A PHYLOGENETIC ASSESSMENT OF PRISMATIC DINOSAUR EGGS FROM THE CRETACEOUS TWO MEDICINE FORMATION OF MONTANA

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ABSTRACT—Two egg types from the Upper Cretaceous Two Medicine Formation of Montana are described and incorporated into a phylogenetic analysis of egg characters. Small (7.5 × 3.5 cm), ellipsoidal eggs with a surface ornamentation consisting of isolated round tubercles represent a new, unnamed ootaxon. The microstructure includes narrow, prismatic shell units with three structural layers. The second egg type, oospecies *Prismatoolithus levis*, belongs to the theropod *Troodon formosus*. Although previously described, the presence of a third, external layer had been overlooked. Both eggs display several features typical of avian eggs: narrowly spaced nucleation sites, barrel-shaped mammillae with blocky crystal habit, a squamatic-like texture in the prismatic layer, and a third, structural layer. In addition, the new egg type exhibits a cuticle layer and the eggs of *Troodon* are asymmetric.

Cladistic analysis of 14 fossil and extant taxa using 15 egg and shell characters favors a phylogeny consistent with more traditional analyses based on osteologic or genetic data and supports a theropod dinosaur origin for birds. No single character unambiguously distinguishes the eggs of avians from those of non-avian theropods, and the new Two Medicine egg type is recognized simply as that of a theropod. Results also indicate that resemblances in egg characters among non-avian and avian theropods are largely homologous and imply a high-level of similarity in reproductive physiology. Egg features are phylogenetically informative; better classifications and greater utility of eggs and eggshell will be gained through their phylogenetic treatment.

INTRODUCTION

Several varieties of supposed dinosaur eggs exhibit features such as two structural layers, prismatic shell units and squamatic ultrastructure, which are unique to birds among living taxa (Hirsch and Quinn, 1990; Mikhailov, 1997; Varricchio et al., 2002; Zelenitsky et al., 2002). However, parataxonomic classification schemes, those used to identify and categorize fossil eggs and eggshell in the absence of osteological remains, group some of these eggs as "ornithoid" and others as "dinosauroid-prismatic" (Hirsch, 1996; Mikhailov, 1997; Carpenter, 1999). Although these morphotypes were intended to represent structural categories and not taxonomic assignments (Mikhailov, 2000), they have been linked with various taxonomic groups within Dinosauria. For example, the ornithoid morphotype was associated with ratites and non-avian theropods and the dinosauroid-prismatic type with neognaths and hypsilophodont and protoceratopsian ornithischians (Hirsch and Quinn, 1990; Hirsch, 1996; Mikhailov, 1997). This mixing of morphologic descriptions and taxonomic names obscures the phylogenetic potential of egg and eggshell features.

Recently, Zelenitsky et al. (2002) challenged the usefulness of eggshell morphotypes. They contend that the use of these categories "constrains workers to assign new egg taxa to established groupings that may or may not represent natural taxa" (Zelenitsky et al., 2002:304). Instead, they suggest researchers adopt a cladistic approach. Phylogenetic analysis of fossil dinosaur eggs would provide important information unobtainable from other data sets. Discerning whether shared features among extant and extinct dinosaurians represent convergences or homologies would help clarify the reproductive biology of non-avian dinosaurs. An egg phylogeny would also provide information on when and possibly how reproductive patterns in modern Aves evolved. Furthermore, a cladistic approach would permit the taxonomic identification of eggs lacking embryos.

Several factors have contributed to the lack of phylogenetic analyses of fossil egg types: (1) an established parataxonomic system; (2) a paucity, until recently, of fossil eggs containing diagnostic embryonic remains; and (3) erroneous taxonomic assignments of eggs, e.g., those of *Oviraptor* and *Troodon* (see Norell et al., 1994, and Varricchio et al., 2002, for histories of these misidentifications). The latter created an appearance of phylogenetic inconsistency in eggshell structure (see Hirsch, 1996:table 11.1). Although fossil eggshell features have been discussed within a phylogenetic framework (Mikhailov, 1992; Kohring, 1999; Makovicky and Grellet-Tinner, 2000), only a few analyses based on largely modern avian eggshell types have tested the phylogenetic significance of egg characters (Grellet-Tinner, 2000, in press; Zelenitsky and Modesto, 2003). Here we conduct a cladistic analysis of a selection of Mesozoic and modern egg types. Because this represents the first analysis of primarily fossil material, we restrict the sample to egg types with identifiable embryonic remains. This allows evaluation of the egg-based phylogeny by comparison with those generated from skeletal or genetic data.

We also describe two egg types from the Upper Cretaceous Two Medicine Formation of Montana that exhibit eggshell features formerly unreported outside avian eggs (Figs. 1–2). The egg types represent the non-avian theropod *Troodon formosus* and a new unnamed ootaxon. Although eggs of the former have been described before (Hirsch and Quinn, 1990; Zelenitsky and Hills,1996; Varricchio et al., 2002; Zelenitsky et al., 2002), we document phylogenetically important structures, either previously overlooked or with controversial interpretations (Zelenitsky et al., 2002). The second egg type, unassociated with embryonic remains, is included in the phylogenetic analysis as an example of how a cladistic rather than a parataxonomic approach would assess an unidentified egg.

MATERIALS AND METHODS

The *Troodon* eggs come from the Two Medicine Formation of Teton County and the Judith River Formation of Hill Country, Montana. All egg specimens are curated at the Museum of the Rockies (MOR). Two Medicine eggs include MOR 675 and 963 from the Willow Creek Anticline, Egg Mountain (locality TM-006); MOR 246 from Egg Island (locality TM-024); and MOR 1139 from an unnamed site (near locality TM-011). MOR 993 is
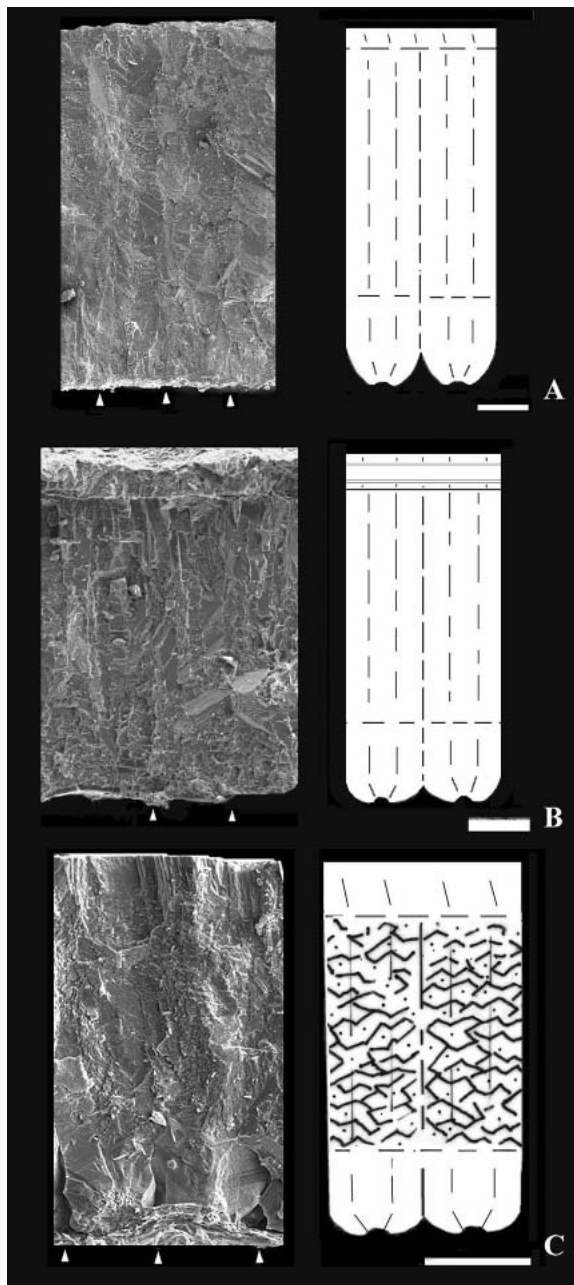
FIGURE 1. SEM images and schematic diagrams of radial sections through fossil and extant eggshells showing the three structural layers: the mammillary, prismatic, and third or external layer. **A**, *Troodon formosus* (MOR 1139). **B**, new Two Medicine egg (ES 101). **C**, domestic hen. White tick marks indicate the margins of a prismatic shell unit. Schematic diagrams represent ideal composites of these and other unfigured specimens. Scale bars equal 100 μm. The hen eggshell shows the clearest example of scale-like squamatic texture in the shell unit on the right. This texture is unevenly distributed in the fossil specimens.

were made with Buehler Omnimet Enterprise image analysis software.

Phylogenetic analysis was conducted using PAUP 4.0 (Swofford, 1998) on 14 fossil and extant taxa using 15 egg and shell characters (Tables 1, 2). Because the structure of flexible or soft, membrane-like eggs of lepidosaurs and some turtles differs radically from that of rigid, hard-shelled eggs (Mikhailov, 1992; Hirsch, 1994), we limited the extant species in our analysis to those that produce hard-shelled eggs. These included three turtles (*Melanochelys trijuga*, *Rhinoclemmys areolata*, and *Malacochersus tornieri*), two crocodilians (*Alligator mississippiensis*, *Crocodylus niloticus*), and two birds, a basal neognath (*Gallus gallus*) and a paleognath (*Struthio* sp). Extinct taxa were limited to those eggs with diagnostic embryonic remains. These included the ornithopod *Maiasaura peeblesorum* (Hirsch and Quinn, 1990; Horner, 1999), an unnamed titanosaurian sauropod (Chiappe et al., 1998), the allosauroid theropod *Lourinhanosaurus antunesi* (Mateus et al., 1997; Antunes et al., 1998), the maniraptoran theropods *Troodon formosus* (Varricchio et al., 2002) and an oviraptorid (Norell et al., 1994), and an unidentified basal bird from the Cretaceous of Argentina (Schweitzer et al., 2002). Because of the significant confusion resulting from taxonomic misidentification of eggs in the past, eggs with more ambiguous taxonomic identification were not included in the analysis. Whereas microscopic examinations of eggshell were carried out directly on all specimens except for those of *Lourinhanosaurus antunesi* (Mateus et al., 1997; Antunes et al., 1998), information on egg dimensions, nest structures, and adult size was obtained from published works (Bent, 1932; Ar et al., 1974; Anderson et al., 1985; Paul, 1988; Dunham et al., 1989; Magnusson et al., 1989; Hirsch and Quinn, 1990; Rootes et al., 1991; Norell et al., 1994,1995; Peczkis, 1995; Terres, 1995; Dong and Currie, 1996; Mateus et al., 1997; Varricchio et al., 1997, 1999, 2002; Antunes et al., 1998; Chiappe et al., 1998; Carpenter, 1999; Clark et al., 1999; Horner, 1999; Schweitzer et al., 2002).

This sample represents nearly all the taxonomically identifiable eggs and eggshell currently available for the Mesozoic. Exceptions include dendroolithid eggs with therizinosaur embryos (Manning et al., 1997), Lower Jurassic eggs with embryos from the Elliot Formation of South Africa (Kitching, 1979), egg material associated with an adult *Deinonychus antirrhopus* (Makovicky and Grellet-Tinner, 2000), and three purported avian egg types from the Cretaceous of Mongolia (Mikhailov, 1997). Eggshell and eggs associated with the therizinosaur embryos (Manning et al., 1997) have not been described in detail nor were they available to the authors. Currently, the embryos of the South African eggs remain unidentified and diagenesis obscures most relevant eggshell features (Zelenitsky and Modesto, 2002). Makovicky and Grellet-Tinner (2000) describe an egg closely adhered to the external aspect of *Deinonychus* gastralia and assign this and associated eggshell to this taxon. Similarly, two of the three Mongolian egg types, *Gobioolithus major* and *Laevisoolithus sochavi*, lack embryos but occur with adult avian bones (Sabbath, 1991; Mikhailov, 1997). As in the *Deinonychus*-associated eggs, taphonomic information is minimal. Embryos exist for the third egg type, *Gobioolithus minor*, but have been variously interpreted as enantiornithine (Martin, 1983), paleognathous (Mikhailov, 1997), or neornithine (Chatterjee, 1997). Because our sample already includes a variety of theropods, we exclude these taphonomically and taxonomically more ambiguous specimens.

EGG DESCRIPTIONS

New Two Medicine Eggs

The new eggs from the Two Medicine Formation are small (7.5 × 3.5 cm), symmetrical and ellipsoid. These eggs apparently oc-

the sole Judith River specimen. Eggshells from the new, unnamed prismatic eggs, Montana State University, Earth Science Collection (ES) 101, 102, are from the lowermost Two Medicine Formation, E-2 Site, Old Trail Museum locality in Teton County. Eggshell thin sections, 30 μm thick, were viewed under a polarizing light microscope (PLM). Additional eggshell was mounted on aluminum stubs, coated with 10 nanometers of gold, and viewed by scanning electron microscope (SEM). Measurements
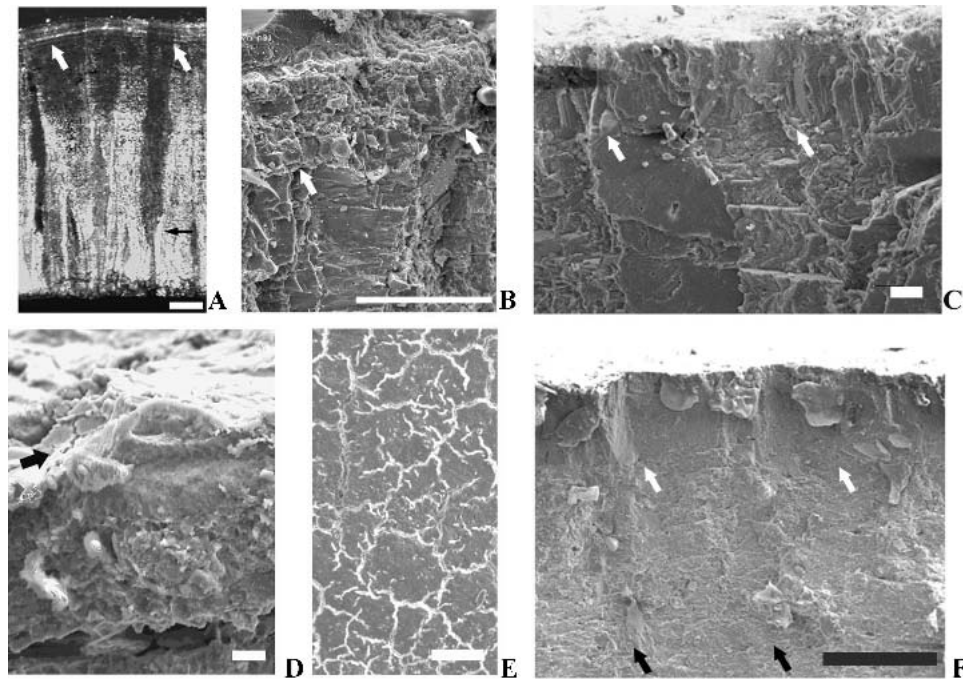
FIGURE 2. Fossil and extant eggshell microstructures. **A**, thin section of new Two Medicine Formation egg (ES 101). Black arrow marks the gradual transition from mammillary to prismatic layer; white arrows denote the abrupt transition to the third structural layer. **B**, SEM of shell from same egg (ES 101). Arrows mark the base of the third, external layer. Note the third layer consists of a porous zone between two strata of blocky crystals. **C**, SEM of the outer portion of *Troodon* eggshell showing the external layer overlying the upper portions of the prismatic shell units. Arrows mark the transition between the second and third structural layers. Note the change in calcite orientation across this transition and also the variation in vesicle abundance and squamatic-like texture in some prisms. **D**, oblique view of the new Two Medicine egg type, ES 101, showing the third structural layer and the outer surface of the shell. Arrow marks the cuticle layer. **E**, SEM of domestic fowl eggshell showing the cracked outer surface of the cuticle. **F**, SEM of domestic fowl eggshell. White arrows mark the transition from squamatic ultrastructure of the second layer to the third structural layer; black arrows indicate the margins of a faint prismatic column largely obscured by the squamatic texture. Scale bar in A equals 100 μm, B equals 50 μm, C–F equals 10 μm.

curred in pairs within the sediment, with their long axis oriented approximately parallel to the strata. Their method of incubation remains uncertain. The thin (0.52–0.85 mm), calcite eggshells (ES 101, 102) exhibit tightly spaced, barrel-shaped mammillae and a second structural layer comprised of narrow prismatic columns with abundant vesicles (Fig. 1B). Patchy squamatic-like texture occurs in the prismatic columns of most eggshells. This feature may represent diagenetic alteration and its biological significance remains uncertain (see further discussion below). A third structural layer comprised of two strata of blocky crystals separated by a porous, vesiculated region displays an abrupt transition from the underlying prismatic columns (Fig. 2A, B). The new eggs exhibit straight and consistently narrow pores. Surface ornamentation consists of discrete and isolated, round tubercles that are overlain by a thin (11–22 μm) amorphous material displaying a cracked surface texture, a feature discernable only under SEM (Fig. 2D). This feature characterizes other specimens of this egg type from elsewhere within the Two Medicine Formation and closely resembles the cuticle found in fossil (Schweitzer et al., 2002) and extant avian eggs (Solomon, 1997:fig. 65; Fig. 2E). Furthermore, the cracked surface texture differs from surficial mineral deposits and recrystallization in

TABLE 1. Egg and eggshell characters used in cladistic analysis.

1. Spacing of nucleation centers relative to shell width: >0.40 (0), 0.33–0.40 (1), 0.24–0.33 (2), >0.24 (3).
2. Shell composition: aragonite (0), calcite (1).
3. Radiating crystal form of mammillary layer: truncated (0), irregular (1), blocky (2).
4. Second structural layer: absent (0), prismatic (1), wedge (2).
5. Third structural layer: absent (0), present with horizontal crystals (1), present with vertical crystals (2), present with porous and crystalline regions (3).
6. Nucleation centers: at base of mammillary layer (0), within layer (1).
7. Transition between first and second structural layers: absent (0), abrupt (1), gradual (2).
8. Squamatic structure in second structural layer: absent (0), present (1).
9. Pore system: straight and consistent width (0), straight with enlarged base (2), straight to oblique (3), irregular and varying (4), branched (5).
10. Transition between second and third structural layers: absent (0), gradual (1), abrupt (2).
11. Egg to adult body size ratio: small, <0.10 E_b (0), medium, 0.10–0.30 E_b (1), large, >0.30 E_b (2). E_b is the mass of an egg predicted for a bird of similar adult body size using an allometric equation based on modern data (Blueweiss et al., 1978).
12. Egg shape: symmetrical (0), asymmetrical (1).
13. Clutch arrangement: random or massed (0); paired (1); single layer and open (2).
14. Composition of the mammillary layer: crystalline (0), organic and crystalline (1).
15. Cuticle: absent (0), present (1).

TABLE 2.   Data matrix for characters in Table 1

Melanochelys trijuga	00000	00000	20000
Malacochersus tornieri	00000	00000	20000
Rhinoclemmys areolata	10000	00010	20000
Alligator mississippiensis	01121	12011	00010
Crocodylus niloticus	01121	12011	00010
Maiasaura peeblesorum	11?00	00030	0000?
Titanosaurian sauropod	11000	00000	0000?
Lourinhanosaurus	21212	02021	1100?
Oviraptorid	310?0	01100	2010?
Troodon formosus	31212	02?01	2110?
New Two Medicine egg	31213	02?02	?0101
Cretaceous bird	31?12	02101	?1?01
Struthio sp.	31012	01141	21201
Gallus gallus	21212	02101	21201

fossil eggshells that result from diagenesis. Similar surface textures occur in modern avian eggs as a result of drying of the protein cuticle following oviposition (Solomon, 1997). The size (7.5 × 3.5 cm); symmetrical, ellipsoid shape; surface ornamentation; and microstructure of the third structural layer of these Two Medicine eggs distinguish them from all previously reported Mesozoic eggs.

Eggs of *Troodon formosus*

Eggs of the small theropod *Troodon formosus* from the Two Medicine and Oldman Formations of Montana and Alberta, respectively, belong to the oospecies *Prismatoolithus levis*. Clutches contain up to 24 eggs arranged in pairs, and standing vertically to slightly obliquely within the sediments. The upper portions of these asymmetric eggs apparently remained subaerially exposed within the nest (Varricchio et al., 1999). These smooth, medium-sized (13 × 6 cm) eggs have a calcite shell, roughly 1 mm thick and composed of narrow, vertical shell units (Hirsch and Quinn, 1990; Varricchio et al., 2002) organized into three structural layers (Fig. 1A). These layers include the basal mammillary layer, a second structural layer consisting of tightly packed prismatic columns, and an external layer. Pores are vertical, straight, and maintain a uniform diameter throughout their length (Hirsch and Quinn, 1990; Varricchio et al., 2002:fig. 5b).

Several papers (Hirsch and Quinn, 1990; Zelenitsky and Hills, 1996; Varricchio et al., 1999, 2002; Zelenitsky et al., 2002) provide extensive descriptions of *Troodon* embryos, clutch morphology, nest structures, and egg size, shape, surface texture, and microstructure. Consequently, the remainder of the description presented here focuses on those eggshell features with contradictory interpretations. These include the mammillary layer, squamatic ultrastructure, and the presence of a third, external layer.

Mammillary Layer—Radial sections show barrel-shaped mammillae comprised of radiating spherulites emanating from the former site of calcite nucleation within the membrane. These spherulites broaden towards their distal ends and change orientation sharply to form closely packed aggregates of vertical, rhombohedral crystals with blocky cleavage (Hirsch and Quinn, 1990, Zelenitsky and Hills, 1996, Zelenitsky et al., 2002; Varricchio et al., 2002). Overall, the mammillary layer exhibits tabular structure and a gradual change to the overlying prismatic layer.

Previous descriptions of *Troodon* eggshell pertain to either presumably hatched eggs or eggs containing embryonic remains (Hirsch and Quinn, 1990:fig. 4a-f; Mikhailov, 1991:plate 27, fig 7; Zelenitsky and Hills, 1996; Varricchio et al., 2002:figs. 5, 6). In these specimens, the basal portion of the mammillary layer is typically absent, most likely a result of calcium dissolution during embryogenesis or possibly diagenesis. However, recently discovered, well-preserved *Troodon* eggshells from Alberta provide a more complete picture of the mammillary layer (Zelenitsky et

al., 2002). Zelenitsky et al. (2002) described specimens that include eisospherites at the base of the mammillae and report a mammillary layer to prismatic layer thickness ratio of 1:1.77 to 1:2.35. This proportion was significantly underestimated in previous descriptions (Hirsch and Quinn, 1990; Zelenitsky and Hills, 1996; Varricchio et al., 2002), a consequence of poor preservation. Therefore, in complete *Troodon* specimens the height of the mammillary layer exceeds the width (Zelenitsky et al., 2002).

Squamatic Structure—As defined by Mikhailov (1997), squamatic ultrastructure consists of a pattern of scale-shaped irregular entities, each 10–30 μm in size and readily visible in eggshell radial sections. These "form a continuous network which cuts across the vertical sub-divisions in the eggshell structure" (Mikhailov, 1997:16). Squamatic ultrastructure characterizes the continuous, second structural layer in avian and ornithoid dinosaurian eggshell (Mikhailov, 1997). Until recently, this feature was considered absent from the second structural layer of *Troodon* eggshell. For this reason *Troodon* eggs were excluded from the ornithoid morphotype and assigned to either dinosauroid-prismatic (Hirsch, 1996; Mikhailov, 1997) or prismatic (Carpenter, 1999) classifications. However, Zelenitsky et al. (2002) identified locally preserved vesicles and squamatic ultrastructure in *Troodon* eggshell from Alberta. They considered this feature most similar to that found in galliform birds. Our examination of *Troodon* specimens (MOR 363, 675, 963, 993) and the new prismatic eggs from Montana (ES 101, 102) confirms the presence of similar textural features within the prismatic layer (Fig. 1). Notably, these specimens and those figured in Zelenitsky et al. (2002:fig. 2b) lack lateral continuity of this texture across the prismatic shell units in radial sections. Instead, the squamatic-like texture occurs in some calcite prisms but may be absent in adjacent ones. This differs from the 'continuous network' defined by Mikhailov (1997) and the more even distribution of squamatic ultrastructure characteristic of most extant avian eggshells (Fig. 2F; Mikhailov, 1995:fig. 1a) and non-avian theropods such as oviraptorids (Mikhailov, 1997:plate 9, fig. 1). This discrepancy in morphology raises questions regarding interpretation of this feature: Does this uneven distribution reflect diagenesis or preservation of the original calcite structure? If the latter, should it be considered equivalent to the squamatic ultrastructure of birds or as a feature peculiar to *Troodon* and the new egg type? We agree with Zelenitsky et al. (2002) in the recognition of this feature, but feel its interpretation remains ambiguous.

External Layer—A subtle five to eight degree change in crystal orientation in the outer portion of the eggshell defines the third, external layer (Figs. 1A, 2C). This third structural layer of calcite contains fewer vesicles than the underlying prismatic columns. The thickness of this layer as a ratio of the preserved shell thickness is roughly 1:10 to 1:13 in specimens examined from numerous eggs from multiple clutches. With the exception of a tentative identification (Varricchio et al., 2002), this feature has not been reported previously. Zelenitsky et al. (2002) suggested that the absence of an external layer in *Troodon* might represent a taphonomic artifact because Cretaceous avian eggs are often missing this feature. In extant avian eggshell, the uniformity of the squamatic ultrastructure provides a sharp contrast with the overlying external layer (Fig. 2F). Poor preservation and/or a more subtle contrast with the underlying prismatic layer may explain the omission of this structure in previous descriptions. Nevertheless, a third structural layer is clearly visible in at least two other previously published figures (Hirsch and Quinn, 1990:fig. 5b, c; Zelenitsky and Hills, 1996:fig. 2d). Furthermore, we interpret the 'recrystallized' portion of *Lourinhanosaurus* as an external, third layer, because both pores and shell-unit extinction patterns extend through this layer (Antunes et al., 1998:text-fig. 1, plate 1).

PHYLOGENETIC ANALYSIS AND DISCUSSION

Troodon and the new Two Medicine eggs share several structural characteristics with avian eggs: narrowly spaced calcite nucleation sites; barrel-shaped mammillae with blocky crystal habits; possible squamatic texture in the second structural layer (Zelenitsky et al., 2002); and a third structural layer overlying the prismatic layer (Figs. 1A, 2C). Furthermore, *Troodon* eggs display an asymmetrical shape typical of avian eggs, and the unnamed Two Medicine eggs bear a crazed external surface (Fig. 2D) that is indistinguishable from the cuticle layer found in many modern birds (Solomon, 1997). This diverse suite of characters raises questions about the taxonomic placement of the unnamed Two Medicine eggs, as well as the phylogenetic origin of the avian egg. Specifically, do structural features present in both Two Medicine egg types represent synapomorphies or simply homoplastic convergences with birds?

Cladistic analysis with PAUP (Swofford, 1998) of 14 fossil and extant taxa using 15 egg and shell characters produces 68 equally parsimonious trees 38 steps in length. Consistency and Retention indices for the most parsimonious trees are 0.89 and 0.94, respectively. A strict consensus tree places the three turtle species as sequential outgroups to an archosaur clade that includes the two crocodilians, the ornithischian *Maiasaura*, the unnamed titanosaur, and a large polytomy consisting of all the non-avian theropods and birds. An Adams consensus tree differs only in that *Lourinhanosaurus* and the oviraptorid represent unresolved sister taxa to a clade containing the remaining theropods (Fig. 3). Additionally, *Troodon* and the Cretaceous bird fall out as sister taxa.

The archosaur and theropod-bird clades were retained in 65% and 76% of the bootstrap replications (N = 1000), respectively. In contrast, these two clades typically persist in trees slightly longer than the most parsimonious trees. For example, the archosaur clade recurs in the majority of trees one to three steps out, while the more robust theropod clade persists in more than 90% of trees that are one to three steps longer and in more than 75% of trees four to six steps longer than the minimum-length tree. Of the two continuous characters, removal of character no. 11 (Table 1), egg to adult body-size ratio, did not affect the topology. However, deletion of character no. 1, spacing of nucleation sites relative to shell thickness, results in the collapse of the theropod clade to the archosaur node.

Although bootstrap retention figures are somewhat low, the resulting topology agrees with those derived from either genetic or skeletal data (Benton and Clark, 1988; Gauthier et al., 1988; Hedges, 1994; Sereno, 1999), suggesting that egg characters retain phylogenetic information. A recent study of extant avian eggshell also demonstrates their phylogenetic utility (Grellet-Tinner, 2000). Further, even with the small number of available characters, egg features independently favor both a dinosaur and theropod origin of birds. The inclusion of the unnamed Two Medicine ootaxon within an exclusively theropod clade suggests that the eggs belong to either a bird or a non-avian theropod.

A single unambiguous character, a rigid calcite eggshell, defines the archosaur clade, whereas the theropod-bird clade is diagnosed by tight spacing of the shell unit nuclei relative to shell thickness and the presence of a second structural layer consisting of parallel, vertical calcite prisms. Further, all theropods but the oviraptorid share the presence of a third structural layer.

Several other features typical of modern bird eggs, e.g., asymmetric egg shape, a cuticle layer, and squamatic texture, are more irregularly distributed among the non-avian theropods. No single feature unambiguously separates avian from non-avian theropod eggshell. Thus, caution is currently warranted in the assignment of fossil eggshell and eggs lacking identifiable embryos to Aves. For example, a Cretaceous egg from Mongolia was recently described as an avialan closer to modern birds than to enantiornithines on the basis of the presence of a third structural layer (Grellet-Tinner and Norell, 2002). However, phylogenetic analysis and the occurrence of this feature in the allosauroid *Lourinhanosaurus*, the maniraptoran *Troodon*, and a primitive avian egg from the Cretaceous of Argentina indicate that a third layer has a wider phylogenetic distribution. Consequently, present knowledge limits the assignment of the Mongolian egg to Theropoda.

Character distributions in our analysis indicate a significant amount of homoplasy in the evolution of eggshell structure. Both the *Troodon* egg type and the unnamed Two Medicine egg type exhibit the three structural layers present in many modern birds (Nys et al., 1999) but may lack the characteristic squamatic texture. In contrast, oviraptorid eggs possess only two structural layers but exhibit squamatic texture (Mikhailov, 1997; Norell et al., 1994). Similarly, *Lourinhanosaurus* has three structural layers but no squamatic texture and relatively small eggs. This mix of derived and primitive features probably results in both *Lourinhanosaurus* and the oviraptorid being pulled to the base of the theropod clade in the Adams consensus tree (Fig. 3). Comparable homoplasy occurs in osteological data sets for theropod clades (Sereno, 1999; Holtz, 2001). For example, oviraptorids exhibit a hypocleideum-like spike on the furcula (Makovicky and Currie, 1998), while an avian-like, pneumatic quadrate is present in troodontids (Norell et al., 2000).

Two factors contribute to the lack of more definitive results from this analysis: a limited set of characters and homoplasy. Although egg features function well in the recognition of clades such as Crocodylia and Theropoda, they were less successful in discerning larger scale relationships. For example, the analysis failed to clarify relationships among the sauropod, hadrosaur,
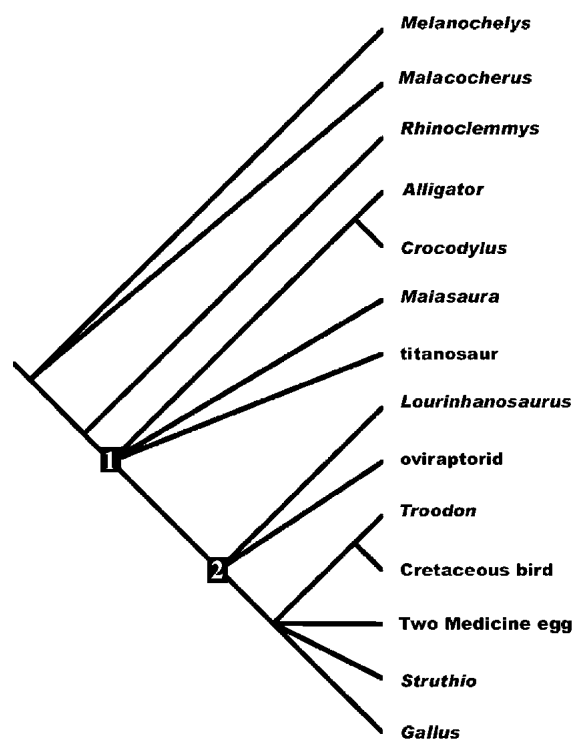

FIGURE 3. Phylogeny (Adams consensus tree) resulting from a cladistic analysis using only egg and eggshell features. A strict consensus tree differs only in that all the theropods form a single polytomy. Node 1 represents archosaurs united by a single unambiguous character, a rigid-calcite eggshell; Node 2 represents theropods including both birds and non-avian theropods. Synapomorphies of this clade include tightly spaced shell units relative to eggshell thickness, a second structural layer of vertical prisms, and possibly a third, external layer.

and crocodilian examples. This emphasizes the difficulties in comparing eggshell of disparate morphologies; drastically different egg types simply lack a significant number of traits that are both phylogenetically meaningful and comparable. Future analyses with a more diverse sample may alleviate this problem, but several major dinosaur clades (e.g., Prosauropoda, Ceratosauria, Thyreophora, and Marginocephalia) currently lack any clearly identifiable egg material. Despite this limitation, a broader phylogenetic analysis of 'dinosaur' egg types, with or without identifiable osteological remains, might move eggshell parataxonomy closer to a phylogenetically based classification.

Currently, cladistic analysis of fossil eggs is somewhat limited by both the number of taxonomically identifiable fossil eggs and distinct eggshell characters. Nevertheless, a phylogeny based only on egg and eggshell characters from a selection of living taxa and several Mesozoic taxa with identifiable eggs concurs with more traditional analyses using either osteological (Benton and Clark, 1988; Gauthier et al., 1988; Sereno, 1999) or genetic data (Hedges, 1994) and independently supports a theropod dinosaur origin for birds (Fig. 3). Further, phylogenetic analysis suggests that most features one would consider typical of modern avian eggs (e.g., asymmetric shape, rigid calcite shell comprised of two or more structural layers, squamatic ultrastructure, closely spaced shell units, and straight narrow pores) first evolved within non-avian theropods. The theropod avian-ancestor produced an egg nearly identical to that of a modern bird; this implies a high level of similarity in oviduct function (Mikhailov, 1992) and reproductive physiology (Varricchio and Jackson, 2004). The extent to which the shared egg character states reflect a correspondence in reproductive behaviors remains debatable. Clearly, non-avian theropods such as *Troodon* and *Oviraptor* differ from modern birds in partially to fully burying their egg clutches (Clark et al., 1999; Varricchio et al., 1999). This is probably associated with higher rates of eggshell gas conductance (Deeming, 2002). However, if eggshell characteristics strongly reflect incubation environment (Deeming, 2002), then the synapomorphies of avian and non-avian eggs would argue for greater parallels in nesting behavior among theropods than between either avian or non-avian theropods and crocodilians.

Although parataxonomic egg names remain practical for otherwise unidentifiable fossil eggs and eggshell, higher parataxonomic groups may cease to be useful as a better phylogenetic understanding of eggs develops. Future revisions and additions to egg parataxonomy should exclude parataxonomic names that incorporate existing taxonomic names (e.g., dinosauroid, ornithoid) since these potentially obscure evolutionary relationships. Phylogenetic approaches will provide both greater understanding and utility of fossil eggs and eggshell.

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