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REVIEW

Reproduction in Mesozoic birds and evolution of the modern avian reproductive mode

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ABSTRACT

The reproductive biology of living birds differs dramatically from that of other extant vertebrates. Although some attributes of modern avian reproduction had their origin within theropod dinosaurs like oviraptors and troodontids, even the most derived non-avian theropods lack key features of modern birds. We review the current knowledge of reproduction in Mesozoic birds and 3 lines of evidence that contribute to our understanding of the evolution of the modern avian reproductive mode: (1) efforts to define the ancestral reproductive condition on the basis of extant birds, (2) the fossil record of non-avian theropod dinosaurs, and (3) the fossil record of reproduction in primitive Mesozoic birds (e.g., Enantiornithes).

The fossil evidence from Mesozoic birds and non-avian theropods suggests that reproduction passed through 5 stages from basal theropods to neornithines: (1) pre-maniraptoran theropods, (2) oviraptor-grade maniraptorans, (3) troodontid-grade paravians, (4) Enantiornithes, and (5) basal Neornithes. Major changes occurred incrementally in egg size, shape, and microstructure; in nest form; in incubation method; and in parental care. Reproduction in troodontid theropods concurs with this clade representing the sister taxon to birds. Reproduction in enantiornithine birds included sequential ovulation from a single ovary and oviduct, eggs planted upright within sediments, and incubation by a combination of sediment and attendant adult or eggs fully buried with superprecocial young. Incubation modes of derived non-avian theropods and enantiornithines may have favored paternal care.

Significant changes between enantiornithines and neornithines include an additional increase in relative egg size and sediment-free incubation. The latter permitted greater adult–egg contact and likely more efficient incubation. Associated changes also included improved egg shape, egg rotation, and chalazae—the albumin chords that suspend the yolk and facilitate proper embryonic development during rotation. Neornithes are the only Mesozoic clade of Dinosauria to nest completely free of sediment, and this may have played a crucial role in their surviving the K–Pg mass extinction event.

Keywords: dinosaurs, eggs, Enantiornithes, evolution, Mesozoic, Neornithes, reproduction, Troodontidae

Reproducción de aves mesozoicas y evolución del modo de reproducción moderna de las aves

RESUMEN

La biología reproductiva de las aves vivientes difiere marcadamente de la de otros vertebrados actuales. Aunque algunos atributos de la reproducción moderna de las aves tuvieron su origen dentro de los dinosaurios terópodos como los oviraptores y los troodóntidos, incluso los terópodos no aviares más derivados no poseen rasgos claves de las aves modernas. Aquí revisamos el conocimiento actual de la reproducción en las aves mesozoicas y tres líneas de evidencia que contribuyen a nuestro entendimiento de la evolución del modo de reproducción de las aves modernas: (1) los esfuerzos para definir la condición reproductiva ancestral tomando como base las aves vivientes, (2) el registro fósil de los dinosaurios terópodos no aviares y (3) el registro fósil de la reproducción en las aves mesozoicas primitivas (e.g., Enantiornites).

La evidencia fósil de las aves mesozoicas y de los terópodos no aviares sugiere que la reproducción pasó a través de cinco estados desde los terópodos basales hasta los neornitines: (1) terópodos anteriores a los maniraptores, (2) maniraptores de grado oviraptor, (3) paraviares de grado troodóntido, (4) Enantiornites, y (5) Neornites basales. Los grandes cambios ocurrieron incrementalmente en el tamaño, la forma y la microestructura del huevo; en la forma del huevo; en el método de incubación; y en el cuidado parental. La reproducción en los terópodos troodóntidos está de acuerdo con que este clado representa el taxón hermano de las aves. La reproducción en las aves enantiornitine incluyó la ovulación secuencial a partir de un único ovario y oviducto, huevos insertos en posición vertical dentro de los sedimentos, e incubación con una combinación de sedimentos y adulto a cargo o de los huevos totalmente enterrados con jóvenes súper precoces. Los modos de incubación de los terópodos no aviares derivados y de los enantiornitines puede haber favorecido el cuidado parental.

Los cambios significativos entre los enantiornitines y los neornitines incluyen un incremento adicional en el tamaño relativo del huevo y la incubación sin sedimentos. Lo último permitió un mayor contacto entre el adulto y el huevo y probablemente una incubación más eficiente. Los cambios asociados también incluyeron una mejora en la forma del huevo, la rotación del huevo y la chalaza—las cuerdas de la albúmina que sostienen la yema y que facilitan el desarrollo embrionario adecuado durante la rotación. Los Neornites son el único clado de Dinosauria del Mesozoico que anidan en ausencia completa de sedimentos, y esto puede haber jugado un papel crucial en sobrevivir el evento de extinción masivo del Cretácico–Paleógeno.

Palabras clave: dinosaurios, Enantiornites, evolución, huevos, Mesozoico, Neornites, reproducción, Troodóntidae

The reproductive biology of living birds differs dramatically from that of other extant vertebrates. From the microstructure of the eggshell, egg production, and incubation to the form of parental care, birds exhibit unique anatomical, physiological, and behavioral adaptations. These features can be used to define a modern avian reproductive mode characteristic of living birds (Table 1). Ornithologists have long sought to understand the origins of these features, particularly the role of parental care and adult-contact incubation (Van Rhijn 1984, Kavanau 1987, Wesołowski 1994, Burley and Johnson 2002, Tullberg et al. 2002, Dial 2003, Deeming 2006). Reoccurring questions include whether the predominant biparental care of modern birds evolved from a state of no care, maternal (female-only) care, or paternal (male-only) care and how the evolution of flight potentially influenced reproduction. Using phylogenetic analyses of character distributions, mathematical modeling, and relic behaviors, researchers have speculated on the interplay of parental care patterns, mating systems, hatchling altriciality, egg size, and other attributes (Kavanau 1987, McKitrick 1992, Owens and Bennett 1994, Sillén-Tullberg and Temrin 1994, Temrin and Sillén-Tullberg 1994, Wesołowski 1994, Burley and Johnson 2002) and, after making a few assumptions about the ancestral state, proposed various scenarios on the evolution of the avian reproductive mode (Kavanau 1987, Wesołowski 1994, Burley and Johnson 2002). A hesitancy to accept the dinosaur origin of birds complicated earlier interpretations (Kavanau 1987, Burley and Johnson 2002), but more recent work (e.g., Dial 2003, Dyke and Kaiser 2010), as advocated by Prum (2002), builds upon this now well-accepted framework. Although these studies have largely failed to reach a general consensus on how the modern avian reproductive mode evolved, particularly within Mesozoic birds, they highlight the distinctiveness of reproduction among extant birds, the wide gap between birds and other extant groups, and the abundant homoplasy and independent originations of specific reproductive attributes among living avian clades.

Dinosaur paleontologists have also speculated on the evolution of reproduction in birds, but from a different perspective. While ornithologists have largely worked from the extant crown clades down the tree to hypothesize about the base of Neornithes, dinosaur paleontologists using various sister taxa of extant birds have worked up the tree toward the primitive condition of Aves. Based on the study of eggs, eggshell, embryos, and nesting traces, paleontologists (e.g., Varricchio et al. 1997, 2002, Grellet-Tinner et al. 2006, Zelenitsky 2006) have largely agreed that various anatomical features—including aspects of egg shape, ornamentation, microstructure, and porosity characteristic of living birds—trace their origin to within non-

TABLE 1. Modern avian reproductive mode: the reproductive attributes that typify modern birds. Features listed are neither universal to nor exclusive to modern birds.

Modern avian reproductive mode		
Nesting	**Eggs**	**Young**
Eggs exposed, uncovered by sediment or vegetation	Relatively large eggs	Synchronous to asynchronous hatching
Incubation by brooding adult	Variable egg color	Primitively precocial
Delayed incubation	Asymmetric egg shape typical	Rapid growth
Egg rotation	Calcitic, multilayered shell	
	Narrow shell units	**Parental care**
Egg production	Closely spaced organic cores	Predominantly biparental
Exclusively oviparous	Possible cuticle layer	Care of eggs
Single functional ovary and oviduct	Two distinct membranes	Care of young
"Assembly-line" oviduct	Low porosity	
Egg production at 1 egg day^{-1}	Air cell present within egg	
Iterative egg laying	Straight, narrow pores	
Female sperm storage	Chalazae	

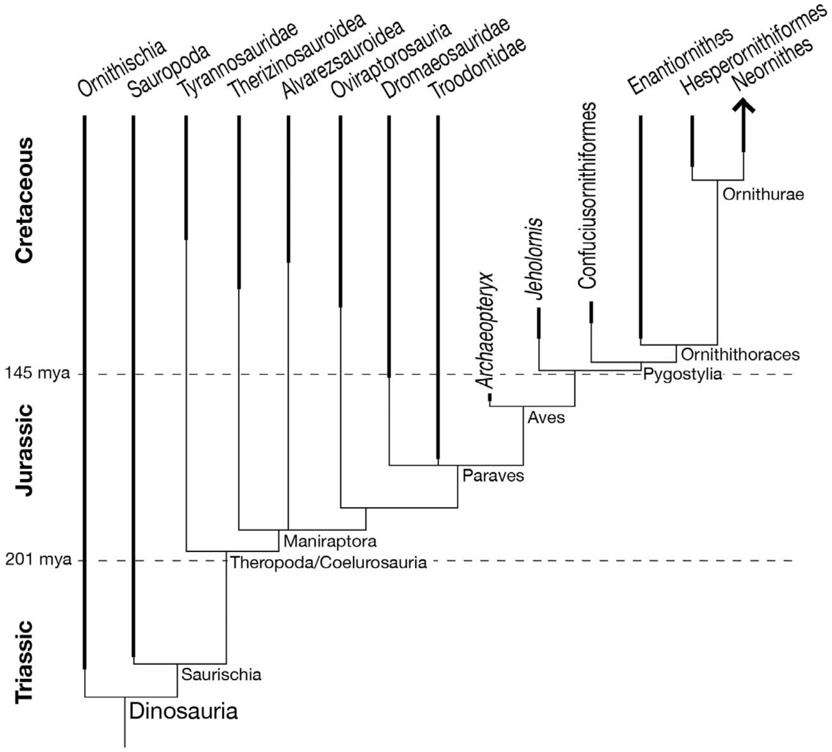

FIGURE 1. Phylogeny of the major taxa discussed in this review. Note that oviraptors and troodontids are more closely related to birds than to any other non-avian dinosaurs, with the exception of the Dromaeosauridae. Modified from Brusatte et al. (2014, 2015).

avian maniraptoran dinosaurs (e.g., oviraptors and troodontids). These features, together with adult–egg associations, clutch configurations, and nest traces, further suggest that accompanying behavioral and physiological attributes may also have evolved before the origin of Aves. However, these more interpretational aspects remain contentious (e.g., Deeming 2002, Ruben et al. 2003, Wesołowski 2004). Nevertheless, although some attributes of modern avian reproduction likely had their origin within non-avian theropod dinosaurs, even the most derived non-avian theropods lack some key features of modern birds (e.g., large egg-to-adult-body size ratios, clutches incubated free of sediment, and egg rotation). Thus, a significant gap still exists between non-avian theropods and modern birds in terms of their reproductive ecology.

Fortunately, over the past 40 yr, paleontologists have amassed an important collection of Cretaceous eggs, embryos, and even clutch-associated adults that can be assigned to Mesozoic birds (e.g., Mikhailov 1991, Sabath 1991, Schweitzer et al. 2002, Dyke et al. 2012, Fernández et al. 2013). During the 1970s, the Soviet–Mongolian and Polish–Mongolian expeditions made the first major discoveries in the Gobi Desert, including dense concentrations of avian eggs. Similar localities are now known from Argentina and Romania (Dyke et al. 2012, Fernández et al. 2013). This material helps bridge the knowledge gap in terms of reproduction between non-avian dinosaurs and modern birds.

Here, we focus on the current knowledge of reproduction in Mesozoic birds and the 3 principal lines of evidence that contribute to our understanding of the evolution of the modern avian reproductive mode: (1) modern birds and the efforts of ornithologists to define the ancestral reproductive condition on the basis of extant neornithines, (2) non-avian theropods and the work of dinosaur paleontologists to elucidate those reproductive attributes that are likely to be primitive for Aves, and (3) the fossil record of reproduction in primitive Mesozoic birds. The first 2 define a phylogenetic bracket that provides important context and interpretational guidance to the third and principal focus of this study, the Mesozoic fossil record.

Before undertaking this largely fossil review, we wish to first highlight a few key aspects of this paleontologic perspective that may be unfamiliar to, or overlooked by, more neontologically oriented researchers. First, this review emphasizes the fossil evidence for 3 extinct clades: Oviraptorosauria, Troodontidae, and Enantiornithes. Oviraptors and troodontids largely consist of small (5–50 kg), bipedal theropod dinosaurs. Together with dromaeosaurids, these carnivorous groups represent the closest dinosaurian relatives to birds and are thus more closely related to modern birds than to any other non-avian dinosaurs (Brusatte et al. 2014; Figure 1). Enantiornithes were the dominant clade of Mesozoic birds, with >60 species exhibiting a diversity of feeding adaptations and a worldwide distribution (O'Connor et al. 2011). More derived than basal birds such as *Archaeopteryx* and *Confuciusornis*, Enantiornithes represent the sister taxon to Ornithurae, the clade consisting of Hesperornithiformes, Neornithes, and a couple additional extinct taxa (Brusatte et al. 2014; Figure 1).

Paleontologic research is inherently specimen based. Accordingly, we provide specimen tables and brief discussion of key taxonomic issues in the Appendix. Eggs unassociated with osteological remains have been classified using ootaxonomy, a system adopted by paleontologists to name and track such specimens. Ootaxonomy is practiced like regular taxonomy but remains an informal system, in that the names do not take precedence over taxonomic names (Mikhailov 1991). Ootaxonomic names are used here because they provide a convenient mechanism for discussing various egg types.

Interpretation of fossil specimens must consider preservation. For example, only a few Cretaceous localities (e.g., Yixian Formation of northeast China; Benton et al. 2008) regularly preserve feathers. Thus, the vast majority of oviraptor and troodontid specimens from elsewhere lack any evidence of the integument. However, these 2 clades are generally regarded as possessing feathers, on the basis of (1) the few exceptional specimens preserving a feathery integument (e.g., Xu et al. 2010, Zheng et al. 2014), (2) occurrence of feathers across a more inclusive clade of theropods, and (3) a similar pattern of preservation vs. nonpreservation in feathered clades such as Enantiornithes (Benton et al. 2008). Preservational issues more directly related to reproduction include (1) interpretation of possible ovarian follicles in a few fossil birds (Mayr and Manegold 2013, Zheng et al. 2013); (2) the importance assigned to, and interpretation of, exceptional specimens such as clutch-associated adults and large clutches; and (3) potential bias favoring preservation of clutches incubated within sediments vs. those above ground (see discussion below).

Admittedly, the record of reproductively relevant fossils among non-avian and avian theropods remains limited in both sheer numbers and taxonomic coverage. For example, there exists only a single dromaeosaurid egg (Grellet-Tinner and Makovicky 2006) and no eggs for any Mesozoic birds other than enantiornithines. One strength of the available specimens is that egg clutches and nests represent the products of animal activity and, potentially, the most direct insight into past reproductive behavior.

In the interpretation of fossil specimens, it is important to allow for both novelty and transitional states that would appear to be inefficient in comparison to the conditions in extant taxa. The modern biota does not encapsulate the entire diversity of vertebrate history. For example, modern vertebrates include neither 4-winged gliders like *Microraptor* (Xu et al. 2003); nor taxa such as *Archaeopteryx* with asymmetrical flight feathers but lacking a keeled sternum and triosseal canal, the osteological correlates of the modern flight stroke (Ostrom 1976, Nudds and Dyke 2010); nor strongly ornamented eggs with a largely avian microstructure as in oviraptors (Grellet-Tinner et al. 2006). Consequently, it would seem unrealistic to expect all past reproductive behaviors to conform to modern standards and patterns of physiology and efficiency. Interpreting reproductive behavior for extinct taxa will likely remain somewhat controversial, particularly given the limitations in sample size, taxonomic coverage, and preservation and the potential for novel structures and behaviors. Consensus will likely result only if evaluation occurs within a phylogenetic framework in which trends and patterns can emerge and be tested.

Deeming (2015) considers the fossil record for extinct theropod species very sporadic and thus difficult to interpret with any certainty. However, we think that the record for both avian and non-avian theropods in the Mesozoic is sufficient to warrant both review and the development of hypotheses that can be tested with future discoveries. Documenting reproduction in early birds should bring clarity to the ancestral reproductive mode and the transitions to the modern condition for birds. Providing a historical and evolutionary context for reproductive traits should deepen our understanding of modern birds. Additionally, reproductive traits may account for the differential survival of bird clades across the Cretaceous–Paleogene (K–Pg) boundary, elucidate the transitions in care strategies among theropods, and shed light on the origins of flight. We conclude this review by presenting a hypothesis on the distribution and transitions of reproductive traits through derived non-avian and avian theropods of the Mesozoic and discuss those aspects that remain most controversial.

Inferring Reproduction in Mesozoic Birds from Modern Taxa

Ornithologists have used a variety of techniques—including physiological arguments, ecological models, and phylogenetic analyses—to predict ancestral reproductive conditions and the changes within premodern and early-modern birds (Kendeigh 1952, Van Rhijn 1984, 1990, Kavanau 1987, Wesołowski 1994, 2004, Ligon 1999, Burley and Johnson 2002, Tullberg et al. 2002, Dial 2003, Deeming 2006). Several reproductive traits, given their near or actual ubiquity among extant birds, are assumed to represent the primitive condition for Neornithes. For

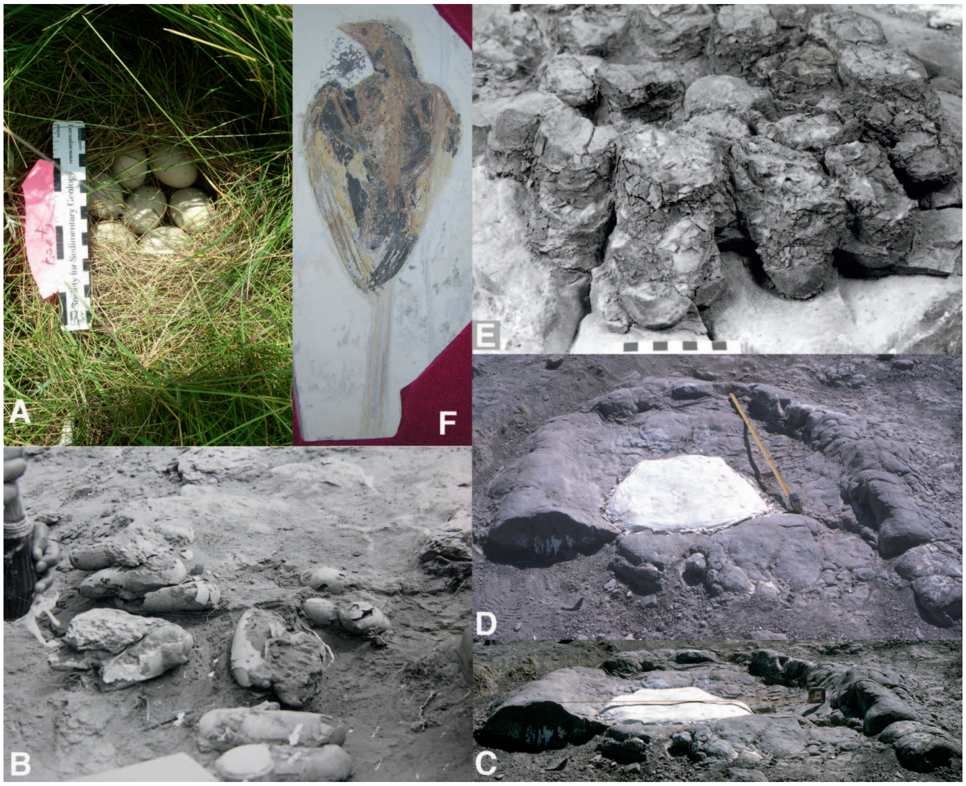

FIGURE 2. (**A**) Modern duck nest. (**B**) Clutch of oviraptor eggs, ZPAL MgOv-II/23, as discovered in the field in the Djadokhta Formation by the Polish Mongolian Expedition of 1970. The pair of eggs at the front are no longer in situ. Note the elongate shape of the eggs in comparison to those of the duck, egg pairing, and the donut-like arrangement of the clutch. Photo from the collections of ZPAL, by W. Skarzynski. (**C**, **D**) *Troodon* nesting trace with clutch of 24 eggs under white plaster jacket from the Two Medicine Formation, Montana. Tape measure = 1 m. (**E**) *Troodon* clutch, MOR 963, from the nesting trace (C, D) in oblique lateral view. Note the elongate form of the eggs as in the oviraptor, the steeply inclined orientation of the long axis, and the tight configuration of the upper blunt ends of the eggs. (**F**) *Confuciusornis* specimen exhibiting long rectrices, potentially reflecting sexual dimorphism.

example, one functional ovary and oviduct (Proctor and Lynch 1993), sequential ovulation, and bird–egg contact incubation occur within the vast majority of living species (Deeming 2002). Additionally, all birds are oviparous, with hard, calcitic, and multilayered eggshells. Deeming (2002) considers eggs "a key evolutionary step in avian reproduction" with "elegant adaptations to the environment in which they exist."

Phylogenetic and other analyses suggest the primitive condition for several other reproductive attributes. McKitrick (1992) and Sillén-Tullberg and Temrin (1994) found self-feeding, precocial young to represent the basal neornithine condition. This may also carry with it corresponding aspects of eggshell morphology, because the greater *in ovo* calcium needs of precocial young require a higher density of mammillary tips on the inner eggshell surface. By contrast, altricial young with faster growth rates and poorly ossified bones on hatching have more widely spaced mammillary cones (Karlsson and Lilja 2008, Österström and Lilja 2012). The basal condition for mating systems is less clear. Temrin and Sillén-Tullberg (1994) suggest monogamy as the primitive state; however, they used the somewhat controversial phylogeny of Sibley and Ahlquist (1990) that unites Palaeognathae with Galliformes and Anseriformes. The primitive condition is likely equivocal within a more traditional phylogeny, given that monogamy is basal for Neognathae, whereas female polygamy appears to be primitive and the male condition equivocal for Palaeognathae (Temrin and Sillén-Tullberg 1994, Moore and Varricchio in press). Overall, Temrin and Sillén-Tullberg (1994) found that transitions to female polygamy occurred more frequently in clades with precocial young. Owens and Bennett (1994) proposed open nests as the primitive state for Neornithes (Figure 2A). Transitions within the clade to "safe nests," such as cavities and colony nesting, were associated with reduced "reproductive effort."

Some form of parental care of eggs and young is found in 99% of all modern birds, the exceptions being only those parasitic species that take advantage of the nurturing attributes of other birds and those that use geothermal or insolation heat (Cockburn 2006). Consequently, the evolution and ancestral condition of parental care in

Neornithes has been the subject of much debate. Some (e.g., Kendeigh 1952) have argued that biparental care, given its preponderance in 81% of extant species (Cockburn 2006), represents the ancestral condition. Others (Handford and Mares 1985, Wesołowski 1994) favor male-only care as the basal condition, based in part on a likely false interpretation of palaeognaths as representing the most primitive living birds (Burley and Johnson 2002). Strictly phylogenetic approaches with no consideration of fossil taxa have recognized the ancestral state as biparental (McKitrick 1992, Tullberg et al. 2002, Birchard et al. 2013, Moore and Varricchio in press), male-only (Vehrencamp 2000), or equivocal (Tullberg et al. 2002). These varying results reflect the choice of phylogeny, the use of ordered or unordered transitions between care states, the inclusion of outgroups, and whether the female care of crocodylians is considered homologous to that of birds. The ambiguity of the ancestral state also stems, in part, from the prevalence of biparental and paternal care in neognaths and palaeognaths, respectively.

Despite the rarity (~1%) of paternal (male-only) care in extant bird species (Cockburn 2006), Van Rhijn (1984, 1990) favored this care strategy as the ancestral condition. His supporting evidence included the wide phylogenetic distribution of paternal care and an apparent difficulty for both maternal and biparental care to give rise to other care strategies. For example, in shorebirds (Charadriiformes) the most common transitions in parental care have been from predominantly male care to either biparental or predominantly female care (Székely and Reynolds 1995). Similar transitions are also typical among fish, in which paternal care represents the most common parental-care strategy to evolve from a state of no care (Gittleman 1981, Gross and Sargent 1985). Using a cost–benefit economic approach of behavioral ecology combined with a historical perspective, Wesołowski (1994, 2004) presented a multistage, male-care-first model for the evolution of parental care in birds. The model begins with a no-care stage in which the main adaptations of flight evolve. Stage 2 is characterized by egg-size increases, sequential ovulation, superprecocial young, and males guarding communal clutches; sequential ovulation is a key feature, necessitated by larger eggs, potentially hindering the evolution of female care but also facilitating both male care and communal nesting. In stage 3, male care increases to include incubation and enables synchronous hatching of the clutch; the latter facilitates the care of young, leading to a decrease in egg size and a dependence on incubation. This, in turn, gives rise to the final stage 4, which features biparental care and monogamy. Wesołowski (2004) regarded non-avian theropods, such as oviraptors and troodontids, as largely irrelevant to the evolution of avian reproduction. Although these theropods may have engaged in nest-guarding, he considered the paleontologic evidence for contact incubation or sequential ovulation (e.g., Norell et al. 1995, Varricchio et al. 1997) insufficient, an interpretation held by others (Deeming 2002, Jones and Geist 2012; see below).

On the basis of experimental manipulation of breeding psittaciforms, Kavanau (1987) postulated that biparental care arose from a state of no care within pre-Aves, and that monochronic ovulation followed earlier stages of polyautochronic, polyallochronic, and monoallochronic ovulation. Later, Kavanau (2007, 2010) revised this scenario to incorporate the dinosaur origin of birds and new data on theropod reproduction, ultimately arguing that troodontids and oviraptors represented secondary flightless birds.

Burley and Johnson (2002) also presented a model outlining the evolutionary stages of avian parental care, but unlike Kavanau (1987), they proposed that biparental care arose from maternal care. Their model was built on a "contemporary understanding of avian evolution" but "does not rely on the correctness of the theropod origin of birds" (Burley and Johnson 2002:241). The model implies the homology of female care across archosaurs, from crocodylians through birds. In their scenario, endothermy represents an important factor decreasing the duration of sperm storage, leading to increased consortship and, eventually, a shift to biparental care.

None of the 3 more extensive models proposed by Kavanau (1987, 2007, 2010), Wesołowski (1994, 2004), and Burley and Johnson (2002) conform to the dinosaur fossil record. However, if one shifts the timing of the origin of flight, then the model of Wesołowski (1994) comes close (Varricchio and Jackson 2003). We will discuss this below, in the section on non-avian dinosaurs.

Dial (2003) addressed the evolution of birds, flight, and avian reproduction by synthesizing data on 5 variables for extant birds: (1) body size, (2) locomotor modules (forelimb, hindlimb, or tail), (3) flight capabilities, (4) nesting mode, and (5) developmental spectrum and parental care. Within extant birds, these traits vary phylogenetically and largely in concert. Basal species including palaeognaths, galliforms, and some anseriforms exhibit large body size, a predominant hindlimb module, flightlessness to burst flight, simple ground nests, and superprecocial to precocial hatchlings requiring minimal parental care. These features appear to be similar to those in advanced non-avian theropods (Dial 2003). More derived avian taxa exhibit small body size, a primary emphasis on the forelimb, more sophisticated flight, elevated and more complex nests, and altricial young requiring extensive parental care. Dial (2003) viewed predation as the primary selective agent driving the shifts in both locomotion and reproduction. Bosque and Bosque (1995) independently demonstrated predation to be an important selective factor in the evolution of developmental rate among altricial birds.

In summary, the perspective based on extant birds indicates that basal neornithines possessed one functional ovary and oviduct; sequential ovulation; hard, calcitic, and multilayered eggshell; open, simple ground nests; incubation by adult–egg contact; precocial, self-feeding young; and likely some form of parental care. However, the mating system and the type of parental care present in this neornithine ancestor remain somewhat controversial.

Non-avian Theropods: Toward the Primitive Condition

The available fossil record related to reproduction in non-avian theropods includes eggs, clutches, nests, embryos, and even adults associated with eggs or clutches. This rich sample includes megalosaurids (Araújo et al. 2013), allosaurs (Mateus et al. 1997), alvarezsaurids (Agnolin et al. 2012), and therizinosaurs (Kundrát et al. 2008), as well as more derived maniraptorans such as oviraptors (Norell et al. 1994, 1995, Dong and Currie 1996, Weishampel et al. 2008, Fanti et al. 2012), dromaeosaurids (Grellet-Tinner and Makovicky 2006), and troodontids (Varricchio et al. 1997, 1999, 2002, 2013, Grellet-Tinner 2006, Bever and Norell 2009). For several reasons, oviraptors and troodontids are the most pertinent in characterization of the reproductive state of ancestral birds. (1) These maniraptoran clades possess the most extensive collection of reproduction-related specimens, providing fairly detailed records of their behavior. (2) Both clades also sit close to the ancestry of birds (Figure 1). Past phylogenetic analyses have found that troodontids and dromaeosaurids comprise Deinonychosauria, the sister taxon to Aves, and collectively form the clade Paraves. Oviraptors then represent the sister taxon to Paraves (Turner et al. 2012). However, some more recent analyses place troodontids as the closest relatives to Aves, with dromaeosaurids and oviraptors each more distantly related (Hendrickx et al. 2015). (3) Oviraptors and troodontids also appear to share a number of reproductive features likely found in the common ancestor of birds. (4) The reproductive anatomy and behavior of these 2 clades differs markedly from that of most other non-avian dinosaurs, including various theropods. For example, most dinosaurs, in contrast to these 2 clades, possess spherical to ovate eggs with high porosity and likely incubated their eggs completely underground (Deeming 2006, Kundrát et al. 2008, Araújo et al. 2013, Tanaka et al. 2015).

Some caveats, however, should be noted in using these 2 maniraptoran clades to characterize the ancestral avian condition. First, the available reproductive information for dromaeosaurids remains sparse. Additionally, eggs and eggshell within the theropod clade Tetanurae, and even Maniraptora, can vary significantly. For example, subspherical and highly porous eggs occur in a torvosaur and a therizinosaur (Kundrát et al. 2008, Araújo et al. 2013) in contrast to those of other tetanurans (Mateus et al. 1997). Thus, inferences of homology among or between non-avian theropods and birds should be viewed cautiously and as hypotheses to be tested as fossil specimens fill phylogenetic gaps in our understanding.

Display arenas. Recently, Lockley et al. (2016) described theropod dinosaur display arenas, or leks, from 4 localities in the mid-Cretaceous of Colorado. The largest site consists of a 50 × 15 m bedrock exposure with ~60 scrapes on its surface. Individual traces consist of large, ≤2 m long, symmetrical and bilobed impressions with multiple parallel scratch marks. Because of their similarity to those of some ground-nesting birds, Lockley et al. (2016) interpret these traces as a product of "nest scrape display" or "scrape ceremonies." Given the density of these traces at all 4 localities, Lockley et al. (2016) suggest that these scrapes indicate that "non-avian theropods engaged in stereotypical avian courtship and lek-like behaviors."

Medullary bone. Many reproductively active female birds possess medullary bone, a complex of irregular bone tissue deposited along the interior endosteal surface of long bones that is used as a mineral reserve for egg formation (Simkiss 1967). Although medullary bone is largely resorbed during egg laying, birds may retain some medullary bone for days to weeks after ovulation (Simkiss 1967). Medullary bone is reported in the theropods *Tyrannosaurus* (Schweitzer et al. 2005) and *Allosaurus*, as well as in the ornithischian *Tenontosaurus* (Lee and Werning 2008); each represents a clade more distantly related to birds than either troodontids or oviraptors (Sereno 1999). Purported medullary bone in both theropod examples is problematic. In *Tyrannosaurus*, which is more closely related to birds, the unusual tissue continues around the circumference of the bone and into the cortex on the opposite side. The *Allosaurus* tissue is lined with endosteal bone. Both features are unexpected in modern avian medullary bone. Histologic examination of an oviraptor with an egg preserved within the body cavity revealed no evidence of medullary bone (He et al. 2012). However, Schweitzer et al. (2016) recently provided biochemical support for their earlier identification of medullary bone in *T. rex* (Schweitzer et al. 2005).

Eggs. Egg size in relation to adult size in both oviraptors and troodontids is large in comparison to the ratios for all other non-avian dinosaurs. Further, these eggs greatly exceed those typical of modern reptiles of similar body mass but are only about half the size expected in a bird of similar adult body mass (Varricchio and Jackson 2004b). Both clades possess moderately to extremely elongated eggs, quite different from those of most other non-avian dinosaurs. The elongation index (length:width ratio) of these eggs, ranging from 2:1 to >3:1, also differs from the proportions of modern bird eggs (López-Martínez and Vicens 2012, Deeming and Ruta 2014) (Figure 2B, 2E).

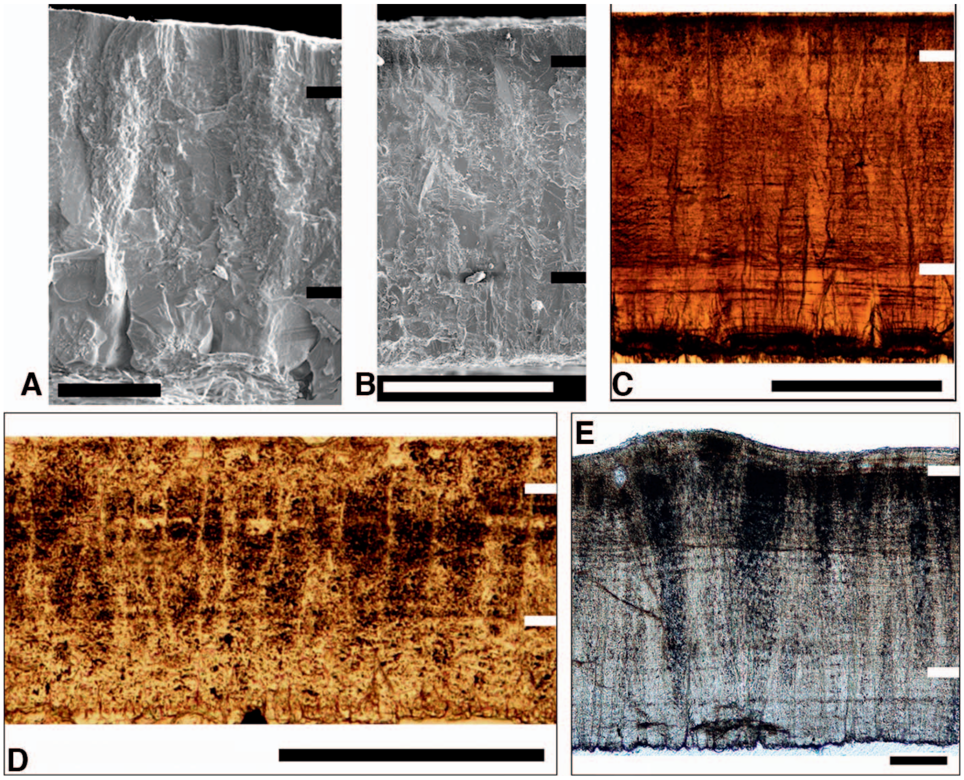

FIGURE 3. Avian and non-avian theropod eggshells. (**A**) SEM image of hen (*Gallus gallus*) eggshell showing 3 structural layers. From the inner to outer eggshell, these include the mammillary layer (ML), continuous layer (CL), and external layer (EL); horizontal bars in this and all images (B–E) indicate transitions between layers. Note closely packed cones in ML and squamatic texture in CL. Scale bar =100 μm. (**B**) SEM image of *Troodon* eggshell from the Two Medicine Formation of Montana. Note narrow prisms and irregular distribution of squamatic texture in CL. Scale bar = 500 μm. (**C**) Same as B in thin section. (**D**) Thin section image of eggshell of a basal bird (probably an enantiornithine) from the Neuquén locality, Bajo de la Carpa Formation of Argentina. Tips of mammillary cones are absent, likely due to recent weathering. Structural layering and narrow prisms in the CL are apparent despite significant calcite alteration. Scale = 250 μm. (**E**) Thin section image of *Triprismatoolithus stephensi*, a non-avian or possible avian theropod eggshell from the Two Medicine Formation of Montana. The EL exhibits a more complex and layered composition compared to the dense crystalline structure of eggshell shown in A–D. Scale bar = 100 μm.

Deeming and Ruta (2014) propose that, in contrast to modern archosaurs (crocodylians and birds), the elongate eggs of these non-avian theropods reflect a lack of albumen, as in squamates, and the absorption of sufficient water within the oviduct to expand the ovum. As a consequence, their embryos would be at an advanced developmental stage at oviposition (Deeming and Ruta 2014). This hypothesis implies that these non-avian theropod eggs were radically different from those of modern birds, despite similar eggshell microstructure (see below).

Oviraptor eggs are weakly asymmetric, whereas those of *Troodon* and other troodontids (ootaxon *Prismatoolithus*) have a more pronounced asymmetry (Hirsch and Quinn 1990, Zelenitsky and Hills 1996, Mikhailov 1997, Clark et al. 1999, Varricchio et al. 2002). Grellet-Tinner et al. (2006) suggest that the asymmetry corresponds to the development of an air cell as in the eggs of modern birds. Reflecting the relative asymmetry of their eggs, oviraptors would have a small proto-air cell, whereas that of *Troodon* would be fully formed (Grellet-Tinner et al. 2006). However, the link between egg shape and the air cell is tenuous. In extant birds the air cell forms because of evaporation of fluids that occurs within open nests (Ar and Rahn 1980). By contrast, egg shape in birds is thought to result from the combination of only a single egg and peristalsis (i.e. muscular contractions) within the oviduct (Iverson and Ewert 1991).

Egg microstructure. Both oviraptors and troodontids possess eggs with hard, calcitic shells that share microscopic attributes with modern birds, including narrow shell units in relation to overall shell thickness, a second structural layer of vertical prisms, sparse and narrow pores, calcium absorption (“cratering”) of the mammillae by the developing embryo, and at least some textural development within the continuous layer that paleontologists refer to as “squamatic structure” (Figure 3A, 3B, 3C; Hirsch and Quinn 1990, Mikhailov 1997, Zelenitsky et al.

2002, Grellet-Tinner and Chiappe 2004, Varricchio and Jackson 2004a, Zelenitsky 2006, Jin et al. 2007, Zelenitsky and Therrien 2008). Eggs of the dromaeosaur *Deinonychus* also share these same features (Grellet-Tinner and Makovicky 2006). The more extensive squamatic structure in oviraptors and *Deinonychus* largely obscures the prisms of the second layer, producing a continuous layer characteristic of palaeognaths (Mikhailov 1997, Jin et al. 2007). By contrast, eggs of *Troodon* exhibit only weakly developed squamatic structure with visible prism margins similar to some modern Neognathae; further, *Troodon* possesses a third, external layer as in a variety of birds (Jackson et al. 2010; Figure 3).

Gas conductance value, an attribute tightly linked to incubation mode (Seymour 1979), is several times higher in oviraptor eggs than is expected in avian eggs of comparable size (Deeming 2006). But conductance in *Troodon* eggs closely approximates expected avian values (Deeming 2006, Varricchio et al. 2013). Some additional values ranging from 1.8 to 4.7 times greater than avian values have been reported for what may be additional troodontid eggs, but the taxonomic and ootaxonomic assignment as well as the methods used to calculate these values are somewhat ambiguous (Sabath 1991, Mikhailov et al. 1994, Deeming 2006). More recently, Tanaka et al. (2015) found porosity in oviraptor and troodontid eggs to be lower than in any other non-avian dinosaurs and consistent with open nests. Troodontid eggs also differ from those of oviraptors in lacking ornamentation (Hirsch and Quinn 1990, Grellet-Tinner et al. 2006, Zelenitsky and Therrien 2008).

Egg arrangements. On the basis of within-clutch egg pairing (Figure 2B), Varricchio et al. (1997) proposed that both troodontids and oviraptors had monoautochronic ovulation (i.e. they produced and laid a pair of eggs, one from each ovary and oviduct, at intervals). The discovery of 2 eggs within or in close proximity to oviraptor adults confirms this pattern of sequential ovulation from 2 reproductive tracks in these taxa (Sato et al. 2005, He et al. 2012). However, Grellet-Tinner et al. (2006) consider the evidence for pairing in *Troodon* clutches to be insufficient. Their criticism stems from a misunderstanding of the tests employed and a false notion that pairing must be visible from all perspectives. Because no specific statistical tests exist for pairedness, one must conduct simulation- or permutation-style tests that compare the data for the recognized pairs with data for large samples of randomly generated pairings (Varricchio et al. 1997). Further, how *Troodon* clutches appear in top view does not falsify pairing observed in bottom view. Some perspectives may simply not provide a proper view of the eggs. For example, eggs in an oviraptor clutch are unlikely to appear paired in a nest cross section. Egg pairing is most easily recognized when the long axes of the eggs are fully visible. Acceptance of egg pairing in oviraptor clutches, which have never been tested in any view, seems incongruent with the rejection of this pattern in *Troodon* clutches that have passed statistical tests. Finally, Grellet-Tinner et al. (2006) further argue that the asymmetry in *Troodon* eggs implies a single oviduct, because the asymmetric shape of avian eggs is considered to result from the presence of a single egg in the oviduct at a time. But this condition in birds says nothing about the number of oviducts. Monoautochronic ovulation is the simultaneous production of one egg per oviduct at a time (Smith et al. 1973), thus still meeting the requirements for producing an asymmetric egg.

The highly organized (Zelenitsky 2006) and partially to nearly fully buried clutches found in troodontids and oviraptors differ markedly from those of modern birds. Oviraptor clutches consist of 1–3 layers of paired eggs lying nearly horizontal in rings (Figure 2B). As evidenced by several specimens, the adult assumed a position in the center of the ring (Norell et al. 1995, Dong and Currie 1996, Clark et al. 1999, Fanti et al. 2012). By contrast, *Troodon* clutches consist of eggs standing with their long axis subvertical to vertical within the sediments, leaning in toward the clutch center where their blunt ends largely contact one another (Figure 2E). A *Troodon* specimen preserves a clutch within a broad nesting trace, a shallow earthen bowl with a distinct rim (Figure 2C, 2D). The upper, exposed portion of the clutch occupies a relatively small area ($\sim$0.5 m^2), which an adult could likely have covered with its abdomen (Varricchio et al. 1999). Two adult troodontids have been found associated with egg clutches, but neither preserves a lifelike pose as is typical of the oviraptor specimens (Varricchio et al. 1997, Erickson et al. 2007). Relative clutch mass in both clades appears to be far greater than predicted on the basis of modern reptilian or avian scaling (Blueweiss et al. 1978, Varricchio and Jackson 2003). These clutches are $\sim$3 times larger than expected for either an extant bird or a reptile of similar adult mass and are proportionally larger than other non-avian dinosaur clutches (Varricchio and Jackson 2003). Horner (1987) suggested that *Troodon* clutches might represent communal nesting.

The partial burial of eggs in both troodontids and oviraptorids likely prohibited egg turning (Varricchio et al. 1997, 1999), a behavior common to nearly all extant birds but absent in crocodylians and other reptiles. In birds, the chalazae (gelatinous structures at either end of the egg) stabilize the position of the yolk within the albumen. This allows the embryo to maintain proper orientation when the egg rotates during egg turning (Romanoff and Romanoff 1949, Baker and Stadelman 1957, Terres 1995, Rahman et al. 2007). The chalazae and the high viscosity of the albumen hold the yolk in a central position, preventing adhesion to the eggshell. By contrast, most reptilian embryos adhere to the eggshell membrane, and egg turning is harmful or fatal in reptiles, rather than beneficial as in birds (Deeming 1991, Deeming and Ferguson 1991). This important distinction suggests that the evolution of chalazae likely occurred in response to, or facilitated, eggs incubated in open nests, completely free of sediment.

Adult–clutch associations are known in 4 oviraptor taxa (*Oviraptor*, *Citipati*, *Nemegtomaia*, and cf. *Machairasaurus*; Norell et al. 1995, Dong and Currie 1996, Fanti et al. 2012) and 2 troodontids (*Troodon* and an unnamed Mongolian form; Varricchio et al. 1997, Erickson et al. 2007). Also, eggs are assigned to the dromaeosaur *Deinonychus* on the basis of their preservation appressed to the exterior of adult gastralia (Grellet-Tinner and Makovicky 2006). Erickson et al. (2007) examined the histology of these clutch-associated adults in order to assess their ontogenetic age and growth state. In contrast to the condition in birds, in which adults complete growth and achieve maximum size before reproducing, these maniraptorans were, in some cases, still growing. The same adults all lacked medullary bone (Varricchio et al. 2008).

Probably the most controversial aspects of oviraptor and troodontid reproduction are the behavioral and evolutionary implications of these clutch-associated adults. The best-preserved oviraptors sit with their legs folded beneath their torso, their feet near the center of the clutch, and their arms draped to either side atop the clutch (Norell et al. 1995, Dong and Currie 1996, Clark et al. 1999, Fanti et al. 2012). Direct adult–egg contact in these specimens consists of various skeletal elements in contact with the upper ends of eggs (Clark et al. 1999). The more poorly preserved troodontid adults provide no insight about their original posture, whereas an intact *Troodon* nesting trace with clutch provides better evidence of reproductive behavior in this taxon (Varricchio et al. 1999; Figure 2C, 2D, 2E).

These oviraptor and troodontid specimens are variously interpreted. Given the limited contact between adult and eggs (Carpenter 1999, Zhao 2000, Deeming 2002, 2006), the presumed inefficiency of transferring body heat to a partially buried clutch, the absence of egg rotation (Ruben et al. 2003, Jones and Geist 2012), the high porosity of oviraptor eggs (Deeming 2006), uncertainty about adult body temperature, and size disparity and perceived asymmetry in the *Troodon* nest structure in relation to the clutch (Carpenter 1999), some consider these adults to have engaged in reptile-like nest attendance or guarding. Incubation would have resulted from soil burial (Zhao 2000, Deeming 2002).

By contrast, others propose that the preserved postures of clutch-associated adults suggest brooding homologous to that in birds, without necessarily implying an incubation function (Norell et al. 1995, Dong and Currie 1996, Clark et al. 1999). However, the presence of feathers in troodontids and oviraptors from other localities would favor egg incubation by adults (Hopp and Orsen 2004, Fanti et al. 2012). Furthermore, sequential laying, together with the complex clutch configurations and presumed synchronous hatching in both groups, would likely have required both adult body and incubation temperatures to be elevated over ambient conditions, consistent with this incubation mode (Varricchio and Jackson 2004b). Finally, the nest structure, egg arrangement, and avian-like porosity in troodontids and oviraptors also favor egg incubation by adults (Varricchio et al. 1999, 2013, Tanaka et al. 2015). The tighter clutch configuration and more extensive exposure of the upper eggs suggest more efficient contact incubation in troodontids than in oviraptors. Troodontids may have incubated their eggs using a combination of sediment and adult body heat in a manner analogous to that of the Egyptian Plover (*Pluvianus aegyptius*; Grellet-Tinner 2006, Grellet-Tinner et al. 2006).

These various interpretations implicitly raise the question of homology. Is the parental care evidenced by these specimens homologous to that of crocodylians, birds, or both, or is it of an independent origination? The sole dromaeosaurid egg represents an adult–egg association, thus suggesting that the 3 dinosaur clades closest to Aves likely exhibited some form of parental care of eggs. Thus, resolving the issue of homology becomes important in the interpretation of reproduction in Mesozoic birds. The possible absence of care in pterosaurs (Unwin and Deeming 2008) and the disparate evidence of care in Ornithischia vs. Saurischia (Varricchio 2011) argue against crocodilian and theropod care being homologous.

The question of homology for parental care of eggs also underlies our expectations of whether females, males, or both provide the care in these dinosaurs. A crocodilian homology would imply maternal care, whereas an avian homology would correspond with either biparental or paternal care. In an effort to address the parental-care issue and the unusually large clutch size in both oviraptors and *Troodon*, Varricchio et al. (2008) examined the scaling of clutch size by taxa and parental care strategy. These non-avian theropod clutches scale most closely to those of birds with paternal care. More recently, Birchard et al. (2013) addressed this same question with an expanded data set that included a large number of Anseriformes but excluded megapodes, one of the few clades of birds with some paternal (male-only) care of eggs (Jones et al. 1995). Results show that these same non-avian clutches scale with maternal or paternal equally well but not with biparental care. However, these authors conclude that parental care cannot be distinguished, in part because of the "confounding effects of hatchling maturity." A more extensive analysis using phylogenetic comparative methods based on generalized estimating equations demonstrates significant influences of body mass, parental care strategy, and hatchling maturity on clutch volume across Diapsida (Moore and Varricchio in press). Applying the results of these models to Dinosauria supports the hypothesis of paternal care in these derived non-avian theropods and as the ancestral condition for birds (Moore and Varricchio in press).

Embryos. Skeletal elements of embryonic oviraptors and troodontids appear to be well formed (Geist and Jones 1996, Norell et al. 2001, Varricchio et al. 2002, Weishampel et al. 2008, Bever and Norell 2009). Furthermore, histologic examination of embryonic limbs reveals relatively thin cartilage caps, some endosteal bone, and coarse, compacted cancellous tissue (Horner and Weishampel 1988, Horner et al. 2001, Weishampel et al. 2008). Thus, both clades possessed precocial young, as is common in most modern reptiles and basal extant birds.

In summary, these maniraptoran dinosaurs share with modern birds sequential ovulation, relatively larger eggs, various aspects of eggshell microstructure, some degree of parental care (possibly paternal), at least some adult–egg contact, and precocial hatchlings. Troodontids further exhibit a more strongly asymmetric egg lacking ornamentation, with potentially 3 structural shell layers and low porosity—an egg more similar to that of modern birds than to that of any non-avian dinosaur. The tighter clutch configuration, greater exposure of eggs, and avian levels of porosity favor contact incubation in troodontids. Nevertheless, important differences remain between these 2 maniraptoran clades (oviraptors and troodontids) and modern birds, including 2 functional reproductive tracts, smaller than expected relative egg size, elongate egg-shape, and eggs still largely buried. These sediment-bound eggs would likely preclude egg rotation and, thus, may have lacked chalazae (Varricchio et al. 1997).

Fossil Avian Evidence

The Mesozoic fossil record for avian reproduction includes a number of unusual discoveries, highlighted by the exceptional preservation from the Early Cretaceous Jehol Biota of Liaoning, China. This locality includes an extensive series of adult *Confuciusornis* with feathers, several adult birds that purportedly retain mature ovarian follicles within their body cavities, and an isolated, articulated embryo. Additionally, the fossil record for avian reproduction includes eggs, embryos, adult–egg associations, and rich nesting localities (Table 2). These specimens and sites provide a wealth of information on egg and shell characters, nesting strategies, embryonic development, hatchling state, and, possibly, parental care. Taxonomic assignments based on associated embryos and adults indicate that identifiable eggs and nesting localities all belong to the enantiornithines. A majority of this fossil record comes from the rich Late Cretaceous deposits of Mongolia. Recent descriptions of nesting localities with abundant eggs and eggshell from the Late Cretaceous of Romania and Argentina (Dyke et al. 2012, Fernández et al. 2013) have greatly expanded the geographic distribution of enantiornithine reproduction. To date, no information is available on reproduction in basal Ornithuromorpha taxa such as *Hesperornis* and *Baptornis*. Note that very small eggs with embryonic remains from the Early Cretaceous of Thailand were originally reported as avian (Buffetaut et al. 2005), but more detailed examination by synchrotron imaging shows the embryos to be those of lizards (Fernandez et al. 2015). These eggs will not be discussed further.

Dimorphism. *Confuciusornis sanctus*, a primitive, beaked pygostylian, is the most common bird from the Early Cretaceous Jehol Biota. The large sample includes >100 individuals, many preserved with long tail feathers (rectrices; Figure 2F). However, after several morphometric investigations (Chiappe et al. 2008, 2010, Peters and Peters 2009, 2010, Marugán-Lobón et al. 2011), the dimorphism remains unclear; interpretations include one species with sexes differing in the presence of rectrices (Feduccia 1996, Chiappe et al. 1999, Zinoviev 2009), one species with size dimorphism (Peters and Peters 2009, 2010), and 2 size-dimorphic species, with and without long tail feathers (Marugán-Lobón et al. 2011). The highly crushed, nearly two-dimensional preservation within the Jehol Biota and small sampling sets have hindered attempts to identify female *Confuciusornis* by the presence of medullary bone (Chinsamy et al. 2013, Zheng et al. 2013).

Ovarian follicles. In addition to feathers, the unusual taphonomic conditions of the Jehol Biota facilitated preservation of 8 birds, the very basal *Jeholornis* and 7 enantiornithines, each with aggregates of round objects within its torso (O'Connor et al. 2013). On the basis of the position and circular form of the enclosed structures, Zheng et al. (2013) identify these as partial ovaries with mature ovarian follicles. Further, O'Connor et al. (2013) suggest a similar explanation for the spherical structures preserved with the Jurassic non-avian theropod *Compsognathus longipes* (Griffiths 1993). These masses appear to be centered on the left side of the torso within several of the birds (Zheng et al. 2013), and the proposed follicles exhibit fairly consistent size, both within individuals and across specimens, with average diameters ranging from 5.4 to 7.7 mm. Counts vary, from highs near 30 and 20 within *Compsognathus* and *Jeholornis*, respectively, to <10 in most of the enantiornithines (O'Connor et al. 2013).

Zheng et al. (2013) propose that the presence of a perivitelline layer and other protective layers found in mature follicles facilitated their preservation in these specimens. They further argue that these specimens indicate that basal Aves possessed a single left ovary (Zheng et al. 2013), a feature typical of modern birds and differing from the primitive paired condition hypothesized for non-avian theropods like troodontids and oviraptors (Varricchio et al. 1997). This implies a loss of function in the right ovary and oviduct near the avian–non-avian transition, potentially as an adaptation for flight. The variation in follicle count suggests differing reproductive strategies among these species, with *Compsognathus* and *Jeholornis* producing much larger clutches but with relatively smaller eggs (in comparison to adult mass; O'Connor et al. 2013, Zheng et al. 2013). At least one enantiornithine individual possesses an unfused carpus, implying that sexual maturity preceded skeletal maturation. Finally, Zheng et al. (2013) note that the minimal variation in follicle size in each individual (i.e. limited follicular hierarchy) differs from that seen in modern birds and is more consistent with lower metabolisms and longer growth periods.

Tempering the above arguments, Mayr and Manegold (2013) and Deeming (2015) question how glycoproteins could selectively preserve organs in the body cavity. Follicle preservation may be even more unexpected in those specimens not preserving feathers (e.g., *Linyiornis*; Wang et al. 2016). Mayr and Manegold (2013) suggest that these masses could represent some sort of stomach contents. If ovarian follicles, the uniformity of the follicle size might seem more consistent with en masse egg production, a mode unexpected both in a volant animal and given the iterative egg production evidenced in derived non-avian theropods. As noted by Wang et al. (2016), independent evidence, such as geochemical analysis, is required to verify and clarify this potential preservation of soft tissue structures.

Eggs. Associated adult skeletons or *in ovo* embryonic remains permit the assignment of 6 egg morphs from the Late Cretaceous of Argentina, Romania, and Mongolia to enantiornithine birds (Table 2, Appendix Table 3, and Figure 4). Three eggs belong to the ootaxa *Styloolithus sabathi*, *Gobioolithus minor*, and *Subtiliolithus microtuberculatus* (Figure 4A, 4B, 4C), whereas the others remain unnamed. Kurochkin et al. (2013) described some, but not all, of the embryonic specimens from Khermeen Tsav and associated with *G. minor* eggs as a new enantiornithine, *Gobipipus reshetovi*. Other embryos, those of Elżanowski (1981), remain unassigned within Enantiornithes (see Appendix). An adult skeleton of *Gobipteryx minuta* (Chiappe et al. 2001) occurred in association with *S. microtuberculatus* eggshell, providing a tentative taxonomic assignment.

Among the unnamed eggs are those from the Late Cretaceous Bajo de la Carpa Formation of Argentina, where a Neuquén locality yields abundant eggs, some with likely enantiornithine embryos (Schweitzer et al. 2002). Although not directly associated with adult skeletal material (Fernández et al. 2013), these eggs may be those of *Neuquenornis volans* (Chiappe and Calvo 1994). A second unnamed egg type comes from the Late Cretaceous Sebeş Formation of Romania and occurs in a calcareous mudstone lens that contains thousands of morphologically identical eggshell fragments, nearly complete eggs, and complete and identifiable enantiornithine bones (Dyke et al. 2012). The third unnamed egg is from the Upper Cretaceous Javkhlant Formation of Mongolia. Originally described as a possible neoceratopsian egg (Balanoff et al. 2008), reexamination of the embryonic remains identifies the specimen as enantiornithine (Varricchio et al. 2015).

Ten additional egg or eggshell varieties from the Early and Late Cretaceous are tentatively considered as avian on the basis of their overall shape, lack of ornamentation, and microstructure. These include 7 named ootaxa as well as 3 unnamed eggs from Mongolia (Grellet-Tinner and Norell 2002), Brazil (Marsola et al. 2014), and the United States (Hirsch and Quinn 1990) (Appendix Table 3). Mikhailov (1997) considers the great similarity between *Subtiliolithus* and *Laevisoolithus* sufficient to recognize the latter as enantiornithine; and, given the similarities between *G. minor* and *G. major*, the latter is also likely assignable to this clade.

Although distributed across 4 continents, these egg varieties (Table 2 and Appendix Table 3) exhibit fairly consistent egg morphology at both the macroscopic and the microscopic scales. The eggs range in size from 26 to 70 mm long and are typically slightly asymmetric, with both tapered and more blunt poles. Diameter varies regularly with total length (Figure 5A). Despite the size range, the elongation index (greatest length:diameter) varies only between 1.6 and 2.2, with perhaps a slight trend toward increase with overall egg length. The eggs of non-avian theropods such as troodontids and oviraptors typically exhibit higher elongation, with values between 2.0 and 3.0, whereas the values for modern birds are lower, at ~1.4 (Sabath 1991, Lopéz -Martínez and Vicens 2012, Deeming and Ruta 2014; Figures 2 and 5). Examined non-avian theropod eggs are also more asymmetric than those of both Mesozoic and modern birds (Deeming and Ruta 2014). Thus, both elongation and symmetric indices and more extensive morphometric analysis of egg shape place these Mesozoic avian eggs between those of non-avian theropods and modern birds in terms of shape (Lopéz-Martínez and Vicens 2012, Deeming and Ruta 2014).

The association of adults with eggs permits evaluation of relative egg size for 3 forms (Figure 6B and Appendix Table 4). In each case, estimated egg mass falls short (49–75%) of the expected egg values for a modern bird of equivalent adult body mass. Eggs of troodontid and oviraptor theropods are relatively smaller, at <50% the value predicted for a bird of equivalent body mass (Varricchio and Jackson 2004b).

TABLE 2. Reproduction-related specimens for Mesozoic birds. List includes eggs, eggshell, embryos, and adults with possible reproductive-related features.

	Location	Specimen no.	Taxon	Ootaxon	Formation	Age	Important finds	References
1	Liaoning, China	Multiple specimens	*Confusciusornis*	–	–	Early Cretaceous	Growth series	Chiappe et al. 2008, Zinoviev 2009
2	Liaoning, China	STM2-51, STM10-45, STM29-8	*Jeholornis* and 2 enantiornithines	–	Jehol Formation	Early Cretaceous	Mature ovarian follicles in one mass	Zheng et al. 2013
3	Liaoning, China	IVPP V14238	Enantiornithes	–	–	Early Cretaceous	Embryo in egg without shell, precocial to superprecocial	Zhou and Zhang 2004
4	Fukui, Japan	FPDM-V-0009175	–	*Plagioolithus fukuiensis*	Kitadani Formation	Upper Baremian–Early Cretaceous	Eggshell	Imai and Azuma 2015
5	Zhejiang, China	JYM F0033	–	*Pachycorioolithus jinyunensis*	Lingtoutang Formation	Albian–Early Cretaceous	Egg	Lawver et al. 2016
6	Gobi Desert, Mongolia	PIN 3142-500/1	–	*Oblongoolithus glaber*	Barun Goyot Formation	Late Cretaceous–Campanian	Eggs	Mikhailov 1996a
7	Bugeen-Tsav, Gobi Desert, Mongolia	PIN 2970/5	–	*Laevisoolithus sochavi*, Laevisoolithidae	Nemegt Formation	Late Cretaceous–Maastrichtian	Eggs	Mikhailov 1991, Sabbath 1991, Mikhailov et al 1994
8	Gobi Desert, Mongolia; and Gujarat, India	Type ZPAL MgR-I/12 and I/32; PIN 4230; PIN 4492-1; IGM 100/1011; VPL/KH 580	*Gobipteryx minuta* (*Nanantius valifanovi*), Enantiornithes	*Subtiliolithus microtuberculatus* and *S. kachchhensis*	Khermeen Tsav; Barun Goyot Formation; Nemegt Formation; third intertrappean level	Late Cretaceous–Campanian–Maastrichtian	Eggshell, an adult–eggshell association	Elżanowski 1974, 1977, Mikhailov 1991, Khosla and Sahni 1995, Kurochkin 1996, Chiappe et al. 2001
9	Khulsan and Bayn Dzak, Mongolia	ZPAL MgOv-II/7, II/25	–	"Larger avian eggs"; *Styloolithus sabathi*	Barun Goyot Formation, Djadokhta Formation	Late Cretaceous–Campanian	Eggs with adults	Sabath 1991, Varricchio and Barta 2015
10	Gobi Desert, Mongolia	PIN 4478-1, 2, 5, 6; 3142/429, 460, 481	–	*Gobioolithus major*, "larger *Gobipteryx* eggs"	–	Late Cretaceous	Eggs	Mikhailov 1991, 1996b, 1997, 2000, D. J. Varricchio and F. D. Jackson personal observation
11	Gobi Desert Mongolia	PIN 4492-3, 4; ZPAL MgOv-III/10, 11, 12, 13, 14; PIN 3142/401, etc.	*Gobipipus reshetovi*, Enantiornithes	*Gobioolithus minor*, "*Gobipteryx minuta*" eggs	Barun Goyot Formation, Khermeen Tsav	Late Cretaceous–Campanian	Embryonic remains	Mikhailov 1991, 1996b, 1997, Sabath 1991, Chatterjee 1997, Kurochkin et al. 2013

TABLE 2. Continued.

	Location	Specimen no.	Taxon	Ootaxon	Formation	Age	Important finds	References
12	Gobi Desert Mongolia	ZPAL MgR-I/33, 34, 88-92	"Elżanowski embryos," "*Gobipteryx minuta*," Enantiornithes	–	Khermeen Tsav	Late Cretaceous–Campanian	Embryonic remains with some eggshell	Elżanowski 1981, 1985, 1995
13	Eastern Gobi Desert, Mongolia	IGM 100/2010	Enantiornithes	–	Javkhlant Formation	Late Cretaceous	Egg, 3D imaging of embryo, eggshell with 3 layers	Balanoff et al. 2008, Mikhailov 2014, Varricchio et al. 2015
14	Bayn Dzak, Mongolia	IGM 100/1027	–	–	Djadokhta Formation	Late Cretaceous–Campanian	Egg with 3-layered eggshell (but Mikhailov disputes this)	Grellet-Tinner and Norell 2002, Mikhailov 2014
15	Lleida, Spain	UM1	–	*Sankofa pyrenaica*	Aren Formation	Late Cretaceous–Campanian–Maastrichtian	Fits intermediate position between non-avians and avians	López-Martínez and Vicens 2012
16	Lleida, Spain	FLL6-1-6	–	*Ageroolithus fontillongensis*	Tremp Formation	Late Cretaceous–Maastrichtian	Eggshell	Vianey-Liaud and López-Martínez 1997
17	Sebes, Romania	–	Enantiornithes	–	Sebes Formation	Late Cretaceous–Maastrichtian	Abundant eggs, shell, and bones; colonial nesting	Dyke et al. 2012
18	São Paulo, Brazil	LPRP-USP 0359	Ornithothoraces	–	Vale do Rio do Peixe Formation	Late Cretaceous	Egg	Marsola et al. 2014
19	Neuquén, Argentina	–	∼Enantiornithes (*Neuqueornis volans*?)	–	Baja de la Carpa Formation, Río Colorado subgroup	Late Cretaceous–Campanian	3-layered shell, embryonic material, nesting locality, colonial, upright eggs	Schweitzer et al. 2002, Grellet-Tinner et al. 2006, Salvador and Fiorelli 2011, Fernández et al. 2013
20	Montana, USA	YPM-PU 23396, HEC 362	–	–	Two Medicine Formation	Late Cretaceous–Campanian	Egg	Hirsch and Quinn 1990

Abbreviations: FPDM = Fukui Prefecture Dinosaur Museum, Japan; FLL = Departmento de Paleontología, Universidad Complutense de Madrid, Fontllonga; HEC = Hirsch eggshell catalogue, University of Colorado Museum, USA; IGM = Mongolian Institute of Geology, Ulaan Baatar, Mongolia; IVPP = Institute of Vertebrate Palaeontology and Paleoanthropology, Beijing, China; JYM = Jinyun Museum, Jinyun, Zhejiang Province, China; LPRP-USP = Laboratório de Paleontologia, Universidade São Paulo, Ribeirão Preto, Brazil; PIN = Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; STM = Tianyu Natural History Museum, Shandong, China; UM = Departmento de Paleontología, Universidad Complutense de Madrid, Spain; VPL/KH = Vertebrate Paleontology Laboratory, Khosla, India; YPM-PU = Yale Peabody Museum of Natural History, Princeton University Collection, USA; ZPAL = Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

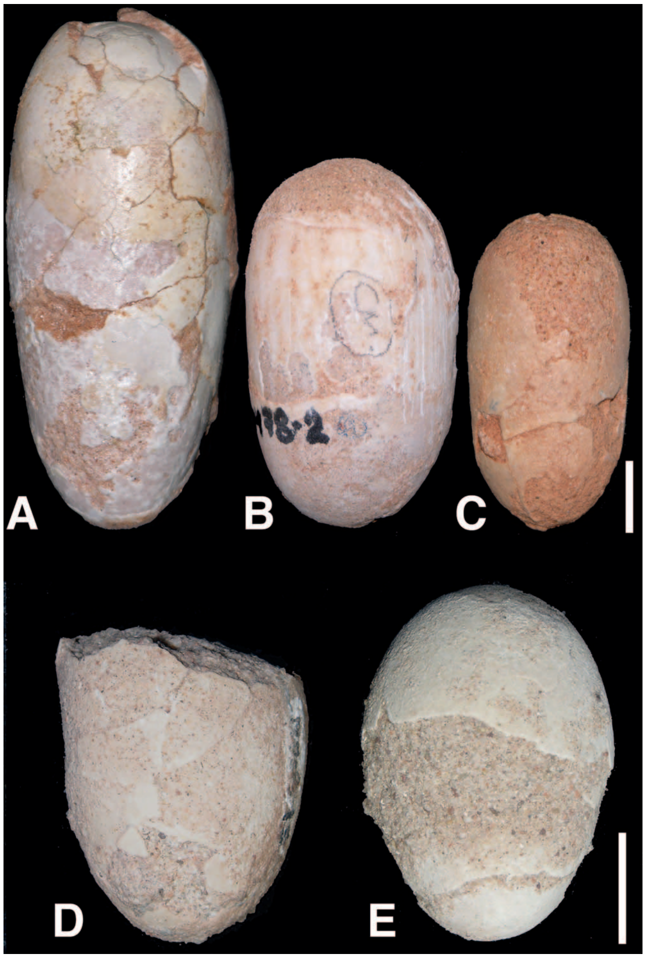

FIGURE 4. Representative enantiornithine eggs. (**A**–**C**) "*Gobioolithus*" eggs, including (**A**) *Styloolithus sabathi* (ZPAL MgOv-II/25) likely representing a distinct oogenus (Varricchio and Barta 2015), (**B**) *G. major* (PIN 4478-2), and (**C**) *G. minor* (ZPAL MgOv-III/10). The former classification of Mikhailov et al. (1994) included eggs such as ZPAL MgOv-II/25, representing the "larger avian eggs" of Sabath (1991) with Soviet-collected specimens as *G. major*. Scale bar = 1 cm. (**D**, **E**) Eggs from the Neuquén locality from the Bajo de la Carpa Formation, Argentina. (**D**) Partial egg, MCUPv13, shows common truncation of upper blunt end. Unnumbered MCUPv specimen (**E**) shows telescoping of blunt end down atop remainder of egg. Both preservation styles reflect the subvertical arrangement of the eggs at Neuquén. Scale bar in D and E = 1 cm.

All of these eggs have a smooth external surface, with the exception of *S. microtuberculatus*, which bears "micronobbules" (Mikhailov 1991). Shell thickness appears to scale only loosely with overall egg size (Figure 5B), with *Laevisoolithus* and the unnamed Two Medicine egg of Montana having particularly thick eggshell for their size. By contrast, the ootaxon *Sankofa pyrenaica* has particularly thin eggshell for its size (Appendix Table 3).

Eggshell microstructure. Mesozoic avian eggs exhibit a shell microstructure with at least 2 layers: a basal, mammillary layer (ML) consisting of radiating calcite with radial or radial and tabular ultrastructure; and an overlying second or continuous layer (CL) with vertically arranged prisms (Figure 3). These prisms may be partially to nearly completely obscured by the development of squamatic ultrastructure as a continuous layer (Mikhailov 1997). The relative proportions of these 2 layers vary among these eggs, but 8 of the 16 exhibit a slightly thicker continuous layer compared to the mammillary layer, and 13 have a CL:ML ratio of 1:1–2:1. The 2 *Subtiliolithus* oospecies are unusual in having a much thicker mammillary layer, greater than twice the thickness of the continuous layer. Some of the overall variability perhaps reflects diagenetic alteration, given that several researchers noted issues in assessing their specimens (Sabath 1991, Mikhailov et al. 1994, Mikhailov 1997, Vianey-Liaud and López-Martínez 1997, Balanoff et al. 2008).

The eggshell of most modern birds also exhibits a third structural layer (Mikhailov 1991, 1997), and the presence of a third layer at times has been considered a synapomorphy of Aves (Mikhailov 1997) or perhaps of a less inclusive clade within Aves (Mikhailov 1991, Kohring 1999, Grellet-Tinner and Norell 2002). The Bajo de la Carpa eggs from Argentina and 2 egg forms from Mongolia possess a third narrow, external layer (Grellet-Tinner and Norell 2002, Schweitzer et al. 2002, Balanoff et al. 2008) (Figure 3). Mikhailov (1991, 2014) and Vianey-Liaud and López-Martínez (1997) also observed an outer layer in *Gobioolithus* and *Ageroolithus* radial sections, respectively. Both, however, interpret these as recrystallized zones of the continuous layer. By contrast, Sellés (2012) includes a third layer as a diagnostic feature of *Ageroolithus*. Mikhailov (2014) further argues that the third layer described in an unnamed Mongolian egg (Grellet-Tinner and Norell 2002) is also a false external zone. The increasing occurrence of a third layer in eggs of enantiornithines (Schweitzer et al. 2002, Balanoff et al. 2008) and in eggs that are likely of Cretaceous non-avian maniraptoran theropods (Bonde et al. 2008, Jackson et al. 2010, Agnolin et al. 2012) from 3 continents argues against a strictly diagenetic origin for this feature and suggests that the trait had an earlier origin than in modern birds (Schweitzer et al. 2002, Jackson et al. 2010). The unnamed Brazilian egg and *Pachycorioolithus* differ from the others in having a thick external layer that exceeds the thickness of the 2 underlying layers (Marsola et al. 2014, Lawver et al. 2016).

The cuticle consists of a thin organic layer deposited on the shell exterior in the final stages of avian egg formation (Tyler 1969). Reports of fossil cuticles remain rare, likely because of the difficulty of preserving their form and composition. Mikhailov (1991) noted a thin (5 μm), mineralized layer draped over the outer surface of a *Gobioolithus* shell. Similarly, a Bajo de la Carpa egg bears a

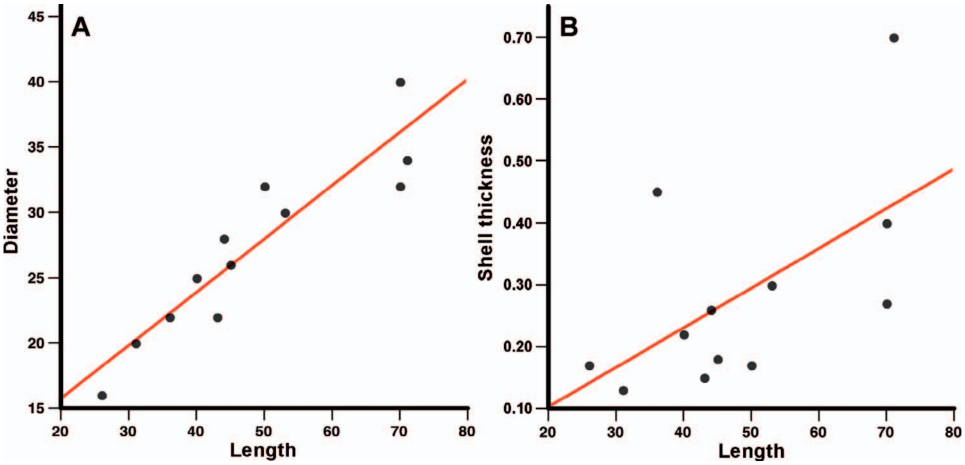

FIGURE 5. Scaling of egg proportions and shell thickness (data from Appendix Table 3; all values in millimeters). (**A**) Egg diameter scales consistently across the Cretaceous avian eggs. Regression equation is $f = 0.407726x + 7.57721$, $r^2 = 0.85$. (**B**) More variation occurs in shell thickness in relation to overall egg length, perhaps reflecting different incubation styles. Regression equation is $f = 0.0064117x - 0.0260329$, $r^2 = 0.35$. Two forms with particularly thick eggshell are the small Two Medicine egg (Hirsch and Quinn 1990) and the larger *Laevisoolithus sochavi* from Mongolia (Mikhailov 1991).

5.5–6.0 μm thick carbonaceous layer on its exterior. Its surface location, granular texture, and abundant vesicles are consistent with an avian cuticle (Schweitzer et al. 2002). *Triprismatoolithus stephensi*, an egg potentially attributable to alvarezsaurids (Agnolin et al. 2012), also possesses a possible cuticle with a more complex structure (Varricchio and Jackson 2004a).

With the exception of *Sankofa*, all of these eggs (Appendix Table 3) can be classified as ornithoid–ratite or ornithoid–neognath, using the terminology of Mikhailov (1991, 1997). These terms reflect the microstructure typical of, but not exclusive to, these modern groups of birds. Thus, the microstructure in these eggs featuring straight, narrow (angusticaniculate) pores, a mammillary layer, prisms, and a second layer with at least some squamatic ultrastructure—and the potential of a third external layer—fall within the morphologic range of eggshells for extant avian taxa.

Given that none of the above microstructural features occur exclusively within the eggs of Aves (Figure 3), some eggs listed here (Table 2 and Appendix Table 3) that lack associated embryonic or adult avian remains potentially represent non-avian theropods. *Sankofa pyrenaica* lacks a well-developed squamatic ultrastructure, and López-Martínez and Vicens (2012) consider it phylogenetically ambiguous but near the non-avian-theropod–avian tran-

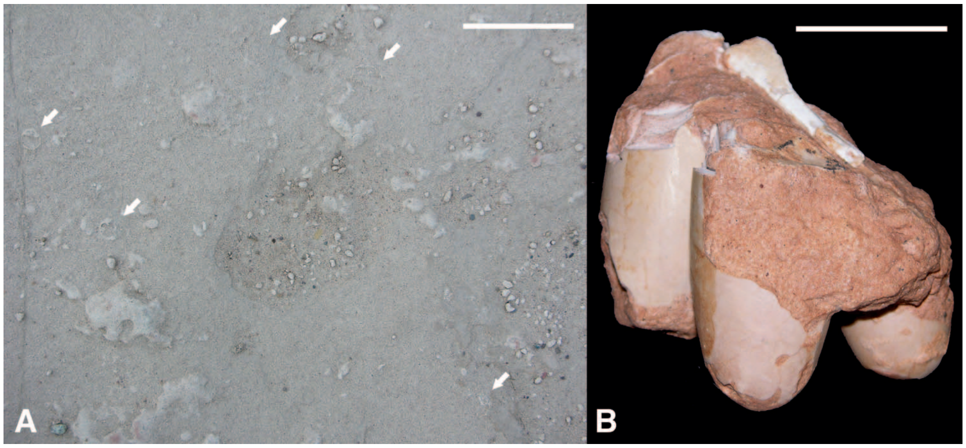

FIGURE 6. Nesting in enantiornithines. (**A**) Weathering surface near parallel to bedding at Neuquén, Argentina, in the Bajo de la Carpa Formation. Erosion has exposed portions of 5 dispersed eggs, marked by arrows. The near circular cross section reflects their largely upright posture in the sand. Scale bar = 10 cm. (**B**) Partial egg clutch for *Styloolithus sabathi*, ZPAL MgOv-II/7a, in oblique-lateral view, showing the steeply inclined orientation of the eggs and the partial avian limb bone lying atop the eggs. Scale bar = 3 cm.

sition. Likewise, the egg *T. stephensi* (Jackson and Varricchio 2010) and eggshell such as "theropod type 2" (Bonde et al. 2008), *Porituberoolithus warnerensis*, *Tristraguloolithus cracioides*, and *Dispersituberoolithus exilis* (Zelenitsky and Hills 1996) could potentially represent avians. All have thin eggshell from 0.27 to 0.53 mm and, with the exception of *P. warnerensis*, have a 3-layered microstructure, features common to some Mesozoic avian eggs. However, these eggs all display prominent ornamentation consisting of discrete and dispersed nodes. Such ornamentation characterizes the eggs of non-avian theropods like oviraptors, ootaxon Elongatoolithidae (Norell et al. 1994), and alvarezsaurids (Agnolin et al. 2012). Surface ornamentation in avian eggs appears to be limited to fine nodes as in *Subtiliolithus microtuberculatus* (Mikhailov 1991) or to variable projections of individual shell units as on the Eocene ootaxon *Metoolithus nebraskensis* (Jackson et al. 2013).

Where observed, pores in these eggs (Appendix Table 3) are described as angusticaniculate, with a simple, non-branching, and tubular form that maintains a relatively consistent diameter throughout its length (Mikhailov 1991, 1996a, 1996b, 1997, Vianey-Liaud and López-Martínez 1997, López-Martínez and Vicens 2012, Sellés 2012). Pores were not observed in samples of 2 unnamed Mongolian eggs, the Two Medicine egg and the Argentine Bajo de la Carpa egg (Hirsch and Quinn 1990, Grellet-Tinner and Norell 2002, Schweitzer et al. 2002, Grellet-Tinner et al. 2006) and are relatively rare in *Sankofa* (López-Martínez and Vicens 2012). Sabath (1991) and Deeming (2006) provide the only estimates of gas conductance based on observed porosity: *Gobioolithus minor* has a conductance value up to 25 times greater than predicted for a modern avian egg of equivalent mass. By contrast, *Styloolithus sabathi* has a value lower than the expected avian value (Sabath 1991). There is some ambiguity in the *S. sabathi* values. First, not all the data for these eggs are presented (Sabath 1991: table 1). Additionally, original conductance values for *G. minor* were only 35% of those determined by Deeming (2006), in part because of miscalculations by Sabath (Deeming 2006). Nevertheless, even if these same discrepancies existed in the *S. sabathi* calculations of Sabath (1991), conductance values would still be much lower than those of *G. minor* and on par with those of modern birds. Nevertheless, these values remain somewhat suspect (Deeming 2015). Fernández et al. (2013) and Salvador and Fiorelli (2011) give conductance values for Bajo de la Carpa eggs based on egg mass and a regression equation for modern birds. Several researchers (Sabath 1991, Deeming 2006, 2015, Jackson et al. 2008, Varricchio et al. 2013), however, would consider this method simply a means of providing an expected modern value to which a porosity-based value could be compared, and not a true measure of porosity in these Cretaceous eggs.

Egg arrangements. Six egg varieties provide information on egg orientation, clutch form, and possible nesting grounds. These group into 3 preservation categories.

(1) Large numbers of *G. minor* and Bajo de la Carpa eggs occur within sandstone horizons, with the subvertical to vertical eggs scattered rather than in discrete clutches (Figure 6A; Mikhailov et al. 1994, Fernández et al. 2013). Both egg varieties occur in formations (Bayun Goyot and Bajo de la Carpa) that preserve a mix of aeolian, fluvial, and lacustrine deposits, representing aeolian dunes crisscrossed by ephemeral streams and water bodies (Fernández et al. 2013, Kurochkin et al. 2013). Bird's Hill at Khermeen-Tsav, Mongolia, has produced hundreds of *G. minor* eggs on multiple horizons, suggesting repeated nesting events (Mikhailov et al. 1994, Kurochkin et al. 2013). On these horizons, "separate eggs always exhibit subvertical position and evenly distributed within a layer of sandy matrix, close to each other: yet these arrangements of eggs are random without any hint of forming a clutch" (Kurochkin et al. 2013:1265).

At the Neuquén locality, Fernández et al. (2013) mapped 65 eggs in place. A majority of these eggs stood vertically oriented, with their narrow pole pointed down. Only a few eggs occurred in a near horizontal orientation. Many eggs lacked their upper blunt pole, perhaps representing hatched eggs (Grellet-Tinner et al. 2006, Fernández et al. 2013). As at Bird's Hill, most eggs (60 of 65) occurred singly (Fernández et al. 2013). Spacing between eggs and their nearest neighbors typically exceeds 22 cm (D. J. Varricchio and F. D. Jackson personal observation; Figure 6A). Given the absence of any discrete bedding planes, it remains unclear how long this surface persisted; nesting events could span multiple years.

Mikhailov et al. (1994) proposed that flooding events accounted for the unusual orientation and dispersion of eggs at Bird's Hill. Flooding of the nesting locality would have floated unhatched eggs in a vertical orientation. As the water level dropped, the sinking eggs slowly became embedded in the soft substrate. Kurochkin et al. (2013) suggested, in addition to this hypothesis, that *Gobipipus* may have incubated eggs separately underground in a manner similar to that of some modern megapode birds (e.g., *Eulipoa wallacei*, the Moluccan Megapode; Jones et al. 1995). The flooding scenario is unlikely to account for the egg arrangements at Khermeen-Tsav or Neuquén. Eggs capable of floating have a density <1 and are unlikely to penetrate the underlying substrate, especially one composed of sand. Experimental efforts to duplicate this hypothesized process at Montana State University failed universally—the eggs always came to rest near horizontally on the underlying substrate (J. Drost personal communication). Sabath (1991) suggested that the well-preserved, three-dimensional form of many of the *G. minor* eggs indicated underground incubation. The high porosity of these eggs (Sabath 1991, Deeming 2006) and the orientation of other enantiornithine eggs further support a burial hypothesis.

(2) Eggs of 2 ootaxa, *Sankofa pyrenaica* and *Styloolithus sabathi*, occur in subvertical to vertical orientations arranged in clutches. No well-preserved clutches exist for *Sankofa*. But available specimens suggest that the eggs stood subvertically, blunt pole up, arranged in clusters of ≤ 5 eggs in ≥ 2 layers (López-Martínez and Vicens 2012).

Two partial clutches for *S. sabathi* from the Cretaceous of Mongolia consist of steeply inclined (45–70°) and closely placed elongate eggs embedded within a fine-grained sandstone (Sabath 1991, Varricchio and Barta 2015; Figure 6B). One specimen retains 4 eggs as a block, their long axes trending in parallel. This asymmetric arrangement (i.e. the eggs are neither vertical nor angle about a central point) suggests that a portion of the clutch is missing (Varricchio and Barta 2015), and 4 additional eggs were collected as part of this clutch as well (Sabath 1991). Articulated avian hindlimbs lie horizontally atop both specimens (Figure 6B). Dimensions of these limbs suggest an animal >1 kg (Appendix Table 4), providing a ratio of egg mass to adult body mass similar to that in other enantiornithines. The very low porosity of these eggs (Sabath 1991), together with their highly angled orientation, suggests that part of the upper portion of the eggs was likely exposed and incubated in a manner similar to that proposed for *Troodon* (Varricchio et al. 2013). Assuming a clutch of 8 eggs gives a clutch mass 1.04 times larger than expected for a bird of similar adult size (Appendix Table 4).

(3) Assemblages of enantiornithine eggshells for an unnamed ootaxon from Romania suggest colonial nesting. An $80 \times 50 \times 20$ cm lens of calcareous mudstone from the Sebeş Formation of Romania contains thousands of eggshell pieces, 7 nearly intact eggs, and 12 complete and 50 fragmentary adult and neonatal bones (Dyke et al. 2012). Dyke et al. (2012) interpret this dense assemblage as the product of a flooding event sweeping through a nesting colony and depositing the remains in a nearby water body. Given the strong flow required to move eggshell fluvially (Imai et al. 2015) and the jumble of whole and broken eggs and bones, the assemblage may represent deposition by a debris flow (Scherzer and Varricchio 2010). This assemblage provides evidence both for waterside colonial nesting and, given the presence of adult bones, some form of parental care (Dyke et al. 2012).

No whole eggs are known for *Subtiliolithus*, but the productive Khaichin-Ula I locality in the Nemegt Formation preserves 30 cm diameter clusters of eggshells, likely representing eggs of a clutch. Mikhailov et al. (1994:107) further state that "the distribution of the eggshell clutches indicates colonial nesting," but no further information is provided. Mikhailov (personal communication) considers the quoted statement a translation error that should be disregarded.

In summary, these 3 modes suggest that enantiornithine eggs primarily exhibit a subvertical to vertical posture within substrates, occur either as single eggs spaced in concentrated horizons or within tightly arranged clutches, and occur in densities suggesting breeding colonies (e.g., Bird's Hill, Mongolia; Neuquén, Argentina; Od assemblage, Romania). Adult–egg associations occur in *Styloolithus sabathi*, *Subtiliolithus*, and with the Romanian enantiornithine. These sites and specimens may indicate 2 different incubation strategies. The first, represented by *G. minor* and the Bajo de la Carpa eggs, would involve buried, scattered eggs in aeolian or waterside sand. The second, represented by *S. sabathi*, and possibly *Subtiliolithus* and the Romanian enantiornithine, would involve clutches partially buried and incubated by an attendant adult. The conductance values of *G. minor* and *S. sabathi* are consistent, respectively, with these 2 strategies (Sabath 1991, Deeming 2006). However, greater confidence could be placed in these interpretations by measuring or remeasuring the conductance values for all the involved ootaxa. On the basis of egg mass and the allometric equation of Deeming et al. (2006) for extant birds, incubation of these enantiornithine eggs would require between 20 (*G. minor*) and 27 days (*S. sabathi*). However, phylogenetic factors play an important role in determining incubation times in modern vertebrates (Deeming et al. 2006), and the differing incubation modes apparent in these fossil taxa would likely also affect the incubation time.

Embryos. Several well-preserved, embryonic avian skeletons have been described from the Cretaceous: a neatly curled skeleton without eggshell from Liaoning (Zhou and Zhang 2004); multiple embryos from Khermeen-Tsav, including the Elżanowski (1981) embryos as well as the type and referred specimens of *Gobipipus reshetovi* (Kurochkin et al. 2013); an *in ovo* embryo, from the Javkhlant Formation of the eastern Gobi, Mongolia (Balanoff et al. 2008, Varricchio et al. 2015); and more fragmentary *in ovo* remains from a Bajo de la Carpa egg (Schweitzer et al. 2002). The Od assemblage from Romania largely contains only scattered and fragmentary neonatal remains but includes one neonatal scapula diagnosable to enantiornithines (Dyke et al. 2012). All the articulated specimens exhibit a consistent posture with the head and neck curled ventrally beneath the body, the head upside down between the limbs, the limbs folded with the humerus lying parallel and adjacent to the vertebral column, the elbow projecting caudally, and the femur angling ventroanteriorly with the knee beneath the forelimb.

Several lines of evidence suggest that the Khermeen-Tsav embryos represent a growth series of a single taxon:

(1) The material is all derived from the same locality associated with a single ootaxon, *Gobioolithus minor* (Sabath 1991, Mikhailov 1997). (2) The specimens show a linear increase in size of >40% but maintain a constant ulna:humerus ratio (Appendix Table 5). (3) The increase in size occurs in association with more complete ossification of the skeleton. For example, the scapular blade, coracoid, and humerus deltopectoral crest become increasingly better defined in progressing through these 3 specimens. Additionally, the largest specimen exhibits fusion of dorsal neural spines, possibly the beginnings of a notarium (Elżanowski 1981). Kurochkin et al.'s (2013) interpretation that the Khermeen-Tsav embryos represent distinct taxa is inherently tenuous, in that it requires one to defend the taxonomic uniqueness of smaller individuals known to represent younger embryonic growth stages. Our argument presented here follows Elżanowski (1981), who attributed the variation among his own samples to differing embryonic age. As a growth series, the largest specimen would represent a late-stage *Gobipipus reshetovi* embryo, which has important implications for the condition of hatchlings.

Enantiornithines clearly hatched at a precocial to superprecocial state, as evidenced by the number of ossified skeletal elements, the definition of the articular ends, and the overall size of the forelimbs. In the Liaoning embryo and the largest "Elżanowski embryo" from Khermeen-Tsav, nearly all elements are present, including those that typically ossify late (Stark 1989), such as vertebrae, rostral bones of the skull, and (in the Liaoning embryo) the furcula. As Elżanowski (1981) noted, the Khermeen-Tsav embryos are remarkable for the well-developed condition of their articular ends of shoulder and forelimb elements. Movies of the three-dimensional renderings of Balanoff et al. (2008) provide excellent views of the articular end of the Javkhlant Formation embryo, particularly the coracoid, distal humerus, and proximal and distal femur (Varricchio et al. 2015). Its limb lengths in relation to its egg size indicate that this embryo was still a long way from hatching, making the definition of these limb articulations more notable. Even the limb bones of precocial young of modern birds lack well-formed articular ends (Stark 1989). Further, in modern birds, forelimb development typically lags in size behind that of the hindlimb (Stark 1989). However, embryos like the Javkhlant Formation specimen and the larger Khermeen-Tsav specimens have relatively massive forelimb elements prior to hatching (Appendix Table 5; Elżanowski 1981: fig. 2). Finally, the Liaoning embryo provides further evidence for precocial young in its preservation of well-developed feather sheets and a large brain case (Zhou and Zhang 2004).

Elżanowski (1981) argues that the degree of ossification in the shoulder and forelimb was well beyond what would be expected in embryos of modern birds. Consequently, he interpreted the Khermeen-Tsav embryos as superprecocial and flight-capable on hatching. Kurochkin et al. (2013) compared the *Gobipipus* type specimen to precocial modern birds and concluded that it was both flight- and run-capable on hatching. Again, this condition is remarkable considering that the individual they examined likely represents a growth stage well before hatching. Elżanowski (1985) argues that superprecociality in these birds would be associated with paternal or male-only care. This hatchling maturity may further support a megapode-like incubation strategy with eggs buried within sediment for sites like Bird's Hill (Kurochkin et al. 2013) and Neuquén. Histologic examination of the Baja de la Carpa embryo (Schweitzer et al. 2002) is consistent with precocial development of enantiornithine embryos. Nevertheless, a close inspection of the histology of the articular ends in embryonic limb elements for enantiornithines has yet to be done.

Discussion

Within Mesozoic birds, *Confuciusornis* provides some evidence for dimorphism either by size or, less likely (Peters and Peters 2009), long rectrices. The tenuous presence of medullary bone (Chinsamy et al. 2013) may indicate that the larger sex was female. In contrast to non-avian theropods, Mesozoic birds appear to have possessed only a single ovary and oviduct. Evidence for this includes the purported concentrations of ovarian follicles in Liaoning avian specimens (Zhou and Zhang 2004) and the absence of egg pairing within clutches and on nesting horizons (Fernández et al. 2013, Kurochkin et al. 2013).

Enantiornithine eggs are intermediate in both relative size and shape between those of non-avian maniraptorans and neornithines, being smaller and more elongate than the latter (Figure 4). Eggshell microstructure resembles that of both more derived maniraptorans and neornithines, and sometimes includes an external layer (Figure 3). The porosity and conductance of these eggs remain largely unexplored, but conductance of *Gobioolithus minor* and *Styloolithus sabathi* are, respectively, much higher than and on par with the predicted value based on modern avian eggs. Several researchers did not observe pores in describing their specimens, which suggests that pores in other ootaxa may be relatively rare.

Egg arrangements include 2 general patterns, both involving near vertical, blunt end-up egg orientations (Figure 6). The first, exemplified by Bird's Hill and the Neuquén localities, consists of a single sandstone bed with many separate and dispersed eggs. Hatchlings were likely superprecocial. In the second pattern, exemplified by *S. sabathi*, eggs occur in a tight clutch associated with an overlying adult, an arrangement similar to those in troodontids. Given the extremely high porosity of *G.*

minor (Deeming 2006), incubation in the first pattern likely involved full burial, whereas the second likely required only partial burial with an attending adult in a *Troodon*-like manner. These planted egg arrangements indicate that, like the eggs of turtles and crocodylians (Deeming 1991), enantiornithine eggs could not be moved during development without significant risk to the embryo (Zelenitsky 2006). In both patterns, hatching would have occurred through the upper blunt pole. Several localities suggest colonial nesting. Enantiornithine embryos appear to be remarkably well ossified, with limb and girdle elements exhibiting well-defined articular surfaces, although this awaits verification through histologic study.

A few features distinguish enantiornithine reproduction from that of troodontids: loss of function in one ovary and oviduct; an increase in relative egg size; and, in some forms, an incubation mode involving single, dispersed, and buried eggs. Egg size increases from approximately 45–50% to an average of 68% the size expected for comparably sized modern birds. This represents a relative size increase of 40–50% from non-avian maniraptorans to enantiornithines and may reflect the shift from monoautochronic ovulation of a pair of smaller eggs to the production of a single larger egg at a time.

Similarly, only a few changes mark the enantiornithine–neornithine transition, but these are likely important. Again, relative egg size increases from Enantiornithes to Neornithes by nearly 50%. This continues a trend that began with the large eggs of non-avian maniraptorans in comparison to those of other non-avian theropods. Major changes occur in the mode of incubation, likely improving the efficiency of heat transfer. Eggs partially to fully buried within sediments during incubation would likely lose significant amounts of heat to the surrounding sediments. Additionally, incubating eggs free of sediment would allow an adult greater and more intimate contact with the eggs while permitting egg turning. The latter would likely necessitate the evolution of chalazae. These chords of albumin stabilize the position of the yolk within the albumen during egg turning and allow the embryo to maintain proper orientation during egg formation and development after laying (Romanoff and Romanoff 1949). Egg turning may allow for a more even distribution of heat, but, importantly, it improves embryonic development by facilitating embryonic use of albumen proteins (Deeming 1991, Turner 1991). In modern birds, egg turning maximizes the efficiency of protein utilization from the albumen and maintains proper embryonic position for the transfer of albumen via the seroamniotic connection (Deeming 1991). Failure to turn eggs drastically reduces the amount of amniotic fluid and retards embryonic growth (Deeming 1991).

The changes in egg shape from the more consistently elongate form of enantiornithines to the more variable form of neornithines may reflect both the egg size increases and the new incubation configuration. Dyke and Kaiser (2010) propose that pubic fusion, present in Early Cretaceous birds such as *Confuciusornis* and Enantiornithes, would have constrained egg size. Elongation of the egg would be a mechanism of increasing overall egg size despite a restricted pelvic diameter. This constraint may explain the changes in eggs from non-maniraptorans to maniraptorans even better, because this is where the major shape change to an elongate egg occurred. Neornithes, with an unfused and open pelvis, would be free to increase relative egg size without adhering to any particular shape. Egg shape appears to be limited from derived non-avian maniraptorans through enantiornithines but then diversifies in Neornithes, moving away from the elongate forms of those earlier groups (Deeming and Ruta 2014). Barta and Székely (1997) modeled egg shape as a product of incubation efficiency and clutch size. They found regular shape changes as the number of eggs in the clutch increased. Consequently, once incubation free of sediments evolved, selection for increased efficiency of heat transfer and within-egg protein use could have acted to alter egg shape.

The fossil evidence from Mesozoic birds and non-avian theropods largely confirms the plesiomorphic nature of a number of the features associated with modern birds: possibly one functional ovary and oviduct; sequential ovulation; hard, calcitic, and multilayered eggshell; precocial, self-feeding young; at least the potential for incubation through adult–egg contact; and likely some form of parental care. We propose that the evolution of the modern avian reproductive mode can be described as passing through 5 stages from basal theropods to neornithines (Figure 7), as follows.

Stage 1: Pre-maniraptoran theropods. Several aspects of avian eggshell microstructure, including a bilaminar structure with a mammillary and a second layer composed of narrow shell units with irregularly distributed squamatic structure, characterize this stage. In several other aspects, reproduction retained a primitive style with relatively small eggs, likely oviposited en masse and randomly distributed within clutches, and incubation of fully buried clutches that likely did not require an attending adult.

Stage 2: Oviraptor-grade maniraptorans. Numerous changes occur here as eggs increase in relative size and become more elongate with slight asymmetry. Egg production was through monoautochronic ovulation; both ovaries and oviducts would produce a single egg simultaneously to be laid at daily or greater intervals. Eggshell microstructure now included a more pronounced continuous layer in which prisms were mostly obscured by well-developed squamatic ultrastructure. Surface ornamentation becomes prominent. Incubation of the unusually large and now highly organized clutches occurred through near,

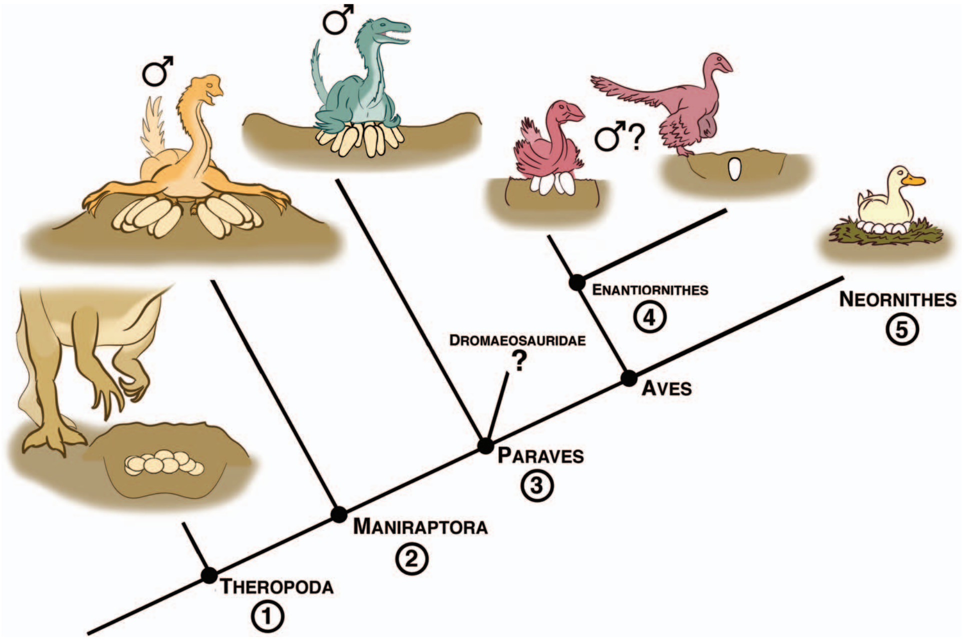

FIGURE 7. Simplified phylogeny showing hypothesized stages in the evolution of reproductive traits toward modern birds. Exact locations of stages 1 and 4 are unclear, given the complex distribution of traits in basal theropods and the lack of information for basal Aves and Ornithuromorpha. Synapomorphies: Stage 1, pre-maniraptoran theropods—bilaminar eggshell with a mammillary and second layer composed of narrow shell units, irregularly distributed squamatic. Stage 2, oviraptor-grade maniraptorans—increase in relative egg size, more elongate egg shape, slight asymmetry, monoautochronic ovulation, iterative laying, eggshell with more pronounced continuous layer and well-developed squamatic ultrastructure, prominent surface ornamentation, large and highly organized clutches, incubation involving nearly full burial with attendant adult, possibly paternal care. Stage 3, troodontid-grade paravians—loss of surface ornamentation, increasing asymmetry, low porosity, potential for third (external) layer in eggshell, clutches of "planted" and near vertical eggs, improved contact incubation with tighter clutch configuration, and exposed upper portions of eggs. Stage 4, Enantiornithes—loss of function in right ovary and oviduct, increasing relative egg size, reduction in egg elongation, incubation as in troodontids or as singleton eggs fully buried in sandstone. Stage 5, basal Neornithes—eggs show further increase in relative size, more variable and less elongate egg shape, clutch free of sediment cover, egg rotation, chalazae with potentially greater incubation efficiency.

but not complete, burial, but with an attendant adult. Large clutch size in relation to adult mass favors paternal care. Delayed incubation likely resulted in synchronous hatching of the eggs.

Stage 3: Troodontid-grade paravians. Eggs now lack surface ornamentation, show increasing asymmetry and low, avian-levels of porosity, and may possess a third (external) layer in their shells. Clutches now consist of "planted" eggs with their long axis nearly vertical and arranged in a more compact configuration. Egg arrangements within these clutches would have permitted greater adult–egg contact for improved heat transfer and insulation. Overall, the reproductive evidence from Mesozoic taxa would favor those phylogenies that place troodontids as the sister taxon to Aves.

Stage 4: Enantiornithes. This stage is marked by a loss of function in the right ovary and oviduct, increasing relative egg size with a reduction in elongation index. Incubation occurred either as in troodontids or as singleton eggs fully buried in sand. Precocial young likely required no or minimal posthatching parental care.

Stage 5: Basal Neornithes. In the final stage, eggs increase to a relative size comparable to modern birds and may adopt a less elongate and more varied shape in the absence of a fused pelvic constraint. Incubation takes place free of sediment and includes chalazae and egg rotation, potentially reflecting greater efficiency. These stages highlight the incremental acquisition of the modern avian reproductive mode, a pattern consistent with current understanding of morphologic evolution across the non-avian to avian theropod transition (Brusatte et al. 2014, 2015).

Issues with the above 5-stage hypothesis include problems of both sampling and interpretation. For example, the fossil record to date provides only a single *Troodon* nesting trace and only poorly preserved enantiornithine clutches and adult–clutch associations in both troodontids and enantiornithines. Lacking a demonstrable preservation mechanism, the proposed ovarian follicles in the Liaoning birds remain questionable. Only limited data are available on porosity for both troodontid and enantiornithine eggs. Interpretational issues include how to interpret clutch-associated adults, whether brooding can occur with only partially exposed eggs, the behavioral significance of the *Gobioolithus* and Neuquén egg localities, and the type of parental care in enantiornithine birds. Finally, our understanding of reproduction in Mesozoic forms may be biased by the favorable preservation of buried eggs as opposed to those incubated in open nests (Deeming 2015). Recognition of the latter will require porosity studies of displaced fragmentary eggshell.

Nevertheless, the record of enantiornithine reproduction would seem to clarify the phylogenetic origin of many aspects of the modern avian reproductive mode. Three trends characterize the changes through the above stages: increasing egg size, modifications to egg shape, and incubation involving greater adult–egg contact. By contrast, function within a single ovary and oviduct remained unchanged from non-avian maniraptorans through Neornithines, as evidenced by the sequential ovulation, consistent microstructure, and potential for asymmetric shape found throughout these groups. It remains unclear whether the 2 enantiornithine incubation strategies favor paternal care through the pre-neornithine stages. Incubation, as in *S. sabathi*, involves slightly larger-than-average clutches with an attending adult in a *Troodon*-like manner (Vehrencamp 2000, Varricchio et al. 2008), but these specimens suffer from poor preservation. The second strategy, involving scattered and sand-buried eggs with superprecocial young, suggests incubation by solar heat, a pattern found in burrow-nesting megapodes (e.g., Maleo, Polynesian Scrubfowl, and Moluccan Megapode) that provide no parental care for the eggs (Elliott 1994, Jones et al. 1995). These megapodes represent the derived condition within the clade, having evolved from species with primitively male-only to male-dominated care of nesting mounds (Jones et al. 1995). Alternatively, a no-care strategy, if potentially represented by *G. minor* and the Bajo de la Carpa taxa and if more widespread taxonomically, would argue for the lack of homology between care in derived non-avian maniraptorans, enantiornithines, and basal neornithines, and would imply a novel origin of both parental care and egg incubation by adults in Neornithes. This would seem a less parsimonious interpretation of the fossil record and would sharply contrast with both the early origin of many reproductive attributes and the trends observed in others across these groups. Neornithes appear to be set off reproductively from earlier avians principally in improved efficiency in adult–egg contact incubation stemming from the removal of eggs from sediment, modifications of egg shape, egg rotation, and the evolution of chalazae.

Recent paleontologic discoveries demonstrate that some non-avian maniraptoran theropods shared a similar respiratory system, brain, feathered integument, and even small body size with Neornithes (Larsson et al. 2000, O'Connor and Claessens 2005, Prum 2005, Turner et al. 2007) and that Mesozoic birds are largely indistinguishable from their closest relatives in morphospace (Brusatte et al. 2014). Enantiornithes were by far the most abundant and diverse group of avians in the Cretaceous, filling a wide array of feeding and flight niches (Chiappe and Walker 2002). Given the slight functional distinction between these groups and Neornithes, it is difficult to envision a Cretaceous–Paleogene (K–Pg) extinction scenario that would selectively affect these groups. Deeming (2002) suggested that "the evolution of true contact incubation" may have been the key adaptation permitting neornithines to survive the end-Cretaceous extinction. Possession of chalazae may have played an important role in distinguishing neornithines from enantiornithines and other Mesozoic birds. This structure would potentially afford Neornithes 3 advantages. First, they could take advantage of a variety of sediment-free nesting environment such as in trees, on rock ledges, or in caves or cavities. Second, Neornithes would be able to adjust their eggs during incubation. For example, gulls during the Mt. St. Helens eruption salvaged their eggs by digging them out from the rain of volcanic ash (Hayward et al. 1982, 1989). Consequently, Enantiornithes of the Cretaceous, compared to Neornithes, would have been restricted to nesting in environments with appropriate sediments and would have had a reduced capability to respond to environmental disturbances once incubation began. Finally, the greater adult–egg contact afforded by brooding eggs free of sediment would have improved incubation efficiency, temperature (Deeming 2015), and embryonic growth. Of all Mesozoic Dinosauria, only the Neornithes, the sole surviving K–Pg clade, apparently possessed chalazae and nested completely free of sediment.

Conclusions

Our current understanding of reproduction in Mesozoic birds is largely limited to the Enantiornithes. Enantiornithine reproduction included sequential ovulation and egg formation from a single ovary and oviduct, eggs planted upright within sediments, incubation of eggs within clutches by a combination of sediment and attendant adult or eggs spread across a horizon, fully buried with superprecocial young. Both incubation strategies required eggs to be deposited within sediments. This reproductive style differed from that of derived maniraptorans in relatively larger, less elongate eggs, and the loss of function in one ovary and oviduct. The 2 incubation modes exhibited by derived maniraptorans and enantiornithines may have favored the presence of paternal care.

The most significant changes between enantiornithines and neornithines are an additional increase in relative egg size and incubation of eggs free of sediment. The latter entailed greater adult–egg contact, potentially improved egg shape, egg rotation, and chalazae. Without this last feature, more basal groups would be forced to plant their eggs within sediment. Neornithes are the only Mesozoic clade of Dinosauria to nest completely free of sediment; this and the associated improvements in incubation efficiency may have played a crucial role in their survival of the K–Pg mass extinction event.

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APPENDIX

Associated adult skeletons or *in ovo* embryonic remains permit the assignment of 6 egg morphs from the Late Cretaceous of Argentina, Romania, and Mongolia to enantiornithine birds (Table 2, Appendix Table 3, and Figure 4). Three eggs belonging to the ootaxa *Subtiliolithus microtuberculatus*, *Gobioolithus minor*, and *Styloolithus sabathi* (Figure 4A, 4B, 4C) from Mongolia have had a far more complicated history than the other eggs, because of conflicting taxonomic and ootaxonomic assignment. *Subtiliolithus microtuberculatus* represents perhaps the most tenuous of these adult–egg associations, being based on some eggshells found adjacent and in situ to the type specimen of the enantiornithine bird *Nanantius valifanovi*, now *Gobipteryx minuta* (Chiappe et al. 2001). An additional 30 eggshell pieces were recovered with weathered-out bones of the bird in a small volume of screened matrix (Kurochkin 1996).

On the basis of a tentative identification of embryos by Elżanowski (1981), past workers informally applied the fossil bird *Gobipteryx minuta* to the *Gobioolithus minor* and *G. major* eggs (Table 1; Mikhailov 1991, 1996a, Sabath 1991). However, Chiappe et al. (2001) synonymized *Nanantius valifanovi* with the adult specimen described previously as *Gobipteryx minuta*. This taxonomic change now links the latter taxon with the oospecies *Subtiliolithus microtuberculatus*. Recently, Kurochkin et al. (2013) named a new enantiornithine, *Gobipipus reshetovi*, based on embryonic remains associated with *Gobioolithus minor* eggs, leaving the embryos of Elżanowski (1981) somewhat problematic in that they are derived from the same locality, Khermeen-Tsav, and oospecies (Sabath 1991, Mikhailov 1991, 1996a). Kurochkin et al. (2013) argue that they represent a distinct taxon and refer them to *Gobipteryx minuta* without the *Nanantius* synonymization. For clarity, we use *G. minuta* sensu Chiappe et al. (2001) and refer to the 2 sets of embryonic material from Khermeen-Tsav as *Gobipipus reshetovi* and "Elżanowski embryos." Likely these 2 sets of embryos, both associated with *Gobioolithus minor* eggs, simply represent growth series of a single taxon (see below). Finally, we follow Varricchio and Barta (2015) in treating the "larger avian eggs" of Sabath (1991) as distinct from *Gobioolithus major* as created by Mikhailov (1996a). In contrast to *G. major*, *Styloolithus sabathi* specimens are clearly associated with skeletal remains, namely adult enantiornithines (Varricchio and Barta 2015; Figure 4A, 4B, 4C).

APPENDIX TABLE 3. Mesozoic avian egg attributes: egg dimensions, microstructure, ornamentation, orientation, skeletal associations, and taxonomic identification for the Mesozoic egg varieties assigned to birds. Specimen numbers correspond to Table 2. All dimensions are in millimeters. Abbreviations: L = egg length, D = egg diameter, CL = continuous layer, ML = mammillary layer, Enant. = Enantiornithes.

Specimen number	Ootaxon (or locality)	L	D	L:D	Asymmetry	Shell thickness	Layers	Squamatic texture	CL:ML	Surface ornamentation	Egg orientation	Associated bones	Taxon
4	*Plagioolithus fukuiensis*	–	–	–	–	0.44	3	Present	1:1	Smooth	–	–	–
5	*Pachycorioolithus jinyunensis*	50	32	1.6	?	0.17	3	Present	1:1	Smooth	–	–	–
6	*Oblongoolithus*	–	<40	–	–	0.3–0.7	2	Present	1:1	Smooth	–	–	–
7	*Laevisoolithus*	71	34	2.1	–	0.7	2	Present	4:3	Smooth	–	–	–
8	*Subtiliolithus*	–	–	–	–	0.3–0.4	2	Present	2:5	Smooth or microtubercles	–	Adult	Enant.
9	*Styloolithus sabathi*	70	32	2.2	Yes	<0.4	3	Present	~1:1	Smooth	Vertical	Adult	Avian Enant.
10	*Gobioolithus major*	53	30	1.8	Yes	0.2–0.4	2	Present	2:1	Smooth	–	–	–
11	*Gobioolithus minor*	43	22	2.0	Yes	0.1–0.2	2 or 3	Present	2:1	Smooth	Vertical	Embryo	Enant.
13	– (Mongolia)	45	26	1.7	No?	0.18	3	Present	4:3	Smooth	–	Embryo	Enant.
14	– (Mongolia)	26	16	1.6	No	0.17	3	Present	2:3	Smooth	–	–	–
15	*Sankofa pyrenaica*	70	40	1.8	Yes	0.27	2	Incipient	–	Smooth	Subvertical	–	–
16	*Ageroolithus fontillongensis*	–	–	–	–	0.25–0.36	2 (3?)	Present	2:1	Smooth	–	–	–
17	– (Romania)	40	25	1.6	Yes	0.22	2	–	1:1	Smooth	–	Embryo and adult	Enant.
18	– (Brazil	31.4	19.5	1.6	?	0.13	3	?	1:0.9	Smooth	–	–	–
19	– (Argentina)	44	28	1.6	Yes	0.26	3	Present	3:2 (or 2:3)	Smooth	Vertical	Embryo	Enant.
20	– (USA)	36	22	1.6	No	0.45	2	–	2:1	Smooth	–	–	–

APPENDIX TABLE 4. Relative egg and clutch sizes (linear dimensions in millimeters, mass in grams, and volume in cubic centimeters). Egg mass and clutch mass were calculated using equations in Field et al. (2013), Campbell and Marcus (1992), and Blueweiss et al. (1978).

Specimen	Measurement	Adult dimension	Adult mass	Egg volume	Egg mass	Predicted egg mass	Percent predicted egg mass	Clutch mass	Predicted clutch mass	Percent predicted clutch mass
Neuquenornis volans	Humerus length	64.3	344	–	–	–	–	–	–	–
	Humerus midshaft diameter	4.6	337	–	–	–	–	–	–	–
	Tibiotarsus length	87.7	528	–	–	–	–	–	–	–
	Tarsometatarsus length	46.8	305	–	–	–	–	–	–	–
	Average adult and egg mass	–	379	17.9	19.0	25.1	75%	–	–	–
Styloolithus sabathi	Least tibiotarsus circumference (ZPAL MgOv-II/7)	14.9	2,700	–	–	–	–	–	–	–
	Least tibiatarsus circumference (ZPAL MgOv-II/25)	12.4	1,700	–	–	79.9	49%	–	305	104%
	Egg and clutch mass	–	–	37.3	39.5	–	–	317	–	–
Romanian enantiornithine	Humerus length	59	293	–	–	–	–	–	–	–
	Egg mass	–	–	13.0	13.8	20.6	67%	–	–	–

APPENDIX TABLE 5. Element lengths in embryos (linear dimensions in millimeters). Most embryos are unidentified to a taxon. The ZPAL and *Gobiopipus* specimens represent the embryos from Kheermen-Tsav.

Element	IVPP V14238, Liaoning	*Gobiopipus reshetovi*, PIN 4492-3	*Gobiopipus reshetovi*, PIN 4492-4	ZPAL MgR-I/33, Mongolia	ZPAL MgR-I/34, Mongolia	IGM 100/2010, Mongolia	MUCPv-284, Bajo de la Carpa
Egg volume (cm^3)	–	10.8	10.8	–	–	15.8	17.9
Skull	21	16	–	–	–	–	–
Scapula	–	9	–	11	–	–	–
Coracoid	6	6	–	–	–	9.4	–
Humerus	12	13	–	14	18.7	∼16.5	–
Ulna	13	15	–	16.1	21.5	–	–
Radius	12	14	–	15.9	–	18.5	–
Ulna:humerus	1.1	1.15	–	1.15	1.15	1.12 [a]	–
Metacarpal II	–	7.2	–	–	11.1	–	–
Metacarpal III	–	–	–	7.5	11.8	–	–
Ilium	–	–	7	–	–	–	–
Pubis	–	–	6	–	–	–	–
Ischium	–	–	–	–	–	–	5
Femur	11	–	9	–	–	13.2	–
Tibiotarsus	13	–	13	–	–	15.6	–
Metatarsal III	9	–	–	–	–	8.8	–
Tibiotarsus:femur	1.18	–	1.44	–	–	1.18	–
MTIII:femur	0.82	–	–	–	–	0.67	–
Humerus:femur	1.09	–	–	–	–	1.25	–

[a] Actually radius:humerus, and likely a low estimate of ulna:humerus.