

Digital preparation of a probable neoceratopsian preserved within an egg, with comments on microstructural anatomy of ornithischian eggshells

Amy M. Balanoff · Mark A. Norell ·
Gerald Grellet-Tinner · Matthew R. Lewin

Received: 26 September 2007 / Revised: 17 December 2007 / Accepted: 12 January 2008 / Published online: 27 February 2008
© Springer-Verlag 2008

Abstract We describe the first known embryo of a neoceratopsian dinosaur, perhaps the most ubiquitous Laurasian group of Cretaceous dinosaurs, which is preserved completely enclosed within an egg. This specimen was collected from Late Cretaceous beds of southern Mongolia, which commonly preserve fossils of the neoceratopsian, *Yamaceratops dorn gobiensis*. The small egg was scanned using high-resolution X-ray computed tomography and digitally prepared from the matrix. The preserved and imaged elements support a diagnosis of the embryo to Neoceratopsia and allow preliminary observations of ontogenetic transformations within this group. The addition of an embryo also adds another important data point to the

already impressive postnatal ontogenetic series that are available for this clade.

Keywords Ornithischia · Computed tomography · Eggshell microstructure · Embryo

Introduction

Neoceratopsia is a diverse group of ornithischian dinosaurs that includes basal, relatively primitive forms like *Liaoceratops*, as well as the more familiar large, derived ceratopsids (e.g., *Triceratops*). Despite often being one of the most common elements of Laurasian Cretaceous dinosaur faunas (Dodson et al. 2004), Neoceratopsia completely lacks a record of indisputable embryos (i.e., found *in ovo*—contained within an egg). Previous neoceratopsian material was considered embryonic based on the size of the specimens, but identifications were made in the absence of associated eggshell (e.g., Bohlin 1953; Maryńska and Osmólska 1975; Dong and Currie 1993). Likewise, eggs have been classified as belonging to Ceratopsia on the basis of egg type without any accompanying skeletal material (see Carpenter and Alf 1994; Mikhailov et al. 1994). It should be noted that simple associations of bones and eggshell have been shown potentially to be misleading (Norell et al. 1995, Grellet-Tinner et al. 2006). If prenatal material for Ceratopsia were available, it would be the ideal lineage within which to better understand the evolution of development because comprehensive growth series already exist, and work continues on the postnatal ontogeny within this group (e.g., Brown and Schlaikjer 1940; Erickson and Tumanova 2000; Goodwin et al. 2006; Makovicky et al. 2006).

Although a long association exists between the fields of paleontology and developmental biology, the record of

Communicated by G. Mayr

Electronic supplementary material The online version of this article (doi:10.1007/s00114-008-0347-2) contains supplementary material, which is available to authorized users.

A. M. Balanoff (✉) · M. A. Norell
Division of Paleontology, American Museum of Natural History,
Central Park West at 79th Street,
New York, NY 10024, USA
e-mail: abalanoff@amnh.org

M. A. Norell
e-mail: norell@amnh.org

G. Grellet-Tinner
Department of Geology and Geological Engineering,
South Dakota School of Mines,
Rapid City, SD 57701, USA
e-mail: Gerald.grellet-tinner@sdsmt.edu

M. R. Lewin
Department of Emergency Medicine, University of California,
San Francisco School of Medicine,
San Francisco, CA 94143, USA
e-mail: aplysia99@yahoo.com

described embryonic non-avian dinosaurs remains sparse (e.g., Horner and Currie 1994; Norell et al. 2001; Varricchio et al. 2002; Reisz et al. 2005; Salgado et al. 2005). Moreover, the connection between these disciplines typically is restricted to observations of developmental patterns in living taxa used to explain patterns seen in the fossil record. Relatively few studies concentrate on understanding the patterns of developmental trajectories across clades. Nevertheless, the recent surge in the number of descriptive works on dinosaur embryos bodes well for our understanding of the evolution of development within this long and interesting lineage. An increased concentration in developmental morphology on the part of paleontologists, the discovery of new fossil embryos, as well as new technologies with which to visualize these unique specimens will aid in the continued endeavor to understand fossil dinosaur embryos.

In this study, we use high-resolution X-ray computed tomography (HRCT) to digitally prepare and subsequently describe a fossilized egg, which contains an embryonic skeleton (Fig. 1). This specimen represents the first indisputable embryonic specimen that can be diagnosed with any confidence to Neoceratopsia. Furthermore, an analysis of the microstructural anatomy of the eggshell was performed to associate this specimen with a specific eggshell type. This embryo *in ovo*, preserved within the egg, provides a new and important data point on the ontogenetic trajectory of Neoceratopsia with which we can begin to make observations of this lineage's growth and development that eventually could be used to shed light on the larger dinosaurian clade.

Materials and methods

IGM 100/2010 (Institute of Geology, Mongolia) was discovered as an isolated egg in the Khugenetslavkant locality (eastern Gobi Desert, Dornogobi Aimag, Mongolia) that is Late Cretaceous in age (Eberth et al., unpublished). The sediments of this locality consist largely of a coarse sandstone that is interpreted as being fluvial in nature (see Makovicky and Norell 2006). The fauna at this locality is dominated by the neoceratopsian, *Yamaceratops dornogobiensis*, and also includes remains of primitive ornithopods, troodontids, dromaeosaurids, and several kinds of mammals and lizards. The egg is small (total volume of $\sim 28.5 \text{ cm}^3$), symmetrical and elongate ($\sim 4.75 \text{ cm}$ greatest length, 2.23 cm greatest width; Fig. 1), and is essentially complete except for one broken pole. The break reveals the presence of fragile bones contained within a coarse sandstone matrix that fills the egg. Several other isolated eggs of identical morphology, but not known to contain embryos, also have been recovered from the locality.

The small size and fragility of the skeletal remains preclude physical preparation of IGM100/2010. Instead, the specimen was scanned using HRCT, and the embryonic skeleton was digitally removed from the matrix (Fig. 2). Digital preparation revealed a large number of bones recognizable in the HRCT slices by their hollow nature that could not otherwise be observed.

The entire egg was HRCT-scanned along its long axis at The University of Texas at Austin. The scan resulted in a total of 1,296 sequential images. Scanning parameters include a slice thickness of 0.036 mm and interslice spacing

Fig. 1 **a** Photograph of IGM 100/2010; **b** three-dimensional digital rendering of IGM 100/2010 in same orientation presented in **a**, with eggshell and matrix rendered semi-transparent. Skeletal elements are opaque

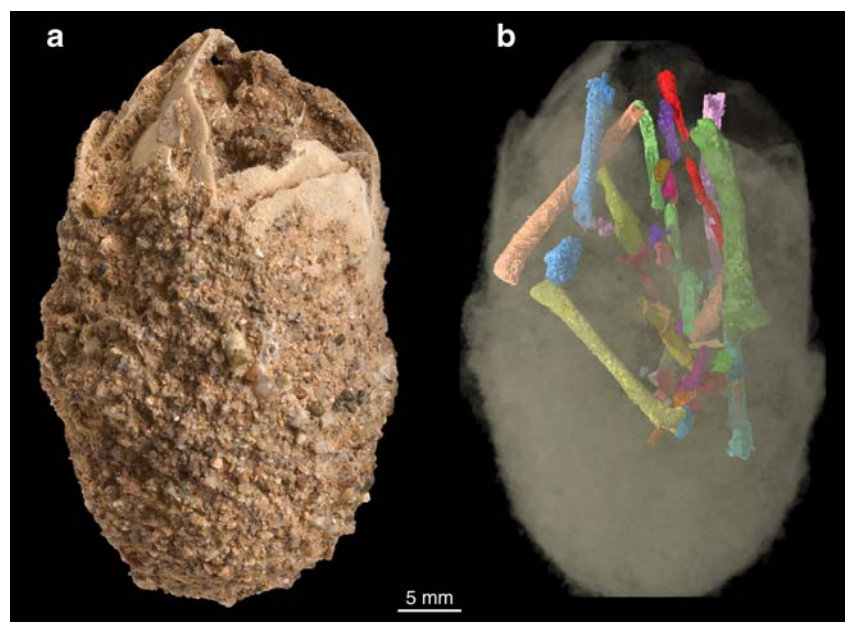
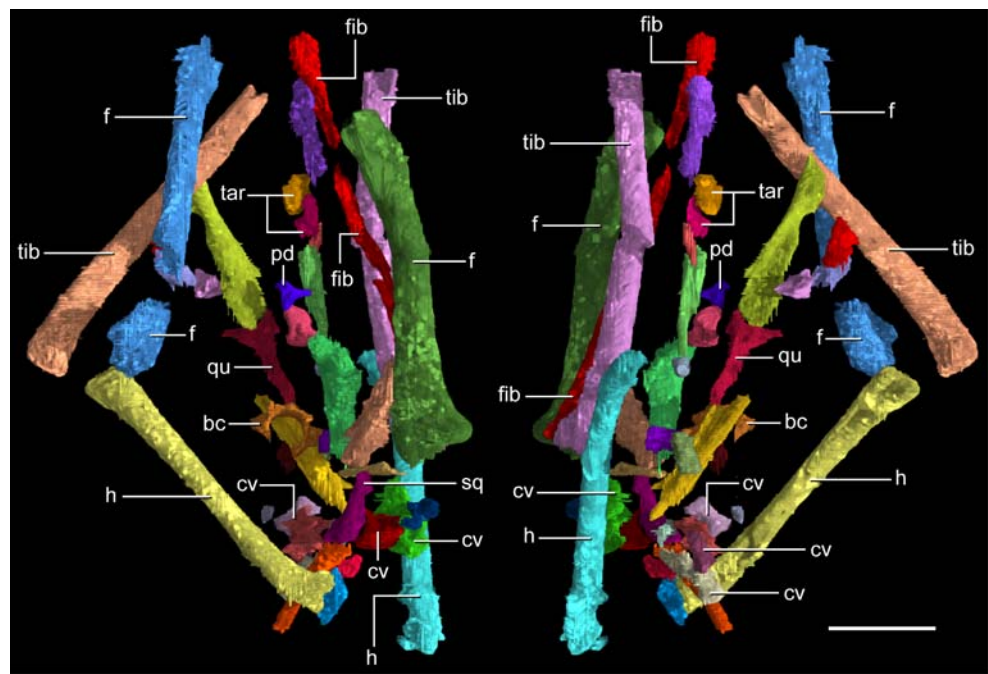


Fig. 2 Two views of the three-dimensional digital rendering of skeletal elements of IGM 100/2010 with eggshell and matrix rendered transparent. *bc* braincase, *cv* cervical vertebra, *f* femur, *fib* fibula, *h* humerus, *pd* prementary, *qu* quadrate, *sq* squamosal, *tar* tarsals, *tib* tibia. Scale bar equals 5 mm



(i.e., z-spacing) of 0.036 mm. The field of reconstruction is 32 mm, and resultant image size is 1,024×1,024 pixels. These parameters yield an interpixel spacing (i.e., x-spacing and y-spacing) of 0.031 mm.

Image processing was done in the program VGStudio-Max© 1.2.1. The two-dimensional slice images were reduced from 1,024×1,024 pixels by one third to 768×768 pixels so that they could more easily be loaded and manipulated. Image processing of these data resulted in separate three-dimensional volume renderings of each isolated embryonic bone without any physical preparation of the egg (see Balanoff and Rowe 2007 for a more comprehensive description of the methods). All original data and image processing are available for viewing on the website *Digital Morphology* (http://www.DigiMorph.org/specimens/neoceratopsian_egg).

For the microstructural analysis of the egg, eggshell fragments were removed from the broken pole of IGM 100/2010. Two fragments were gently cleaned with air and then broken into two smaller fragments that were immediately gold-coated to preserve their integrity, avoid contamination before examination, and facilitate scanning electron microscopy (SEM) observations. SEM examinations were performed at 12–15 KV on a Hitachi H-7000 FA transmission electron microscope and scanning transmission electron microscope.

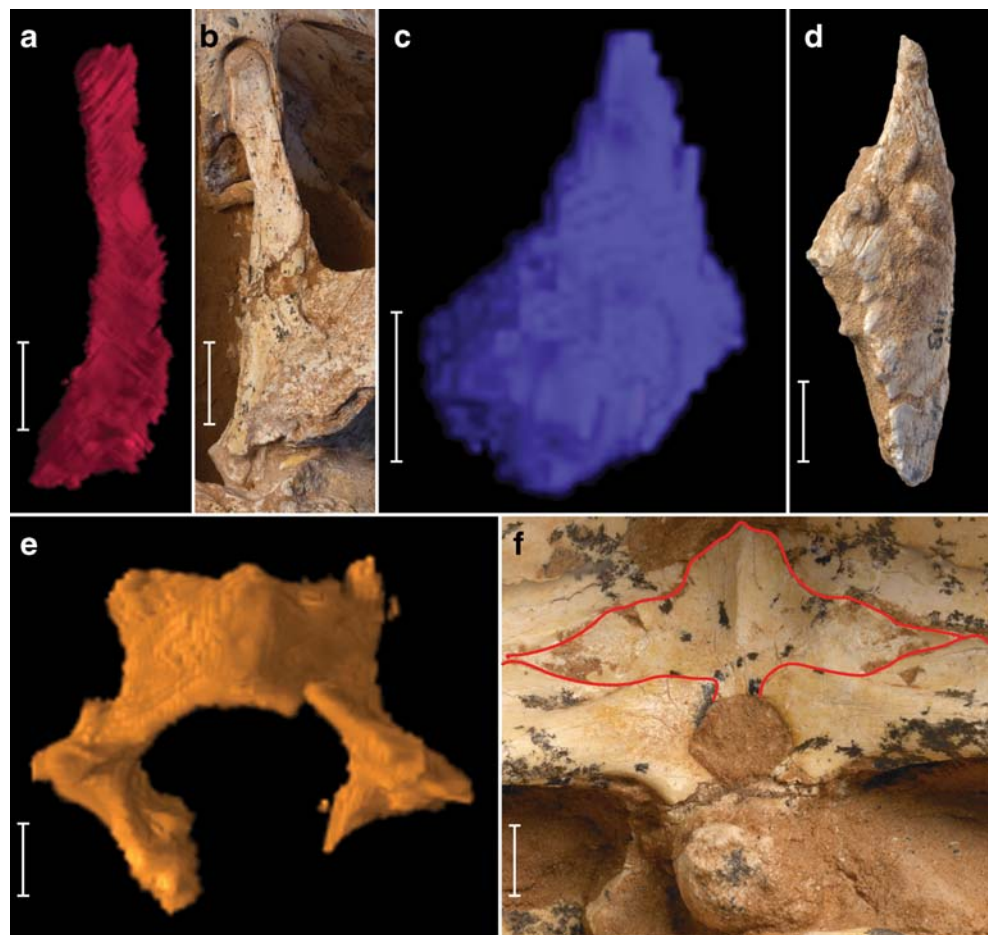
Results

Much of the embryonic skeleton is present, and approximately 40 elements were digitally prepared from all regions

of the skeleton including the skull, vertebral column, and fore- and hindlimbs (Fig. 2). Because of the extremely small size of the specimen (many bones being on the scale of 1 mm) and early stage of development, some of the elements are not recognizable. The majority of the skeleton has settled to one side of the egg yet remains semi-articulated, a taphonomic feature indicating that IGM 100/2010 was filled with sediment before extensive decomposition or resorption could occur (Dong and Currie 1993; Sato et al. 2005). Although many skeletal elements are in an advanced state of ossification, the relatively small size of the embryo compared to the egg volume suggests that hatching was not imminent (Ricklefs and Starck 1998; Starck and Ricklefs 1998); however, a more rigorous analysis of the ontogenetic maturity of this specimen is forthcoming. The hindlimbs are preserved in articulation (Electronic supplementary material; Fig. 2). Other regions of the skeleton, although not in articulation, are positioned roughly where they would be expected in life.

Cranial elements such as part of the braincase, quadrate, and prementary are easily discernable. Skeletal immaturity is particularly evident in the recovered braincase, which consists of the exoccipitals and supraoccipital. These elements are closely associated, but not yet fused (Fig. 3e and f), and have been identified as being a portion of the braincase based on their overall morphology, lack of a neural spine, and the extremely large opening (foramen magnum). Cervical vertebrae are also present in this specimen and have elongate neural spines and relatively smaller openings for the neural canal (Fig. 2). The general morphology of the braincase is similar to immature *Protoceratops andrewsi* in that the paroccipital processes

Fig. 3 **a** Digital rendering of lateral view of quadrate of IGM 100/2010. Scale bar equals 1 mm. **b** Photograph of lateral view of quadrate of adult *Protoceratops* (IGM 100/1246). Scale bar equals 3 cm. **c** Digital rendering of right lateral view of predentary of IGM 100/2010. Scale bar equals 500 μ m. **d** Photograph of right lateral view of predentary of adult *Protoceratops* (IGM 100/1113). Scale bar equals 1 cm. **e** Digital rendering of posterior view of braincase of IGM 100/2010. Scale bar equals 5 mm. **f** Photograph of posterior view of braincase of adult *Protoceratops* (IGM 100/2012). Sutures between the exoccipital and supraoccipital are outlined in red. Scale bar equals 1 cm



do not reach as far laterally relative to the adult and the foramen magnum remains relatively large. The braincase is similar to other described juveniles (see Goodwin et al. 2006) as well as that of fully mature *P. andrewsi* and *Yamaceratops dorn gobiensis* in that the supraoccipital forms the dorsal margin of the foramen magnum (Brown and Schlaikjer 1940; Makovicky and Norell 2006; Fig. 3e and f). It is not apparent if the exoccipital contribution to the occipital condyle is present at this early ontogenetic stage. The predentary of IGM 100/2010 closely resembles that of *Y. dorn gobiensis* in that it is a relatively solid bone with a slightly concave buccal surface. The ventral process is missing probably due to its young ontogenetic age. The quadrate possesses a dorsal shaft that is elongate and compressed rostrocaudally, as seen in other basal neoceratopsians. The pterygoid flange extends medially from the ventral portion of the quadrate, but does not extend the length of the shaft as it does in the adult of *Y. dorn gobiensis* (Makovicky and Norell 2006).

The postcranium is better ossified than the cranium, and cross-sectional data derived from HRCT slices suggest that the epiphyses of the long bones are formed in calcified

cartilage (Horner and Currie 1994). Recovered vertebrae are derived from the anterior part of the cervical series as indicated by the size and morphology of the neural arches, particularly that of the expanded neural spines (Fig. 2). Included among the anterior cervical vertebrae is the axis (Fig. 2) that possesses an expanded, hatchet-shaped neural spine that extends over the succeeding vertebra. The proximal ends of the femora and distal ends of the tibiae and fibulae are broken, and therefore, measurements were not obtainable from the hindlimb. Although these measurements are not available, the femur clearly exceeds the length of the humerus, which is 15.6 mm. Postcranial elements are morphologically similar to neoceratopsians, and the limbs possess a gracile aspect that is strikingly similar to that exhibited by younger specimens of *P. andrewsi* (Brown and Schlaikjer 1940). There is a small process on the midshaft of the femur that we interpret as the fourth trochanter based on shape and spatial arrangement. This feature is difficult to discern in the three-dimensional reconstructions but much more easily seen in the original CT slices (slice 259 of the horizontal movie; http://www.DigiMorph.org/specimens/Neoceratopsian_egg).

Phylogenetic diagnosis

Comprehensive growth series are only known in extinct dinosaurs in a few exceptional cases (e.g., *Protoceratops*, Brown and Schlaikjer 1940; *Maiasaura*, Horner et al. 2000). The lack of comprehensive ontogenetic data in closely related clades combined with the generally poor state of preservation (due to the presence of poorly ossified bones and a lack of developed morphology) makes it extremely difficult to diagnose particular fossil embryos to specific taxa (see Norell et al. 2001). The digitally isolated elements of IGM 100/2010, however, allow the specimen to be diagnosed to the successively nested clades of Ornithischia and Neoceratopsia based on derived cranial features. The presence of a prementary bone (Fig. 3c and d) unequivocally diagnoses the specimen as an ornithischian (Sereno 1986). IGM 100/2010 is diagnosed further to Neoceratopsia based on a quadrate shaft that is straight in lateral view (Fig. 3a and b; Makovicky 2002; Xu et al. 2002). This feature is described by Makovicky (2002) as being diagnostic of Neoceratopsia and consisting of a quadrate shaft that is straight in lateral view from articulation with the squamosal to the condylar end. This character has not been surveyed in all ornithischians, but rather only ceratopsians and a few outgroups (i.e., Ornithopoda and Pachycephalosauria). Therefore, the diagnosis to Neoceratopsia is tenuous, pending a more comprehensive study of this character within all of Ornithischia.

It should be noted that the above identification is made using a strictly apomorphy-based approach. Other features provide additional support for IGM 100/2010 as a neoceratopsian. Most notably, the dorsally concave shape of the prementary is shared with all other neoceratopsians (Fig. 3c and d), in contrast to the much straighter prementary of ornithopods and basal ceratopsians (Norman et al. 2004; You and Dodson 2004). The prementary also lacks the severe scoop-like shape characteristic of forms such as *Leptoceratops gracilis*, *P. andrewsi*, and ceratopsids (Makovicky and Norell 2006), although this feature could be correlated with the young ontogenetic maturity of the specimen. The lack of this character also does not prohibit the specimen from being a more derived ceratopsian.

On the postcranial skeleton, the presence of a fourth trochanter on the midshaft of the femur further supports a diagnosis to Ornithischia (Sereno 1986). Furthermore, the reduction of the fourth trochanter distinguishes IGM 100/2010 from ornithopods, which possess well-developed fourth trochanters even at the earliest known stages of their development (Horner and Currie 1994). The fourth trochanter, however, also is reduced in immature specimens of *Psittacosaurus*; therefore, this feature is useful only to distinguish the specimen as a ceratopsian.

These similarities suggest that this specimen is a neoceratopsian. However, the similarities are not included in the explicit diagnosis of this specimen because they have not been established as derived for these taxa in a more global phylogenetic analysis. Any questions addressed using this specimen must be restricted to Neoceratopsia or a more inclusive clade to avoid introducing circularity.

Embryonic growth within Neoceratopsia

Although a more refined diagnosis cannot currently be supported, even with this less refined diagnosis to the level of Neoceratopsia, observations concerning the ontogenetic development of neoceratopsians in general still can be made. The paroccipital processes have a positive correlation with ontogenetic maturity within Ceratopsia, as there is a marked distal expansion of the processes through time beginning with the rudimentary processes present in the embryo (see Maryńska and Osmólska 1975 and Makovicky 2002). There is a negative allometry between the size of the foramen magnum relative to the rest of the braincase through ontogeny (Fig. 3e and f). This pattern supports a broader pattern that is derived for vertebrates in general in which the maturation of the nervous system is delayed relative to the remainder of the skull (see Emerson and Bramble 1993). The morphology of the prementary undergoes perhaps one of the most dramatic changes (Fig. 3c and d). The ventral process is not present in the embryo, yet is present in the earliest postnatal examples of ceratopsians, which suggests that this process, if not broken, may ossify sometime in late prenatal development or the earliest stages of postnatal development.

Several transformations in the postcranial development of Neoceratopsia also are made evident by IGM 100/2010 (Fig. 2). The anterior cervical vertebrae of the embryo are free and not yet fused into a syncervical, as in basal neoceratopsians, indicating that this fusion occurs in late prenatal or early postnatal development. The fore- and hindlimbs are very gracile elements in the embryo with little curvature along their long axis, whereas the same elements of adult basal neoceratopsians are more curved, robust, and relatively short. The limbs thus demonstrate a negative allometry with the body as a whole (see also Chinnery 2004). Although this study presents only a few examples of changes in characters throughout ontogeny, work continues to be done on growth series within Ceratopsia (e.g., Erickson and Tumanova 2000; Makovicky and Norell 2006; Makovicky et al. 2006; Goodwin et al. 2006; Horner and Goodwin 2006), and this specimen provides an important new addition to the comprehensive series that are already available.

Eggshell microstructure

The eggshell of IGM 100/2010 is very friable and covered by siliciclastic sediments that likely are the cause of moderate acidification of the carbonate shell (Faccio 1994). Nevertheless, sparse and randomly distributed nodes (Fig. 4a and b) are preserved on the outer eggshell surface, but no pore canals or apertures were observed on the studied samples. A secondary epitaxial growth blankets the inner shell surface and probably is due to bacterial mediation originating from the decomposing embryo and mobilization of calcium ions (Grellet-Tinner 2005; Fig. 4c). We estimate, based on four digital measurements, the total thickness of the eggshell to be 183–184 μm .

The eggshell is divided into three structural layers (Fig. 4c and d). The innermost layer averages 61–62 μm and displays semicircular spherulites at its base that surround the loci of eggshell units (Fig. 4c). The spherulites

form layer 1 and consist of blocky, blade-shaped crystals (Fig. 4c) which are vertically elongate. Layer 2 (81 μm in thickness) is not clearly demarcated from layer 1 but is differentiated by larger and more numerous vesicles (although the latter may be exaggerated by dissolution during diagenesis) and a sub-horizontal crystal orientation. Layer 2 is capped by a third structural layer that is 40 μm with a vertical crystallographic orientation similar to that of layer 1.

Eggs with clear taxonomic association that exhibit a trilaminated eggshell structure have been referred to avian theropods (Schweitzer et al. 2002; Buffet et al. 2005; Grellet-Tinner 2006; Grellet-Tinner and Makovicky et al. 2006). However, these theropod eggs are always asymmetric (Grellet-Tinner et al. 2006). The symmetry found in IGM 100/2010 is a feature normally associated with basally diverging reptiles (Reptilia *sensu* Gauthier et al. [1988]) such as crocodylians, snakes, and turtles. Because the data

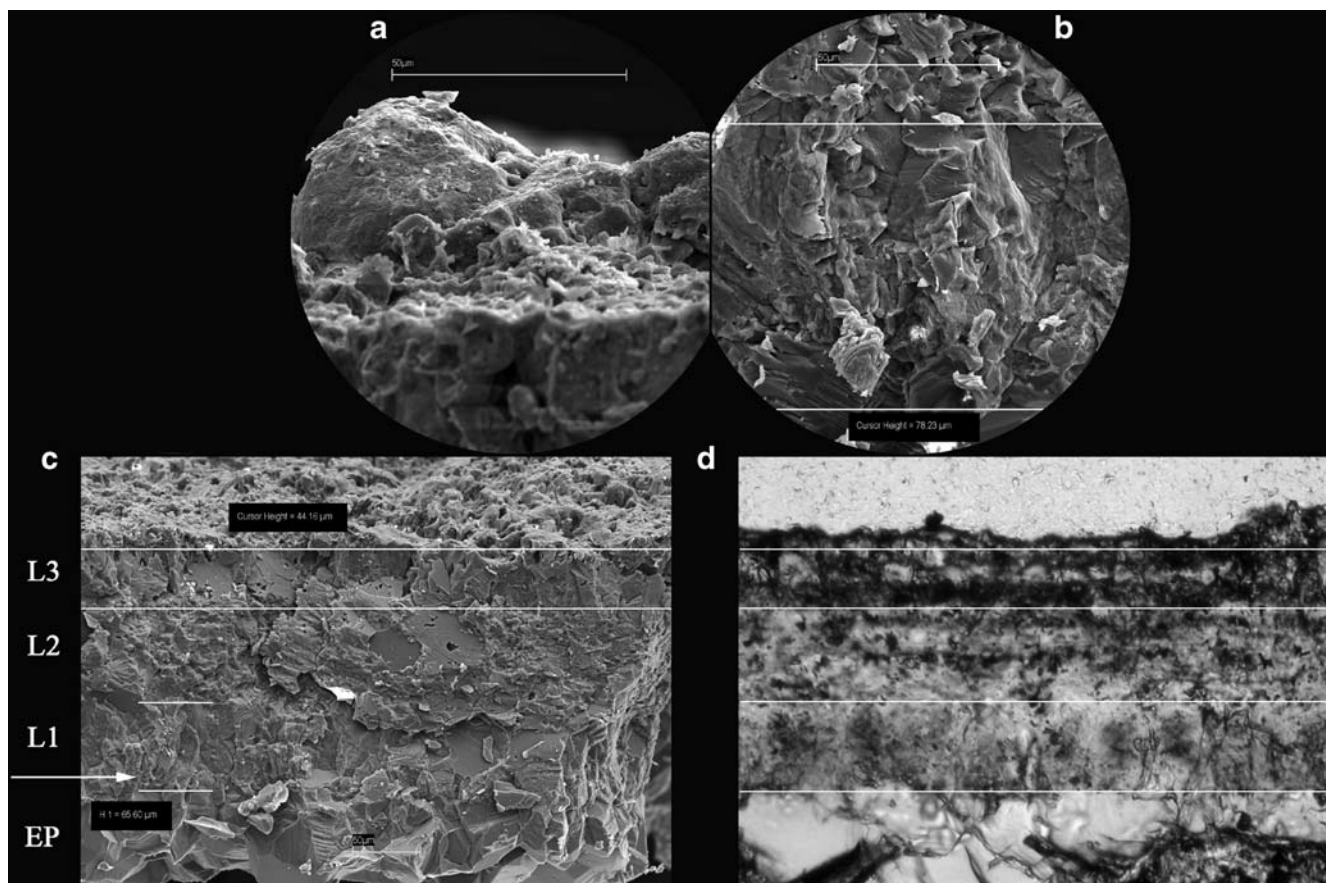


Fig. 4 **a** SEM of surficial ornamentation. Note the node on the left and the overall scaled appearance of the egg surface due to post-burial acidification. The dimensions of the nodules approximate 2.9 μm (at the base) and 1.9 μm in height. **b** SEM of layer 1 (L1), the innermost structural layer. Although very thin, fragile, and partially weathered, the crystals in L1 still display a vertical orientation and a bladed shape. **c** SEM of the entire eggshell thickness. Note that L1 is distinguishable from layer 2 (L2) by the orientation and shape of its calcite crystals and also by lesser amount of vesicles. Despite

moderate diagenetic alteration, some of the spherulites (SP) at the base of the eggshell units are still visible. L2 differs from L1 by its nearly horizontally orientated smaller crystals and by more numerous and larger vesicles. Layer 3 (L3) is proportionally wide and differs from L2 by its vertically orientated crystals. Note the epitaxial calcitic growth (EP) that underlies L1, a feature likely due to mobilization of CaCO_3 during diagenesis. **d** Transmitted light micrograph of a thin section through the entire eggshell thickness illustrating the three structural layers of the eggshell

from eggshell microstructure and egg shape conflict, it is evident that more than one character system is required to accurately diagnose fossil eggs that are not taxonomically identified by clearly associated skeletal remains (i.e., embryos, brooding adults, or eggs present in the body cavity; Grellet-Tinner 2006; Grellet-Tinner and Makovicky et al. 2006).

Conclusions

Fossil embryos are difficult to study in a phylogenetic context because their early state of ossification and small size complicates the identification of apomorphic characters. Yet, even if taxonomic identifications cannot be made to refined levels, embryonic specimens can still be used to support statements about broader patterns of development. In particular, they provide a unique opportunity to address large-scale evolutionary questions such as the evolution of developmental constraints, the evolution of growth rates, the acquisition and allometric growth of osteological features, and the paleobiological properties of organisms (e.g., altricial vs. precocial), but these specimens must be placed within a larger context of where they sit within their own developmental progression as well as where they sit on the tree of life (phylogenetic diagnosis). These issues would seem to be intuitive to any analysis that includes embryonic fossils; however, such matters have not been dealt with explicitly in the literature.

Using a strictly apomorphy-based approach, IGM 100/2010 is diagnosed unequivocally to Ornithischia based on the presence of a predepository and to Neoceratopsia based on a straight quadrate shaft. Thus, this unique specimen represents the first associated embryo and egg for this important dinosaur clade and provides a basis to begin to understand the earliest parts of development within Neoceratopsia.

The taxonomic identification allows the association of this clade of dinosaurs with an eggshell type, which previously was identified based on eggs that lacked skeletal remains (Mikhailov 1995, 1997). Eggshell characters usually are fairly stable within higher taxa of dinosaurs (Grellet-Tinner et al. 2006). The presence of three layers suggests that the three groups of asymmetric and larger eggs with two microstructural layers that previously were assigned to protoceratopsids (Mikhailov et al. 1994; Mikhailov 1995) cannot presently be assigned with certainty to Neoceratopsia.

This study illustrates that despite the long history of descriptive embryology (extending back well over 150 years; see Russell 1916), future attention should be directed toward this endeavor. There still exists a paucity of available descriptions useful to providing both an ontogenetic and phylogenetic diagnosis for fossil embryos. The

wider the taxonomic distribution of these data, the more refined the conclusions that can be drawn from the fossil record. If the fossil record can actually shed light on the evolution of development, then such refinement will be beneficial to paleontologists, neontologists, and biology in general. Fossil embryos provide a direct window into the evolutionary history of development. Ornithischians, and specifically the growing number of ontogenetically informative specimens of ceratopsians, provide an exciting opportunity to better understand the evolution of development in dinosaurs.

Acknowledgments GGT would like to acknowledge E. Duke at the Analytical Facilities of Engineering and Mining Experiment Station of SDSMT for the use of the SEM. MRL would like to thank E. Kernberg, UCSF, for preliminary radiological analyses of the specimen. Mick Ellison provided much help in the preparation of figures. Jessie Maisano assisted in the preparation of the web-based imagery accompanying this paper. Thanks to Gabe Bever, Peter Makovicky, and three anonymous reviewers for their useful comments. CT scanning was performed by the HRCT Facility at The University of Texas at Austin. Support for this project came from the American Museum of Natural History, Division of Paleontology and DEES, Columbia University.

References

- Balanoff AM, Rowe T (2007) Osteological description of an embryonic skeleton of the extinct elephant bird, *Aepyornis* (Palaeognathae: Ratitae). Soc Vert Paleontol Memoir 9, J Vert Paleontol 27(suppl. to 4):1–53
- Bohlin B (1953) Fossil reptiles from Mongolia and Kansu. The Sino-Swedish Expedition, Publication no. 37, pp 1–105
- Brown B, Schlaikjer EM (1940) The structure and relationships of *Protoceratops*. Ann NY Acad Sci 40:133–266
- Buffetaut E, Grellet-Tinner G, Suteethorn V, Cuny G, Tong H, Košir A, Cavin L, Chitsing S, Griffiths PJ, Tabouelle J, Le Loeuff J (2005) Minute theropod eggs and embryo from the Lower Cretaceous of Thailand and the dinosaur-bird transition. Naturwissenschaften 92:477–482
- Carpenter K, Alf K (1994) Global distribution of dinosaur eggs, nests, and babies. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur eggs and babies. Cambridge University Press, Cambridge, pp 15–30
- Chinnery B (2004) Morphometric analysis of evolutionary trends in the ceratopsian postcranial skeleton. J Vert Paleontol 24:591–609
- Dodson P, Forster CA, Sampson SD (2004) Ceratopsidae. In: Weishampel DB, Dodson P, Osmólska H (eds) The Dinosauria. University of California Press, Berkeley, pp 494–513
- Dong Z-M, Currie PJ (1993) Protoceratopsian embryos from Inner Mongolia, People's Republic of China. Can J Earth Sci 30:2248–2254
- Emerson SB, Bramble DM (1993) Scaling, allometry, and skull design. In: Hanken J, Hall BK (eds) The skull, volume 3: functional and evolutionary mechanisms. University of Chicago Press, Chicago, pp 384–416
- Erickson GM, Tumanova TA (2000) Growth curve of *Psittacosaurus mongoliensis* Osborn (Ceratopsia: Psittacosauridae) inferred from long bone histology. Zool J Linn Soc–Lond 130:551–566

- Faccio G (1994) Dinosaurian eggs from the upper Cretaceous of Uruguay. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur eggs and babies. Cambridge University Press, Cambridge, pp 47–55
- Gauthier J, Kluge AG, Rowe T (1988) Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209
- Goodwin MB, Clemens WA, Horner JR, Padian K (2006) The smallest known *Triceratops* skull: new observations on ceratopsid cranial anatomy and ontogeny. *J Vert Paleontol* 26:103–112
- Grellet-Tinner G (2005) The membrana testacea of titanosaurid dinosaur eggs from Auca Mahuevo (Argentina): implications for the exceptional preservation of soft tissue in Lagerstätten. *J Vert Paleontol* 25:99–106
- Grellet-Tinner G (2006) Phylogenetic interpretation of eggs and eggshells: implications for oology and Paleognathae phylogeny. *Alcheringa* 30:130–180
- Grellet-Tinner G, Makovicky PJ (2006) A possible egg of the theropod *Deinonychus antirropus*: phylogenetic and biological implications. *Can J Earth Sci* 43:705–719
- Grellet-Tinner G, Chiappe L, Bottjer D, Norell M (2006) Paleobiology of dinosaur eggs and nesting behaviors. *Palaeogeogr Palaeoclimatol* 232:294–321
- Horner JR, Currie PJ (1994) Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur eggs and babies. Cambridge University Press, Cambridge, pp 312–336
- Horner JR, Goodwin MB (2006) Major cranial changes during *Triceratops* ontogeny. *Proc R Soc B* 273:2757–2761
- Horner JR, de Ricqlès A, Padian K (2000) Long bone histology of the hadrosaurid dinosaur *Matiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *J Vert Paleontol* 20:115–129
- Makovicky PJ (2002) Taxonomic revision and phylogenetic relationships of basal neoceratopsia (Dinosauria: Ornithischia). Ph.D. dissertation, Columbia University, p 279
- Makovicky PJ, Gao KQ, Zhou CF, Erickson G (2006) Ontogenetic changes in *Psittacosaurus*: implications for taxonomy and phylogeny. *J Vert Paleontol* 96(suppl. to 3):94A
- Makovicky PJ, Norell MA (2006) *Yamaceratops dornobienses*, a new primitive ceratopsian (Dinosauria: Ornithischia) from the Cretaceous of Mongolia. *Am Mus Novit* 3530:1–42
- Maryńska T, Osmólska H (1975) Protoceratopsidae (Dinosauria) of Asia. *Palaeontol Pol* 33:133–181
- Mikhailov KE (1995) Systematic, faunistic and stratigraphic diversity of Cretaceous eggs in Mongolia: comparison with China. In: Sun A, Wang, Y (eds) Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. China Ocean Press, Beijing, pp 165–168
- Mikhailov KE (1997) Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Spec Pap Palaeontol* 56:1–80
- Mikhailov KE, Sabath K, Kurzanov S (1994) Eggs and nests from the Cretaceous of Mongolia. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur eggs and babies. Cambridge University Press, Cambridge, pp 98–102
- Norell MA, Clark JM, Chiappe LM, Dashzeveg DY (1995) A nesting dinosaur. *Nature* 378:774–776
- Norell MA, Clark JM, Chiappe LM (2001) An embryonic oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Mongolia. *Am Mus Novit* 3315:1–17
- Norman DB, Witmer LM, Weishampel DB (2004) Basal Ornithischia. In: Weishampel DB, Dodson P, Osmólska H (eds) The Dinosauria. University of California Press, Berkeley, pp 325–334
- Reisz RR, Scott D, Sues H-D, Evans DC, Raath MA (2005) Embryos of an Early Jurassic prosauropod dinosaur and their evolutionary significance. *Science* 309:761–764
- Ricklefs RE, Starck JM (1998) Embryonic growth and development. In: Starck JM, Ricklefs, RE (eds) Avian growth and development: evolution within the Altricial–Precocial Spectrum. Oxford University Press, New York, pp 31–58
- Russell ES (1916, 1982 reprint) Form and function: a contribution to the history of animal morphology. University of Chicago Press, Chicago
- Salgado L, Coria RA, Chiappe L (2005) Osteology of the sauropod embryos from the Upper Cretaceous of Patagonia. *Acta Palaeontol Pol* 50:79–92
- Sato T, Cheng YN, Wu X-C, Zelenitsky DK, Hsiao YF (2005) A pair of shelled eggs inside a female dinosaur. *Science* 308:375–376
- Schweitzer MH, Jackson F, Chiappe L, Schmitt JG, Calvo JO, Rubilar DE (2002) Late Cretaceous avian eggs with embryos from Argentina. *J Vert Paleontol* 22:191–195
- Sereno PC (1986) Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *Natl Geogr Res* 2:234–256
- Starck JM, Ricklefs RE (1998) Patterns of development: the altricial-precocial spectrum. In: Starck JM, Ricklefs RE (eds) Avian growth and development: evolution within the Altricial–Precocial Spectrum. Oxford University Press, New York, pp 3–30
- Varricchio DJ, Horner JR, Jackson FD (2002) Embryos and eggs for the Cretaceous theropod dinosaur *Troodon Formosus*. *J Vert Paleontol* 22:564–576
- Xu X, Makovicky PJ, Wang X, Norell MA, You H (2002) A ceratopsian dinosaur from China and the early evolution of Ceratopsia. *Nature* 416:314–317
- You H, Dodson P (2004) Basal Ceratopsia. In: Weishampel DB, Dodson P, Osmólska H (eds) The Dinosauria. University of California Press, Berkeley, pp 478–493