and Chiappe	2004	Turtle, *Alligator*, non-avian dinosaurs, birds	11	11
Zelenitsky	2004, unpublished dissertation	Paleognath and galliform birds	10	13
Zelenitsky	2004, unpublished dissertation	Paleognath birds	8	15
Zelenitsky	2004, unpublished dissertation	Non-avian dinosaurs, birds	27	16
Varricchio and Jackson	2004	Turtles, crocodilians, non-avian dinosaurs, birds	14	15
Grellet-Tinner	2005, unpublished dissertation	Paleognath birds	7	15
Grellet-Tinner	2005, unpublished dissertation	Crocodilian, non-avian dinosaurs, birds	14	24
Grellet-Tinner	2006	Non-avian dinosaurs, birds	14	15

Table 1 Continued.

Grellet-Tinner and Makovicky	2006	*Alligator*, non-avian dinosaurs, birds	14	19
Winkler	2006	Turtles	12	13
Garcia et al.	2006	Turtles, crocodilians, non-avian dinosaurs, birds	19	27
Moreno-Azanza et al.	2008	Crocodilians, non-avian dinosaurs	12	27
Zelenitsky and Therrien	2008a	Non-avian dinosaurs, birds	7	12
Zelenitsky and Therrien	2008b	Non-avian dinosaurs, birds	7	12
Jin et al.	2010	Turtles, crocodilians, non-avian dinosaurs, birds	17	19
Tanaka et al.	2011	Non-avian dinosaurs, birds	28	16
López-Martínez and Vicens	2012	Non-avian dinosaurs, birds	11	12
Sellés	2012, unpublished dissertation	Turtles, crocodilians, non-avian dinosaurs, birds	24, 21	22, 20
Ribeiro et al.	2014	Turtles, crocodilians, non-avian dinosaurs, birds	19, 29	19, 16
Moreno-Azanza et al.	In press	Turtles, crocodilians, non-avian dinosaurs, birds	15, 14, 10, 12	15, 19, 12, 12
Barta	This study	Turtles, crocodilians, pterosaurs, non-avian dinosaurs, birds	48	36

Methods

Radial thin sections of 40 turtle, crocodilian, and dinosaur eggshells (n = 48 total) were examined and photographed with a Nikon Eclipse LV100POL petrographic

microscope and coded for the 36 binary, multistate, and continuous characters described in the following section and listed in Appendix I. All thin sections are 30 μm thick, unless otherwise noted in the Description of Taxa and Ootaxa section. Characters were constructed according to the contingent/reductive coding method detailed by Brazeau (2011), in order to best capture potentially synapomorphic information contained in the presence or absence of a feature, separate from the states it expresses when present. Collapse of zero-length branches was specified in order to circumvent the potential problems introduced by the treatment of inapplicable states as identical to missing data in PAUP*, as recommended by Brazeau (2011). Please see the following section for more detailed descriptions of the methodology used to code each character. Character phrasing generally follows that recommended by Sereno (2007).

An additional eight egg types (*Pterodaustro guinazui,* ornithocheirid, *Hypacrosaurus stebingeri*, *Massospondylus*, *Lufengosaurus*, *Torvosaurus gurneyi*, *Deinonychus antirrhopus*, and *Bonapartenykus ultimus*) were coded entirely from previously published figures and descriptions. Oospecies or the lowest assignable parataxonomic level was chosen as the operational taxonomic unit (OTU) for ootaxa; likewise, species or the lowest assignable taxonomic level was chosen as the OTU for taxa with identified eggs. The turtle, crocodilian, and pterosaur taxa were designated together as a paraphyletic outgroup with the topology (*Elseya novaeguineae*, *Apalone mutica*, ((*Alligator mississippiensis*, *Crocodylus niloticus*), (*Pterodaustro guinazui*, ornithocheirid))). Designating the outgroup in this way provides the maximum possible information about possible character polarities for Dinosauria, given the possibility that turtles, crocodilians, and pterosaurs may have evolved hard-shelled eggs independently from one another, and from dinosaurs.

Eggshell fragments from 21 of the egg types (*Spheroolithus irenensis*, *Spheroolithus* cf. *zhangtoucaoensis*, *Ovaloolithus chinkangkouensis*, *Faveoloolithus ningxiaensis*, *Faveoloolithus* oosp., *Dendroolithus xichuanensis*, therizinosauroid, *Dendroolithus verrucarius*, *Dendroolithus microporosus*, *Allosaurus* sp., *Oblongoolithus glaber*, *Subtiliolithus microtuberculatus*, *Citipati osmolskae*, *Macroolithus rugustus*, *Trachoolithus faticanus*, Elongatoolithidae indet., *Protoceratopsidovum fluxuosum*, *Protoceratopsidovum minimum*, *Parvoolithus tortuosus*, and *Gobipipus reshetovi*) were mounted on aluminium stubs, coated with gold and imaged at 15 kV with a JEOL 6100 scanning electron microscope (SEM). The ootaxa for which personal examination with SEM was not conducted, due to either the unavailability of eggshell fragments or the availability of high quality published images, were coded using previously published SEM images. Unpublished SEM images for *Macroelongatoolithus* oosp. were provided by D. Simon.

The data matrix was created as a MacClade spreadsheet (Maddison and Maddison 2003) and analyzed using PAUP* 4.0 (Swofford 2003). Missing data were coded as "?" and inapplicable states were scored as "-." The data matrix was subjected to a heuristic search utilizing, for two different trials, both ACCTRAN and DELTRAN optimization, which bias toward secondary losses, and independent gains, respectively. Multistate taxa were treated as polymorphic. I utilized a heuristic search with 100 random-addition-sequence replications. Branch swapping was conducted with a tree bisection-reconnection algorithm. The MaxTrees limit was set to 300,000. A bootstrap analysis with 1000 replicates and a consensus level of 50% was performed utilizing a heuristic search with a random addition sequence, one repetition, and branch-swapping with a tree-bisection-reconnection algorithm. All characters were run as unweighted, and continuous characters (Characters 3, 8, 19, 27, 28, 29) were run as both unordered and ordered in two

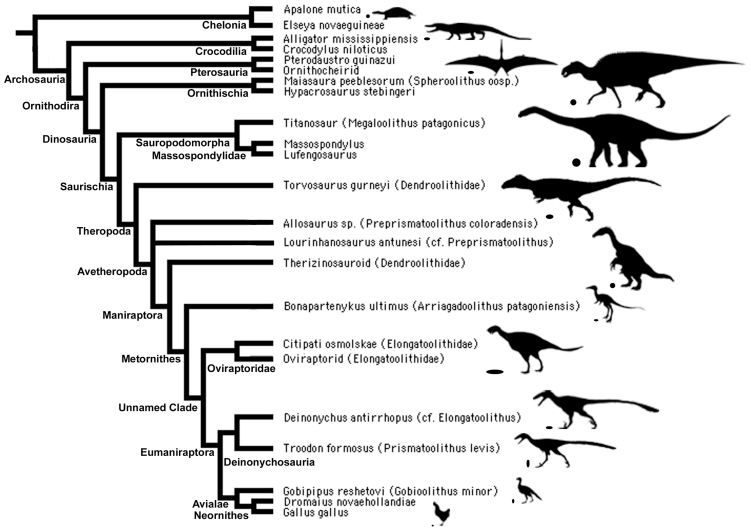
different trials. Though including more taxa than characters in an analysis [as in Tanaka et al. (2011)] produces a large number of most parsimonious trees (Sanderson and Doyle 1993), which tends to decrease resolution of conensus trees, the inclusion of the widest possible range of representative oospecies is necessary to provide a more complete picture of eggshell evolution than previous studies that suffer from limited taxon sampling (see Previous Work section for examples). Sanderson and Doyle (1993) also note that relatively few trees out of a large number of recovered trees can explain most topological variation, with the others constituting minor variations.

A backbone constraints analysis was conducted, utilizing the same parameters as those above in order to examine the recovered positions of unassigned ootaxa relative to the "known" relationships of taxa with identified eggs. For the constrained analysis, the following clades (Figure 1), with their member taxa in parentheses, were used to form the backbone constraint, as reflected by current consensus phylogenetic studies of skeletal material. Clade names and consensus tree topologies follow Hedges (2012), Parrish (2012), Benton (2012), Holtz (2012), Naish (2012), and Yates (2012) and the membership lists given here apply solely to the taxa included for purposes of this analysis and may not reflect those of other authors. **Chelonia** (*Apalone mutica*, *Elseya novaeguineae*), **Archosauria** (*Alligator mississippiensis*, *Crocodylus niloticus*, *Pterodaustro guinazui*, ornithocheirid, *Maiasaura peeblesorum*, *Hypacrosaurus stebingeri*, *Massospondylus*, *Lufengosaurus*, titanosaur, *Torvosaurus gurneyi*, therizinosauroid, *Allosaurus*, *Lourinhanosaurus antunesi*, *Citipati osmolskae*, oviraptorid, *Deinonychus antirrhopus*, *Bonapartenykus ultimus*, *Troodon formosus*, *Gobipipus reshetovi*, *Dromaius novaehollandiae*, and *Gallus gallus*), **Crocodilia** (*A. mississippiensis, C. niloticus*), **Ornithodira** (all archosaur taxa minus Crocodilia), **Pterosauria** (*P. guinazui*, ornithocheirid), **Dinosauria** (all ornithodiran taxa minus

Pterosauria), **Saurischia** (all dinosaur taxa minus *M. peeblesorum* and *Hypacrosaurus stebingeri*), **Sauropodomorpha** (the titanosaur and Massospondylidae), **Massospondylidae** (*Massospondylus* and *Lufengosaurus*), **Theropoda** (all saurischians minus Sauropodomorpha), **Avetheropoda** (all theropods minus *Torvosaurus gurneyi*), **Maniraptora** (all avetheropods minus *Allosaurus*, *L. antunesi*), **Metornithes** (all maniraptorans minus the therizinosauroid),), **Unnamed clade** (all metornithes minus *Bonapartenykus ultimus*), **Oviraptoridae** (*C. osmolskae*, oviraptorid), **Eumaniraptora** (all members of the unnamed clade minus Oviraptoridae), **Deinonychosauria** (*D. antirrhopus*, *T. formosus*), **Avialae** (all eumaniraptorans minus Deinonychosauria), and **Neornithes** (*D. novaehollandiae*, *G. gallus*; = all avialans minus *G. reshetovi*).

The Trace Characters option in MacClade (Maddison and Maddison 2003) was utilized to find the synapomorphies or unique suites of character states that unite the clades recovered by the constrained analysis on an Adams consensus tree, under both ACCTRAN and DELTRAN optimization.

Figure 1. Consensus phylogeny of the taxa with identified eggs included in this study. These clades were enforced as backbone constraints for the constrained phylogenetic analysis in this study. Sihlouettes are from Phylopic (phylopic.org) and are by S. Hartman, S. Traver, M. Martyniuk, FunkMonk, T. Tischler, L. Claessens, P. O'Connor, and D. Unwin.

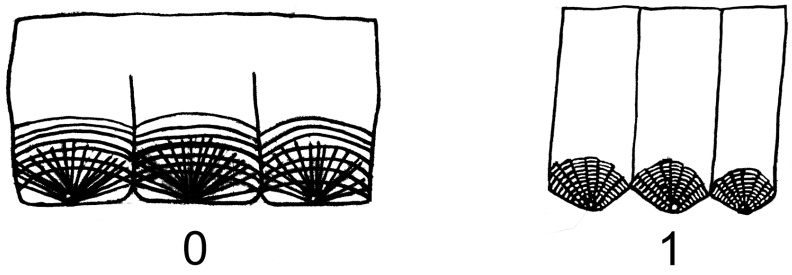


Description of Characters

The following character descriptions are intended to serve as a guide to interpreting the current analysis, and to provide a basis for standardization of descriptive terminology for future cladistic analyses of eggs. Illustrations of character states are intended to be diagrammatic and do not necessarily represent any specific specimen or taxon in order to aid in recognition of these character states in eggs that may be described by future authors.

1. **Eggshell, composition: aragonite (0); calcite (1) after Varricchio and Jackson (2004) (Figure 2).** Turtles are the only known extant taxa that lay eggs with a crystalline component of aragonite, which displays a needle-like morphology (Mikhailov 1991). In contrast, the absence of primary aragonite and the blade- or wedge-like morphology of the crystalline part of the shell units in well-preserved dinosaur eggshell suggest an originally calcitic composition.

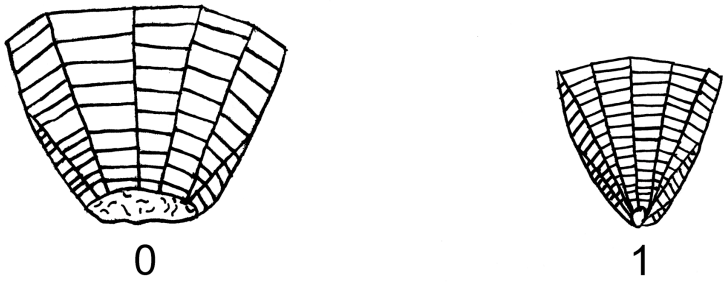
Figure 2. Character 1, states 0 and 1.



2. **Eggshell, first structural layer, organization of nucleation site: loosely organized basal knob (0); highly organized organic core (1) (Figure 3).** The nucleation sites are the points on the shell membrane from which individual shell units begin their growth. Crocodilians possess a loosely organized structure of protein fibers and calcite microcrystals from which the shell unit originates, the

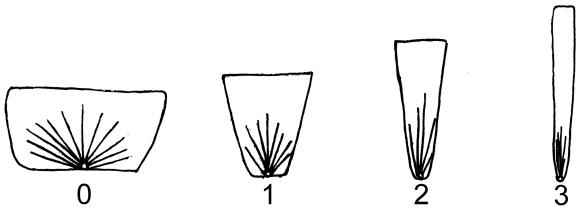
basal knob (Hirsch 1985, Moreno-Azanza et al. 2014). The organic core is a highly organized sub-spherical organic body from which calcite crystals grow radially (Mikhailov 1997a, Moreno-Azanza et al. 2014).

Figure 3. Character 2, states 0 and 1.



3. **Eggshell, first structural layer, height/width ratio of mammillae or shell units (if only one structural layer present): <1 (0); 1.0-2.0 (1); 2.01-7.0 (2); >7.01 (3) (Figure 4).** This character represents categories of shell unit/mammilla height and width measurements measured from thin sections and SEM photographs using ImageJ software, which were then averaged before being divided to obtain a ratio of the averages. Shell unit/mammilla width was measured at its widest point, either at the exterior surface of the eggshell or at the transition to the overlying second layer (if present). The breaks between character states were determined by examining the distribution of the ratio data on a histogram.

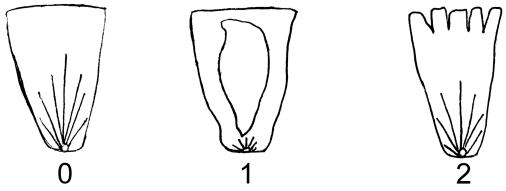
Figure 4. Character 3, states 0, 1, 2, 3.



4. **Eggshell, shell units: unbranched (0); first branched near interior of shell (1); first branched near exterior of shell (2) (Figure 5).** Shell units are considered branched when two or more divisions of an individual shell unit arise from a single organic core at its base. If the shell units first branch in the interior half of the total thickness of the eggshell, state 1 applies. If the shell units first branch in the exterior half of the eggshell, state 2 applies. The presence of secondary shell units in dinosaur eggs (Zhao 1994) remains controversial (Jin et al. 2010, Barta et al. 2014). Mikhailov (1997a) interprets Mongolian dendroolithid eggs as possessing a second layer of spherulitic shell units towards the exterior surface of the eggshell; however, I feel that his earlier interpretation of dendroolithid shell units as finely branching in three dimensions (Mikhailov 1991, Figure 7) best agrees with the morphology of the shell units seen in broken radial section (Mikhailov 1991, Plate 24, figure 7) and under SEM (observed here). I further suggest that reports of secondary spherulites in these and some other eggshells may be due to a geometric artifact of thin sectioning, namely, the cut occurs where branches of a shell unit join the main body. This idea remains to be tested, however. Given that SEM images fail to show true nucleation sites at the bases of the branching points in any of the eggshell examined for this study and another study (Jin et al. 2010), I feel that my interpretation above is more parsimonious than the mechanism of "secondary shell unit" formation proposed by Zhao (1994). Therefore, I code the Mongolian dendroolithids and therizinosauroid eggshell as state 2 for this character. Likewise, I do not include any other characters related to "secondary shell units" in this analysis. Grellet-Tinner et al. (2010) provide an additional possible explanation for the "secondary nucleation sites" observed along the pore margins of other eggshell types (Wang et al. 2011, Wang et al. 2012), which may be different than those proposed for the Mongolian *Dendroolithus* oospecies. Grellet-Tinner et al. (2010) note that if dissolution occurs within a pore canal, the

ends of fibers comprising the organic component of the eggshell can become exposed in the walls of pore canals and potentially serve as nucleation points for diagenetic calcite. This explanation applies particularly well to eggshells in which the "secondary nucleation sites" are primarily observed within pore canals [as noted by Barta et al. (2014) for *Mosaicoolithus* (Wang et al. 2011) and Wang et al. (2012) for the Stalicoolithidae].

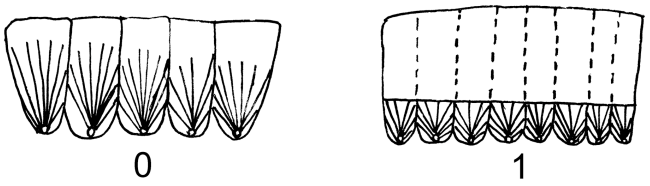
Figure 5. Character 4, states 0, 1, 2.



5. **Eggshell, second structural layer: absent (0); present (1) (Figure 6).** The second structural layer in non-avian and avian theropod eggshell is variously referred to as the spongy (Tyler 1964), continuous (=single) (Mikhailov 1991). column (Tyler 1969), palisade (Schmidt 1957), prismatic (Mikhailov 1991), aprismatic (Grellet-Tinner and Norell 2002), or cryptoprismatic (Jin et al. 2007) layer. The use of these terms depends on the degree of squamatic structure visible throughout the prismatic columns present in the second layer. I follow Jin et al. (2007) in rejecting use of the term "aprismatic" (Grellet-Tinner and Norell 2002), as eggshells with well-developed squamatic structure (to which the term "aprismatic" was originally applied) will sometimes still preserve visible prismatic shell units within the second layer (Jin et al. 2007). The term "spongy layer" was originally designated as a general term to apply to both the continuous (=single) layer of "ornithoid ratite" and the palisade layer of "ornithoid neognath" eggshells (Mikhailov 1991). As discontinuation of the use of eggshell

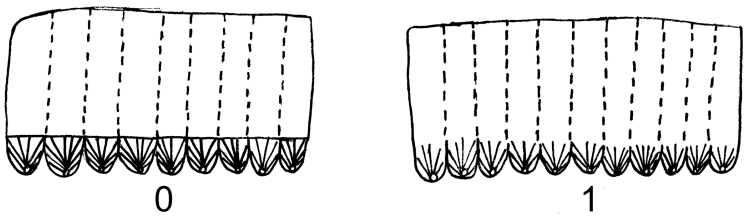
morphotypes has been recommended (Zelenitsky et al. 2002) and as using different terminology (palisade vs. continuous layer) to describe each of these morphotypes reinforces the erroneous notion that all fossil non-avian and avian theropod eggshells can be neatly classified as one morphotype or the other I prefer to use the descriptive terms "prismatic" and "cryptoprismatic" to refer to the second layer, depending on the degree to which prisms are visible through the squamatic structure. Jackson and Varricchio (2010) describe such a spectrum of squamatic structure development. The description of Character 12 provides more discussion of variation in squamatic structure within the second structural layer. The second layer of crocodilian eggshell was split into the organic and honeycomb layers by Ferguson (1982), but is now referred to simply as the middle layer (Moreno-Azanza et al. 2014, Marzola et al. In Press). I follow the use of "middle layer" and avoid using terms reserved for avian eggshell (e.g., continuous layer) so as not to bias interpretations towards considering this layer homologous to the second structural layer of avian eggshell. A second layer is coded as "present" for both crocodilian and avian eggshell for purposes of this analysis, as they both meet the generally understood (though not formalized) criteria for identifying a structural layer [zones of eggshell that possess a distinctive ultrastructure and extend continuously around the egg (Moreno-Azanza et al. 2014)]. I note however, that the homology of crocodilian and avian eggshell should not be assumed, as they exhibit many differences (as becomes clear upon coding them for the other characters in this analysis) beyond sharing three structural layers *sensu lato*.

Figure 6. Character 5, states 0 and 1.



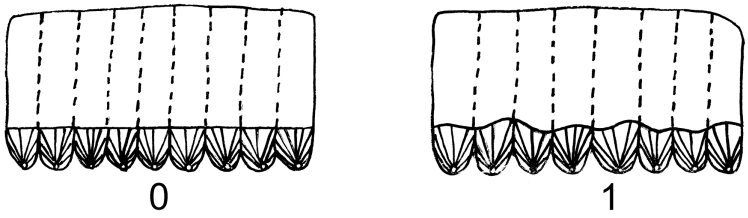
6. **Eggshell, transition between first and second structural layers: abrupt (0); gradual (1). modified after Varricchio and Jackson (2004) and Zelenitsky and Therrien (2008a) (Figure 7).** The transition between the first and second structural layer is coded as 'abrupt' if the first structural layer forms a distinct mammillary layer, the individual shell unit boundaries of which immediately become obscured at the junction with the overlying second layer. If a transition zone exists, within which the shell unit boundaries gradually become less distinct proceeding into the second structural layer, then this character is coded as 'gradual.'

Figure 7. Character 6, states 0 and 1.



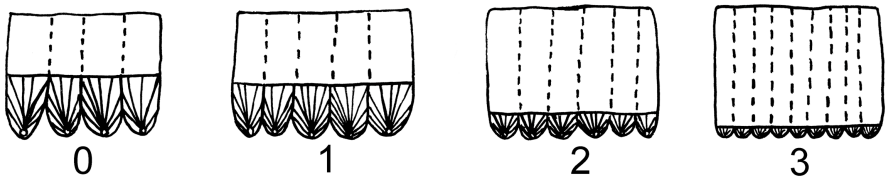
7. **Eggshell, boundary between first and second structural layers: straight (0); undulating (1) (Figure 8).** The boundary between the two layers can either remain straight across the tops of all mammillae, or undulate. For eggshell with a gradual boundary, it is often difficult to determine whether or not it is straight or undulating; such cases are scored as "?" for this character.

Figure 8. Character 7, states 0 and 1.



8. **Eggshell, ratio of second to first structural layer thicknesses: <2:1 (0); 2:1-3:1 (1); 3.01:1-4:1 (2); >4:1 (3) (Figure 9).** This ratio has been used to diagnose Mongolian elongatoolithid and other theropod ootaxa in the past (Mikhailov 1994a, 1997). Thickness measurements were made using ImageJ software and averaged. The breaks between character states for this continuous character were determined based on where breaks occurred between measured ratios in Mikhailov's (1994a) data.

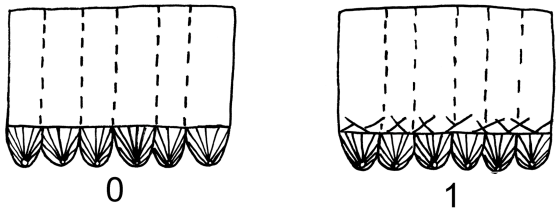
Figure 9. Character 8, states 0, 1, 2, 3.



9. **Eggshell, crystal splaying (sensu Jin et al. 2007) in first and second layers: absent (0); present (1) (Figure 10).** This character is presently only observed in specimens of *Macroelongatoolithus xixiaensis* (Jin et al. 2007), an indeterminate elongatoolithid (Simon et al. 2013 and this study), the oospecies *Elongatoolithus frustrabilis* (D. Barta pers. obs. of PIN 614/611), *Sankofa pyrenaica* (López-Martínez and Vicens 2012), and the extant guinea fowl, *Numida meleagris* (Panheleux et al. 1999). Only *Macroelongatoolithus* and the indeterminate elongatoolithid are included in my data matrix. All of the above egg types exhibit

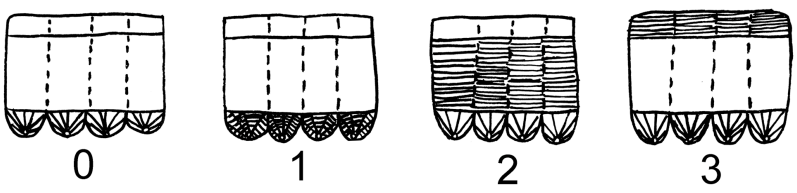
a splaying of the crystals of both the mammillary and cryptoprismatic layers along their shared boundary, forming an interlocking structure, which may hold functional significance for increasing the eggs' breaking strength (Panheleux et al. 1999, Jin et al. 2007).

Figure 10. Character 9, states 0 and 1.



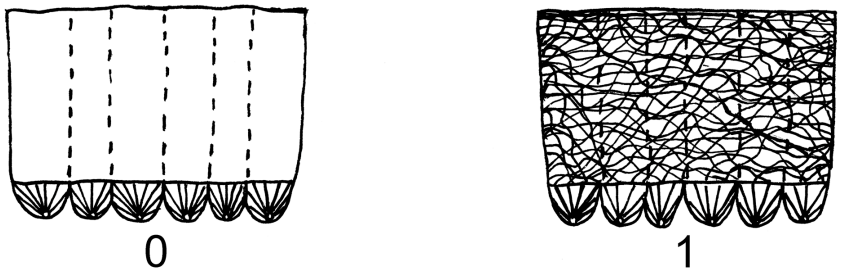
10. Eggshell, tabular structure: absent (0); present in first layer (1); present in second layer (2); present in third layer (3) (Figure 11). Tabular structure refers to the "regular transverse striations" (Mikhailov 1997a) of calcite best observed under SEM. Mikhailov (1997a) states "There is no demonstration of homology between tabular ultrastructure in avian and crocodilian eggshell." However, a hypothesis of homology should be allowed to emerge after analysis from mapping this character on the resulting tree topology. Further detailed developmental and biochemical studies could be undertaken to test a hypothesis of homology. Taxa that possess tabular structure in more than one layer are coded as polymorphic for the relevant states.

Figure 11. Character 10, states 0, 1, 2, 3.



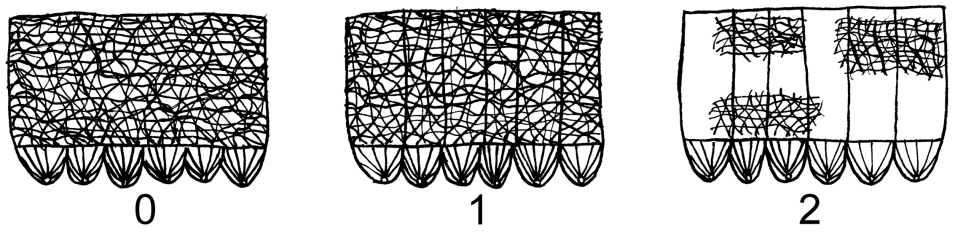
11. Eggshell, second layer: squamatic structure absent (0); present (1) (Figure 12). Squamatic structure is the polycrystalline aggregate of calcite crystals bound together by organic membranes, resulting in a scale-like appearance in SEM, that makes up the three-dimensional structure of the second structural layer of derived theropod and avian eggshell (Mikhailov 1997a).

Figure 12. Character 11, states 0 and 1.



12. Eggshell, prisms: primarily obscured by squamatic structure (0); with well-developed squamatic texture and visible margins (1); with irregular squamatic texture (2) modified after Jackson and Varricchio (2010) (Figure 13). If the squamatic structure visibly extends across all shell units and conceals their boundaries, this character is coded as obscuring the prisms. In cases where defined prism boundaries are present, but squamatic structure is still well developed within the confines of each shell unit, then State 2 applies. If the

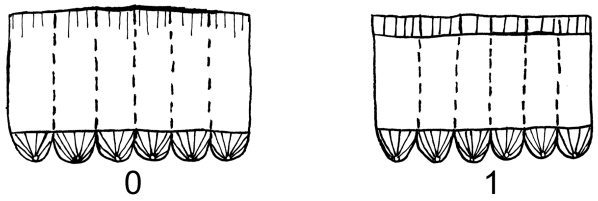
Figure 13. Character 12, states 0 and 1.



squamatic structure is patchy and fails to obscure all shell unit boundaries in the second structural layer, then it is coded as 'irregular.'

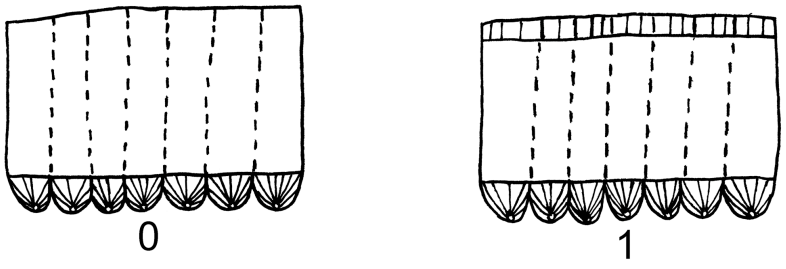
13. Eggshell, transition between second and third structural layers: gradual (0); abrupt (1) after Varricchio and Jackson (2004) (Figure 14). The transition between the second and third structural layers is coded as 'gradual' if not clearly demarcated (as in *Troodon*, see Varricchio and Jackson 2004, figure 2). If the transition is more clearly defined so that the boundary can be easily seen in thin section (as in *Triprismatoolithus* and avian eggshell), then it is coded as 'abrupt.'

Figure 14. Character 13, states 0 and 1.



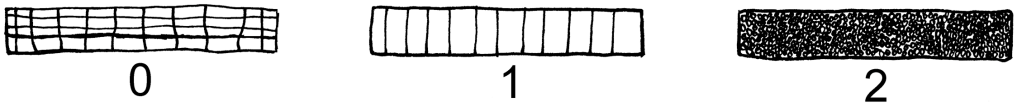
14. Eggshell, third structural layer: absent (0); present (1) (Figure 15). Varricchio and Jackson (2004) documented third structural layers in *Troodon formosus* (*Prismatoolithus levis*) and *Triprismatoolithus stephensi*. The third layer was previously thought absent in all non-avian dinosaur taxa, though has subsequently been found in other eggshells (Bonde et al. 2008, Agnolin et al. 2012).

Figure 15. Character 14, states 0 and 1.



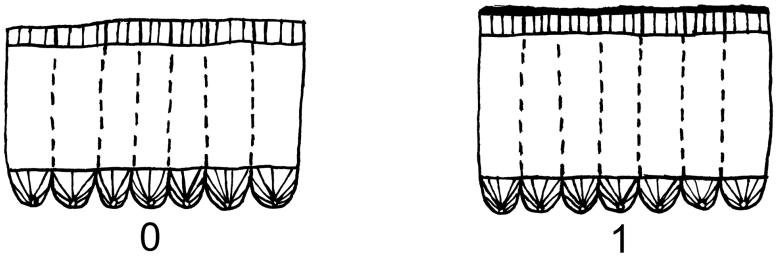
15. Eggshell, third structural layer: with horizontal crystals and vertical fibrous fabric (0); with vertical crystals (1); with granules that obscure crystal orientation (2) modified after Varricchio and Jackson (2004) (Figure 16). Some crocodilians exhibit state 0 (Marzola et al. In press), while theropods and birds show states 1 and 2.

Figure 16. Character 15, states 0, 1, 2.



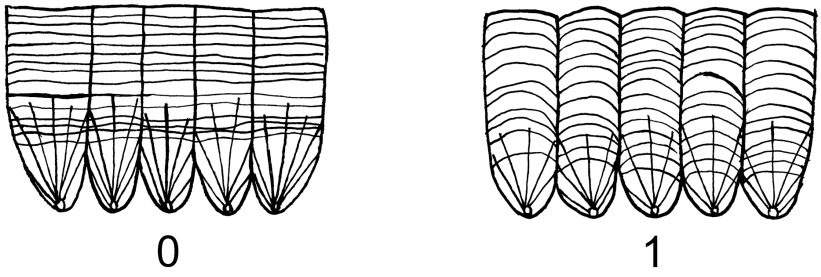
16. Eggshell, cuticle: absent (0); present (1) after Varricchio and Jackson (2004) (Figure 17). The cuticle, though rarely preserved in fossil eggs, is an important protective feature of extant avian eggshell, and is included here for its potential occurrence among dinosaurs [*Triprismatoolithus stephensi*, see Jackson and Varricchio (2010, figure 5)]. This character is scored as "?" for most egg types, other than extant taxa for which the absence or presence of a cuticle is known, and the two arriagadoolithid egg types *T. stephensi* and *Bonapartenykus utimus* (*Arriagadoolithus patagoniensis*).

Figure 17. Character 16, states 0 and 1.



17. Eggshell, accretion lines: straight at shell unit boundaries (0); arched at shell unit boundaries (1) (Figure 18). Accretion lines are generally thought to represent the consequence of a sequential growth pattern of the eggshell from interior to exterior (Schweitzer et al. 2005, and references therein). If the accretion lines extend horizontally across the shell units, parallel to the bounding surfaces of the eggshell, then this character is coded as "straight." If the accretion lines curve strongly towards the interior eggshell surface at the boundaries of the shell units, then this character is coded as "curved."

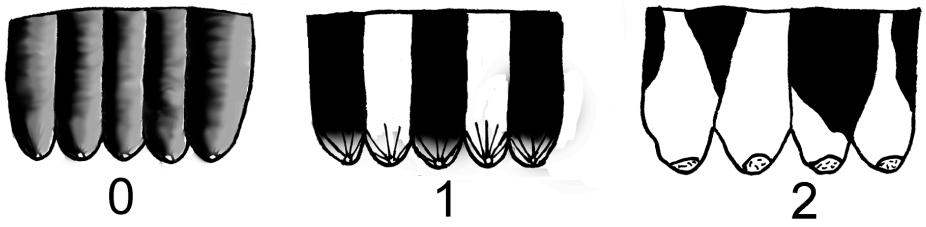
Figure 18. Character 17, states 0 and 1.



18. Eggshell, shell units, extinction pattern under cross polars: sweeping (0); columnar (1); blocky (2) (Figure 19). When examined in thin section under a petrographic microscope, if the shell units show a fan-like pattern of extinction (a psuedouniaxial cross) upon rotating the stage, then this character is coded as "sweeping." If alternating shell units across the extent of the eggshell instead become completely extinguished, then this character is coded as "columnar." For eggs with two or more structural layers, this character was coded as polymorphic if a sweeping extinction pattern is seen in the mammillae and a more "patchy" columnar extinction pattern is seen in the second layer, as in some elongatoolithid

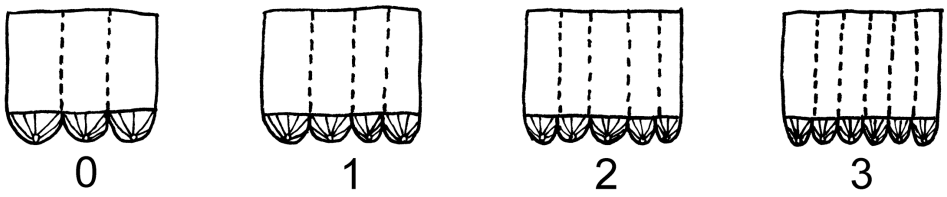
eggs. Crocodilian eggshell exhibits a “blocky” extinction pattern, which consists of “large tabular crystals that extinguish individually” (Moreno-Azanza et al. 2014).

Figure 19. Character 18, states 0, 1, 2.



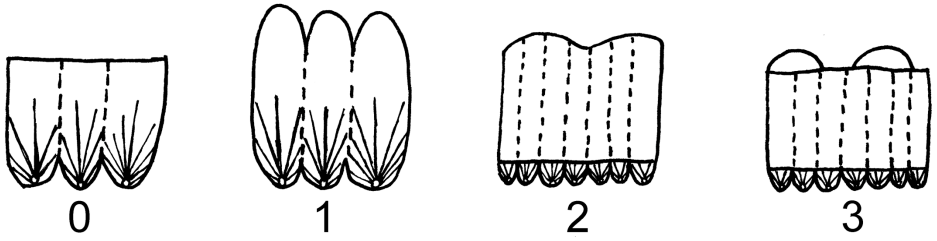
19. Eggshell, nucleation centers, spacing relative to shell thickness: >0.40 (0); 0.33-0.40 (1); 0.24-0.33 (2); <0.24(3) after Varricchio and Jackson (2004) (Figure 20). Measurements for this character were taken using ImageJ software. The spacing of nucleation centers was measured from the center of one organic core to the next, if present. If organic cores are not preserved, then the spacing was measured center-to-center between the lowermost portions of sequential preserved shell units. Thickness was measured from the base of the shell units to the outermost point (including ornamentation) of the shell surface, and averaged.

Figure 20. Character 19, states 0, 1, 2, 3.



20. Eggshell, surface ornamentation: absent (0); present, composed primarily of a single shell unit (1); present, composed of multiple shell units (2); present, not formed by shell units (3) (Figure 21). If only a single shell unit, occasionally with one or two of its neighbors, contributes to the expression of a surficial node, such that the node appears to be an extension of the shell unit, then this character is coded as 'single shell unit.' If multiple shell units extend past their neighbors to contribute to the expression of a single node at the exterior eggshell surface, then this character is coded as 'multiple shell units.' In the emu, the ornamentation is not formed by the shell units (state 3), but instead consists of isolated hillocks of calcite that lack continuity with the underlying shell units.

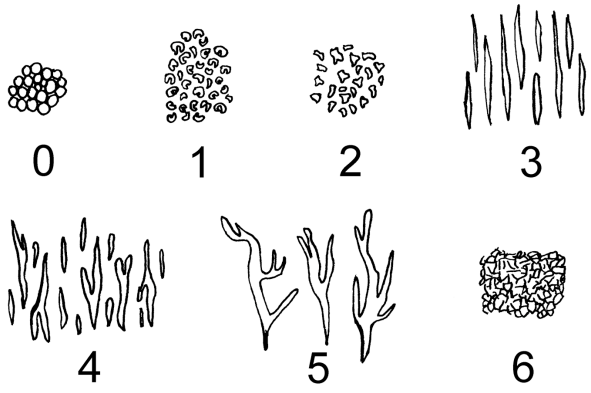
Figure 21. Character 20, states 0, 1, 2, 3.



21. Eggshell, surface ornamentation, type if present and formed by shell units: compactituberculate (0); sagenotuberculate (1); dispersituberculate (2); lineartuberculate (3); ramotuberculate (4); anastomotuberculate (5); irregular (6) (Figure 22). This character describes several types of surface ornamentation (see Carpenter 1999, figure 8.21 for illustrations) considered here as distinct from one another, although further study may show gradation. Thus, care should be taken in assigning ornamentation to one of these categories if it is outside the range of variation for each type as figured by Carpenter (1999). Variation in ornamentation across a single egg, as in many elongatoolithids, is coded as a polymorphism. Further study may suggest that *Maiasaura*

ornamentation is better coded as ramotuberculate or anastomotuberculate, instead of sagenotuberculate, as presented here.

Figure 22. Character 21, states 0, 1, 2, 3, 4, 5, 6.



22. Eggshell, pores, shape in radial section: unbranching (0); branching (1) (Figure 23). Though this character may be difficult to observe in eggshell that also displays branching shell units (see Character 5), in other eggs (e.g. ostrich, see Carpenter 1999, figure 6.13) it is more apparent. Branched pores are nonetheless observed in some members of the Faveoloolithidae, Dendroolithidae, Dictyoolithidae, and Megaloolithidae (*Megaloolithus siruguei*).

Figure 23. Character 22, states 0 and 1.



23. Eggshell, pores, shape in radial section: irregular (0); tubular (1) (Figure 24). Pore margins coded as 'irregular' include both those that are largely tube shaped, but with a rough or undulating interior surface, and those that are wider, irregular, non-tubular cavities within the eggshell (i.e. 'prolatocanaliculate' and 'rimocanaliculate' pore types of Mikhailov 1997a, figure 9). Pore margins coded as 'smooth or tubular' include, but are not limited to, the margins of pore types traditionally referred to as 'angusticanaliculate' and 'tubocanaliculate' by Mikhailov (1997, see figure 9).

Figure 24. Character 23, states 0 and 1.



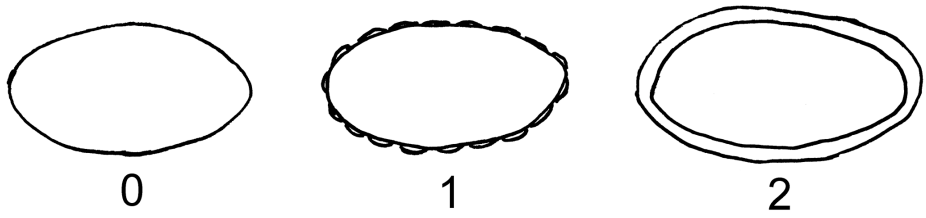
24. Eggshell, pores, orientation to eggshell surface: perpendicular (0); oblique (1) (Figure 25). Pores that are not situated at an angle approximating 90 degrees to the surface are coded as 'oblique.' See Mikhailov (1997, figure 9) for examples of varying pore orientation. For ootaxa (e. g. *Preprismatoolithus*) for which both perpendicular and oblique pores are present, this character is coded as polymorphic.

Figure 25. Character 24, states 0 and 1.



25. Eggs, mechanical properties: soft, no mineralization (0); semi-rigid, discontinuous mineralization (1); rigid, continuous mineralization (2) (Figure 26). Semi-rigid discontinuous mineralization refers to the condition of isolated (not contacting) shell units deposited on a shell membrane. Continuous mineralization refers to the condition in which shell unit margins contact each other across the eggshell. The only non-mineralized egg in this analysis is that of the ornithicheirid pterosaur (Ji et al. 2004, Wang and Zhou 2004).

Figure 26. Character 25, states 0, 1, 2.



26. Eggs, shape: symmetrical about the equator (0); asymmetrical about the equator (1) after Zelenitsky and Therrien (2008a) (Figure 27). Eggs were coded as "symmetrical" or "asymmetrical" on the basis of simple visual inspection. Spherical eggs are scored as "symmetrical about the equator." The symmetry of elongatoolithid eggs remains controversial [see Jin et al. (2007) and references therein, also see López-Martínez and Vicens (2012) for a discussion of the difficulty of using simple egg symmetry distinctions as a phylogenetic character]. Elongatoolithid eggs that appear nearly symmetric, but are too obscured by matrix (Norell et al. 1995) or crushed (Young 1965) to make a clear symmetry determination are herein coded as "symmetrical about the equator" in accordance with Mikhailov (1997a) and Zelenitsky et al. (2000). I consider these eggs to have been likely only weakly asymmetric at most. A previous description

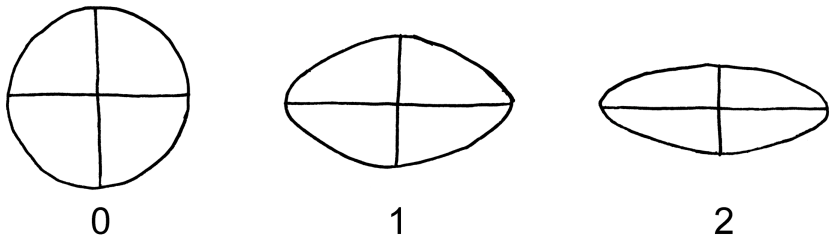
of *Citipati osmolskae* eggs as asymmetrical (Grellet-Tinner et al. 2006) was based on partially crushed Mongolian elongatoolithid eggs (IGM 100/1125) from which a good deal of eggshell is missing from the seemingly more pointed end. Additionally IGM 100/1125 cannot be definitively assigned to *C. osmolskae* on the basis of embryonic remains or an associated adult, nor did Grellet-Tinner et al. (2006) discuss any microstructural comparisons of these eggs with those of *Citipati*. Future detailed examination of *C. osmolskae* and *Macroolithus rugustus* eggs may reveal the same slight asymmetry present in *Macroelongatoolithus* oosp. from the Upper Cretaceous Wayan Formation of Idaho (Simon et al. 2012), potentially necessitating recoding of these eggs as asymmetrical, or the recoding of all weakly asymmetrical eggs as symmetrical.

Figure 27. Character 26, states 0 and 1.



27. Eggs, shape, elongation index (ratio of egg length to width): 1.0-1.5 (0); 1.5-2.0 (1); >2.0 (2) (Figure 28). An extensive list of elongation indices of a range of ootaxa were compiled by Mikhailov (1994a,b) and form the basis for placing the breaks between states of this continuous character. Measurements were compiled from the literature, or personal observation of whole eggs when possible (see Supp. Info. for references and measurements).

Figure 28. Character 27, states 0, 1, 2.



28. Eggs, ratio of actual eggshell thickness to predicted eggshell thickness based on egg mass using an avian regression (Eggshell Thickness Quotient = ETQ): < 0.50 (0); 0.50-1.75 (1); >1.75 (2). Eggshell thickness holds physiological significance as a proxy for pore length, which is one control on gas conductance through the eggshell (Ar et al. 1974, Seymour 1979). Eggshell thickness also affects eggshell breaking strength, and thicker eggshell may have been an adaptation to compensate for the relative weakness of particular microstructures (Sabath 1991). For these reasons, volume-specific shell thickness may vary phylogenetically according to the functional demands imposed by the different types of incubation and microstructure of different taxa. Egg masses were calculated using volumes either obtained from previously calculated values in the literature, or calculated using simple geometric models of spheres and ellipsoids for spherical and elongate eggs, respectively. Dinosaur egg density was assumed to be 1.08 gm/cm^3, a standard avian density calculated from the average of 29 species in Paganelli et al. (1974) with mass data from *Aepyornis* (Jackson et al. 2008) added, using the equation of Paganelli et al. (1974) to calculate density. Average turtle egg density was calculated from the range of mean densities given by Iverson and Ewert (1990). Crocodilian egg density used the value calculated by Varricchio et al. (2008), who used the original data of Ferguson (1985). Data from *Aepyornis* were added to the dataset of Ar and Rahn (1985) to constrain the

upper boundary of the regression line, and the regression equation for shell thickness against mass was recalculated, giving $ST=58.368*M^{0.4218}$, where ST=predicted eggshell thickness, and M=egg mass. The actual eggshell thicknesses were then divided by the predicted values to obtain the ETQ used to code this character. Breaks between character states were determined by visual inspection of a histogram of the ETQ values.

29. **Eggs, ratio of calculated egg mass relative to body size to predicted egg mass relative to body size using an extant avian regression (Egg Mass Quotient = EMQ): small, <0.10 E_b (0); medium, 0.10-0.30 E_b (1); large, >0.30 E_b (2) from Varricchio and Jackson (2004).** E_b is the predicted egg mass for a hypothetical bird of similar adult size to the included taxa, calculated using the allometric equation of Blueweiss et al. (1978), which is based on data from extant taxa. Adult body sizes for extinct taxa with identified eggs were obtained from previous estimates in the literature, which primarily used Anderson et al.'s (1985) method for mass estimation from femur circumference. The exception is *Pterodaustro guinazui*, for which estimated body mass based on a three-dimensional digital model was used (Henderson 2010).
30. **Eggs, pairing: unpaired (0); paired (1) (Figure 29).** Pairing was determined by simple visual estimation of pairing in clutches. Statistical techniques to determine pairing (Varricchio et al. 1997) were not used in the present study, though they provide an avenue for future refinement of this character.
31. **Eggs, orientation of long axis within clutch: subhorizontal (<45 degrees from surface of substrate) (0); subvertical (> or = 45 degrees from surface of substrate) (1); modified after Zelenitsky and Therrien (2008a) (Figure 30).** A simple visual inspection of egg orientation angle was used to code this character.

Figure 29. Character 30, states 0 and 1.

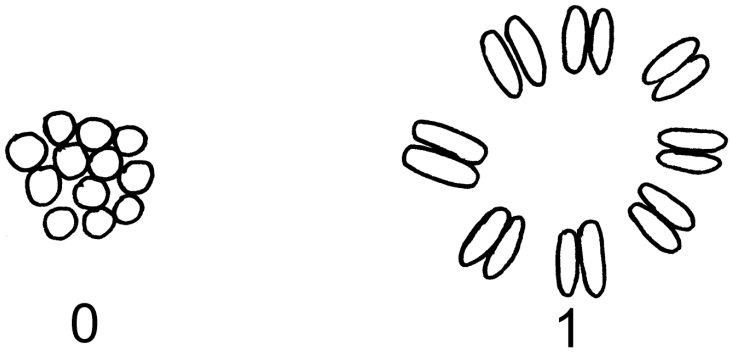


Figure 30. Character 31, states 0 and 1.



32. Eggs, location within nest: unburied (0); partially buried (1); completely buried (2) (Figure 31). "Buried" in states 0 and 1 can refer to either burial within a substrate or underneath a vegetation mound. The mode of burial was inferred from previously published estimates of gas conductance [with high gas conductance values (compared to an avian model) suggesting burial] and on the basis of clutch arrangement and preserved nest traces. Direct observations of nest type from the literature were used to code this character for extant taxa.

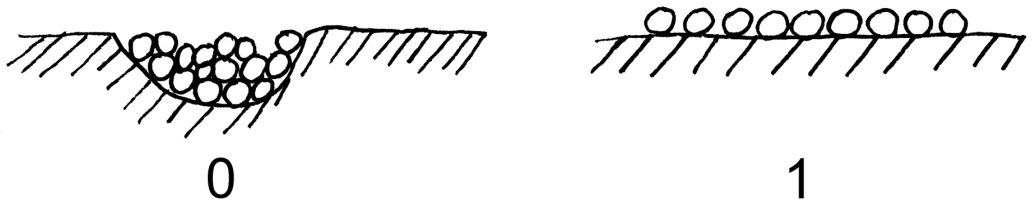
Figure 31. Character 32, states 0, 1, 2.



33. Clutch, contact with adult: absent (0); present (1). Inferences of adult contact for extinct taxa were made on the basis of adults preserved on top of eggs. Inferences of absence of adult contact for taxonomically identified eggs were made on the basis of water vapor conductance evidence for buried eggs and a lack of clutch-associated adults.

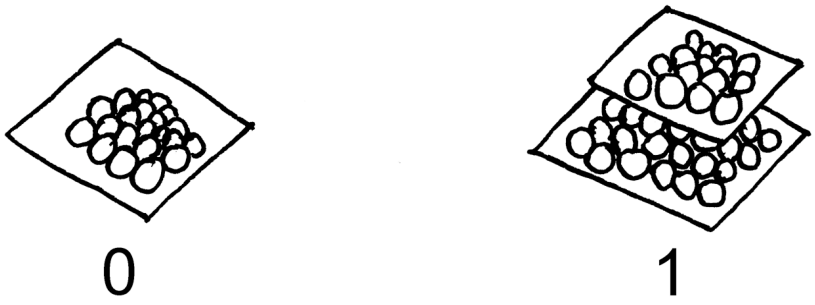
34. Clutch, egg layers: absent (massed) (0); present (1) (Figure 32). If the clutch lacks any kind of planar arrangement and instead appears to conform simply to the shape of its enclosing nest, as in some turtles, then it is scored as State 0. If any planar arrangement(s) of eggs are present, State 1 applies.

Figure 32. Character 34, states 0 and 1.



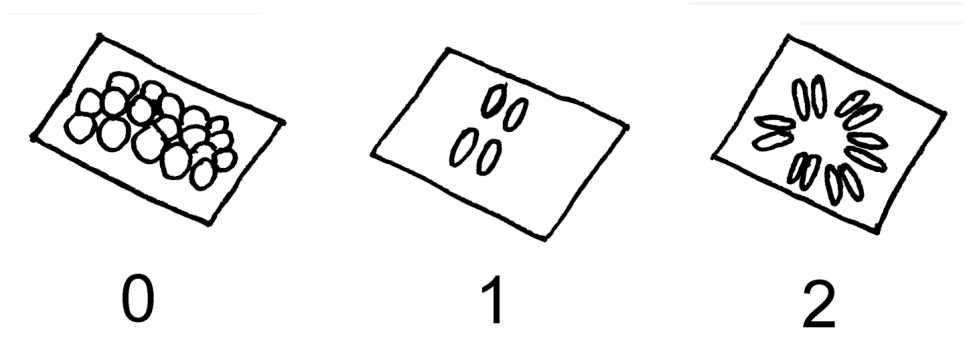
35. Clutch, egg layers, number if present: one (0); two or more (1) (Figure 33). **"**Egg layers" refers to the number of planar arrangements of eggs within the clutch. This character was coded on the basis of visual inspection of clutches.

Figure 33. Character 35, states 0 and 1.



36. Clutch, arrangement of eggs within layers: irregular (0); linear or rectangular (1); ring-shaped with central opening (2) (Figure 34). This character refers to the spatial arrangement of eggs within the plane of each individual layer of a clutch, provided that the clutch possesses layers. 'Irregular' refers to a clutch without a discernible pattern of egg arrangement. 'Linear or rectangular' refers to a layer of eggs that are grouped into repeating rows or columns. 'Ring-shaped' can refer to clutches with any size of roughly circular central opening.

Figure 34. Character 36, states 0, 1, 2.



Description of Taxa and Ootaxa

The following brief descriptions of the taxa and ootaxa included in the current analysis are intended to familiarize the reader with the spatial and temporal occurrences of these egg types, as well as document the material examined and comment on any special considerations involved with the inclusion of each ootaxon. Age and locality data are given for examined material only, and do not necessarily reflect the total spatial and temporal distribution of a given egg type. Readers are encouraged to consult the cited references in this section for further information used to aid in character coding for the taxa and ootaxa in question. Ootaxonomic assignments largely follow those of previous authors, but were examined, and in some cases revised, on a case-by-case basis, as detailed in the comments section for each egg type. For all figures in this section, ML = mammillary layer, CL = continuous or cryptoprismatic layer, and EL = external layer. Institutional abbreviations: AMNH, American Museum of Natural History, New York, New York; CAGS, Chinese Academy of Geological Sciences, Beijing, China; CXMVZA, Chuxiong Prefectural Museum, Chuxiong, China; ES, Department of Earth Sciences, Montana State University, Bozeman, Montana; IGM, Geological Institute, Mongolian Academy of Sciences, Ulanbataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; JZMP, Jinzhou Paleontological Museum, Jinzhou, China; MHIN-UNSL-GEO, Museo de Historia Naturale, Universidad Nacional de San Luis, San Luis, Argentina; ML, Museu da Lourinhã, Portugal; MOR, Museum of the Rockies, Bozeman, Montana; MWC, Museum of Western Colorado, Grand Junction, Colorado; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; RTMP, Royal Tyrell Museum of Paleontology, Drumheller, Alberta; UCM, University of Colorado Museum of Natural History, Boulder, Colorado; ZMNH,

Zhejiang Museum of Natural History, Hangzhou, China; ZPAL, Institute of Paleobiology, Polish Academy of Sciences.

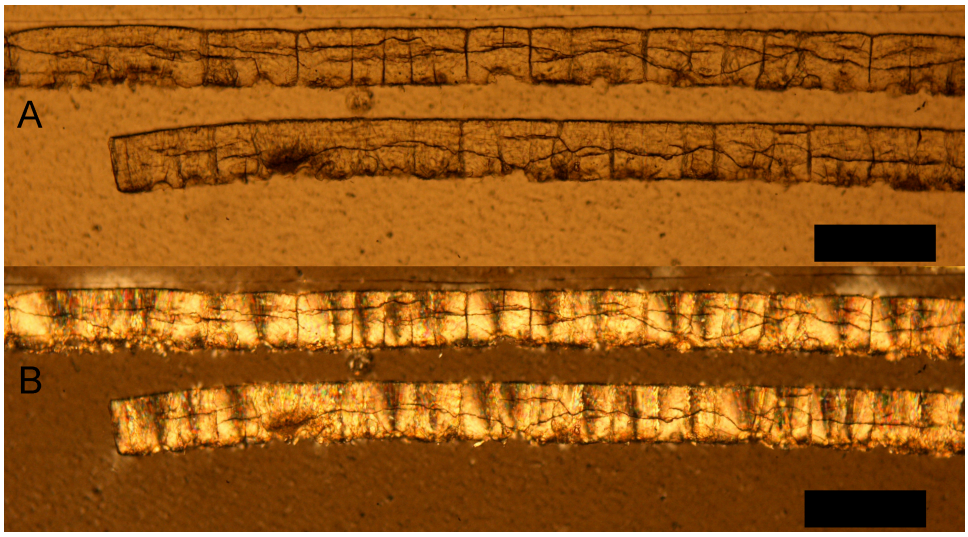
1. *Apalone mutica* LeSueur 1827 (Chelonia) (Figures 35A,B)

Age and Locality: Extant, central United States.

Material Examined: Thin section ES 203. Data on whole eggs and clutches used in coding was obtained from Ernst and Lovich (2009) and Bonin et al. (2006).

Comments: The extant smooth softshell turtle (*Apalone mutica*) is designated as an outgroup for this analysis, along with *Elseya novaeguineae*. Despite controversy over the phylogenetic position of turtles, all studies agree that they are basal to the other archosaur groups included in this study (Hedges 2012), and are designated as such in the outgroup topology.

Figure 35. *Apalone mutica* (ES 203) eggshell under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



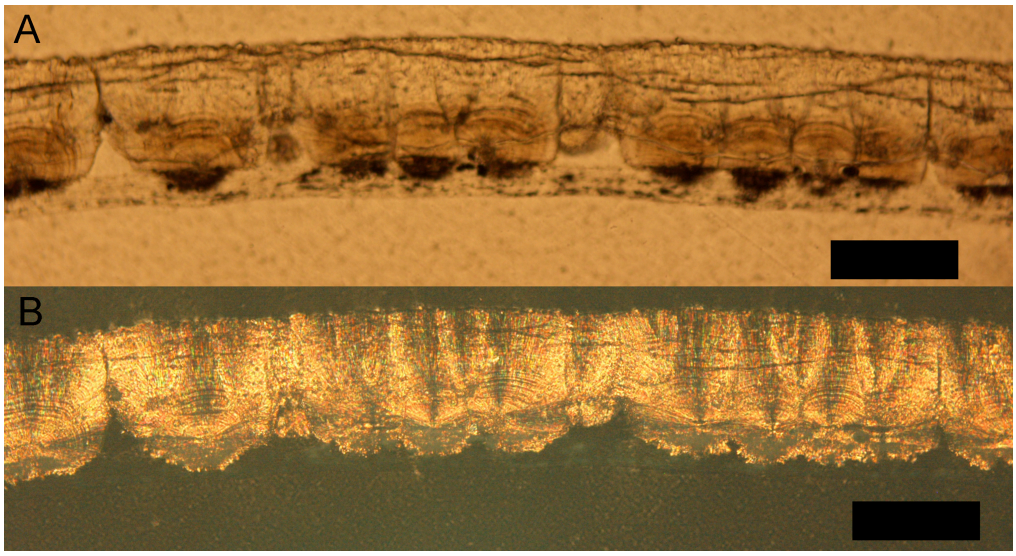
2. *Elseya novaeguineae* Meyer 1874 (Chelonia) (Figures 36A,B)

Age and Locality: Extant, Papua New Guinea and Indonesia.

Material Examined: Thin section ES 194. Data on whole eggs and clutches used in coding was obtained from Bonin et al. (2006).

Comments: The New Guinea snapping turtle (*Elseya novaeguineae*) is designated as part of the outgroup for this analysis.

Figure 36. *Elseya novaeguineae* eggshell (ES 194) under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



3. *Alligator mississippiensis* Daudin 1801 (Archosauria: Crocodilia) (Figures 37A,B)

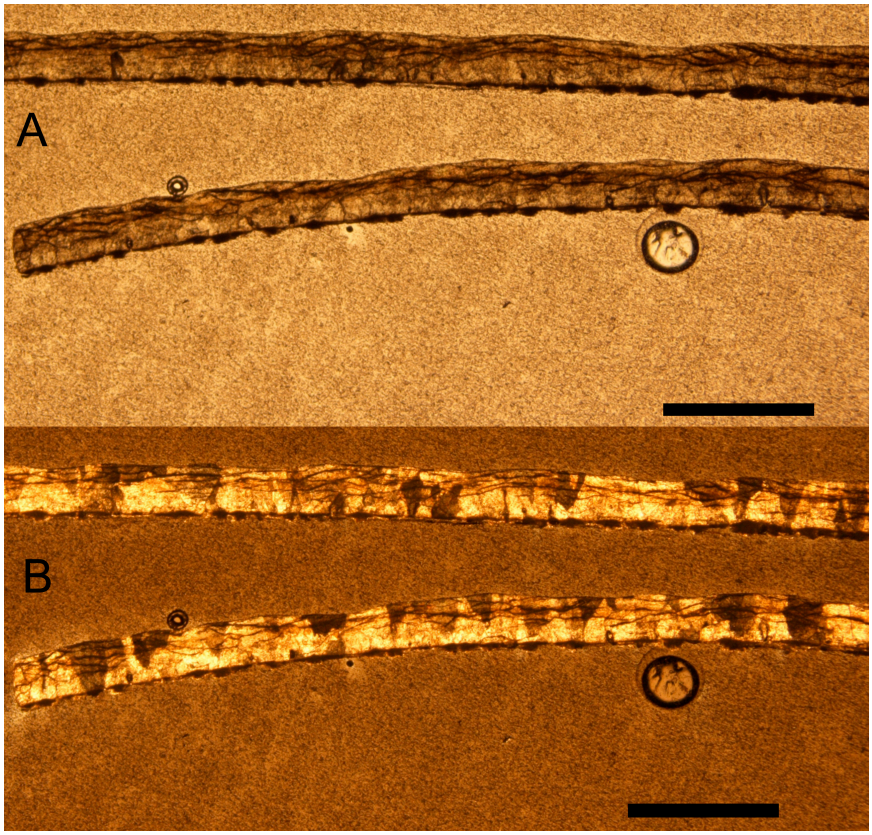
Age and Locality: Extant, southeastern United States

Material Examined: Thin section ES 345. Data on whole eggs and clutches used in coding was obtained from Ferguson (1982) and Deeming and Ferguson (1990).

Comments: Though widely considered by previous authors (Hirsch 1985, Mikhailov 1991, Grellet-Tinner and Chiappe 2004) to possess only a single structural layer, recent studies (Moreno-Azanza et al. 2014, Marzola et al. In press) have confirmed the presence of up to three structural layers of calcite within crocodilian eggshell, as originally noted by Ferguson

(1982) (though he included the eggshell membrane as a layer, and split the middle layer into two separate layers, for a total of five), and coded for cladistic analysis by Varricchio and Jackson (2004). The question of the homology of these structural layers to those seen in non-avian dinosaurs and birds calls for further developmental, ultrastructural, and biochemical investigation that is outside the scope of the current study. *Alligator mississippiensis* forms part of the outgroup for this study.

Figure 37. *Alligator mississippiensis* eggshell (ES 345) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



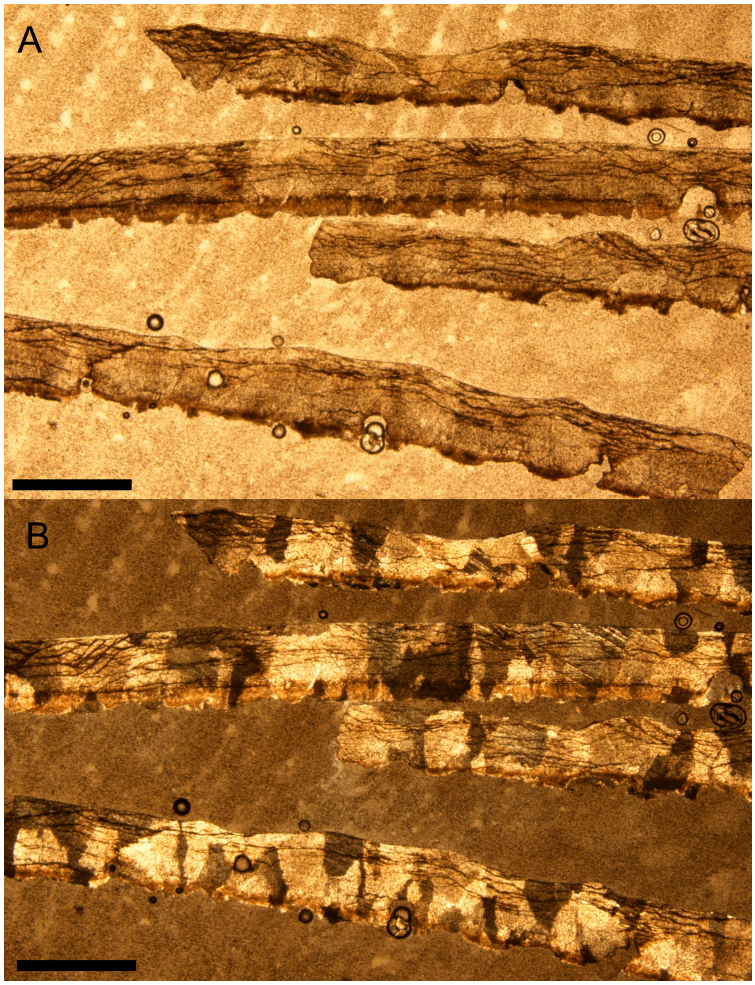
4. *Crocodylus niloticus* Laurenti 1768 (Archosauria: Crocodilia) (Figures 38A,B)

Age and Locality: Extant, Africa.

Material Examined: Thin section ES 343. Data on whole eggs and clutches used in coding was obtained from Hirsch and Kohring (1992).

Comments: See comments for *A. mississippiensis* above. *Crocodylus niloticus* is part of the outgroup for this analysis.

Figure 38. *Crocodylus niloticus* eggshell (ES 343) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



5. *Pterodaustro guinazui* Bonaparte 1969 (Archosauria: Pterosauria)

Age and Locality: Lower Cretaceous Lagarcito Formation, central Argentina.

Material Examined: Coded from data on MHIN-UNSL-GEO V246 presented by Chiappe et al. (2004), Grellet-Tinner et al. (2007), and Unwin and Deeming (2008).

Comments: The identification of this egg as *Pterodaustro* is based on the occurrence of a *Pterodaustro* embryo in the only known egg of this type (Chiappe et al. 2004). *Pterodaustro guinazui* is part of the outgroup for this study.

6. Ornithocheiridae Seeley 1870 (Archosauria: Pterosauria)

Age and Locality: Lower Cretaceous Yixian Formation, Jingangshan, Liaoning Province, China.

Material Examined: Coded from data on IVPP V13758 and JZMP 03-03-2 presented by Wang and Zhou (2004), Ji et al. (2004), and Unwin and Deeming (2008).

Comments: These two eggs both contain embryos that are identified to Ornithicheiridae (probably the same taxon for both) by Wang and Zhou (2004) and Unwin and Deeming (2008). I follow Unwin and Deeming's (2008) assignment of JZMP 03-03-2 to an ornithocheirid, rather than the tentative assignment to *Beipiaopterus* by Ji et al. (2004). As the only presumably soft-shelled egg included in this analysis, many character states are coded as inapplicable ("-") for this taxon. The ornithocheirid forms part of the outgroup for this study.

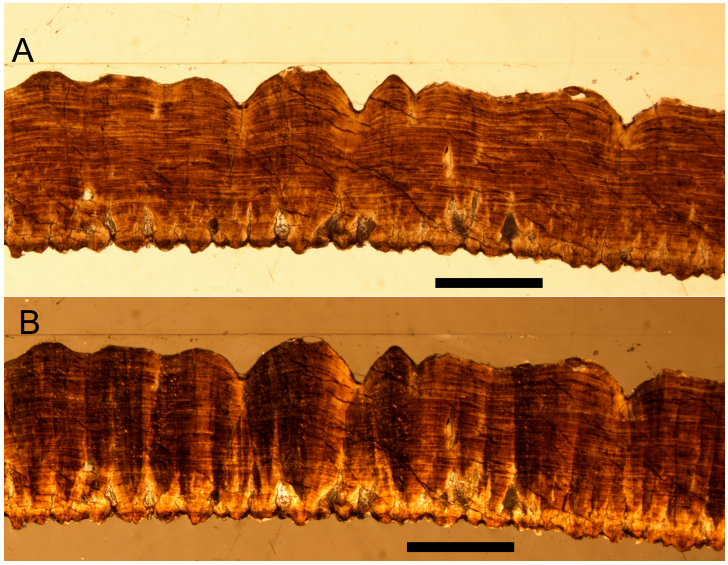
7. *Maiasaura peeblesorum* Horner and Makela 1979 (Oospecies *Spheroolithus* oosp. Zhao 1979) (Dinosauria: Ornithischia) (Figures 39A,B)

Age and Locality: Upper Cretaceous Two Medicine Formation, Willow Creek Anticline, Montana, United States.

Material Examined: Thin section ES 333. I used additional thin section, SEM, and whole egg and clutch data presented by Hirsch and Quinn (1990), as well as personal examination of clutch MOR 281 to aid in coding this taxon. Gas conductance values for *S. albertensis* from Deeming (2006) and Oser (unpubl.) were used as proxies for *M. peeblesorum*, as both of these eggshell types are quite similar to *M. peeblesorum* in microstructure and pore shape.

Comments: The examined thin section is assigned to *Maiasaura* because it is almost identical to the material associated with hatchling *Maiasaura* bones examined by Hirsch and Quinn (1990). Despite previous authors' assignments of *M. peeblesorum* eggshell to *Spheroolithus albertensis* (Jackson and Varricchio 2010), I note that Zelenitsky and Hills (1997), who provide the only diagnosis of *S. albertensis*, did not formally assign the eggs of *M. peeblesorum* to this oospecies. Horner (1999) assigned *Maiasaura* eggs to the oospecies *Spheroolithus maiasauroides* from the Upper Cretaceous of Mongolia, but differences in surface ornamentation and calculated egg size between *Maiasaura* and *S. maiasauroides* (Mikhailov 1994b) call into question this assignment. Until a more thorough review of all *Spheroolithus* oospecies is completed, I choose to assign the eggs of *M. peeblesorum* to *Spheroolithus* oosp.

Figure 39. *Maiasaura peeblesorum* (*Spheroolithus* oosp.) eggshell (ES 333) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



8. *Hypacrosaurus stebingeri* Horner and Currie 1994 (Dinosauria: Ornithischia)

Age and Locality: Upper Cretaceous Two Medicine Formation, Landslide Butte and Blacktail Creek localities, Montana; Upper Cretaceous Oldman Formation, Devil's Coulee locality, Alberta, Canada.

Material Examined: SEM images of RTMP 1987.079.0085 figured by Grellet-Tinner and Chiappe (2004) and clutch and whole egg data from Horner and Currie (1994) and Horner (1999) were utilized in coding.

Comments: These eggs are assigned to *Hypacrosaurus stebingeri* on the basis of embryos *in ovo* (Horner and Currie 1994). Tazaki et al. (1994) describe *Hypacrosaurus* eggshell as having two structural layers; however, given the highly diagenetically altered nature of the specimens (Grellet-Tinner and Chiappe 2004, Jackson and Varricchio 2010), I choose to code *Hypacrosaurus* eggshell as "?" for most microstructural characters until a detailed reexamination of eggshells from more specimens can be

made. Araújo et al. (2013) state that *Hypacrosaurus* eggshell does not possess individualized shell units. Such an assertion is not tenable given the recrystallization of the eggshell, which indeed obscures any shell unit boundaries that may have been present originally.

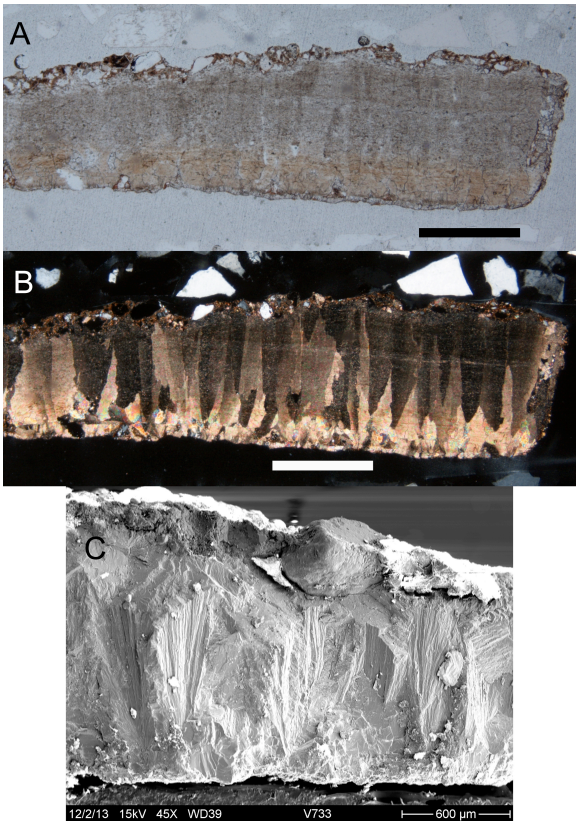
9. *Spheroolithus irenensis* Zhao and Jiang 1974 (Oofamily Spheroolithdae) (Figures 40A,B,C)

Age and Locality: Upper Cretaceous Wangshi Group, Laiyang, Shandong Province, China.

Material Examined: Thin section and SEM stub for IVPP V733 (material housed in PIN collections). Whole egg and clutch data presented by Young (1954) and Zhao and Jiang (1974) were used to code relevant characters.

Comments: Though often assigned to hadrosauroids on the basis of co-occurrence at the same localities as adult *Tanius* and *Bactrosaurus* remains (Young 1954, Zhao and Jiang 1974), I feel that this is not strong enough evidence to warrant assignment of *Spheroolithus irenensis* to any particular dinosaur genus.

Figure 40. *Spheroolithus irenensis* eggshell (IVPP V733) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 1 mm. Scale bar for (C) equals 0.6 mm.



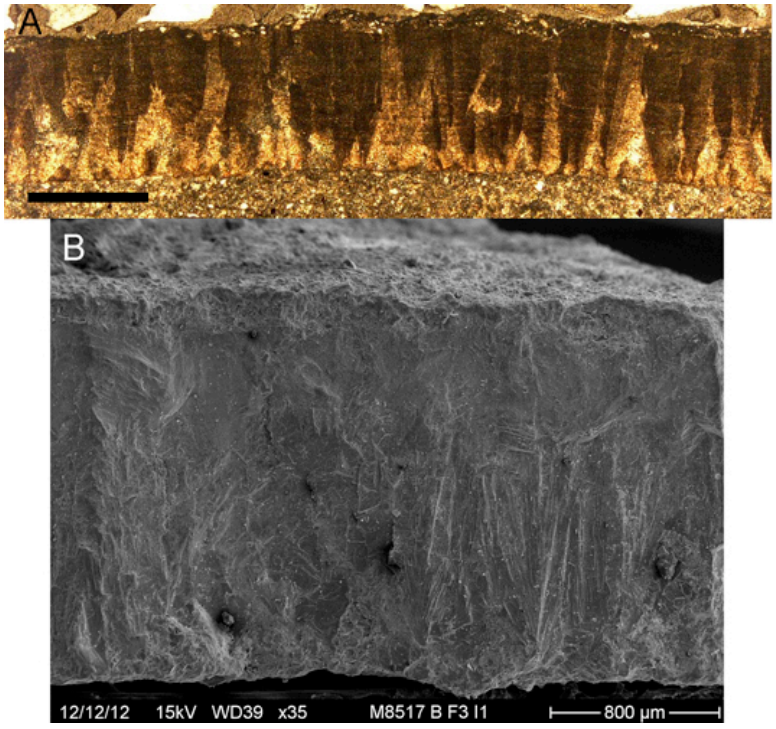
10. *Spheroolithus* cf. *zhangtoucaoensis* Fang, Wang, and Jiang 2000 (Oofamily Spheroolithidae) (Figures 41A,B,C)

Age and Locality: Upper Cretaceous Liangtoutang and Chichengshan Formations, Tiantai basin, Zhejiang Province, China.

Material Examined: Thin sections ZMNH M8517F, M8535 D2 and M8572 D1 E and SEM stubs ZMNH M8517 B and M8517 D1 C. Barta et al. (2014, also see supplementary information) provide a list of whole eggs and clutches used in coding.

Comments: See Barta et al. (2014) for further description and a discussion of the referral of these eggs to *Spheroolithus* cf. *zhangtoucaoensis*. No embryo, hatchling, or adult associations are known for this oospecies.

Figure 41. *Spheroolithus* cf. *zhangtoucaoensis* eggshell under crossed polars (A, M8517 F) and SEM (B, M8517 B). Scale bar for (A) equals 1 mm. Scale bar for (B) equals 0.8 mm.



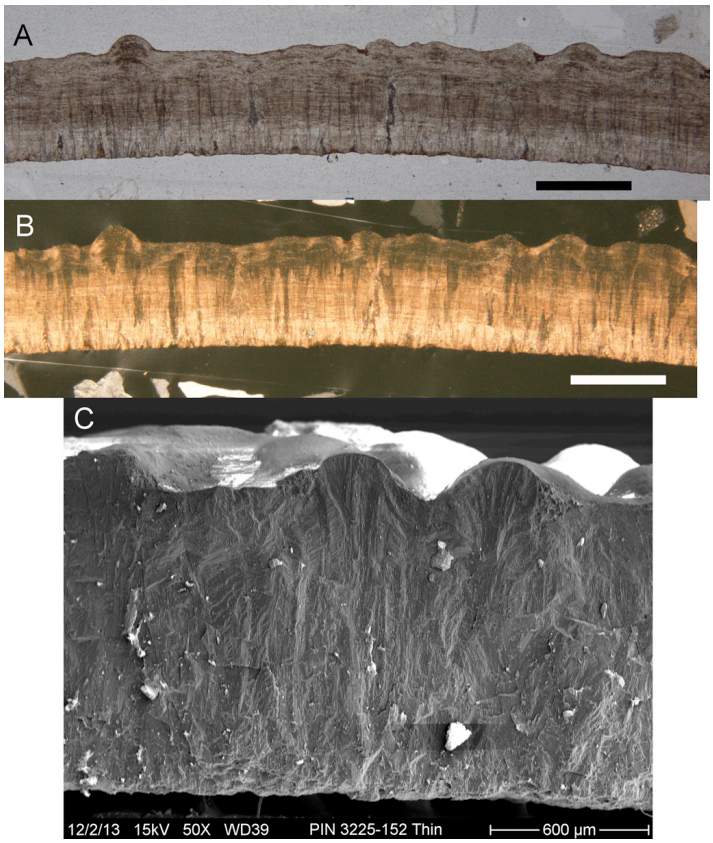
11. *Ovaloolithus chinkangkouensis* Zhao and Jiang 1974 (Oofamily Ovaloolithidae) (Figures 42A,B,C)

Age and Locality: Upper Cretaceous Bayn-Shireh Formation, Dariganga locality, Mongolia

Material Examined: Thin section and SEM stub of PIN 3225-152. Additional whole egg measurements were obtained from Mikhailov (1994b).

Comments: Similarities with the Spheroolithidae and co-occurrence of Ovaloolithidae with hadrosaurs at some localities led Mikhailov (1997) to tentatively posit an ornithopod identify; however, no identifiable embryonic bones are known from ovaloolithid eggs. See Sochava (1972) for description of unidentifiable embryonic bones (nevertheless identified as likely belonging to a "horned dinosaur" similar to *Leptoceratops* or *Protoceratops*) associated with an ovaloolithid egg.

Figure 42. *Ovaloolithus chinkangkouensis* eggshell (PIN 3225-125) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 1 mm. Scale bar for (C) equals 0.6 mm.



12. *Massospondylus* Owen 1854 (Dinosauria: Saurischia)

Age and Locality: Lower Jurassic Upper Elliot Formation, Rooidraai locality, South Africa.

Material Examined: Data on whole eggs and clutches were obtained from Reisz et al. (2005, 2010, 2012). SEM images of eggshell microstructure were obtained from Grine and Kitching (1987) and Zelenitsky and Modesto (2002).

Comments: These eggs are identified as belonging to *Massospondylus* based on embryos *in ovo* (Reisz et al. 2005). The eggshell is heavily diagenetically altered (Zelenitsky and Modesto 2002), and is thus coded as "?" for most microstructural characters.

13. *Lufengosaurus* Young 1941 (Dinosauria: Saurischia)

Age and Locality: Lower Jurassic Lower Lufeng Formation, Dawa locality, Lufeng County, Yunnan Province, China.

Material Examined: Specimen CXMVZA C2019 2A233 was coded from data presented by Reisz et al. (2013, including supplementary information).

Comments: This egg type is tentatively referred to *Lufengosaurus* on the basis of its close association with embryonic bones (Reisz et al. 2013) and is known only from eggshell fragments.

14. Titanosauria Bonaparte and Coria 1993 (Oospecies *Megaloolithus patagonicus* Calvo, Engelland, Heredia, and Salgado 1997) (Dinosauria: Saurischia) (Figures 43A,B)

Age and Locality: Upper Cretaceous Anacleto Formation, Auca Mahuevo locality, Argentina.

Material Examined: Thin section ES 328. Thin section, SEM, and whole egg and clutch data from Chiappe et al. (1998), Jackson et al. (2008), and Sander et al. (2008) were used to aid in coding some characters.

Comments: These eggs are assigned to a titanosaur on the basis of embryos *in ovo* (Chiappe et al. 1998).

Figure 43. Titanosaur (*Megaloolithus patagonicus*) eggshell (ES 328) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



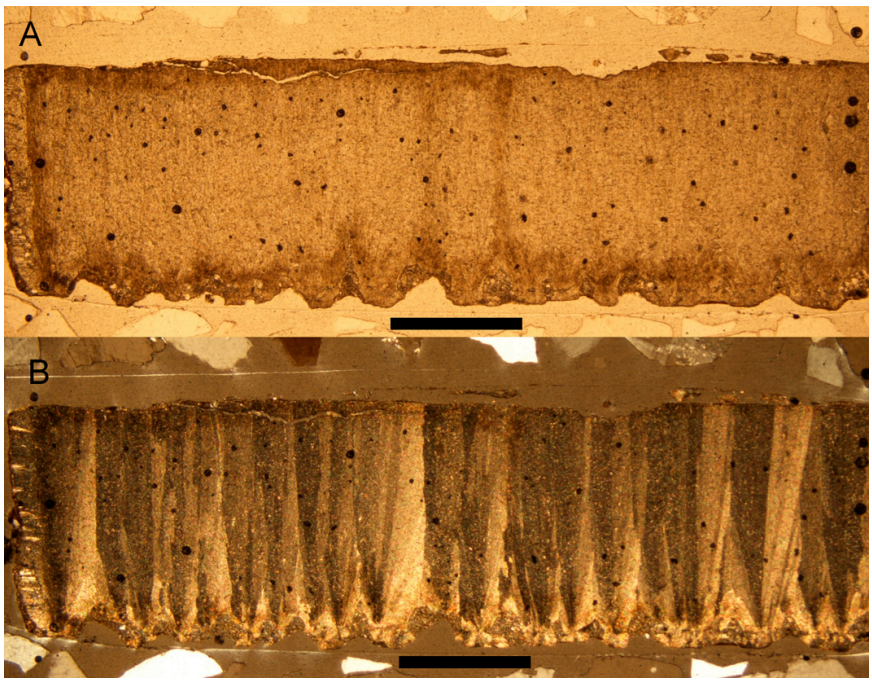
15. *Cairanoolithus dughii* Vianey-Liaud, Mallan, Buscail, and Montgelard 1994 (Oofamily Megaloolithidae) (Figures 44A,B)

Age and Locality: Upper Cretaceous Renne-les Chateau locality, France.

Material Examined: Thin section ES 318. Thin section and whole egg and clutch data from Williams et al. (1984), Vianey-Liaud et al. (1994) and Vianey-Liaud et al. (2003) were used to aid in coding some characters.

Comments: Sellés (2012) reasonably suggests that *Cairanoolithus* belongs to an oofamily distinct from other megaloolithids; however, in deference to him until the name of the oofamily is published, I here retain the original megaloolithid assignment of Vianey-Liaud et al. (1994).

Figure 44. *Cairanoolithus dughii* eggshell (ES 318) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



16. *Megaloolithus* cf. *mammilare* Vianey-Liaud, Mallan, Buscail, and Montgelard 1994 (Oofamily Megaloolithidae) (Figures 45A,B)

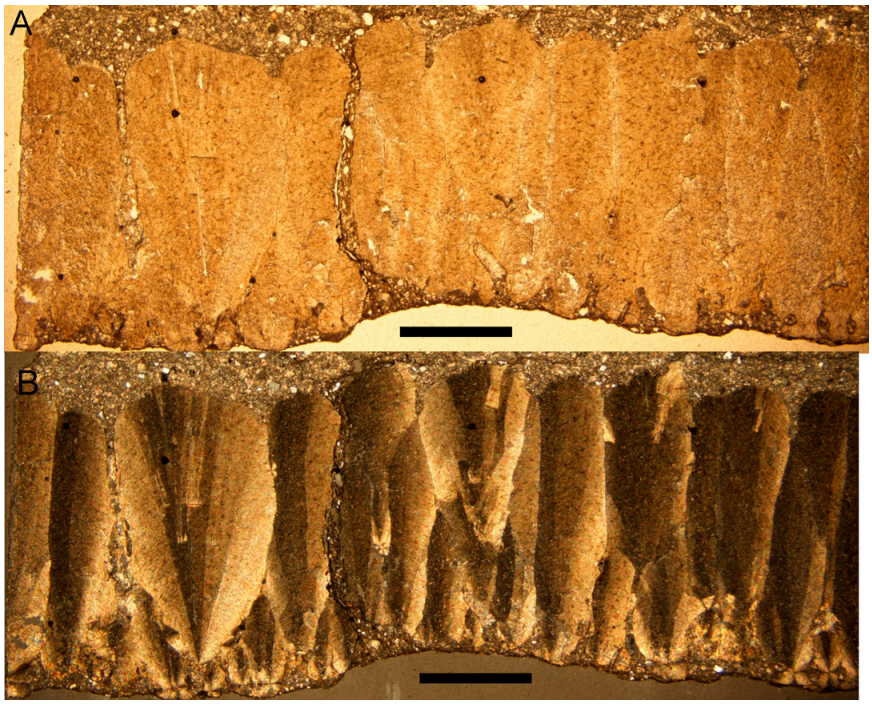
Age and Locality: Upper Cretaceous Tremp Formation, Coll de Nargo locality, Spain.

Material Examined: Thin section ES 317. Thin section and whole egg and clutch data from Vianey-Liaud et al. (2003) and Sander et al. (2008) were used to aid in coding some characters.

Comments: As this eggshell is slightly thicker than the shell thickness range given as diagnostic of *M. mammilare* by Vianey-Liaud et al. (1994),

but is more similar to it than to other *Megaloolithus* oospecies in all other respects [also see Sander et al. (2008) for an argument in favor of the synonymy of all Catalan *Megaloolithus* oospecies with *M. mammilare*], this eggshell is here designated *Megaloolithus* cf. *mammilare*, to indicate a slightly uncertain referral.

Figure 45. *Megaloolithus* cf. *mammilare* eggshell (ES 317) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



17. *Faveoloolithus ningxiaensis* Zhao and Ding 1976 (Oofamily Faveoloolithidae) (Figures 46A,B)

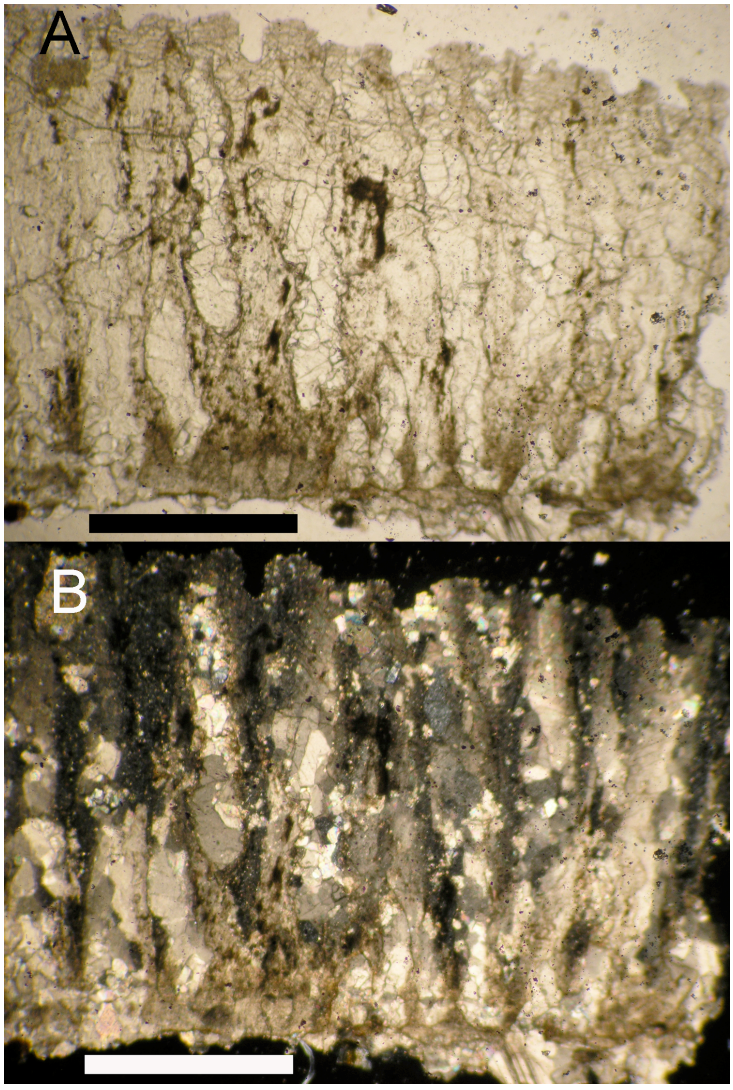
Age and Locality: Upper Cretaceous Barun Goyot Formation, Ikh-Shunkht locality, Mongolia. [Also see Mikhailov et al. (1994) for a possible Lower Cretaceous occurrence at the Algui-Ulan Tsav locality.]

Material Examined: Thin section and SEM stub for PIN 4477-5, thin section ZPAL MgOv-III/18b; Additional whole egg data and gas

conductance values were obtained from Sabath (1991), Mikhailov (1994b), and Mikhailov et al. (1994).

Comments: Mikhailov (1991) tentatively assigned Faveoloolithidae to sauropod dinosaurs on the basis of large egg size and inferred nesting mode. However, such an identification must remain tentative, as no embryonic or hatchling associations are yet known for this oofamily.

Figure 46. *Faveoloolithus ningxiaensis* eggshell (ZPAL MgOv-III/18b) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



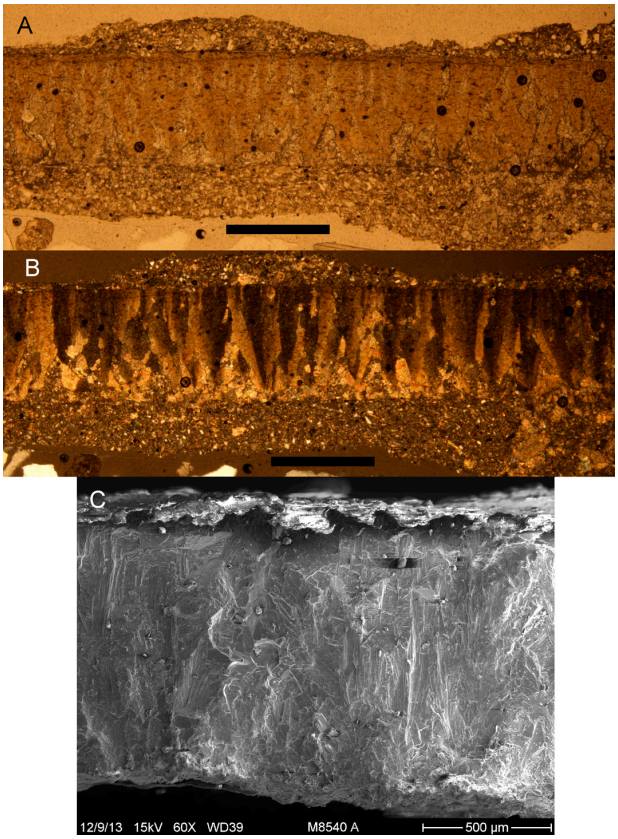
18. *Faveoloolithus* oosp. Zhao and Ding 1976 (Figures 47A,B,C)

Age and Locality: Upper Cretaceous lower Liangtoutang Formation, Tiantai basin, Zhejiang Province, China.

Material Examined: Thin sections ZMNH M8540-2 and M8540-D4 G and SEM stub ZMNH M8540. Additional whole egg measurements were obtained from Jin (2009).

Comments: Jin (2009) named this *Faveoloolithus* oospecies in his unpublished dissertation, but this name remains unpublished, so the specimens are herein referred simply to *Faveoloolithus oosp*.

Figure 47. *Faveoloolithus* oosp. eggshell under plain light (A, ZMNH M8540-D4 G), crossed polars (B, ZMNH M8540-D4 G), and SEM (C, ZMNH M8540 A). Scale bars for (A) and (B) equal 1 mm. Scale bar for (C) equals 0.5 mm.



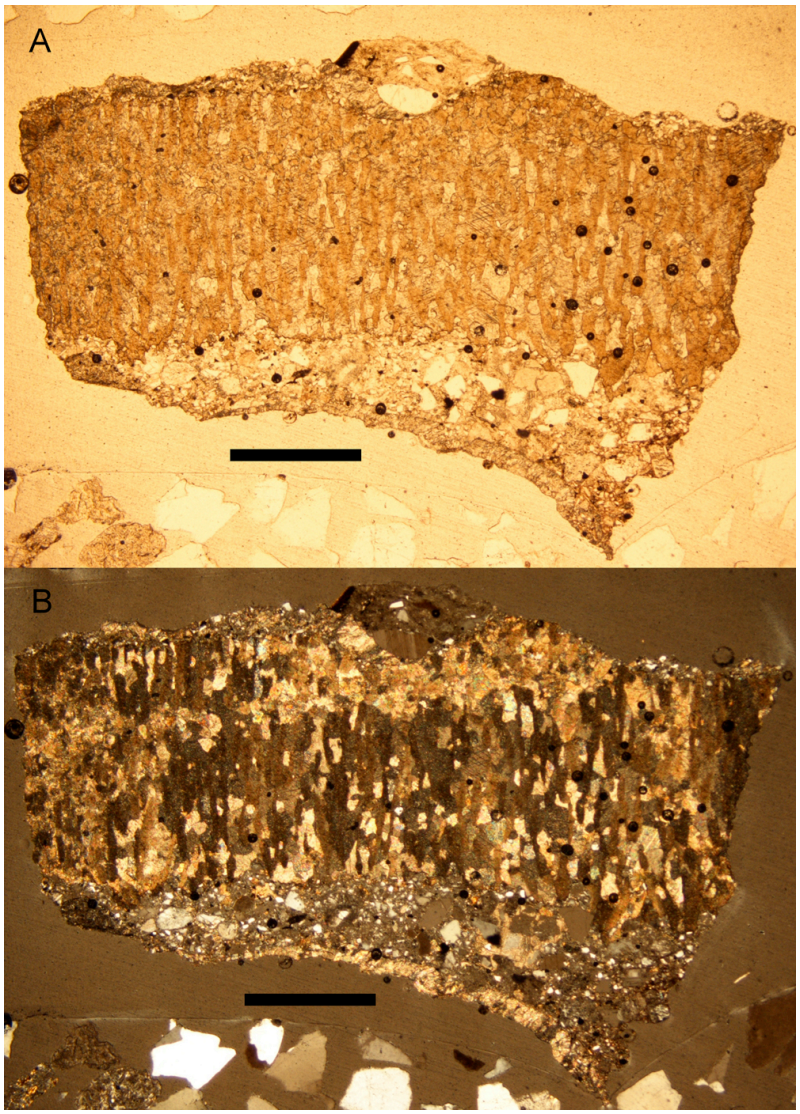
19. *Dictyoolithus hongpoensis* Zhao 1994 (Oofamily Dictyoolithidae) (Figures 48A,B)

Age and Locality: Upper Cretaceous Fangyan Formation, Xianju County, Zhejiang Province, China, and Upper Cretaceous Chichengshan Formation, Lishui basin, Zhejiang Province, China.

Material Examined: Thin section ES 324 from ZMNH uncatalogued specimen. Additional data obtained from Jin et al. (2010).

Comments: Though Jin et al. (2010) tentatively identified a possible "structural transition" in the lowermost one-fifth of radial sections of *D. hongpoensis* eggshell, reexamination of the innermost of the two possible structural layers shows that only a single layer of calcite is present. Personal observation by the author suggests that the appearance of a structural transition between the two layers is caused by the greater prevalence of secondary calcite-filled pore spaces in the innermost part of the eggshell, causing this part to appear brighter than the overlying "layer" when viewed under crossed polars (Jin et al. 2010, Figure 3A,B). No demarcation between layers is observed under plane polarized light or SEM, or under crossed polars in a different thin section (ES 324); thus, *D. hongpoensis* is coded as possessing a single structural layer in this analysis.

Figure 48. *Dictyoolithus hongpoensis* eggshell (ES 324, ZMNH uncatalogued) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



20. *Dendroolithus verrucarius* Mikhailov 1994b (Oofamily Dendroolithidae) (Figures 49A-C)

Age and Locality: Upper Cretaceous Barun Goyot Formation, Khermeen-Tsav locality, Mongolia.

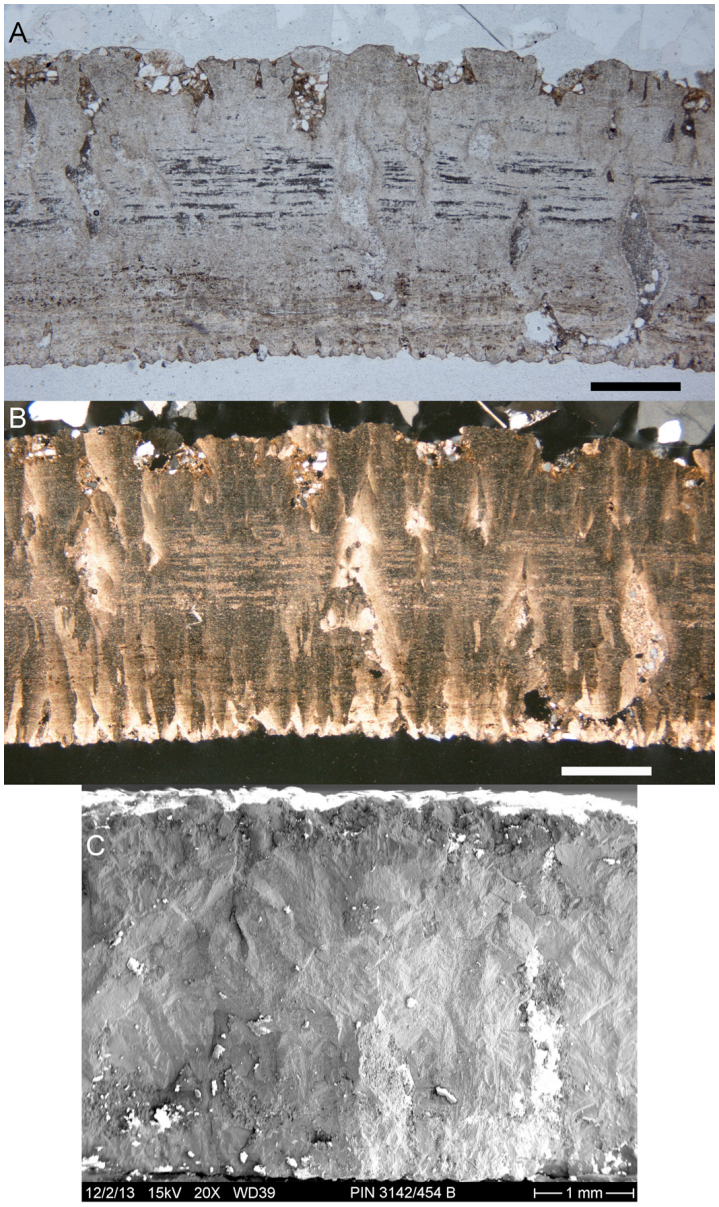
Material Examined: Thin section and SEM stub PIN 3142/454.

Additional data obtained from Mikhailov (1994b) and Mikhailov et al.

(1994). An estimation of gas conductance was obtained from Sabath (1991).

Comments: See comments for Character 5 for a discussion and reinterpretation of Mongolian dendroolithid eggshell structure.

Figure 49. *Dendroolithus verrucarius* eggshell (PIN 3142/454) under plain light (A), crossed polars (B), and SEM (C). Scale bars equal 1 mm.



21. *Dendroolithus microporosus* Mikhailov 1994b (Oofamily Dendroolithidae)

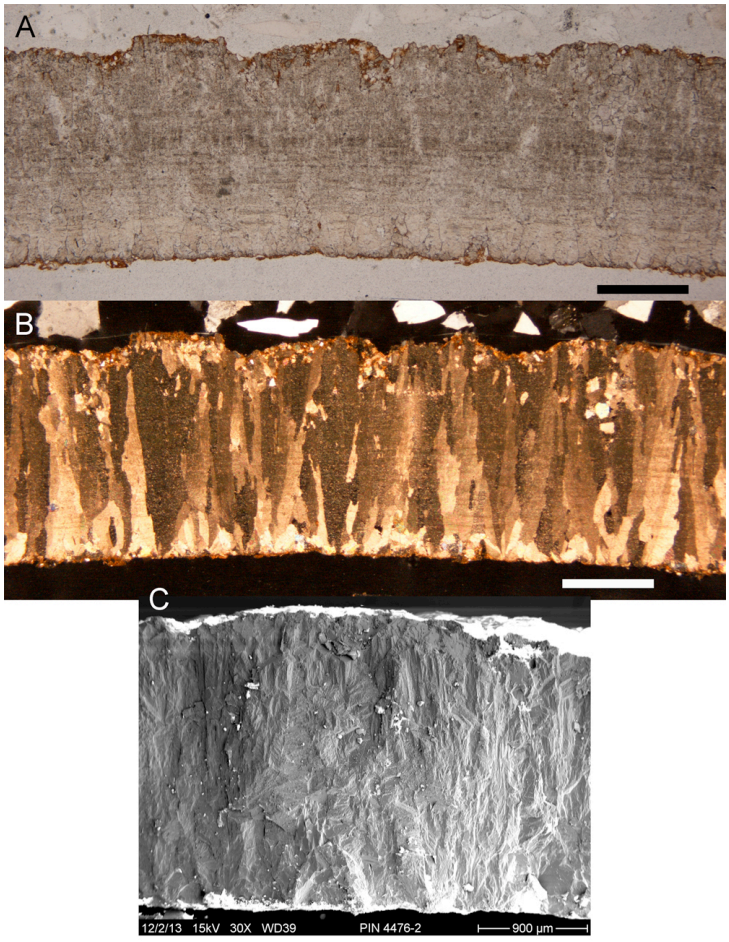
(Figures 50A,B,C)

Age and Locality: Upper Cretaceous ?Barun Goyot Formation, Shilyust-Ula locality, Mongolia.

Material Examined: Thin section and SEM stub PIN 4776-2. Whole egg measurements were obtained from PIN 4476-1 (a nearly complete egg).

Comments: See comments for Character 5 for a discussion and reinterpretation of Mongolian dendroolithid eggshell structure.

Figure 50. *Dendroolithus microporosus* eggshell (PIN 4776-2) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 1 mm. Scale bar for (C) equals 0.9 mm.



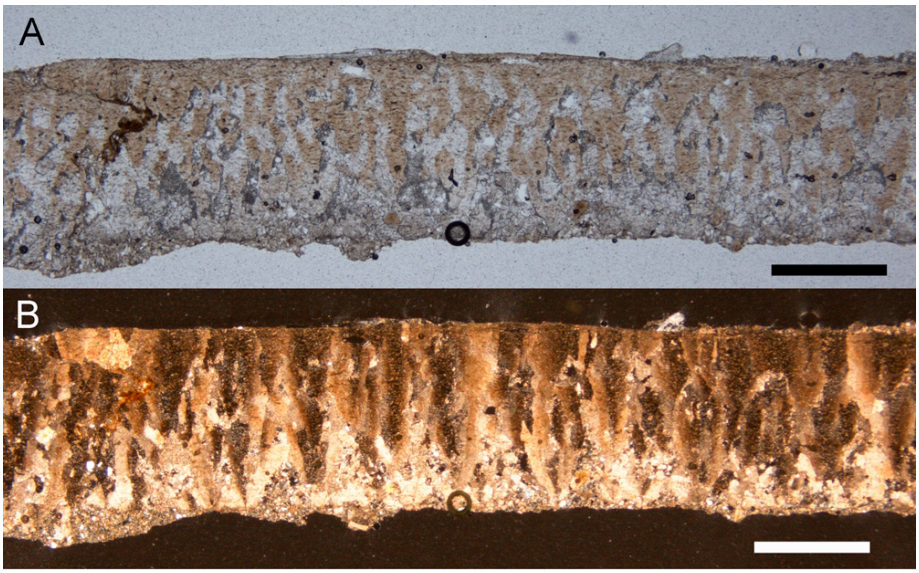
22. *Dendroolithus xichuanensis* Zhao and Zhao 1998 (Oofamily Dendroolithidae) (Figures 51A,B,C)

Age and Locality: Upper Cretaceous Liangtoutang Formation, Tiantai basin, Zhejiang Province, China.

Material Examined: Thin section ZMNH M8690. Whole egg measurements obtained from personal examination and Jin (2009).

Comments: *Dendroolithus xichuanensis* was originally named by Zhao and Zhao (1998) for eggshell fragments from the Gaogou Formation in Henan Province. Jin (2009) assigns the studied Zhejiang specimens to this oospecies and provides further description.

Figure 51. *Dendroolithus xichuanensis* eggshell (ZMNH M8690) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



23. *Torvosaurus gurneyi* Hendrickx and Mateus 2014 (Oofamily Dendroolithidae) (Dinosauria: Saurischia)

Age and Locality: Upper Jurassic Lourinhã Formation, Porto das Barcas locality, Portugal.

Material Examined: Specimen ML1188 was coded from data presented by Araújo et al. (2013), including supplementary information) and from specimen ML1842 (Ribeiro et al. 2014).

Comments: These eggs are assigned to *Torvosaurus* on the basis of a clutch mingled with embryonic bones, and were further assigned to *Torvosaurus gurneyi* by Hendrickx and Mateus (2014). I choose to use the oofamily name Dendroolithidae for these eggs in accordance with Araújo et al. (2013) instead of the potentially synonymous (but earlier) name Phaceloolithidae used by Ribeiro et al. (2014). I do this because Zeng and Zhang (1979) only briefly described and did not figure Phaceloolithidae in the paper that diagnosed this oofamily. Additionally, most subsequent authors have used Dendroolithidae (Zhao and Li 1988) in preference to Phaceloolithidae, and Mikhailov (1997a) did not consider the two oofamilies synonymous.

24. Therizinosauroidea Maleev 1954 (Oofamily Dendroolithidae) (Dinosauria: Saurischia) (Figures 52A-C)

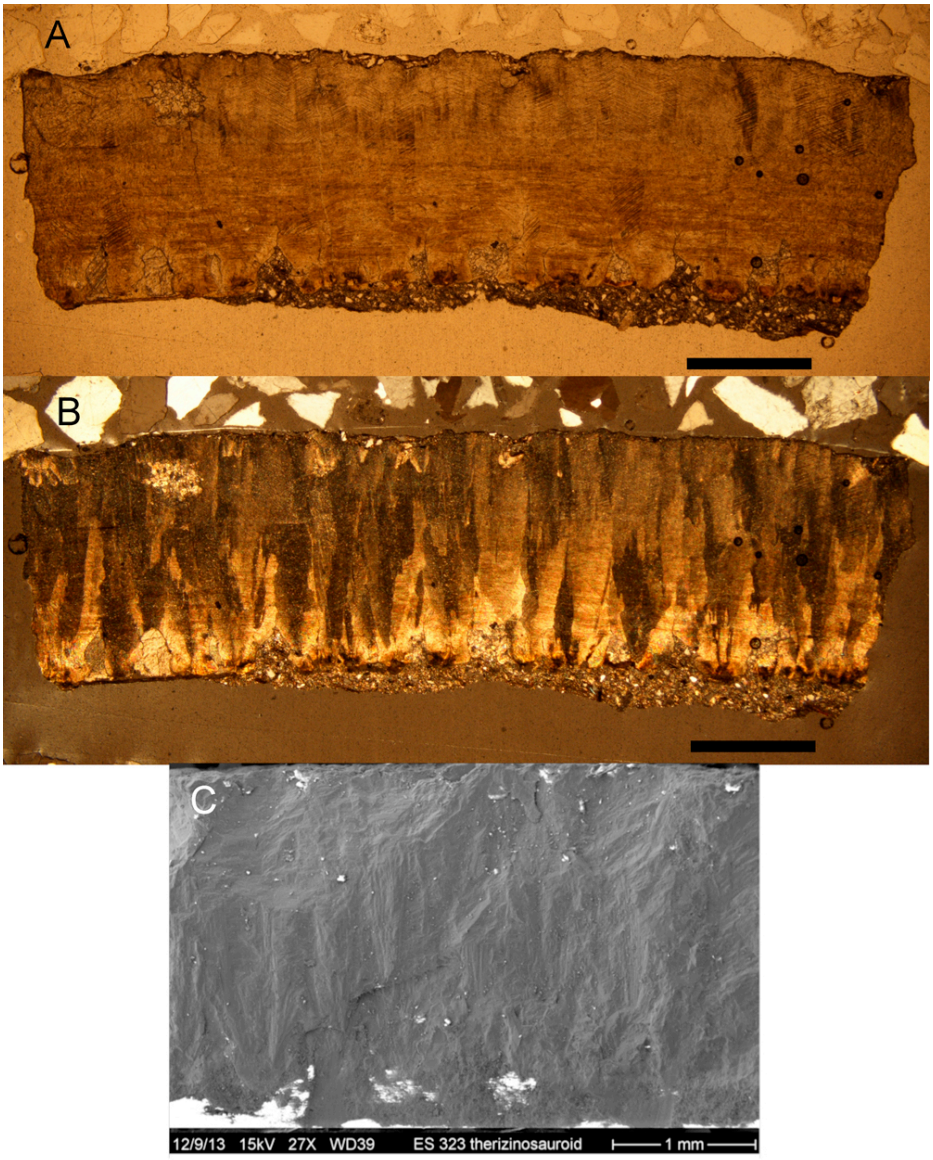
Age and Locality: Upper Cretaceous Nanchao Formation, Henan Province, China.

Material Examined: Thin section and SEM stub for ES 323 (from CAGS unnumbered fragment) and thin sections UCM 777-1 and 777-2. Both thin sections were lapped to 50 μm instead of the standard 30 μm. Whole egg measurements and clutch data were taken from Kundrát et al. (2005, 2008).

Comments: These eggs are identified as therizinosauroid on the basis of embryos *in ovo* (Kundrát et al. 2008). Though assigned to Dendroolithidae by Mikhailov (1997a), Zelenitsky (2004) and Barta et al.

(2014) described some similarities between this eggshell and the Spheroolithidae. M. Kundrát and colleagues are conducting a full description of this eggshell (Kundrát pers. comm.). See comments for Character 5 above for a reinterpretation of Mongolian dendroolithid and therizinosauroid eggshell structure.

Figure 52. Therizinosauroid (Dendroolithidae) eggshell (ES 323 from CAGS unnumbered specimen) under plain light (A), crossed polars (B), and SEM (C). Scale bars equal 1 mm.



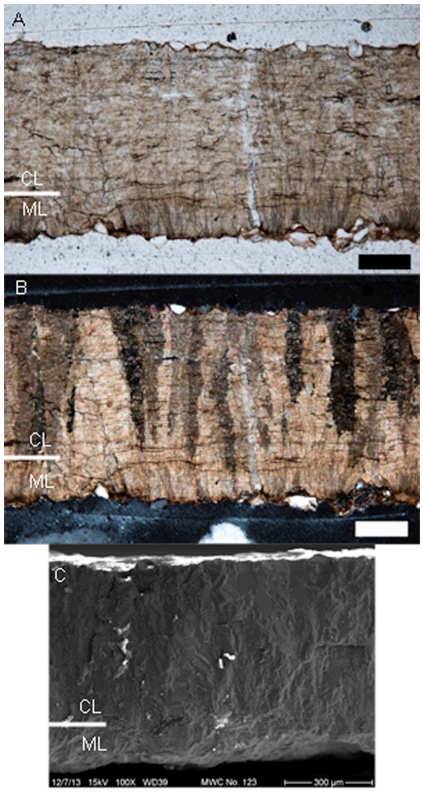
25. *Allosaurus* sp. Marsh 1877 (Oospecies *Preprismatoolithus coloradensis* Hirsch 1994) (Dinosauria: Saurischia) (Figures 53A,B,C)

Age and Locality: Upper Jurassic Morrison Formation, Kirkland and Young localities, Colorado, United States.

Material Examined: Thin sections and SEM stubs ES 445 and ES 446 (originally MWC, uncatalogued material). Additional data were obtained from Hirsch (1994) and Carpenter (1999).

Comments: The assignment of *Preprismatoolithus coloradensis* eggs to *Allosaurus* is based on a co-occurrence of embryonic or perinatal *Allosaurus* bones with a possible clutch from Wyoming (Carrano et al. 2013).

Figure 53. *Allosaurus* (*Preprismatoolithus coloradensis*) eggshell (ES 446 from MWC uncatalogued specimen) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 0.2 mm. Scale bar for (C) equals 0.3 mm.



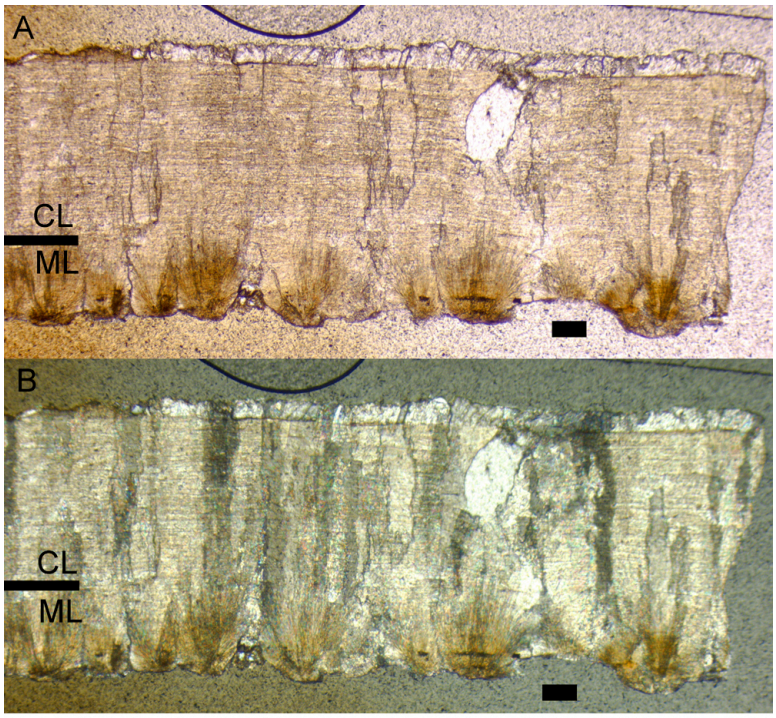
26. *Lourinhanosaurus antunesi* Mateus 1998 (Oogenus cf. *Preprismatoolithus* Zelenitsky and Hills 1996) (Dinosauria: Saurischia) (Figures 54A,B)

Age and Locality: Upper Jurassic Lourinhã Formation, Paimogo locality, Portugal.

Material Examined: Thin section UCM 607-1-2. This thin section was lapped to 62 μm instead of the standard 30 μm. Additional data were obtained from Mateus et al. (1998) and Antunes et al. (1998).

Comments: Assignment of these eggs to *Lourinhanosaurus antunesi* is based on associated embryonic remains (Mateus et al. 1998).

Figure 54. *Lourinhanosaurus antunesi* (cf. *Preprismatoolithus*) eggshell (UCM 607-1-2) under plain light (A) and crossed polars (B). Scale bars equal 0.1 mm.



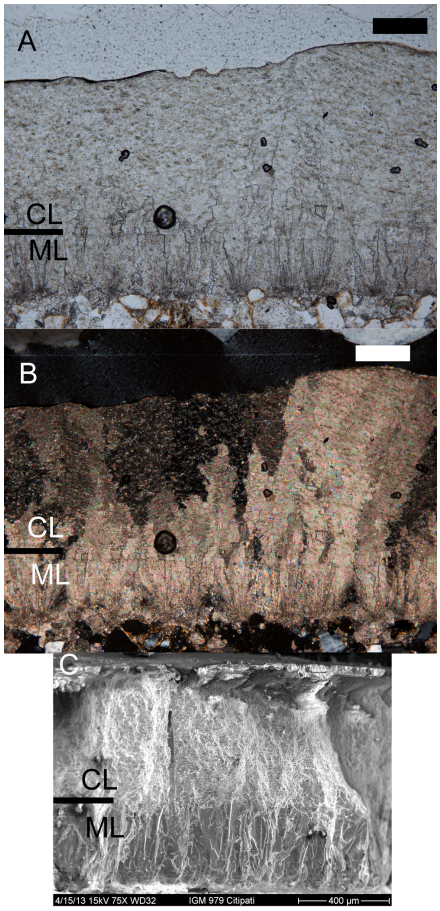
27. *Citipati osmolskae* Clark, Norell, and Barsbold 2001 (Oofamily Elongatoolithidae) (Dinosauria: Saurischia) (Figures 55A,B,C)

Age and Locality: Upper Cretaceous Djadokhta Formation, Bayn Dzak and Ukhaa Tolgod localities, Mongolia.

Material Examined: Thin sections and SEM stubs from IGM 100/971 and 100/979. Additional data were obtained from Norell et al. (1994, 1995) and Clark et al. (1999).

Comments: These specimens are attributed to *Citipati osmolskae* on the basis of an embryo *in ovo* (IGM 100/971), and an adult on top of a clutch (IGM 100/979). See comment for Character 23 regarding the symmetry of *C. osmolskae* eggs.

Figure 55. *Citipati osmolskae* (Elongatoolithidae) eggshell under plain light (A, IGM 100/971), crossed polars (B, IGM 100/971), and SEM (C, IGM 100/979). Scale bars for (A) and (B) equal 0.2 mm. Scale bar for (C) equals 0.4 mm.



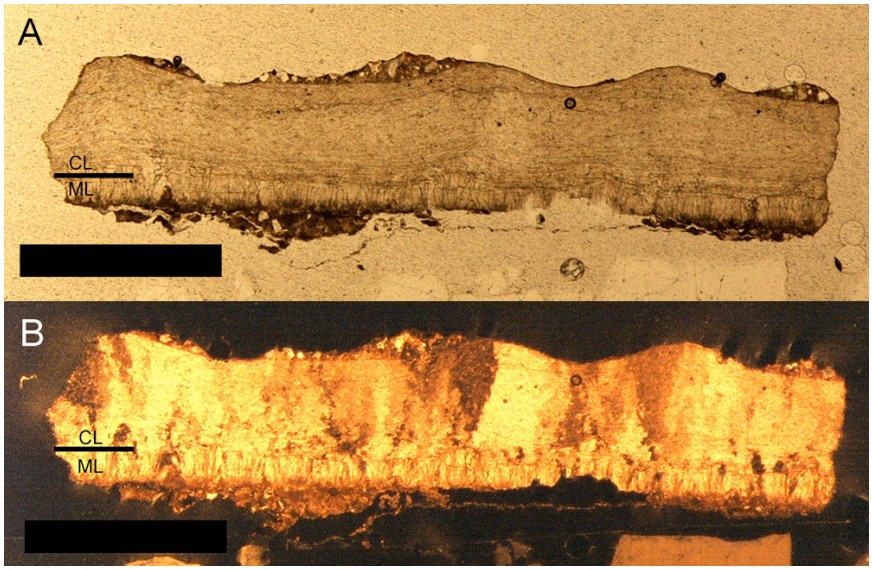
28. Oviraptoridae Barsbold 1976 (Oofamily Elongatoolithidae) (Dinosauria: Saurischia) (Figures 56A,B)

Age and Locality: Upper Cretaceous Nemegt Formation, Bugin-Tsav locality, Mongolia.

Material Examined: Thin section ES 297. Additional data obtained from Weishampel et al. (2008).

Comments: This specimen is assigned to an unspecified oviraptorid on the basis of eggs containing embryos (Weishampel et al. 2008).

Figure 56. Oviraptorid (Elongatoolithidae) eggshell (ES 297) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



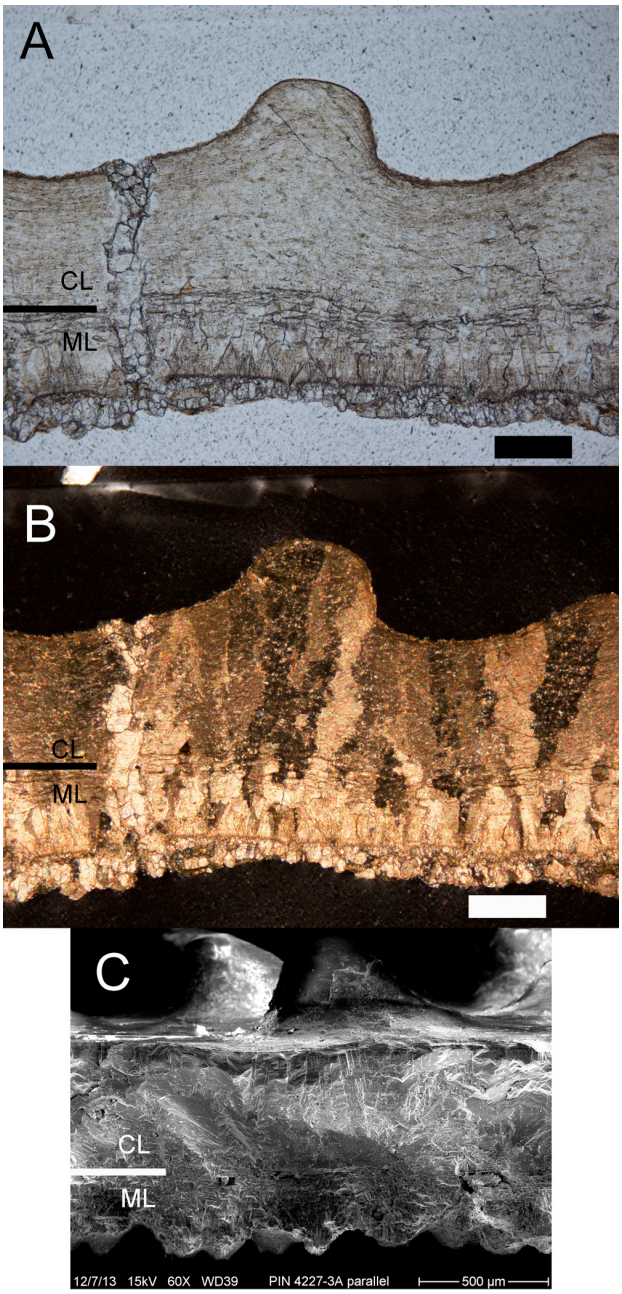
29. *Trachoolithus faticanus* Mikhailov 1994a (Oofamily Elongatoolithidae) (Figures 57A-C)

Age and Locality: Lower Cretaceous Dushih Ula Formation, Buylyasutuin-Khuduk locality, Mongolia.

Material Examined: Thin section and SEM stub from PIN 4227-3.

Comments: *T. faticanus* is known only from eggshell fragments (Mikhailov 1994a).

Figure 57. *Trachoolithus faticanus* eggshell (PIN 4227-3) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 0.2 mm. Scale bar for (C) equals 0.5 mm.



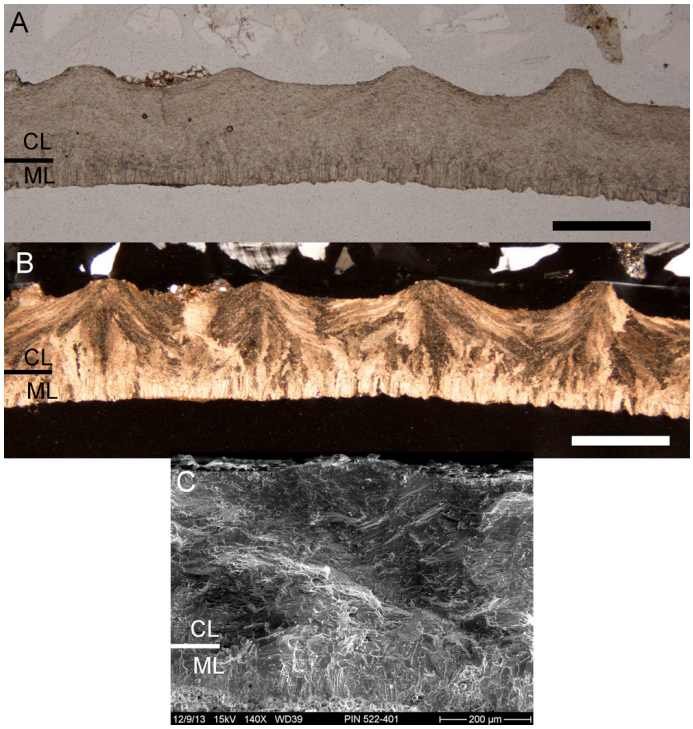
30. *Macroolithus rugustus* Young 1965 (Oofamily Elongatoolithidae) (Figures 58A-C)

Age and Locality: Upper Cretaceous Manrak Svita, Zaisan locality, Kazakhstan, and Upper Cretaceous Nemegt Formation, Tsagan-Khushu locality, Mongolia.

Material Examined: Thin sections and SEM stubs PIN 2710/6-2 and PIN 522-401. Additional clutch data obtained from Young (1965).

Comments: Other specimens of the oogenus *Macroolithus* from China have been associated with adult and embryonic oviraptorosaur remains (Sato et al. 2005, Cheng et al. 2008), but the Kazakhstani and Mongolian material currently lacks such associations. See comment for Character 23 regarding the symmetry of *M. rugustus* eggs.

Figure 58. *Macroolithus rugustus* eggshell (PIN 522-401) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 1 mm. Scale bar for (C) equals 0.2 mm.



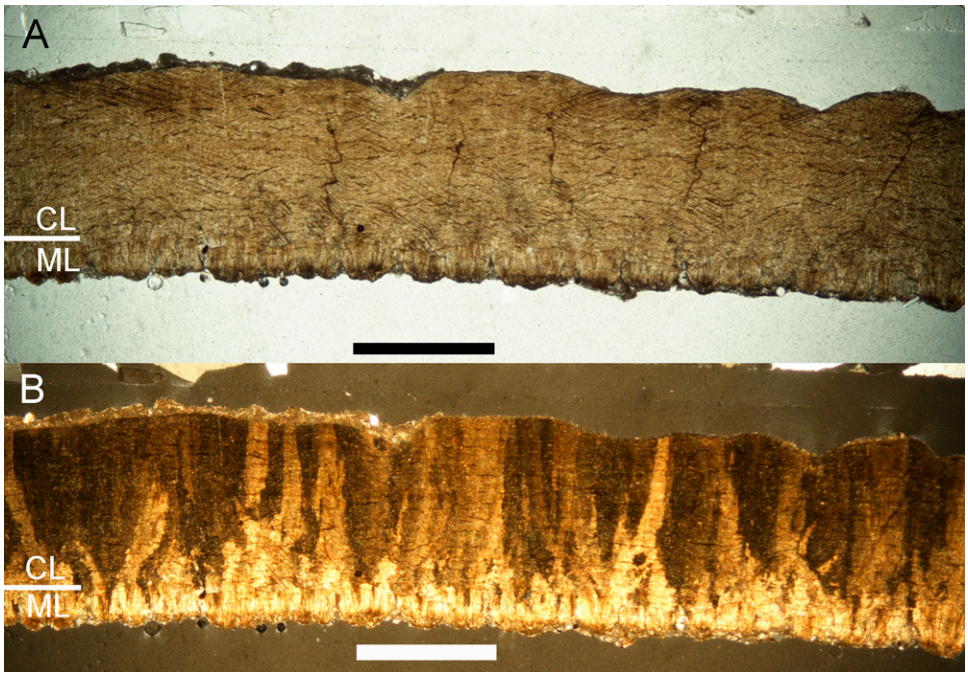
31. *Macroelongatoolithus* oosp. Li, Yin, and Liu 1995 (Oofamily Elongatoolithidae) (Figures 59A,B)

Age and Locality: "mid-Cretaceous" Wayan Formation, Idaho, United States.

Material Examined: Thin section ES 392-1. Additional data obtained from Simon et al. (2012), and Simon (pers. comm.).

Comments: A full description of this material by D. Simon and colleagues is pending (Simon pers. comm.). See Huh et al. (2014) for a discussion of the assignment of *Macroelongatoolithus* eggs to the oofamily Elongatoolithidae, rather than the Macroelongatoolithidae (Wang and Zhou 1995, Wang et al. 2010).

Figure 59. *Macroelongatoolithus* oosp. eggshell (ES 392-1) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



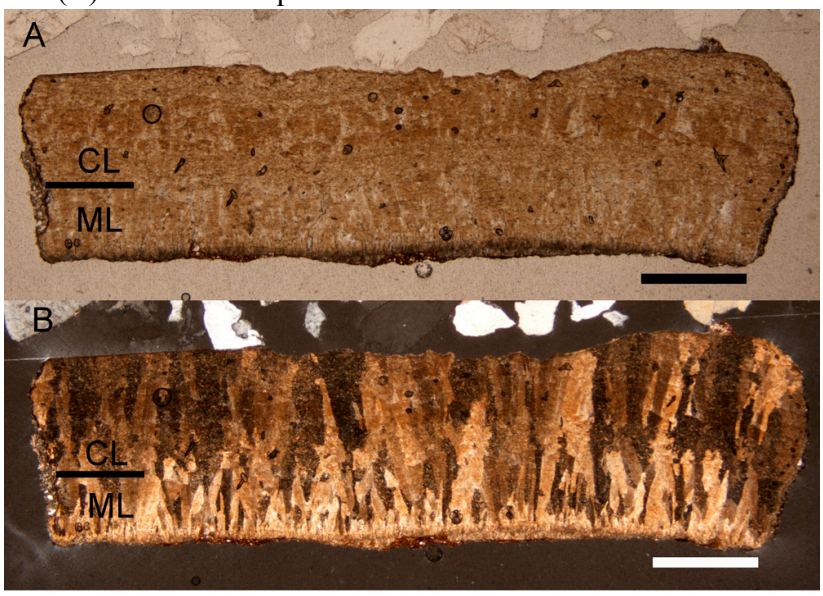
32. *Macroelongatoolithus xixiaensis* Li, Yin, and Liu 1995 (Oofamily Elongatoolithidae) (Figures 60A,B)

Age and Locality: Upper Cretaceous Chichengshan Formation, Tiantai basin, Zhejiang Province, China.

Material Examined: Thin sections ES 116 DV2, DV4, and DV4-1. Additional SEM, whole egg, and clutch data were obtained from Jin et al. (2007) and Grellet-Tinner et al. (2006).

Comments: A *Macroelongatoolithus* specimen from China with an associated ?oviraptorid embryo likely allows for assignment of this oogenus to oviraptorids (Grellet-Tinner 2005); however, this specimen has not been fully described.

Figure 60. *Macroelongatoolithus xixiaensis* eggshell (ES 116 DV2) under plain light (A) and crossed polars (B). Scale bars equal 1 mm.



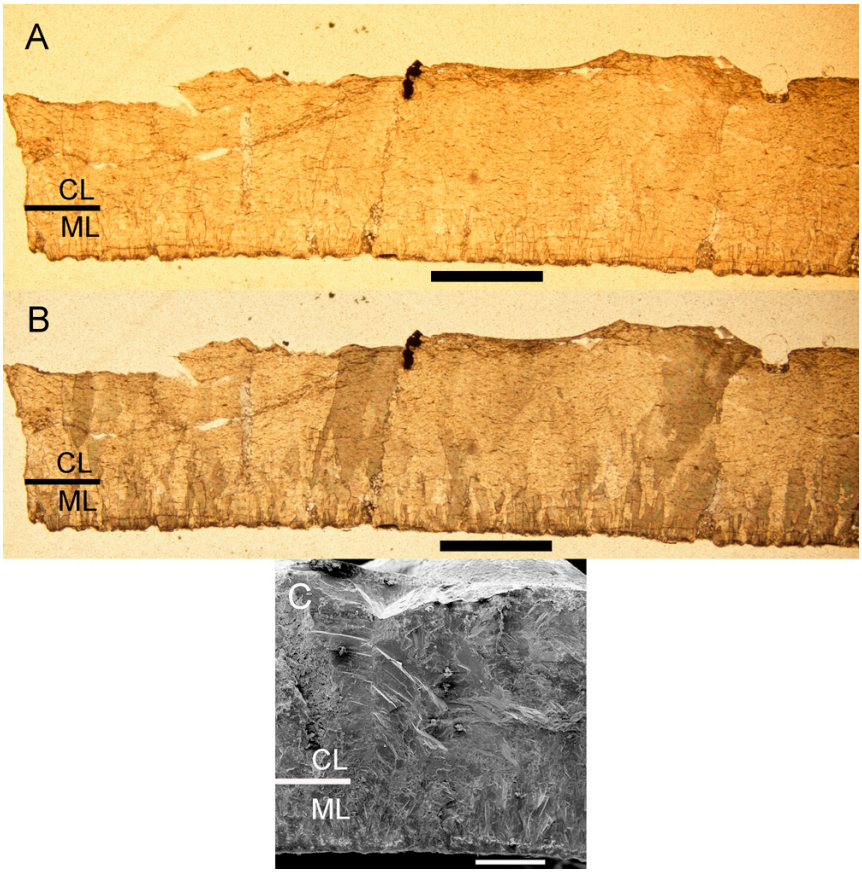
33. Elongatoolithidae indet. Zhao 1975 (Figures 61A,B)

Age and Locality: Lower Cretaceous Cloverly Formation, Locality near Edgar, Montana, United States.

Material Examined: Thin sections and SEM stubs ES 399-1,2; ES 400-1,2; ES 401-1,2.

Comments: Simon et al. (2013) presented a preliminary study of this eggshell; further description is forthcoming from those authors. This egg type is known only from eggshell fragments, and cannot be assigned at this time to a more specific ootaxon or dinosaur taxon.

Figure 61. Elongatoolithidae indet. eggshell under plain light (A, ES 401-1), crossed polars (B, ES 401-1), and SEM (C, ES 401-2). Scale bars for (A) and (B) equal 1 mm. Scale bar for (C) equals 0.5 mm.



34. *Deinonychus antirrhopus* Ostrom 1969 (Oogenus cf. *Elongatoolithus* Zhao 1975) (Dinosauria: Saurischia)

Age and Locality: Lower Cretaceous Cloverly Formation, Cashen Pocket Locality, Montana, United States.

Material Examined: Specimen AMNH 3015 was coded from data presented by Grellet-Tinner and Makovicky (2006).

Comments: This eggshell is assigned to *Deinonychus* on the basis of a partial egg adhering to gastralia of an adult of this taxon. Referral of this eggshell to cf. *Elongatoolithus* (Jin et al. 2010) was not elaborated upon with further description and comparisons to other *Elongatoolithus* and thus may not be supported by further study.

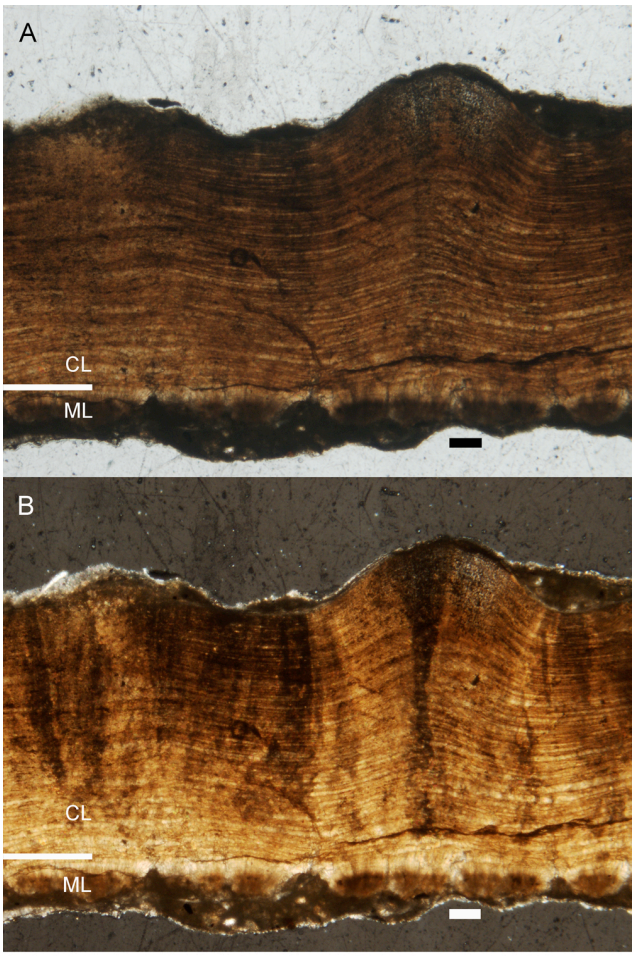
35. *Continuoolithus canadensis* Zelenitsky, Hills, and Currie 1996 (Oofamily incertae sedis) (Figures 62A,B)

Age and Locality: Upper Cretaceous Two Medicine Formation, Egg Mountain locality, Montana, United States.

Material Examined: Thin sections from MOR 326 (TM-006). Additional SEM, whole egg, and clutch data were obtained from Hirsch and Quinn (1990) and Schaff (2012).

Comments: Though previous authors (Horner 1984, Hirsch and Quinn 1990) made mistaken tentative assignments to *Troodon*, no adult associations or taxonomically identifiable embryonic remains (Horner 1997) are known for any *Continuoolithus canadensis* specimens.

Figure 62. *Continuoolithus canadensis* eggshell [MOR 326 (TM-006)] under plain light (A) and crossed polars (B). Scale bars equal 0.1 mm.



36. *Bonapartenykus ultimus* Agnolin, Powell, Novas, and Kundrát 2012 (Oospecies *Arriagadoolithus patagoniensis* Agnolin, Powell, Novas, and Kundrát 2012) (Dinosauria: Saurischia)

Age and Locality: Upper Cretaceous Allen Formation, Salitral Ojo de Agua locality, Patagonia, Argentina.

Material Examined: Whole egg and SEM data were obtained from Agnolin et al. (2012).

Comments: These eggs and eggshell fragments are assigned to *Bonapartenykus ultimus* on the basis of their close association with a

partial adult skeleton of this taxon. Agnolin et al. (2012) established the oofamily Arriagadoolithidae for these eggs and *Triprismatoolithus stephensi* (see below).

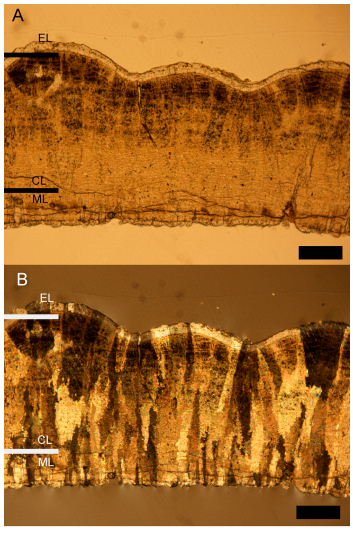
37. *Triprismatoolithus stephensi* Jackson and Varricchio 2010 (Oofamily Arriagadoolithidae) (Figures 63A,B)

Age and Locality: Upper Cretaceous Two Medicine Formation, Sevenmile Hill locality, Montana, United States.

Material Examined: Thin section ES 101. Additional data obtained from Jackson and Varricchio (2010).

Comments: *Triprismatoolithus stephensi* was recently assigned to the oofamily Arriagadoolithidae by Agnolin et al. (2012). Other arriagadoolithid eggs from Argentina are associated with an adult specimen of the alvarezsaurid *Bonapartenykus ultimus* (Agnolin et al. 2012, see above), though adult or embryonic associations remain unknown for *T. stephensi*.

Figure 63. *Triprismatoolithus stephensi* eggshell (ES 101) under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



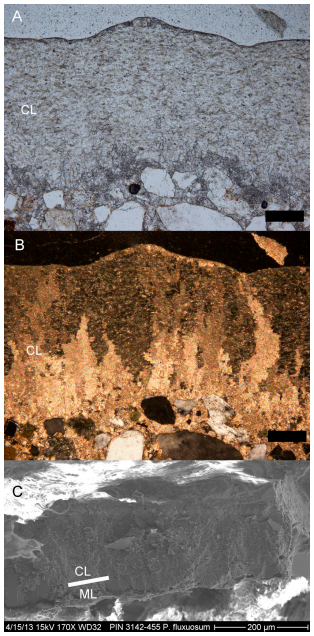
38. *Protoceratopsidovum fluxuosum* Mikhailov 1994a (Oofamily Prismatoolithidae) (Figures 64A-C)

Age and Locality: Upper Cretaceous Barun Goyot Formation, Khulsan and Khermeen-Tsav localities, Mongolia.

Material Examined: Thin sections PIN 4478-4 and 3142/455 and SEM stub from PIN 3142/455. Additional data were obtained from Sabath (1991) and Mikhailov (1994a).

Comments: Though Mikhailov (1994a) assigned the oogenus *Protoceratopsidovum* to protoceratopsids, this is based solely on the prevalence of protoceratopsid remains at the same Mongolian localities. As no embryonic or close adult associations are known for any of the *Protoceratopsidovum* oospecies, I consider this oogenus to remain unassigned to a particular dinosaur taxon.

Figure 64. *Protoceratopsidovum fluxuosum* eggshell under plain light (A, PIN 4478-4), crossed polars (B, PIN 4478-4), and SEM (C, 3142-455). Scale bars equal 0.2 mm.



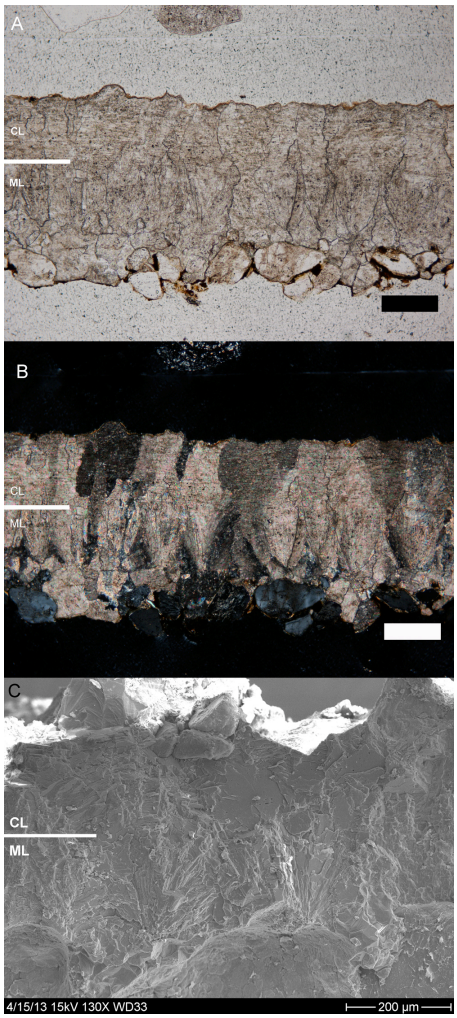
33. *Protoceratopsidovum sincerum* Mikhailov 1994a (Oofamily Prismatoolithidae) (Figures 65A-C)

Age and Locality: Upper Cretaceous Djadokhta Formation, Bayn-Dzak and Tugrikiyn-Shireh localities, Mongolia.

Material Examined: Thin sections PIN 614-58/1 and PIN 3143/121 and SEM stub from PIN 3143/121. Additional data were obtained from Sabath (1991) and Mikhailov (1994a).

Comments: See above comments for *P. fluxuosum*.

Figure 65. *Protoceratopsidovum sincerum* eggshell (PIN 3143/121) under plain light (A), crossed polars (B), and SEM (C). Scale bars equal 0.2 mm.



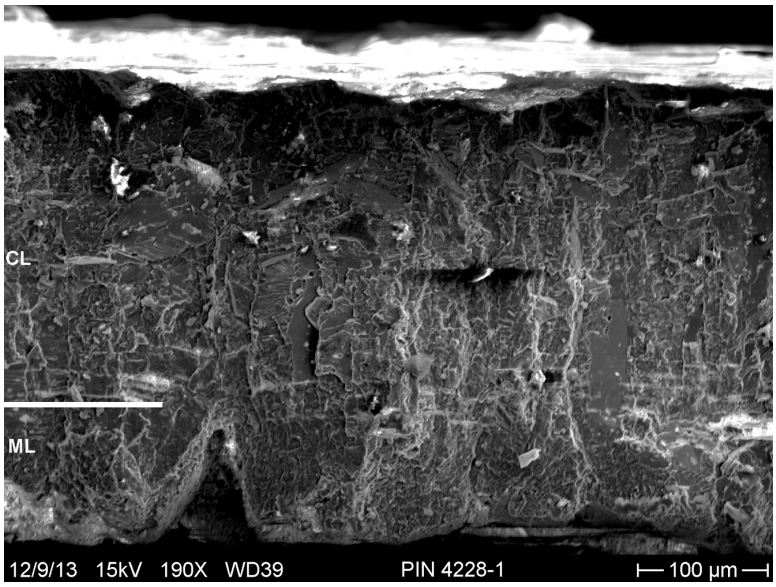
34. *Protoceratopsidovum minimum* Mikhailov 1994a (Oofamily Prismatoolithidae) (Figure 66)

Age and Locality: Upper Cretaceous Djadokhta Formation, Baga-Tariach locality, Mongolia.

Material Examined: SEM stub from PIN 4228-1. Additional data were obtained from Sabath (1991) and Mikhailov (1994a, 1997a).

Comments: See above comments for *P. fluxuosum*.

Figure 66. *Protoceratopsidovum minimum* eggshell (PIN 4228-1) under SEM. Scale bar equals 0.1 mm.



35. *Troodon formosus* Leidy 1856 (Oospecies *Prismatoolithus levis* Zelenitsky and Hills 1996) (Dinosauria: Saurischia) (Figure 67A,B)

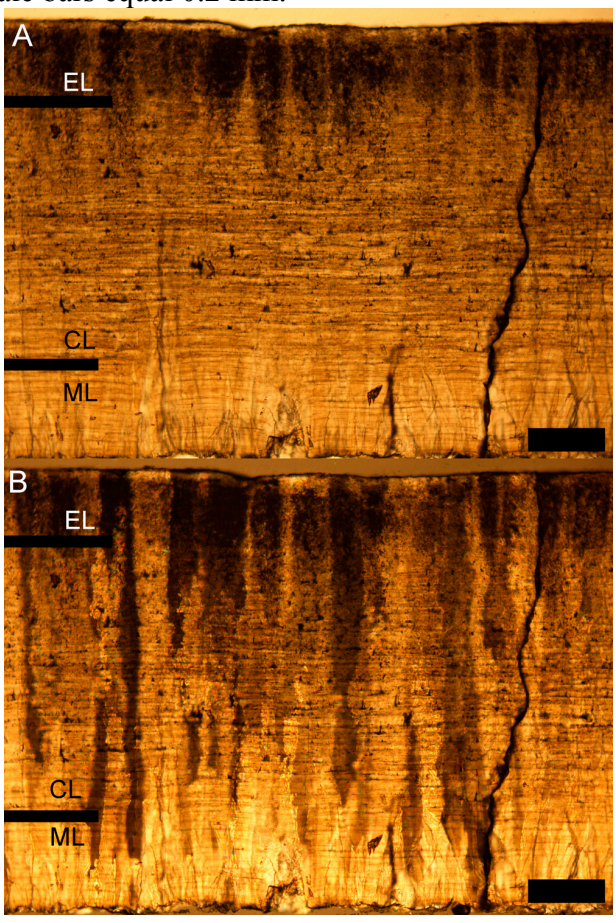
Age and Locality: Upper Cretaceous Two Medicine Formation, Egg Mountain locality, Montana, United States.

Material Examined: Thin section ES 347. Additional SEM, whole egg, clutch, and gas conductance data were obtained from Hirsch and Quinn

(1990), Varricchio et al. (1997, 1999, 2002, 2013), and Jackson et al. (2010).

Comments: The examined material is assigned to *Troodon formosus* on the basis of close similarity of eggshell microstructure to *Troodon* eggs containing embryos *in ovo* (Varricchio et al. 2002) and those of a clutch found in close association with an adult individual (Varricchio et al. 1997). Past descriptions of these eggs as those of the basal ornithopod *Orodromeus makelai* are erroneous [see Varricchio et al. (2002) and discussion therein].

Figure 67. *Troodon formosus* (*Prismatoolithus levis*) eggshell under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



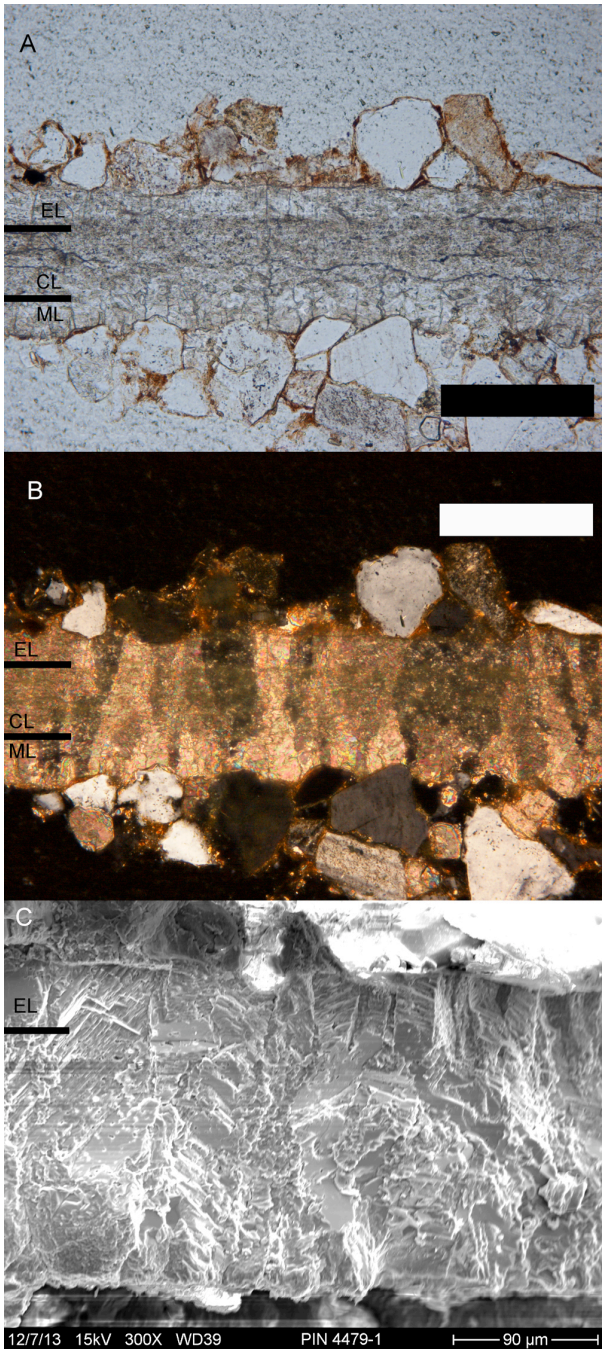
36. *Parvoolithus tortuosus* Mikhailov 1996b (Oofamily incertae sedis) (Figure 68A-C)

Age and Locality: Upper Cretaceous ?Barun Goyot Formation, Khongil locality, Mongolia.

Material Examined: Thin section and SEM stub PIN 4479-1. Additional data were obtained from Mikhailov (1997a).

Comments: *P. tortuosus* was established on the basis of a single incomplete egg (Mikhailov 1996b), though Mikhailov (1997a) suggests that multiple eggs are known [one of these is described by Zelenitsky (2004)]. Carpenter (1999) erroneously considers Mikhailov's (1996b) *P. tortuosus* egg to be a pupa chamber. Zelenitsky (2004) and the current study confirm Mikhailov's (1996b) original interpretation of *Parvoolithus* as an egg.

Figure 68. *Parvoolithus tortuosus* eggshell (PIN 4479-1) under plain light (A), crossed polars (B), and SEM (C). Scale bars for (A) and (B) equal 0.2 mm. Scale bar for (C) equals 0.09 mm.



37. *Oblongoolithus glaber* Mikhailov 1996b (Oofamily incertae sedis) (Figures 69A-C)

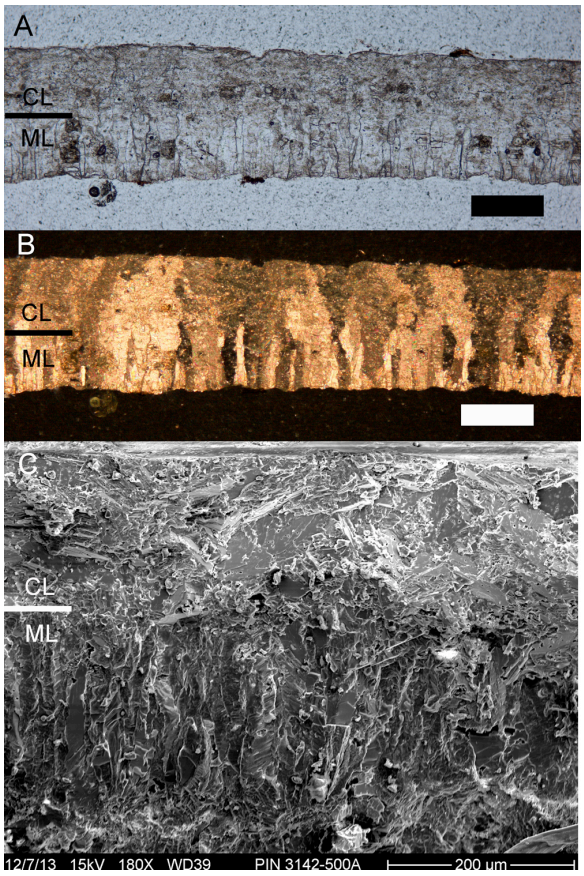
Age and Locality: Upper Cretaceous Barun Goyot Formation, Khermeen-Tsav locality, Mongolia.

Material Examined: Thin section and SEM stub PIN 3142-500.

Additional data were obtained from Mikhailov (1997a).

Comments: *O. glaber* was named on the basis of a single incomplete egg (Mikhailov 1996b), though Mikhailov (1997a) makes reference to multiple Mongolian eggs of this oogenus.

Figure 69. *Oblongoolithus glaber* eggshell (PIN 3142-500) under plain light (A), crossed polars (B), and SEM (C). Scale bars equal 0.2 mm.



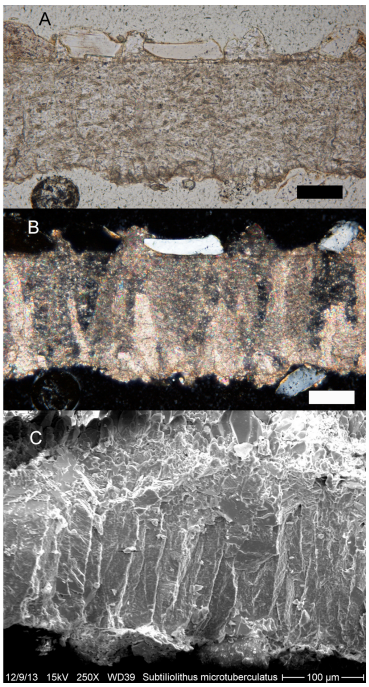
38. *Subtiliolithus microtuberculatus* Mikhailov 1991 (Oofamily Laevisoolithidae) (Figures 70A-C)

Age and Locality: Upper Cretaceous Nemegt Formation, Khaychin-Ula I locality, Mongolia.

Material Examined: Thin section and SEM stub from PIN 4230-7 and SEM stub from PIN uncatalogued eggshell.

Comments: An occurrence of *Subtiliolithus* oosp. eggshell fragments in association with a juvenile or subadult individual of the enantiornithine bird *Nanantius valifanovi* led Kurochkin (1996) to assign this oogenus to enantiornithines. Chiappe et al. (2001) later suggested that *Nanantius* is a junior synonym of *Gobipteryx*. I choose not to assign *S. microtuberculatus* to a particular taxon at this time, though I note that it likely belongs to an enantiornithine. *Subtiliolithus* is known only from eggshell fragments.

Figure 70. *Subtiliolithus microtuberculatus* eggshell under plain light (A, PIN 4230-7), crossed polars (B, 4230-7), and SEM (PIN uncatalogued). Scale bars for (A) and (B) equal 0.2 mm. Scale bar for (C) equals 0.1 mm. These specimens are too recrystallized to allow for confident placement of the ML/CL boundary.



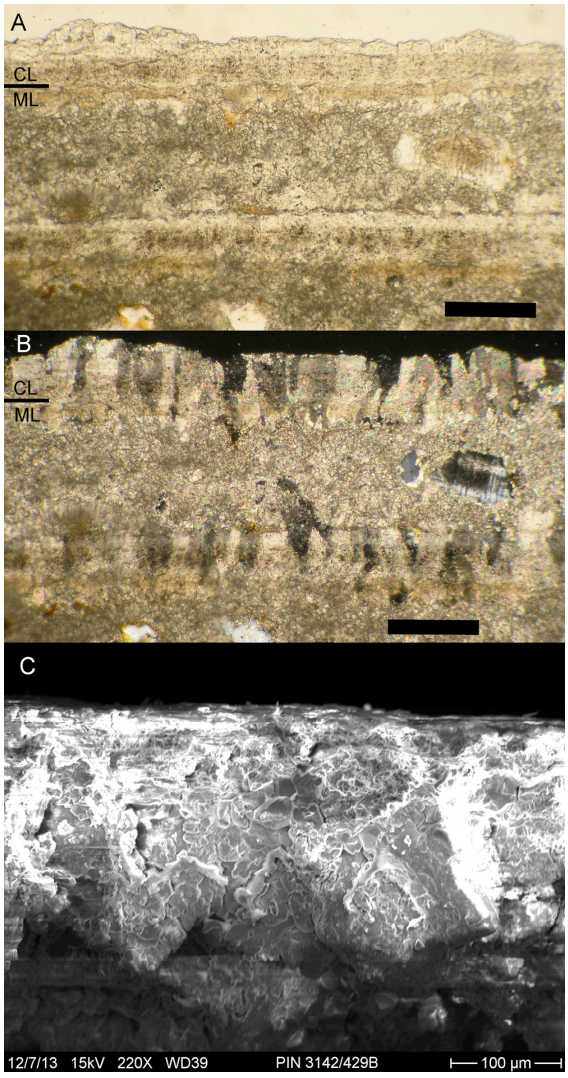
39. *Gobipipus reshetovi* Kurochkin, Chatterjee, and Mikhailov 2013 (Oospecies *Gobioolithus minor* Mikhailov 1996a) (Dinosauria: Saurischia) (Figures 71A-C)

Age and Locality: Upper Cretaceous Barun Goyot Formation, Khermeen-Tsav locality, Mongolia.

Material Examined: Thin section and SEM stub from PIN 3142/429, thin section from ZPAL Mg-Ov-III/11b, and numerous whole and partial eggs in the PIN and ZPAL collections. Additional data were obtained from Sabath (1991), Mikhailov (1997a), and Kurochkin et al. (2013).

Comments: Though previously assigned to *Gobipteryx minuta* on the basis of embryos with adhering eggshell fragments (Elzanowski 1981, Sabath 1991, Mikhailov 1991), recently *Gobioolithus minor* eggs have been reassigned to the enantiornithine *Gobipipus reshetovi* on the basis of embryos *in ovo* (Kurochkin et al. 2013). Given the difficulty of comparing the eggshell adhering to the *Gobipteryx* eggs with *Gobioolithus minor* due to extensive diagenetic alteration and the possible synonymy of *Nanantius valifanovi* (which is associated with laevisoolithid eggshell, see above) with *Gobipteryx* (Chiappe et al. 2001), it seems reasonable to tentatively consider *Gobipipus* as the best candidate for the parent of the *G. minor* eggs.

Figure 71. *Gobipipus reshetovi* (*Gobioolithus minor*) eggshell under plain light (A, ZPAL MgOv-III/11b), crossed polars (B, ZPAL MgOv-III/11b), and SEM (PIN 3142/429). Scale bars for (A) and (B) equal 0.2 mm. Scale bar for (C) equals 0.1 mm. Note that (C) is highly recrystallized.



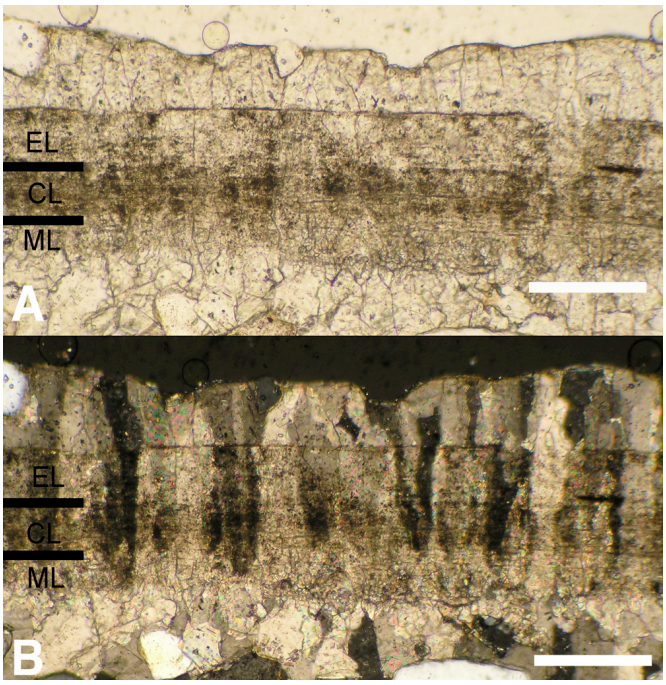
40. "Larger Avian Eggs" of Sabath (1991) (Dinosauria: Saurischia) (Figures 72A,B)

Age and Locality: Upper Cretaceous Volcano and Ruins localities, Bayn Dzak, Barun Goyot and Djadokhta Formations, Mongolia.

Material Examined: Egg clutch ZPAL MgOv-II/7a-e, eggs and partial eggs ZPAL MgOv-I/19, MgOv-I/21a-c, and MgOv-I/25c-d, MgOv-II/6a-g, and MgOv-II/25 and thin sections ZPAL MgOv-II-6.

Comments: These eggs were originally referred to *Gobioolithus major* by Mikhailov (1996a); however, subsequent redescription by Varricchio and Barta (In review) reveals them to be a new oogenus and oospecies. I consider the eggs to be avian on the basis of associated likely avian hind limb elements overlying egg clutch ZPAL MgOv-II/7a-e (Sabath 1991), and the results of cladistic analyses of the eggs, using preexisting data matrices that differ from this study (Varricchio and Barta In review).

Figure 72. Eggshell from the "Larger Avian Eggs" of Sabath (1991) (ZPAL MgOv-II-6) under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



41. *Dromaius novaehollandiae* Latham 1790 (Dinosauria: Saurischia) (Figures 73A,B)

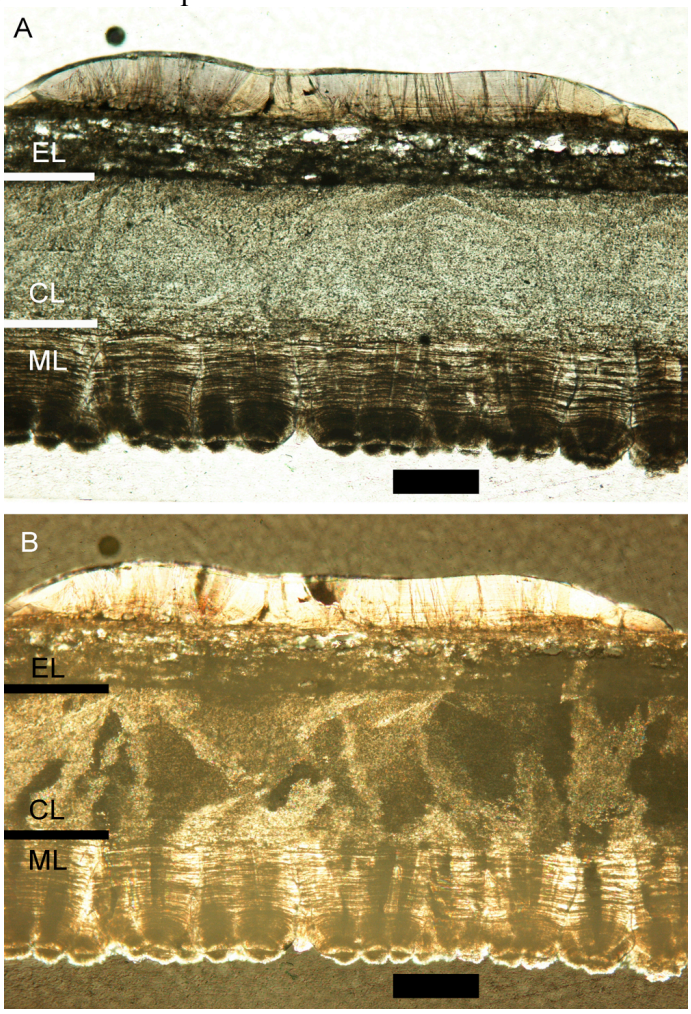
Age and Locality: Extant, United States.

Material Examined: ES uncatalogued thin section. Additional unpublished data were obtained from D. Simon and D. Lawver. A

published egg volume was obtained from Paganelli et al. (1974) and compared with calculated values. Clutch data were taken from Folch (1992). SEM images used in coding were obtained from Grellet-Tinner and Chiappe (2004).

Comments: *Dromaius novaehollandiae* is included as a representative paleognath bird.

Figure 73. *Dromaius novaehollandiae* (ES uncatalogued) eggshell under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



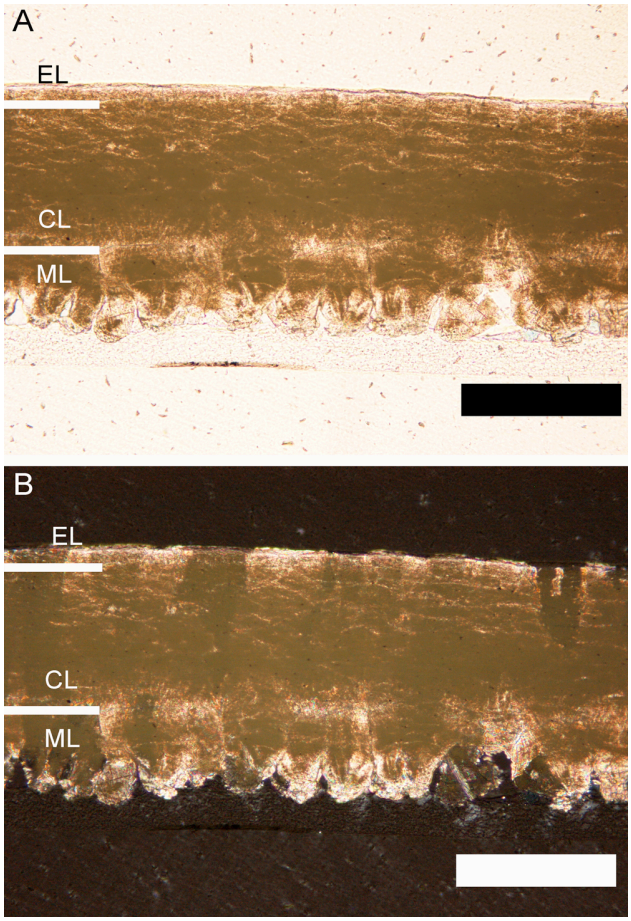
42. *Gallus gallus* Linnaeus 1758 (Dinosauria: Saurischia) (Figures 74A,B)

Age and Locality: Extant, United States.

Material Examined: Thin section ES 247. Egg dimensions were obtained from Oates (1901) and a volume from Paganelli et al. (1974). Clutch data were obtained from McGowan (1994).

Comments: *Gallus gallus* is included as a representative neognath bird. Thin section ES 247 is thicker than the standard 30 µm, thus characters relating to some obscured features (e.g. prisms) were coded from previously published SEM images (Nys and Gautron 2007, Chien et al. 2008, Hincke et al. 2012).

Figure 74. *Gallus gallus* eggshell (ES 247) under plain light (A) and crossed polars (B). Scale bars equal 0.2 mm.



Results

Unconstrained Analyses

The unconstrained analysis including all 48 egg types and 36 characters terminated at the maximum designated limit of 300,000 trees. Tree statistics (tree length, consistency = CI, retention = RI, and rescaled consistency =RC indices) are listed in Table 2. Tree length was slightly greater and the aforementioned indices slightly less when characters 3, 8, 19, 27, 28, 29 were set as ordered, rather than unordered. Given the potentially untenable assumption that all of the states for these characters transitioned sequentially to one another, further discussion of the unconstrained analysis only deals briefly with topologies recovered by analyses in which the continuous characters were ordered. However, the similar CI, RI, and RC between the analyses with and without ordered characters (Table 2), even with the added steps imposed by ordering, suggests that ordering continuous characters produces similarly-supported results to trees with unordered characters.

Slightly better resolution of clades on consensus trees was found when using ACCTRAN optimization rather than DELTRAN; these differences are likely a consequence of transforming characters more towards internal nodes (under ACCTRAN) than distal branches (under DELTRAN), or could instead result from slightly different trees being found under the two separate heuristic searches. I discuss the topology of the trees using ACCTRAN optimization, given their slightly better resolution and the fact that ACCTRAN optimization is the default setting in PAUP* 4.0 (Swofford 2003) and helps to identify all potentially synapomorphic character states. Two characters (24 and 25) were parsimony-uninformative in all analyses, and only CI values (Table 2) excluding these characters are reported. The characters are retained for the interest of

future researchers, as they could become informative if they were coded for more taxa, or upon the inclusion of additional taxa.

The strict consensus tree (Figure 75) consists of a polytomy of dinosaur eggs that includes the clades (titanosaur, *Megaloolithus* cf. *mammilare*); (*Torvosaurus gurneyi*, *Faveoloolithus ningxiaensis*, (*Faveoloolithus* oosp., *Dictyoolithus hongpoensis*, *Dendroolithus xichuanensis*)); (*Spheroolithus irenensis*, *Spheroolithus* cf. *zhangtoucaoensis*, (therizinosauroid, (*Dendroolithus verrucarius*, *Dendroolithus microporosus*))); and (*Bonapartenykus ultimus*, *Triprismatoolithus stephensi*).

I choose to report the Adams consensus tree (Figure 76) as it allows for greater resolution than the strict consensus tree (Felsenstein 2004). Adams consensus trees preserve all of the nesting information common to the set of fundamental trees (Adams 1972). One drawback of Adams consensus trees is that they may display clades that were not found in any of the original subset of recovered trees (Barrett et al. 1991). However, I feel that the increased resolution provided by the Adams consensus, particularly for a data matrix such as ours with a large number of taxa with missing data and/or widely varying placements on the most parsimonious trees outweighs these concerns. I note, however, that polytomies recovered in the Adams consensus should be viewed as ambiguous (Wilkinson 1994). The Adams consensus tree resolves taxa with many missing or conflicting character states as early branches of clades in which they are resolved in an unstable manner (Wiley and Lieberman 2011). These unstable ootaxa include *Protoceratopsidovum fluxuosum* and *Subtiliolithus microtuberculatus*, though they are still recovered within a clade containing derived theropod eggs in both the Adams and 50% majority rule consensus trees.

The unconstrained Adams Consensus tree produced from an analysis in which the continuous characters were ordered (Figure 77) is similar overall to that of the analysis

with unordered characters (Figure 76), but differs mostly in its greater resolution of derived theropod and avian egg clades. Avian eggs are recovered as successively basal to other theropod eggs, which is the opposite result compared to osteological trees.

Table 2. Tree statistics for cladistic analyses conducted with continuous characters 3, 8, 19, 27, 28, 29 set as both unordered and ordered, ACCTRAN and DELTRAN optimization used, and *Spheroolithus* cf. *zhangtoucaoensis* and the indeterminate elongatoolithid included and deleted. CI = consistency index, RI = retention index, RC = rescaled consistency index.

Unconstrained Analyses			Constrained Analyses		
	All Taxa	Reduced		All Taxa	Reduced
Unordered Characters	Length: 155 CI: 0.58 RI: 0.76 RC: 0.45	Length: 152 CI: 0.57 RI: 0.75 RC: 0.45	Unordered Characters	Length: 170 CI: 0.52 RI: 0.70 RC: 0.38	Length: 168 CI: 0.52 RI: 0.69 RC: 0.37
Ordered Characters	Length: 162 CI: 0.57 RI: 0.77 RC: 0.44		Ordered Characters	Length: 180 CI: 0.52 RI: 0.71 RC: 0.36	

Figure 75. Unconstrained strict consensus tree. All continuous characters unordered.

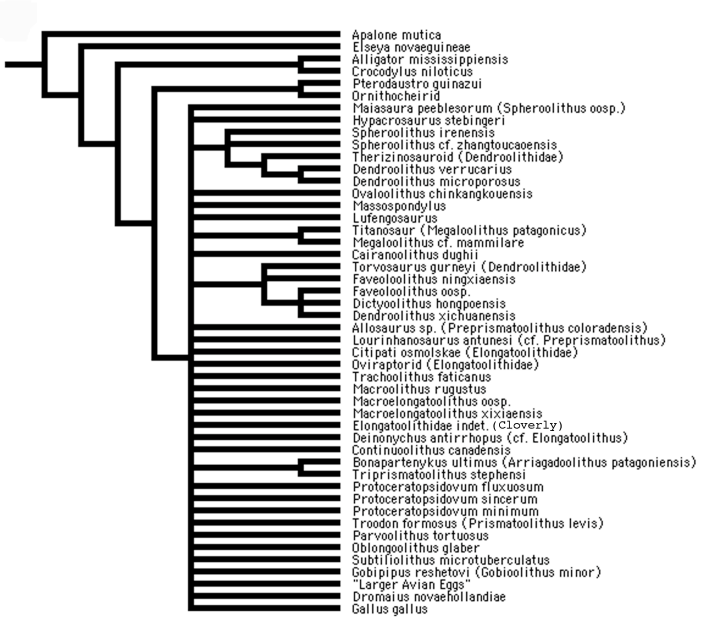


Figure 76. Unconstrained Adams consensus tree. Values above nodes are 50% majority rule bootstrap values. Nodes with a 100% value were constrained to be appear in the outgroup. All continuous characters unordered.

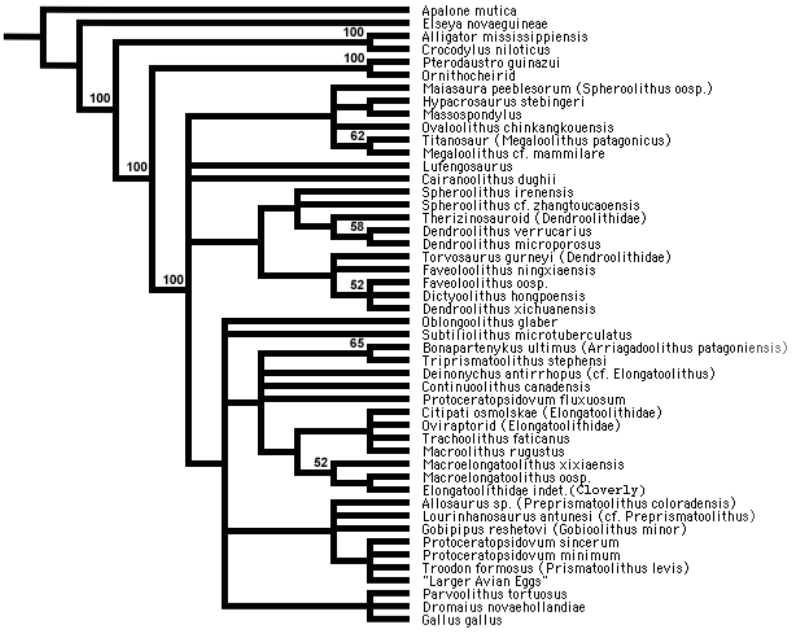


Figure 77. Unconstrained Adams Consensus tree with continuous characters ordered.



Constrained Analyses

The lack of congruence between portions of the unconstrained trees and topologies derived from analyses of osteological data prompt, for the first time, a constrained cladistic analysis of dinosaur eggs. This analysis terminated at the maximum of 300,000 trees. Tree statistics are listed in Table 2. The lower support found for this tree may be attributable to the constraints breaking up groupings based on homoplasy that would otherwise contribute to a shorter tree length and higher CI and RI scores. As for the unconstrained analysis, ordering the continuous characters contributed to a slightly greater tree length and lower CI and RC values. Only minor topological differences were detected between the analysis using ACCTRAN optimization and the analysis using DELTRAN optimization. For the reasons noted above for the unconstrained analysis, I choose to discuss only the results of the analysis using all unordered characters and ACCTRAN optimization, though synapomorphies of clades are examined under both ACCTRAN and DELTRAN optimization below.

The strict consensus tree (Figure 78) recovered a monophyletic Dinosauria comprising a large polytomy containing the clades (*Spheroolithus irenensis*, *S.* cf. *zhangtoucaoensis*, (therizinosauroid, (*Dendroolithus verrucarius*, *D. microporosus*))); (*Faveoloolithus* oosp., *Dictyoolithus hongpoensis*, *Dendroolithus xichuanensis*, *Torvosaurus gurneyi*); (*Allosaurus* sp., *Lourinhanosaurus antunesi*); (oviraptorid, *Macroolithus rugustus*); and (*Bonapartenykus utlimus*, *Triprismatoolithus stephensi*). As with the unconstrained analysis, better resolution was found in the Adams consensus (Figure 79) tree. The least stable ootaxa revealed by the Adams consensus tree in comparison to the 50% majority rule consensus tree are *Ovaloolithus chinkangkouensis* and *Cairanoolithus dughii*, which both moved from within the theropod clade (in the 50% majority rule consensus tree) to a polytomy at the base of Dinosauria (in the Adams

consensus tree). Additionally, *Oblongoolithus glaber* moves from a derived position within Theropoda to a polytomy at the base of this clade.

The constrained Adams Consensus tree produced from an analysis in which the continuous characters were ordered (Figure 80) differs from the analysis with unordered characters (Figure 79) mainly in its placement of *Macroelongatoolithus* outside Eumaniraptora, and its recovery of a clade of all avian and potential avian eggs.

Figure 78. Constrained strict consensus tree with continuous characters unordered.

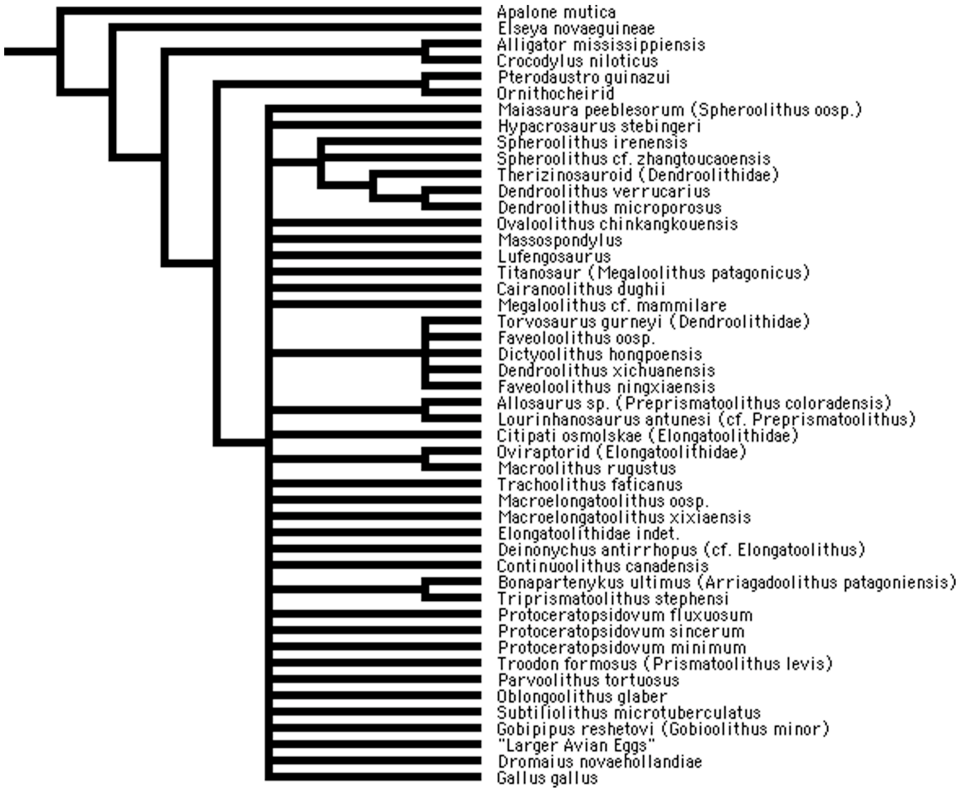


Figure 79. Constrained Adams consensus tree with continuous characters unordered. Numbers above nodes are 50% majority rule bootstrap support values. Letters below nodes correspond to the unnamed clades listed in Table 3. Unnamed clade F is not resolved under ACCTRAN optimization (presented here), but contains *Oblongoolithus glaber* as the sister ootaxon to *Subtiliolithus microtuberculatus* at the position indicated.

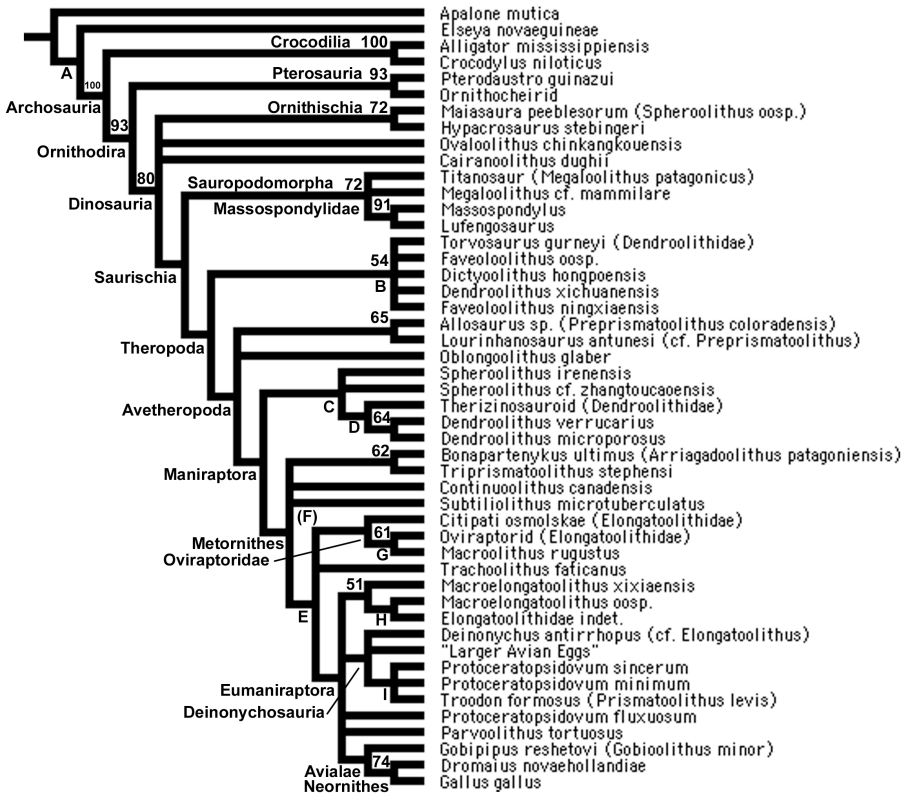
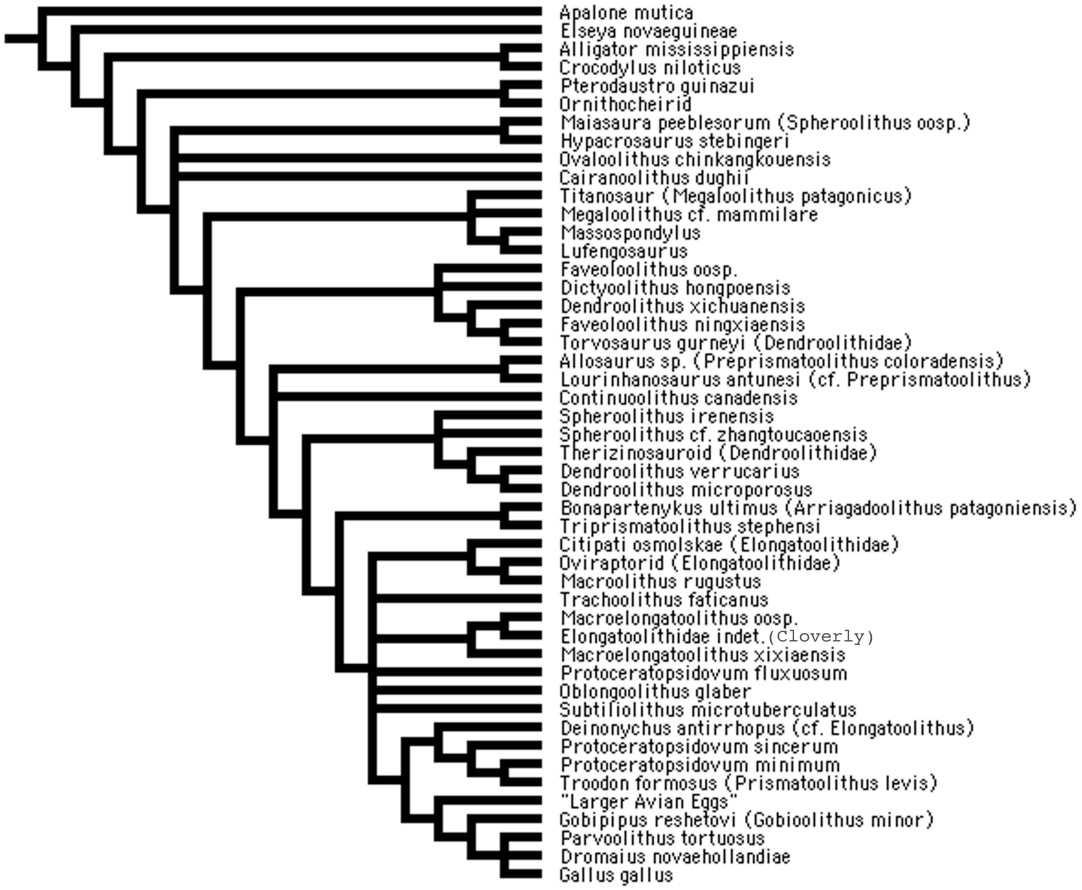


Figure 80. Constrained Adams Consensus tree with continuous characters ordered.



Taxonomic Reduction

Safe taxonomic reduction (Wilkinson 1995) is a method of identifying for deletion from a data matrix those taxa that do not affect the relationships of other taxa, but do contribute to a high number of most parsimonious trees. I performed safe taxonomic reduction for both the unconstrained and constrained analyses with unordered characters by deleting two ootaxa, *Spheroolithus* cf. *zhangtoucaoensis* and Elongatoolithidae indet. These egg types coded identically (apart from some missing data for the indeterminate elongatoolithid) to two other ootaxa in the analysis,

Spheroolithus irenensis and *Macroelongatoolithus* oosp., respectively. Though the unconstrained reduced analysis produced fewer (299,941) than the designated maximum of 300,000 trees, the effectiveness of the heuristic search may have been diminished due to tree-buffer overflow. Safe taxonomic reduction of the constrained tree produced the maximum of 300,000 trees. The main differences in topology on the unconstrained strict consensus tree were a failure to recover the titanosaur + *Megaloolithus* cf. *mammilare* clade, the *Bonapartenykus ultimus* + *Triprismatoolithus stephensi* clade. *Allosaurus* sp., *Lourinhanosaurus antunesi*, and *Gobipipus* eggs were not recovered as unresolved potential sister taxa to a clade of the other prismatoolithids and the "Larger Avian Eggs" in the taxonomically reduced analysis, though they occupy this position when all taxa are included. Safe taxonomic deletion produced one difference between the constrained strict consensus trees; namely, the position of the oviraptorid and *Macroolithus rugustus* eggs were unresolved relative to one another (instead of being sister taxa) after taxonomic reduction. For the constrained Adams consensus trees, taxonomic reduction lead to a loss of some internal resolution within Oviraptoridae and caused both *Macroelongatoolithus* OTUs to drop out of Eumaniraptora into an unresolved position basal to that clade. *Protoceratopsidovum sincerum, P. minimum*, and the "Larger Avian Eggs" also dropped out of Deinonychosauria to an unresolved position basal to that clade after taxonomic reduction.

As the tree statistics of the taxonomically reduced trees are substantially similar to those that include all taxa (Table 2), as the number of trees obtained was not greatly reduced, and as *Spheroolithus* cf. *zhangtoucaoensis* and the indeterminate elongatoolithid are older than the ootaxa most closely related to them in this analysis (Simon et al. 2013, Barta et al. 2014), and thus may be important to understanding the early evolution of

these egg types, I choose to only discuss the results of the analyses with all taxa and ootaxa included.

Synapomorphies of Clades

The following clade membership lists and the synapomorphies that unite them (Table 3) are taken from the Adams consensus tree of the constrained analyses (Figure 79), with all characters run as unordered. I feel that this best represents the trade-off between decreased clade support and increased resolution, all within a constrained framework that prevents the recovery of clades that conflict with well-established clades based on osteological characters. I note, however, that the use of consensus trees to trace characters has been criticized because consensus trees have lost the information about the trees that contributed to making them (Maddison and Maddison 2003). However, I feel this practice is justified, as it is not feasible to examine character evolution across each of the 300,000 most parsimonious trees recovered by PAUP* for my analysis.

In some cases the listed character states are not unambiguous synapomorphies that evolve only once on the tree, but instead may represent reversals or independent appearances of character states that contribute to unique combinations of character states that diagnose clades. Unambiguous synapomorphies are marked with an asterisk. Listed synapomorphies are those that the clade shares basally; nested, less-inclusive clades and their more derived members may not share all features. As clade membership and synapomorphies varied slightly when using ACCTRAN versus DELTRAN optimization, the source of each taxon and synapomorphy (whether recovered under ACCTRAN or DELTRAN) is noted in Table 3. The listed synapomorphies should only be considered as uniting those ootaxa and taxa included in the current analysis, and may or may not be present in all members of a given clade.

Synapomorphies recovered on the constrained Adams Consensus tree, utilizing ordered continuous characters, were largely the same as those from the analysis with all characters unordered. The major differences when continuous characters were ordered are a less inclusive Eumaniraptora, united by a lack of surface ornamentation, subvertically oriented eggs, and partially buried eggs, and a more inclusive Aviales, united by the presence of prisms with well-developed squamatic structure, an abrupt transition between the second and third structural layers, and an EMQ > 0.30 E_b.

Table 3. Membership and synapomorphy lists for clades recovered on Adams consensus trees with all characters designated as unordered, under both ACCTRAN (A) and DELTRAN (D) optimization. Unambiguous synapomorphies are marked with an asterisk.

Clade Name	Membership	Synapomorphies
Unnamed Clade A	*Elseya novaeguineae*, all other taxa (A,D)	Elongation index of 1.5-2.0 (A,D)
Archosauria	Crocodilia, Ornithodira (A,D)	Eggshell composed of calcite (A*,D*); accretion lines straight at shell unit boundaries (A,D)
Crocodilia	*Alligator mississippiensis*, *Crocodylus niloticus* (A)	Loosely organized basal knob (A*); second structural layer present (A); tabular structure present in second and third layers (A); squamatic structure absent from second layer (A*); third structural layer present (A); third structural layer with horizontal crystals and vertical fibrous fabric (A*); blocky extinction pattern (A*); EMQ <0.10 (A)

Table 3 Continued.

Ornithodira	Pterosauria, Dinosauria (A,D)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A,D)
Pterosauria	*Pterodaustro guinazui*, ornithocheirid (A,D)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A,D)
Dinosauria	Ornithischia, Saurischia, *Ovaloolithus chinkangkouensis*, *Cairanoolithus dughii* (A,D)	Height/width ratio of mammillae or shell units is 2.01-7.0 (A*,D*); tabular structure present in the first layer (A*,D*); nucleation site spacing/shell thickness ratio <0.24 (A*,D*); elongation index of 1.0-1.5 (A,D); layers of eggs present within clutch (A*,D*)
Ornithischia	*Maiasaura peeblesorum*, *Hypacrosaurus stebingeri* (A,D)	Eggshell ornamentation composed primarily of a single shell unit (A,D); sagenotuberculate ornamentation (A,D) Sagenotuberculate ornamentation is also present in *Ovaloolithus*, which is recovered in an unresolved position relative to Ornithischia.
Saurischia	Sauropodomorpha, Theropoda (A,D)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A,D)

Table 3 Continued.

Sauropodomorpha	Massospondylidae, titanosaur, *Megaloolithus* cf. *mammilare* (A,D)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A,D)
Massospondylidae	*Massospondylus*, *Lufengosaurus* (A)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A,D)
Theropoda	Unnamed Clade B, Avetheropoda (A,D)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A,D)
Unnamed Clade B	*Torvosaurus gurneyi*, *Faveoloolithus ningxiaensis*, *Faveoloolithus* oosp., *Dictyoolithus hongpoensis*, *Dendroolithus xichuanensis* (A,D)	Shell units first branched near interior of shell (A*,D*); branching pores (A*,D*); irregular pore shape (A,D)
Avetheropoda	*Preprismatoolithus* (A,D), *Oblongoolithus glaber* (A only), Maniraptora (A,D)	Second structural layer present (A,D); squamatic structure present in second layer (A*,D*); columnar extinction pattern (A,D)

Table 3 Continued.

Preprismatoolithus	*Allosaurus* sp., *Lourinhanosaurus antunesi* (A,D)	Height/width ratio of mammillae equals 1.0-2.0 (A,D); gradual transition between first and second layers (A,D); tabular structure present in second layer (A,D); prisms with irregular squamatic texture (A); nucleation site spacing/eggshell thickness ratio of 0.24-0.33 (A,D); pores perpendicular and oblique to eggshell surface (A,D); asymmetrical eggs (A,D)
Maniraptora	Unnamed Clade C, Metornithes (A,D)	ETQ >1.75 (A,D)
Unnamed Clade C	*Spheroolithus irenensis*, *Spheroolithus* cf. *zhangtoucaoensis*, Unnamed Clade D (A,D)	Second structural layer absent (A,D); Tabular structure absent (A,D); sweeping extinction pattern (A,D); irregular pore shape (A,D)
Unnamed Clade D	therizinosauroid, Mongolian *Dendroolithus* (A,D)	Shell units first branched near exterior of shell (A*,D*)
Mongolian *Dendroolithus*	*Dendroolithus verrucarius*, *Dendroolithus microporosus* (A,D)	Surface ornamentation composed primarily of a single shell unit (A,D); irregular surface ornamentation (A*,D*)

Table 3 Continued.

Metornithes	Arriagadoolithidae (A,D), *Continuoolithus canadensis* (A,D), *Subtiliolithus microtuberculatus* (A only), Unnamed Clade E (A,D)	Second structural layer present (A,D); cuticle present (A*,D*); ornamentation composed of multiple shell units (A,D); paired eggs (A*,D*)
Arriagadoolithidae	*Bonapartenykus ultimus*, *Triprisamtoolithus stephensi* (A)	Gradual transition between first and second structural layers (A); tabular structure present in first and second layers (A); prisms with irregular squamatic texture (A): third structural layer present (A)
Unnamed Clade E	Oviraptoridae (A,D), *Trachoolithus faticanus* (A,D), Unnamed Clade F (D only); Eumaniraptora (A,D)	Prisms primarily obscured by squamatic structure (D); ETQ equals 0.50-1.75 (A,D); Adult contact with clutch (A*,D*); lineartuberculate ornamentation (A*);
Unnamed Clade F	*Oblongoolithus glaber*, *Subtiliolithus microtuberculatus* (D only)	No features that were not also potentially plesiomorphic for Unnamed Clade E or synapomorphic for Eumaniraptora were found to support this clade, given its unresolved position at the base of Unnamed Clade E and consequent difficulty in reconstructing basal character states when Unnamed Clade F differs from the other basal members of Unnamed Clade E (D).

Table 3 Continued.

Oviraptoridae	*Citipati osmolskae*, Unnamed Clade G (A,D)	Two or more layers of eggs in a clutch (A,D); ring-shaped clutch with central opening (A,D)
Unnamed Clade G	oviraptorid, *Macroolithus rugustus* (A,D)	Undulating boundary between first and second layers (A,D); second to first layer thickness ratio equals 3.01:1-4:1 (A*,D*)
Eumaniraptora	*Macroelongatoolithus*, Deinonychosauria, *Protoceratopsidovum fluxuosum, Parvoolithus tortuosus*, Aviales (A,D)	Ratio of second to first layer thickness <2:1 (A); columnar extinction (A); asymmetrical egg shape (A,D)
Macroelongatoolithus	*Macroelongatoolithus xixiaensis*, Unnamed Clade H (A,D)	Undulating boundary between first and second structural layers (A,D); Crystal splaying between first and second layers (A*,D*)
Unnamed Clade H	*Macroelongatoolithus* oosp., Elongatoolithidae indet. (A,D)	Ratio of second to first structural layer thicknesses >4:1 (A,D)
Deinonychosauria	*Deinonychus antirrhopus* (A,D), "Larger avian eggs" (A only), Unnamed Clade I (A,D)	Nucleation center spacing/eggshell thickness ratio equals 0.24-0.33 (D); Eggs oriented subvertically in the substrate (A) (this is unknown for *Deinonychus*)
Unnamed Clade I	*Protoceratopsidovum sincerum* (A,D), *Protoceratopsidovum minimum* (A,D), *Troodon formosus* (A,D); "Larger Avian Eggs" (D only)	Prisms with irregular squamatic texture (A); Gradual transition between first and second layers (D); Surface ornamentation absent (D); Eggs oriented subvertically in the substrate (D)

Table 3 Continued.

Aviales	*Gobipipus reshetovi*, Neornithes (A,D)	This clade was constrained to appear on the tree, and no synapomorphies support it. (A); Elongation index of 1.5-2.0 (D) (This is also shared with *Parvoolithus tortuosus*.)
Neornithes	*Dromaius novaehollandiae*, *Gallus gallus* (A,D)	EMQ >0.30 (A,D); unpaired eggs (A,D); subhorizontal egg placement (A,D); unburied eggs (A*,D*); irregular arrangement of eggs in layer within clutch (A,D)

Discussion and Conclusions

Comparisons with Previous Work

The current work likely recovers a greater number of less well-supported trees than previous analyses because of the inclusion of greater number of taxa and ootaxa. Though it also includes a greater number of characters than any past work, the large expansion in the number of taxa and ootaxa with conflicting and homoplastic character states greatly complicates parsimony analysis. However, I feel that inclusion of such egg types is vital to obtain a more accurate picture of the totality of dinosaur egg evolution. Nevertheless, the tree topologies recovered in both the constrained and unconstrained analyses broadly agree with those of previous authors, yet highlight many important differences related to taxon selection and specifics of character coding. In terms of breadth of taxon selection, the current analysis is perhaps most comparable to that of Tanaka et al. (2011), and in character selection and coding to that of Jin et al. (2010).

Strong support is found among all trees (strict consensus trees for both unconstrained and constrained analyses) for a clade containing *Faveloolithus* oosp., *Faveoloolithus ningxiaensis*, *Dictyoolithus hongpoensis*, *Dendroolithus xichuanensis*, and *Torvosaurus gurneyi* eggs. Past studies did not include all of these ootaxa, and the fact that they group together to the exclusion of the other dendroolithids in the analysis is an interesting finding that will be discussed further in the Hypothesized Ootaxon Identities and the Monophyly of Oofamilies section below. The oofamily Arriagadoolithidae and a clade containing the oviraptorid and *Macroolithus rugustus* are consistently recovered among the unconstrained Adams consensus tree and both the strict and Adams consensus tree for the constrained analysis.

Differing from all previous studies, a clade containing Chinese spheroolithid eggs, therizinosauroid eggs, and Mongolian dendroolithid eggs is recovered in both the strict and Adams consensus trees for both the constrained and unconstrained analyses. This is again particularly interesting given the failure of these eggs to group with other members of their oofamilies included in the analysis (see Hypothesized Ootaxon Identities and the Monophyly of Oofamilies section for further discussion). This clade may be the same as the recently named oofamily Stalicoolithidae (Wang et al. 2012), as both contain Mongolian "dendroolithid" eggs and Chinese "spheroolithid" eggs, though disagreement exists over the validity of some related forms, specifically *Paraspheroolithus* and *Mosaicoolithus* (Barta et al. 2014, Zhang et al. In press).

The rather disparate nature of the two turtle egg types and my designation of the outgroup as paraphyletic relative to the ingroup may explain their failure to form a clade, even when they are constrained as monophyletic within the outgroup. Dinosauria (the ingroup) is monophyletic for both the constrained and unconstrained analyses, as was specified for both.

Pterosaur eggs are not recovered as monophyletic on the basis of character evidence in any of the current analyses. This is not surprising, given the disparate nature of *Pterodaustro* and ornithocheirid eggs and the large amounts of missing or inapplicable data for both taxa. Nevertheless, constraining Pterosauria to be monophyletic allows for more accurate character polarization across the remainder of the tree and removes conflict with consensus osteological trees.

The following section compares the topology of the unconstrained Adams consensus tree of the current study (utilizing ACCTRAN optimization and unordered characters) to the topologies of previously published cladistic analyses of dinosaur oological characters. The topology of the tree resulting from the constrained analysis and its implications for the possible taxonomic identities of unassigned ootaxa will be discussed in the Hypothesized Ootaxon Identities and Monophyly of Ootaxa section below. Discussing the unconstrained tree here allows for more direct comparison to previous studies, none of which utilized constraints. Unpublished theses (Zelenitsky 2004, Grellet-Tinner 2005) mentioned in the Previous Work section are not discussed here, as the results of very similar analyses by the same authors have now been published elsewhere. The exceptions are the analyses of Sellés (2012), which contain unique results not yet published elsewhere.

Grellet-Tinner and Chiappe (2004): This study produced a strict consensus tree in which a monophyletic Dinosauria consists of a basal polytomy that includes Ornithischia, Sauropoda, and Theropoda. The unconstrained analyses of the current study recovered a similarly monophyletic Dinosauria, though I specifically designated the ingroup as monophyletic relative to my paraphyletic outrgroups. The present study disagrees with Grellet-Tinner and Chiappe (2004) in its recovery of oviraptorid and extant avian eggs in an unresolved position relative to those of *Troodon*.

Varricchio and Jackson (2004): As in my study, the turtle outgroups of Varricchio and Jackson (2004) fail to form a clade. In the current analysis, *Maiasaura* is recovered in a clade with titanosaur eggs, rather than in an unresolved position, as Varricchio and Jackson (2004) found. Unlike in their tree, *Lourinhanosaurus* groups with more derived Eumaniraptoran eggs in my study. Also unlike their study, the current analysis surprisingly recovers *Triprismatoolithus stephensi* as closer to oviraptorid eggs than to Eumaniraptora. Similar to their tree, the relationship of Eumaniraptora relative to Oviraptoridae remains unresolved. Both my and Varricchio and Jackson's (2004) analyses recovered likely enantiornithine eggs as closer to *Troodon* than to other avian eggs.

Garcia et al. (2006): Garcia et al.'s (2006) findings differ greatly from mine in placing prismatoolithids, elongatoolithids, and bird eggs in a successive series basal to all other ootaxa in the analysis. In the current unconstrained analysis, *Cairanoolithus dughii* is basal to all megaloolithids, as in the analysis of Garcia et al. (2006). One difference is that I recover *Maiasaura* eggs as closer to *Megaloolithus* than they do. Garcia et al. (2006) recover avian eggs as more derived than other theropods, unlike in my unconstrained analysis, where they occupy an unresolved position relative to other derived theropods. As in Garcia et al. (2006), I recover *Troodon formosus* (*Prismatoolithus levis*) eggs in a clade with *Preprismatoolithus coloradensis*. See the Previous Work section for reasons why Garcia et al. (2006) may have recovered such an unusual topology that differs from most other cladistic analyses of eggshell and lacks congruence with analyses of osteological characters.

Grellet-Tinner and Makovicky (2006): As in their analysis, I do not recover a basal split between saurischian and ornithischian eggs. My analysis places *Deinonychus antirrhopus* eggshell as outside a clade containing *Citipati osmolskae* and

Macroelongatoolithus xixiaensis, unlike in their study, in which *D. antirrhopus* was found to be the sister taxon to *M. xixianesis*. Grellet-Tinner and Makovicky (2006) recover avian eggs as more derived than other theropods, unlike in my unconstrained analysis, where their relationships remain unresolved.

Moreno-Azanza et al. (2008): This analysis utilizes the characters and some ootaxa of Garcia et al. (2006), but shares only a few included ootaxa with the current study, as it focuses mostly on the interrelationships of megaloolithid oospecies. As in Garcia et al. (2006) and the current study, Moreno-Azanza et al. (2008) find *Cairanoolithus dughii* to be basal to other megaloolithids.

Zelenitsky and Therrien (2008a): My unconstrained tree topology differs from that of Zelenitsky and Therrien (2008a) by placing *Maiasaura* and titanosaur eggs in a clade with one another, rather than as successive outgroups to the theropod eggs in the analysis. As in my analysis, Zelenitsky and Therrien (2008a) recover *Protoceratopsidovum* in a clade with the eggs of *Troodon*. *Parvoolithus* also falls out in a clade with extant avian eggs in my analysis, similar to its position as the sister taxon to *Numida* in Zelenitsky and Therrien's (2008a) paper.

Zelenitsky and Therrien (2008b): The main difference between the present study and theirs not already discussed under the section for Zelenitsky and Therrien (2008a) above is my placement of *Deinonychus* eggshell in a clade with *Citipati*, to the exclusion of the clade containing *Troodon* eggs.

Jin et al. (2010): This study differs from the current analysis and consensus osteological phylogenies by placing *Maiasaura peeblesorum* and the titanosaur in a clade that forms the sister group to crocodilian eggs. Like the present study, it positions *Dictyoolithus* outside the clade containing the eggs of *Lourinhanosaurus* (cf. *Preprismatoolithus*). I, however, recover a monophyletic Neornithes, whereas they failed to do so. As in my

analysis, Jin et al. (2010) recover a clade containing the eggs of *Deinonychus*, an oviraptorid, and *Macroelongatoolithus*.

Tanaka et al. (2011): Their study differs from the current analysis in recovering megaloolithid eggs as more derived than other "dinosauroid-spherulitic" egg types, the interrelationships of which are better resolved in my study. As in the current study, *Megaloolithus* cf. *mammilare* and titanosaur eggs (*Megaloolithus patagonicus*) are recovered in a clade together [note in their Figure 5 that the "eggs of therizinosaurs" listed within Megaloolithidae is likely a typing error, based on comparison with the original analysis of Zelenitsky (2004), and should instead read "eggs of titanosaurs."]. The eggs of *Lourinhanosaurus* are also recovered as sister to those of *Preprismatoolithus coloradensis*, whereas in the current analysis their precise relationship remains unresolved. These egg types are placed more basally within Theropoda in Tanaka et al.'s (2011) analysis, than in ours, where they occur in a larger clade with other prismatoolithids. Tanaka et al. (2011) also found a clade of *Deinonychus* and elongatoolithid oospecies, as in my study, though the finer details of the topology of this clade differ between the two analyses. Tanaka et al. (2011) recovered *Macroelongatoolithus* as closer to the other elongatoolithids than to *Deinonychus*, as I also did. Tanaka et al. (2011) recover avian eggs as more derived than those of non-avian theropods, where the relationships of the two groups remain unresolved in the current analysis. The Comment on Ootaxonomy section provides a further discussion of the naming of ooclades by Tanaka et al. (2011).

López-Martínez and Vicens (2012): This study combines the data matrices of Zelenitsky and Therrien (2008a) and Zelenitsky and Therrien (2008b) and further incorporates *Sankofa pyrenaica* and the Bajo de la Carpa enantiornithine egg (Schweitzer et al. 2002) into the resulting data matrix. The tree topology does not differ substantially

from that of Zelenitsky and Therrien (2008a) and Zelenitsky and Therrien (2008b), and comparisons with the current study can be found under the entries for those two works.

Sellés (2012): This author modified the data matrix of Jin et al. (2010) to include new and rephrased characters and additional ootaxa. My recovery of *Faveoloolithus* far from the megaloolithids forms a major difference with the analyses of Sellés (2012, Fig. 26). Other parts of the trees are in close agreement with ours, such as the placement of *Cairanoolithus* outside Megaloolithidae. However, I do not find that *Cairanoolithus* falls out in the same clade as *Ovaloolithus* or any of the *Spheroolithus* oospecies, as Sellés (2012) does. As in my tree, most of Sellés' (2012) trees (with the exception of his majority rule consensus tree with *Cairanoolithus* added) fail to resolve the positions of possible ornithischian, sauropod, and theropod eggs relative to one another at the base of Dinosauria.

Ribeiro et al. (2014): The placement of the Porto das Barcas (probable *Torvosaurus gurneyi* eggs) concurs with that of the current study, as they are recovered in a polytomy with *Dendroolithus*, *Faveoloolithus*, and therizinosauroid eggshell when added to the data matrix of Tanaka et al. (2011), and as the sister taxon to *Dictyoolithus* when added to the data matrix of Jin et al. (2010). These placements are compatible with its position on the tree generated by the current analysis, where *Torvosaurus* eggs are a possible sister taxon to a clade containing *Dendroolithus xichuanensis*, *Dictyoolithus hongpoensis*, and *Faveoloolithus* oosp. The placement of the Casal da Rola eggshell (*Preprismatoolithus*) within the same clades as *Lourinhanosaurus* eggshell by Ribeiro et al. (2014) in both of the existing data matrices they utilized argues in favor of their assignment of the eggshell to *Lourinhanosaurus*, though these eggs occupy a more derived position within Theropoda on my unconstrained tree.

Moreno-Azanza et al. (In press): The addition of *Trigonoolithus amoae* to the data matrices of Jackson and Varricchio (2004), Grellet-Tinner and Makovicky (2006), Zelenitsky and Therrien (2008a), and López-Martínez and Vicens (2012) does not substantially change the recovered tree topologies of any of those analyses; thus comparisons with the current study can be found under the entries for those papers.

Comparison of Osteological and Oological Tree Topologies

Comparison of unconstrained cladistic analyses of oological characters and those of osteological characters helps to reveal problematic areas of the oological phylogeny in which homoplasy in eggshell and other reproductive characters may be rampant. Such discrepancies between the two types of datasets necessitate the use of backbone constraints to prevent the placement of taxonomically identified eggs in groupings that conflict with clades established on the basis of skeletal data, and to highlight the potential identities of taxonomically unassigned eggs. The unconstrained Adams consensus tree obtained by my study differs from the topologies of consensus trees of osteological data in the following ways:

1. *Maiasaura peeblesorum* and *Hypacrosaurus stebingeri* eggs, the only definite ornithischian eggs in the analysis, are not recovered as the sister taxa to all identified saurischian eggs. This is likely due to the large amount of missing data for *Hypacrosaurus* and a lack of basal ornithischian eggs that could shed light on the ancestral condition of dinosaur eggs.

2. *Lufengosaurus* eggshell does not form a sauropodomorph clade with *Massospondylus* eggshell, which instead groups with *Hypacrosaurus stebingeri* eggs. Neither egg type forms a sister group to the titanosaur. This is due to the large amount of missing data for both of the massospondylids, and the largely non-overlapping nature of the characters

that they can be coded for (mostly microstructural characters for *Lufengosaurus*, mostly whole-egg and clutch characters for *Massospondylus*).

3. Therizinosauroid eggs and *Torvosaurus gurneyi* eggs are recovered in a clade to the exclusion of all other taxonomically identified theropod eggshell. This is likely due to the fact that both eggs lack a second structural layer of eggshell. This character represents a reversal for the therizinosauroid, whereas it may be a retention of the primitive single-layered dinosaurian (or ornithodiran?) condition for *T. gurneyi*.

4. *Deinonychus antirrhopus* eggshell is not recovered as closer to *Troodon formosus* than to oviraptorid eggs. This placement may result from the lack of a third structural layer and presence of an ornamented eggshell surface for *Deinonychus*, both of which are characteristics shared with oviraptorid eggs.

5. *Allosaurus* sp. and *Lourinhanosaurus antunesi* eggs fall out in a derived position close to *Troodon formosus* eggs and other prismatoolithids. This may be the result of independently evolved characters originally used to unite the oofamily Prismatoolithidae, such as the presence of visible prisms that remain largely unobscured by squamatic structure.

Other placements of taxonomically identified eggs are consistent with osteological phylogenies.

Hypothesized Ootaxon Identities and the Monophyly of Oofamilies

This section and Table 4 utilize the Adams consensus tree topology (Fig. 79) obtained through the constrained analysis with ACCTRAN optimization, all characters unordered, and all taxa included. It is important to posit hypothetical identities for ootaxa within the relatively stable phylogenetic framework afforded by the topologies of osteological phylogenies that are based on a greater number of characters than are available to oological cladistic analyses.

Table 4. List of oofamilies with their member egg types. An assessment of monophyly and a possible taxonomic identification is made for each based on the constrained Adams consensus tree (Fig. 77). Only those taxa whose eggs have been subjected to thorough comparisons before formal assignment to an oofamily are included in the list. For example, the eggs of lambeosaurines and *Deinonychus antirrhopus* have been assigned to the Spheroolithidae (Horner 2000) and Elongatoolithidae (Jin et al. 2010), respectively, though neither assignment was based on an explicit microstructural comparison.

Oofamily	OTUs included in analysis	Monophyletic?	Inferred Taxonomic Identity(ies)
Spheroolithidae	*Maiasaura peeblesorum* (*Spheroolithus* oosp.), *S. irenensis*, *S.* cf. *zhangtoucaoensis*	No; The two Asian *Spheroolithus* oospecies are closer the therizinosauroid than to the eggs of *M. peeblesorum*.	Hadrosaurid (*M. peeblesorum*); Indeterminate tetanuran (*S. irenensis*, *S.* cf. *zhangtoucaoensis*)
Ovaloolithidae	*Ovaloolithus chinkangkouensis*	N/A	Indeterminate dinosaur
Megaloolithidae	Titanosaur (*Megaloolithus patagonicus*), *Megaloolithus* cf. *mammilare*, *Cairanoolithus dughii*	No; *C. dughii* falls outside the clade containing the other two megaloolithids.	Sauropod (*Megaloolithus*); Indeterminate dinosaur (*C. dughii*)
Faveoloolithidae	*Faveoloolithus ningxiaensis*, *Faveoloolithus* oosp.	Uncertain; The two faveoloolithids in the analysis fall out in a polytomy with some dendroolithids and *Dictyoolithus hongpoensis*.	Basal tetanuran
Dictyoolithidae	*Dictyoolithus hongpoensis*	N/A	Basal tetanuran

Table 4 Continued.

Dendroolithidae	*Torvosaurus gurneyi* (Dendroolithidae), *Dendroolithus xichuanensis*, Therizinosauroid (Dendroolithidae), *D. verrucarius, D. microporosus*	No; *T. gurneyi* and *D. xichuanensis* fall out in a polytomy together, basal to the clade containing the therizinosauroid, *D. verrucarius*, and *D. microporosus*	Basal tetanuran (*T. gurneyi*, *D. xichuanensis*); therizinosauroid (*D. verrucarius*, *D. microporosus*)
Oblongoolithidae	*Oblongoolithus glaber*	N/A	Indeterminate avetheropod
Arriagadoolithidae	*Bonaparetnykus ultimus* (*Arriagadoolithus patagoniensis*), *Triprismatoolithus stephensi*	Yes	Alvarezsaurid
Laevisoolithidae	*Subtiliolithus microtuberculatus*	N/A	Indeterminate metornithine
Elongatoolithidae	*Citipati osmolskae* (Elongatoolithidae), oviraptorid (Elongatoolithidae), *Macroolithus rugustus*, *Trachoolithus faticanus*, *Macroelongatoolithus xixiaensis*, *Macroelongatoolithus* oosp., Elongatoolithidae indet.	No; *C. osmolskae*, the oviraptorid, and *M. rugustus* form a clade (Oviraptoridae) to the exclusion of the other ootaxa. *Macroelongatoolithus* and the indeterminate elongatoolithid form a more derived clade. The position of *T. faticanus* is unresolved relative to Oviraptoridae.	oviraptorid (*M. rugustus*), Indeterminate eumaniraptorans (*Macroelongatoolithus*, indeterminate elongatoolithid)

Table 4 Continued.

Prismatoolithidae	*Allosaurus* sp. (*Preprismatoolithus coloradensis*), *Lourinhanosaurus antunesi* (cf. *Preprismatoolithus*), *Protoceratopsidovum fluxuosum*, *Protoceratopsidovum sincerum*, *Protoceratopsidovum minimum, Troodon formosus* (*Prismatoolithus levis*)	No; *Allosaurus* sp. and *L. antunesi* eggs form a much more basal clade than do the other prismatoolithids in the analysis. *P. fluxuosum* is placed in an indeterminate position within Eumaniraptora relative to *P. sincerum*, *P. minimum*, and *P. levis*, which are united in a polytomy.	Allosaurids and possibly basal coelurosaurs (Carrano et al. 2012) (*Preprismatoolithus*); Indeterminate eumaniraptoran (*P. fluxuosum*); troodontids (*P. sincerum*, *P. minimum*, *P. levis*)
Gobioolithidae	*Gobipipus reshetovi* (*Gobioolithus minor*)	N/A	non-neornithine bird

The theropod identities posited herein for faveoloolithid and some spheroolithid eggs conflict with previous attributions of Faveoloolithidae to sauropods (Mikhailov 1991, Grellet-Tinner and Fiorelli 2010, Soto et al. 2012), pachycephalosaurs (Kundrát 2000), and ornithopods (Zhao 1979b, Sabath 1991) and of Spheroolithidae to Ornithopoda (Mikhailov 1991). A basal tetanuran parentage for faveoloolithids, dictyoolithids, and some dendroolithids, known mostly from the Late Cretaceous, would imply a long ghost lineage for such a basal clade. No megalosaurids are known from the Cretaceous (Holtz 2012). This argues strongly against a basal tetanuran identity for these egg types posited solely on the basis of cladistic analysis and suggests two alternative hypotheses: 1) Faveoloolithid, dictyoolithid, and some dendroolithid eggs were laid by a taxon outside Theropoda and represent an example of convergence with *Torvosaurus*

gurenyi eggshell, or 2) they represent another case of reversal to a more "basal" dinosaur egg type among derived theropods, as is the case with therizinosauroids (see below). I did not include any South American faveoloolithids in this analysis, which are often hypothesized to be the eggs of sauropods (Faccio 1994, Grellet-Tinner and Fiorelli 2010 and references therein). My recovery of *Dictyoolithus hongpoensis* as a potential theropod egg type agrees with the cladistic analysis presented by Jin et al. (2010). Zelenitsky (2000) notes that there is a "gradation between the eggshell structure of dendroolithids and faveoloolithids" which may be the result of varying degrees of diagenetic alteration. Thus, it is cautioned that the grouping of these egg types together in this analysis may result from a taphonomic, rather than a phylogenetic signal. Further testing of Zelenitsky's (2000) idea through the use of cathodoluminescence and other techniques is needed.

Recovery of *Dendroolithus verrucarius* and *D. microporosus* as derived members of a clade containing therizinosauroid eggshell suggests that they might plausibly be assigned to therizinosauroids or closely related taxa. This, combined with the occurrence of therizinosauroids in Late Cretaceous Mongolia, lends support to a therizinosauroid identity for these eggs, as put forward by Mikhailov (1997a). Extension of this identification beyond *D. verrucarius and D. microporosus* to the whole of Dendroolithidae is not warranted, *contra* Mikhailov (1997a), as the Chinese *Dendroolithus xichuanensis* falls out in a polytomy with *Torvosaurus gurneyi* eggshell far from the Mongolian dendroolithids and Chinese therizinosauroid eggs.

The recovery of *Ovaloolithus chinkangkouensis* and *Cairanoolithus dughii* as indeterminate dinosaurs on an Adams consensus tree highlights that any of the dinosaur clades remain potential candidates for parent taxa. The placement of *C. dughii* as outside

Megaloolithidae concurs with the results of Sellés (2012). He considered *Cairanoolithus* to be potential ornithopod eggs.

Oblongoolithus glaber, the sole known member of the Oblongoolithidae, is recovered as an indeterminate avetheropod in this analysis, in agreement with a previously posited theropod identity (Mikhailov 1997a).

The recently named oofamily Arriagadoolithidae (Agnolin et al. 2012) is recovered as the only monophyletic oofamily in this analysis, supporting the assertion that *Triprismatoolithus stephensi* may be the eggs of a Two Medicine Formation alvarezsaurid that is currently unknown from skeletal remains (Agnolin et al. 2012).

Subtiliolithus microtuberculatus, the sole laevisoolithid egg included in my data matrix, is recovered as an indeterminate metornithine. This is broadly consistent with the identification of this egg type as enantiornithine based on the co-occurrence of eggshell fragments with a subadult specimen of *Nanantius valifanovi* (Kurochkin 1996) (=*Gobipteryx minuta*, Chiappe et al. 2001).

Contrary to the results of a previous analysis that broadly sampled elongatoolithid ootaxa (Tanaka et al. 2011) and my own unconstrained Adams consensus tree, Elongatoolithidae is paraphyletic in the constrained analysis. The *Macroelongatoolithus* oospecies and the indeterminate Cloverly Formation elongatoolithid are grouped within Eumaniraptora to the exclusion of other elongatoolithid eggs that are hypothesized to belong to oviraptorids. While this possibly argues in favor of the validity of Macroelongatoolithidae (Wang and Zhou 1995), Huh et al. (2014) argue against use of this oofamily due to strong similarities with Elongatoolithidae and the potentially insufficient nature of diagnostic characters used to define Macroelongatoolithidae. The findings of the current study may reveal previously overlooked taxonomic diversity within Elongatoolithidae, though I note that further description of a possible perinatal

oviraptorid skeleton associated with Chinese *Macroelongatoolithus* eggs (Grellet-Tinner 2005) may help to provide a taxonomic constraint for this egg type to be used in future reanalyses of this dataset. Perhaps the phylogenetic signal actually represented by the separation of elongatoolithid eggs from one another on the current constrained tree is the potential difference between the eggs of Oviraptoridae, and Caenagnathidae. Caenagnathidae is a group recently recognized as monophyletic and distinct from Oviraptoridae that contains taxa large enough to have plausibly laid *Macroelongatoolithus* eggs (Lamanna et al. 2014). This idea necessarily remains highly speculative until definitive caenagnathid remains are found in association with eggs. The relationships of the Early Cretaceous elongatoolithid ootaxon *Trachoolithus faticanus* to other elongatoolithids remain unresolved, likely because it is known solely from eggshell fragments (Mikhailov 1994a).

As in previous cladistic analyses (Jin et al. 2010, Tanaka et al. 2011), Prismatoolithidae is found to be polyphyletic because of the inclusion of *Preprismatoolithus* eggshell, which belongs to *Allosaurus* sp. (Carrano et al. 2013) and *Lourinhanosaurus antunesi* (Mateus et al. 1998), with the eggs of *Troodon formosus*, a more derived theropod. Excluding *Preprismatoolithus*, "core Prismatoolithidae" consisting of *Protoceratopsidovum sincerum*, *P. minimum*, and *Prismatoolithus levis*, is monophyletic. An exeception is *Protoceratopsidovum fluxuosum*, a problematic ootaxon that shares some features (such as lineartuberculate ornamentation) with elongatoolithids and is recovered in this analysis as an indeterminate eumaniraptoran egg. Nevertheless, the finding of all *Protoceratopsidovum* eggs as theropod concurs with previous analyses (Zelenitsky and Therrien 2008a, Tanaka et al. 2011) and makes a previously hypothesized protoceratopsian identity (Mikhailov 1994a) very unlikely.

Gobioolithus minor, the sole representative of Gobioolithidae in the analysis, is constrained to group with extant avian eggs in my analysis on the basis of enantornithine (*Gobipipus reshetovi*) embryos *in ovo* (Kurochkin et al. 2013). The incertae sedis ootaxon *Continuoolithus canadensis*, included here for the first time in a cladistic analysis, falls out as an indeterminate metornithine, consistent with all previous studies that have identified it as a likely theropod egg (Hirsch and Quinn 1990, Zelenitsky et al. 1996, Jackson and Varricchio 2010). The incetae sedis oospecies *Parvoolithus tortuosus* occupies an unresolved position at the base of Eumaniraptora, a finding that agrees broadly with the analyses of Zelenitsky and Therrien (2008a) and Tanaka et al. (2011), which further resolve it as a possible avian egg.

The "Larger Avian Eggs" of Sabath (1991) are here recovered within Deinonychosauria, suggesting a non-avian theropod identity. However, Varricchio and Barta (In review) redescribe the adult bones associated with a clutch of these eggs, finding a possible avian character. Additionally, the unusually thick external layer possessed by these eggs is not seen in any non-avian theropod eggs, but is seen among some extant bird orders (Mikhailov 1997b). The overall smaller egg size and lesser eggshell thickness of the "Larger Avian Eggs" in comparison to prismatoolithids also may indicate an avian identity. Nevertheless, the troodontid-like clutch configuration of this egg type suggests that if the tentative avian identification of Varricchio and Barta (In review) proves incorrect, a troodontid identity is a good alternative possibility.

Comments on Ootaxonomy

Of the twelve oofamilies included in this study (Table 4), only one, Arriagadoolithidae, was recovered as monophyletic under its current membership, six (Megaloolithidae, Faveoloolithidae, Dendroolithidae, Spheroolithidae, Elongatoolithidae, and Prismatoolithidae) were recovered as non-monophyletic, and five (Dictyoolithidae,

Ovaloolithidae, Gobioolithidae, Oblongoolithidae, and Laevisoolithidae) were represented in the analysis by a single oospecies.

The non-monophyletic nature of most oofamilies for which two or more representatives were sampled for this analysis might suggest that the ootaxonomic system itself is not useful and that its use should be discontinued. I do not agree. Though it may be necessary to redefine most currently recognized oofamilies to provide explicitly phylogenetic definitions and membership lists based on the results of cladistic analysis, parataxonomy still plays a vital role in helping researchers to avoid making erroneous or unjustified assignments of eggs to parent taxa. Parataxonomy further aids in biostratigraphic and biogeographic comparisons among oofaunas for which most eggs lack associated embryonic or adult remains (Mikhailov 2014, Sellés et al. 2014, Varricchio et al. 2014).

Arguments in favor of the usefulness of ootaxonomy aside, this study supports the general statements of Zelenitsky (2004), Varricchio and Jackson (2004), and Grellet-Tinner (2005) that paleoology would benefit from the use of explicit phylogenetic definitions in the description and classification of eggs. I further extend this argument to suggest that a phylogenetic framework constrained to current consensus osteological phylogenies should be utilized in future cladistic analyses of oological material in order to bring about greater congruence and reduce conflict between the content of "ooclades" (Zelenitsky 2004) and osteological clades.

I choose not to apply the names of previously defined "ooclades" (Zelenitsky 2004, Tanaka et al. 2011) to the results of my analysis. Though the tree topologies are broadly congruent (see discussion under Comparisons with Previous Work above), until more cladistic analyses of eggshell are conducted and a broad consensus among different researchers arrived at, it would be best not to complicate ootaxonomy with more names,

particularly ones that include existing taxon names, as the "ooclades" do (e.g. Neotetanuroomorpha, Maniraptoroomorpha). The use of clade names in this study is strictly based on the clades formed by the taxonomically identified eggs specified in the backbone constraint. I prefer to leave unnamed those clades whose membership does not correspond to any osteological clade, though I note that some of these, if consistently recovered in the future, could be named as new oofamilies, or redefinitions of existing ones.

Major Trends in Dinosaur Eggshell Evolution

Understanding of general trends in the evolution of archosaur egg and eggshell evolution is complicated by several factors. No eggs are known for basal archosaur or archosauromorph taxa; indeed, the earliest known hard-shelled eggs are those of prosauropod dinosaurs (Bonaparte and Vince 1979). Given this temporal and phylogenetic distribution of early Mesozoic eggs and the fact that at least some pterosaur taxa possessed non-mineralized or semi-rigid eggs, it remains possible that crocodilian eggshell was evolved independently from that of non-avian dinosaurs and birds, complicating use of the Extant Phylogenetic Bracket (EPB, Witmer 1995) to infer ancestral eggshell structure. Similarly, a lack of identified ornithischian eggshells in the fossil record until those of Late Cretaceous hadrosaurs complicates efforts to confidently reconstruct ancestral character states for dinosaur eggs. Nevertheless, the present analysis provides potential synapomorphies (Table 3) that unite dinosaur eggs to the exclusion of other taxa. These ancestral states of egg characters can be tested by future discoveries of basal egg types near those nodes. These potential synapomorphies include a height/width ratio of shell units equal to 2.01-7.0, tabular structure present in the first structural layer, a nucleation site spacing/shell thickness ratio less than 0.24, the presence of layers of eggs within a clutch, and an elongation index of 1.0-15. This last character is

ambiguous with respect to the whole tree, as spherical to subspherical eggs are also laid by some turtles (e.g., *Apalone mutica* in the current study). No synapomorphies were found to support Saurischia, Sauropodomorpha, or Massospondylidae, and these clades only appear on the constrained tree because they were specified as part of the backbone constraint,

Because of the inclusion of the disparate *Torvosaurus* eggshell in the current study, no common oological features were found to unite all of Theropoda in the present study. Nevertheless, within the constrained framework some trends within theropod eggshell evolution become apparent. Basally, the clade retains "primitive" dinosaur egg characters also seen in hadrosaur eggs, such as presence of a single structural layer of calcite and irregular pore shape. The second structural layer apparently first evolved within Avetheropoda, and with it appeared squamatic structure and a columnar extinction pattern. A possible feature that may diagnose Maniraptora is an eggshell thickness quotient (ETQ) greater than 1.75, as this is a trait found among both therizinosauroid and oviraptorid eggs. Therizinosauroid eggs represent a major reversal within Theropoda, and a mark a reappearance of such "primitive" dinosaur eggshell features as the lack of a second structural layer and irregular pore shape. Interestingly, they appear to lack tabular structure, which is optimized as basal to Dinosauria in this analysis and is present among many theropod eggs (Jin et al. 2010).

The Metornithes possess at least two structural layers of calcite, have ornamentation that is composed of multiple shell units, were the first dinosaurs to exhibit egg pairing within clutches, and may have been the first dinosaurs to possess a cuticle, though this feature could only be scored as present for the two arriagadoolithids and the extant avian taxa in the analysis; thus, it remains unclear if the egg types bracketed by

these taxa actually possessed a cuticle or not, but its presence is predicted by the character optimization on the Adams consensus tree.

The unnamed clade of Oviraptoridae + Eumaniraptora may have been the first group for which adults made contact with their clutches, and the first to possess lineartuberculate ornamentation. Additional ambiguous synapomorphies optimized at this node include prisms that are primarily obscured by squamatic structure, and an ETQ of 0.50-1.75.

Eumaniraptorans possess asymmetrical eggs and columnar extinction, characters also present in *Preprismatoolithus* lower on the tree. Neornithes was the first dinosaur clade to have an EMQ greater than 0.30. Additional differences between neornithine eggs and those of troodontids include upaired eggs, subhorizontal egg placemet, unburied eggs, and an irregular arrangement of eggs within the single-layered clutch. All of these differences suggest a major shift in reproduction style on the line leading to extant avians, concurring with the results of Varricchio et al. (1997).

Taken together, all of these transitions suggest that the whole of dinosaur egg evolution on the line leading to modern birds has been marked by an increasing complexity of eggshell structure (as demonstrated by the addition of second and third structural layers) that produces eggshell microstructure of comparable complexity to those of crocodilians, though the evolutionary history of Pseudosuchian eggs remains largely unknown. Within theropods, a stepwise accumulation of avian-like eggshell traits is seen, with a major reversal to a more basal dinosaur condition in Therizinosauroidea.

Implications for Interpreting the Mesozoic Fossil Record of Eggs

The findings of this study argue against *a priori* reasoning that the majority of unassigned ootaxa could belong to ornithischians or sauropodomorphs. Though the relationships of *Ovaloolithus* and *Cairanoolithus* are unresolved relative to the remainder

of Dinosauria, the number of remaining egg types that might plausibly be considered sauropod or ornithischian on the basis of oological (particularly microstructural) characters alone is small. The fact that *Ovaloolithus* and *Carianoolithus* are restricted to the Late Cretaceous of Asia and North America (Mikhailov 1994b, Bray 1999), and Europe (Vianey-Liaud et al. 1994), respectively, suggests that eggs that might be considered even potential ornithischian eggs remain unknown for most of the Mesozoic, and from Gondwana. Additionally, an egg containing a possible titanosaur embryo (Grellet-Tinner et al. 2011) may be similar to *Ovaloolithus* or *Spheroolithus* (Mikhailov 2014), further complicating assignment of all eggs of either of these ootaxa to ornithischians if the identification of the embryo is upheld. An association of perinatal hadrosaur bones with megaloolithid eggs from the Late Cretaceous of Romania (Grigorescu et al. 2010) remains problematic, as it would suggest convergence between hadrosaur and titanosaur eggs. My unconstrained phylogenetic analysis does suggest there is some degree of convergence between hadrosaur and titanosaur eggs; however, the sole unassigned megaloolithid (*Megaloolithus* cf. *mammilare*) included in my analysis groups with the titanosaur egg to the exclusion of hadrosaur eggs on the strict consensus tree. Future inclusion of the particular oospecies to which the Romanian material is assigned (*Megaloolithus siruguei*) in a phylogenetic analysis also including the eggs of hadrosaurs could help to provide some insight as to its affinities. Until further study of this association is made, I accept the argument of Weishampel and Jianu (2011) that the perinatal remains may have been washed in to the nests from a short distance away, as none have yet been found inside well-preserved eggs. This contrasts with titanosaur embryos found within megaloolithid eggs (Chiappe et al. 1998), which provide for a more confident assessment of the parentage of megaloolithid eggs.

The results of the cladistic analysis and the observations above highlight biases against the preservation of ornithischian eggshell, which possibly result from 1) a bias in the amount of preserved rock from the time in which ornithischians lived, 2) ornithischians laying eggs in areas of non-deposition, 3) ornithischians employing an alternative reproductive strategy that is not conducive to egg preservation (e.g. use of vegetation mounds, eggs with pliable shells, ovoviviparity, or viviparity), or 4) some combination of any or all of the above. The global prevalence of ornithischians throughout the Mesozoic, across a range of basins with different tectonic styles and geographic areas with varying degrees of continuous deposition for varying amounts of time argues against 1). The presence of *Maiasaura* and lambeosaurine eggshell (Horner 1999) in different depositional environments suggests that at least some ornithischians laid their eggs in a variety of environments where they were likely to be preserved, arguing against 2). Application of the Extant Phylogenetic Bracket (EPB, Witmer 1995) would argue against 3); however, the existence of apparently pliable-shelled pterosaur eggs (Wang and Zhou 2004, Ji et al. 2004) complicates strict application of the EPB, and necessitates that the hypothesis that some ornithischians evolved hard-shelled eggs independently from other dinosaurs at least merit consideration.

Alternatively, this analysis highlights that the extensive scope of theropod egg disparity and suggests that homoplasy with the eggs of other clades may be greater than previously thought, potentially causing the mistaken recovery of unidentified eggs from other clades as theropod. Such homoplasy may result from functional considerations involved with water vapor conductance such as the length and width of pores and the total area of an egg they occupy (Seymour 1979, Garcia et al. 2006, Grigorescu et al. 2010). Shell thickness, both in terms of its controls on pore length and egg breaking strength (Sabath 1991) is another character with functional significance and the potential

to exhibit convergence among egg types. An interesting case of convergence is the shared characters between therizinosauroid and other herbivorous dinosaur eggs, including the presence of a single structural layer and spherical egg shape. Spherical egg shape may be a result of the need to pack larger numbers of eggs together in the cloaca before being laid *en masse* as in some turtles (Carpenter 1999), but I note that somewhat elongated eggs are also known for crocodilians which also exhibit mass-laying. Perhaps mass-laying only prevents the development of highly elongate eggs (more elongate than those of crocodilians) or perhaps there are as-yet-unknown dietary controls that influence egg formation and result in convergence among these taxa, such as the enlarged guts of herbiovores reducing the body cavity space in which to fit a highly elongate egg.

In the end, there are likely only so many ways to form an egg that still allow for viable offspring to hatch. These overall functional controls that limit the range of possible egg diversity likely cause the reappearance of certain features across disparate taxa. Still, a few major transitions (unambiguous synapomorphies recovered in this analysis) can be said to exhibit a clear phylogenetic signal.

These unambiguous synapomorphies include, for Archosauria, calcitic eggshell; for Dinosauria, the taller-than-wide shell units, tabular structure in the first structural layer, narrowly spaced nucleation sites, and prescence of a layer(s) of eggs; for the clade of Faveoloolithidae, Dictyoolithidae, and some dendroolithid eggshell, shell units that branch near their bases and branching pores; for Avetheropoda, the presence of squamatic structure in the second structural layer of eggshell; for the clade of the therizinosauroid and Mongolian *Dendroolithus*, shell units that first branch near the exterior of the eggshell; for the clade of Mongolian *Dendroolithus*, irregular surface texture; for Metornithes, a cuticle and paired eggs; for the clade of Oviraptoridae, Eumaniraptora and others, adult contact with the clutch; for the clade of the unidentified

oviraptorid and *Macroolithus*, a second to first structural layer thickness ratio of 3.01:1-4:1; for *Macroelongatoolithus*, crystal splaying between the first and second structural layers (though this is present in other taxa not included in the analysis, see discussion for Character 9); and for Neornithes, unburied eggs.

The absence of oological synapomorphies for many of the major dinosaur clades (Saurischia, Sauropodomorpha, Theropoda) highlights the relative lack of eggs for basal members of these clades, and highlights the disparate nature of the eggs that are known for these clades. The relative lack of unambiguous oological synapomorphies for some derived theropod and avian clades reveals the complex nature of the mosaic evolution of egg characters on this part of the tree.

Summary and Prospectus

Major findings of this study include:

- Eggshell characters are marked by significant homoplasy, which may produce misleading groupings of eggs in the absence of a toplogically constrainted framework based on the consensus osteological relationships of taxa with identified eggs.
- This analysis finds a stepwise accumulation of avian-like eggshell traits within theropods before the appearance of extant avians, as in previous studies.
- Therizinosauroid eggs represent a major reversal to a more basal dinosaur condition within Theropoda.
- All taxonomically unassigned ootaxa except for *Ovaloolithus chinkangouensis* and *Cairanoolithus dughii* were recovered as saurischian eggs, suggesting that the observed near-absence of ornithischian eggs in the fossil record is not simply an artifact of a lack of embryonic or adult

associations for currently known, yet taxonomically unassigned ootaxa. This further suggests that there were real biases acting against the preservation of ornithichian eggs, and that the independent evolution of hard-shelled eggs within this clade remains a possibility.

- Only one oofamily (Arriagaoolithidae) for which two or more oospecies were included was recovered as monophyletic. This suggests that revision of the ootaxonomic system within an explicitly phylogenetic framework is needed, but awaits the results of future cladistic analyses that may or may not support the clades found here. The non-monophyletic nature of many oofamilies should not, however, diminish the usefulness of ootaxonomy for biostratigraphic, biogeographic, and communication purposes (Mikhailov 2014).

In many ways, oological data forms a "worst-case-scenario" for the application of cladistic analysis. The high degree of homoplasy among egg types and the small number of characters available for analysis work to complicate cladistic results (Varricchio and Jackson 2004), drive up the number of trees recovered, and drive down measures of tree support. Future work should focus on novel methods of reducing the influence of homoplasy on oological data matrices, including the continued use of backbone constraints and incorporation of egg characters into an osteological data matrix to generate a total evidence phylogeny, as has been done for paleognath birds (Zelenitsky and Modesto 2003) and four maniraptoran taxa (Grellet-Tinner 2005). Generation of new characters through novel sources is another means whereby the robustness of oological cladistic results may be improved. One promising method is electron backscatter diffraction (EBSD), a means of precisely identifying the orientation of calcite crystal c-axes within eggshell (Shaw 2009, Trimby and Grellet-Tinner 2011, Moreno-Azanza et al.

2013). Other methods, such as epifluorescence microscopy, help to clarify character codings and sort out diagenetic from biological features of eggshell (Jackson et al. 2010). Further attempts to standardize descriptive terminology applied to eggs and their microstructure will facilitate communication among researchers and help to resolve underlying differences in the interpretation of features that become reflected in the nomenclature applied to those features.

In spite of the above difficulties, cladistic analysis of oological datasets holds much promise for further understanding and untangling the roles of both function and phylogeny in producing the observed diversity of eggshell microstructure, egg morphology, and clutch arrangements. A greater knowledge of eggshell phylogeny serves to provide a framework whereby the meaning of Mesozoic fossil egg diversity may be elucidated.

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APPENDICES

APPENDIX A

CHARACTERS USED IN PHYLOGENETIC ANALYSIS

1. Eggshell, composition: aragonite (0); calcite (1) after Varricchio and Jackson (2004).
2. Eggshell, first structural layer, organization of nucleation site: loosely organized basal knob (0); highly organized organic core (1).
3. Eggshell, first structural layer, height/width ratio of mammillae or shell units (if only one structural layer present): <1 (0); 1.0-2.0 (1); 2.01-7.0 (2); >7.01 (3).
4. Eggshell, shell units: unbranched (0); first branched near interior of shell (1); first branched near exterior of shell (2).
5. Eggshell, second structural layer: absent (0); present (1).
6. Eggshell, transition between first and second structural layers: abrupt (0); gradual (1) modified after Varricchio and Jackson (2004) and Zelenitsky and Therrien (2008a).
7. Eggshell, boundary between first and second structural layers: straight (0); undulating (1).
8. Eggshell, ratio of second to first structural layer thicknesses: <2:1 (0); 2:1-3:1 (1); 3.01:1-4:1 (2); >4:1 (3).
9. Eggshell, crystal splaying (sensu Jin et al. 2007) in first and second layers: absent (0); present (1).
10. Eggshell, tabular structure: absent (0); present in first layer (1); present in second layer (2); present in third layer (3).
11. Eggshell, second layer: squamatic structure absent (0); present (1).
12. Eggshell, prisms: primarily obscured by squamatic structure (0); with well-developed squamatic texture and visible margins (1); with irregular squamatic texture (2) modified after Jackson and Varricchio (2010).
13. Eggshell, transition between second and third structural layers: gradual (0); abrupt (1) after Varricchio and Jackson (2004).
14. Eggshell, third structural layer: absent (0); present (1).
15. Eggshell, third structural layer: with horizontal crystals and vertical fibrous fabric (0); with vertical crystals (1); with granules that obscure crystal orientation (2)modified after Varricchio and Jackson (2004).
16. Eggshell, cuticle: absent (0); present (1) after Varricchio and Jackson (2004).
17. Eggshell, accretion lines: straight at shell unit boundaries (0); arched at shell unit boundaries (1).
18. Eggshell, shell units, extinction pattern under cross polars: sweeping (0); columnar (1); blocky (2).
19. Eggshell, nucleation centers, spacing relative to shell thickness: >0.40 (0); 0.33-0.40 (1); 0.24-0.33 (2); <0.24(3) after Varricchio and Jackson (2004).
20. Eggshell, surface ornamentation: absent (0); present, composed primarily of a single shell unit (1); present, composed of multiple shell units (2); present, not formed by shell units (3).
21. Eggshell, surface ornamentation, type if present and formed by shell units: compactituberculate (0); sagenotuberculate (1); dispersituberculate (2); lineartuberculate (3); ramotuberculate (4); anastomotuberculate (5); irregular (6).
22. Eggshell, pores, shape in radialsection: unbranching (0); branching (1).
23. Eggshell, pores, shape in radial section: irregular (0); tubular (1).
24. Eggshell, pores, orientation to eggshell surface: perpendicular (0); oblique (1).
25. Eggs, mechanical properties: soft, no mineralization (0); semi-rigid, discontinuous mineralization (1); rigid, continuous mineralization (2).
26. Eggs, shape: symmetrical about the equator (0); asymmetrical about the equator (1) after Zelenitsky and Therrien (2008).

27. Eggs, shape, elongation index (ratio of egg length to width): 1.0-1.5 (0); 1.5-2.0 (1); >2.0 (2).
28. Eggs, ratio of actual eggshell thickness to predicted eggshell thickness based on egg mass using an avian regression (Eggshell Thickness Quotient = ETQ): < 0.50 (0); 0.50-1.75 (1); >1.75 (2).
29. Eggs, size relative to adult body size (Egg Mass Quotient = EMQ): small, <0.10 E_b (0); medium, 0.10-0.30 E_b (1); large, >0.30 E_b (2) from Varricchio and Jackson (2004).
30. Eggs, pairing: unpaired (0); paired (1).
31. Eggs, orientation of long axis within clutch: subhorizontal (<45 degrees from surface of substrate) (0); subvertical (> or = 45 degrees from surface of substrate) (1) modified after Zelenitsky and Therrien (2008).
32. Eggs, location within nest: unburied (0); partially buried (1); completely buried (2).
33. Clutch, contact with adult: absent (0); present (1).
34. Clutch, egg layers: absent (massed) (0); present (1).
35. Clutch, egg layers, number if present: one (0); two or more (1).
36. Clutch, arrangement of eggs within layers: irregular (0); linear or rectangular (1); ring-shaped with central opening (2).

APPENDIX B

DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

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                                  .5    .10   .15   .20   .25   .30   .35
Apalone mutica                  01000 ----0 ---0- 01000 -0102 00110 0200- -
Elseya novaeguineae             01100 ----0 ---0- 01000 -0102 01120 0200- -
Alligator mississippiensis      10001 0010{23} 0-110 00202 50102 01100 0200- -
Crocodylus niloticus            10001 0000{23} 0-110 00200 -0102 01100 0200- -
Pterodaustro guinazui           11?00 ----0 ---0- ????? ????1 0202? ?2??? ?
Ornithocheirid                  ----- ----- ----- ----- ----0 01-?? ????? ?
Maiasaura peeblesorum           11200 ----1 ---0- ?0031 10002 00100 02011 0
Hypacrosaurus stebingeri        1???? ????? ????? ????1 1???2 00010 0??10 0
Spheroolithus irenensis         11200 ----0 ---0- ?0030 -0002 002?0 0??10 0
Spheroolithus cf. zhangtoucaoensis 11200 ----0 ---0- ?0030 -0002 002?0 0??10 0
Ovaloolithus chinkangkouensis   11300 ----1 ---0- ?0032 10102 00??? ????? ?
Massospondylus                  1???? ????1 ????? ????? ????2 00000 0??10 0
Lufengosaurus                   11100 ----? ---0- ???0? ????2 ????? ????? ?
Titanosaur                      11200 ----1 ---0- ?1021 00102 001?0 0??11 0
Cairanoolithus dughii           11200 ----? ---0- ?0030 -0102 001?0 02?10 0
Megaloolithus cf. mammilare     11200 ----? ---0- ?1031 00102 001?0 02?10 0
Faveoloolithus ningxiaensis     11210 ----? ---0- ?0030 -1002 001?0 02?11 0
Faveoloolithus oosp.            11210 ----? ---0- ?0020 -1002 001?0 0??10 0
Dictyoolithus hongpoensis       11310 ----1 ---0- ?0020 -1002 001?0 0??10 0
Dendroolithus verrucarius       11320 ----0 ---0- ?0031 600?2 ??2?? ?2??? ?
Dendroolithus microporosus      11220 ----0 ---0- ?0031 60002 002?? ????? ?
Dendroolithus xichuanensis      11210 ----0 ---0- ?0020 -1002 001?? ????? ?
Torvosaurus gurneyi             11210 ----0 ---0- ?0?31 51002 ????? ?2??? ?
Therizinosauroid                11220 ----0 ---0- ?0030 -0002 002?0 0??10 0
Allosaurus sp.                  11101 1?302 12-0- ?0120 -01{01}2 11100 0??10 0
Lourinhanosaurus antunesi       11101 1?102 12-0- ?0120 -01{01}2 10110 02?10 0
Citipati osmolskae              11101 00101 10-0- ?0{01}32 {34}0102 02111 0?111 2
Oviraptorid                     11101 0120? 10-0- ?0032 3???2 ????? ????? ?
Trachoolithus faticanus         11201 0110{12} 10-0- ?0{01}32 {234}0102 ????? ????? ?
Macroolithus rugustus           11101 01201 10-0- ?0032 {234}0102 02??1 0??11 2
Macroelongatoolithus oosp.      11101 0131{12} 10-0- ?0{01}32 {234}0102 121?? 0???? ?
Macroelongatoolithus xixiaensis 11101 0101{12} 10-0- ?0132 {234}01{01}2 ?21?1 0??10 2
Elongatoolithidae indet.        11101 0131{12} 10-0- ?0{01}32 40102 ????? ????? ?
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                                    .5    .10      .15      .20   .25   .30   .35
Deinonychus antirrhopus          11101 0000? 10-0- ?0?22 40102 ????? ????? ?
Continuoolithus canadensis       11001 0030{12} 11-0- ?0{01}22 20102 112?1 02?10 1
Bonapartenykus ultimus           11201 1?30{123} 12111 1??32 {24}01{01}2 ????? 0??10 ?
Triprismatoolithus stephensi     11201 1?30{12} 12112 10132 20102 022?1 0??10 ?
Protoceratopsidovum fluxuosum    11?01 ????? 10-0- ?01?2 {34}0102 121?? ????? ?
Protoceratopsidovum sincerum     11101 1?002 12??? ?0120 -0102 121?? 11?10 ?
Protoceratopsidovum minimum      11101 1?102 12??? ?0?20 -0102 121?1 11?10 ?
Troodon formosus                 11201 1?10{12} 12011 ?0130 -0102 12111 11110 2
Parvoolithus tortuosus           11101 0000{123} 12111 ?0130 -???2 11??? ????? ?
Oblongoolithus glaber            11201 00001 10-0- ?0130 -0102 0???? ????? ?
Subtiliolithus microtuberculatus 11201 00001 10-0- ?0132 20102 ????? ????? ?
Gobipipus reshetovi              11101 0000? 11??? ?010? ?0102 111?? 11??? ?
"Larger Avian Eggs"              11101 1?00? 11111 ?0120 -0102 1212? 11110 ?
Dromaius novaehollandiae         11201 00001 10112 10133 -0102 11120 00110 0
Gallus gallus                    11101 1?00{12} 11011 10130 -0102 10120 00110 0
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