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OOLOGY AND THE EVOLUTION OF THERMOPHYSIOLOGY IN SAURISCHIAN DINOSAURS: HOMEOTHERM AND ENDOTHERM DEINONYCHOSAURIANS?

GERALD GRELLET-TINNER[1]

ABSTRACT

The origin of avian endothermy is a long-held question the answer of which cannot be provided by first level observations. Oological and reproductive characters have collectively provided a new source of data useful for phylogenetic analyses and paleobiological inferences. In addition, the observations of reproductive and oological evolutionary trends in saurischian dinosaurs lead to the interpretation that not only, the thermophysiology of these dinosaurs progressively became more avian-like but after re-examination allows to infer that deinonychosaurians represented here by three troodontids and one dromaeosaurid might already have developed an avian-like endothermy, thus predating the rise of avians. These results based on reproductive traits are independently corroborated by the discoveries of troodontid dinosaurs 1) in high latitudes, 2) covered with feathers in Chinese Lagerstätten, and recently 3) fossilized in a death pose identical to an avian sleeping posture.

KEYWORDS: endothermy, avian, troodontid theropod dinosaurs, oology, reproductive behaviors.

INTRODUCTION

Oological and reproductive characters known to be useful for phylogenic analyses (Grellet-Tinner, 2000; Makovicky and Grellet-Tinner, 2000; Grellet-Tinner and Chiappe, 2004; Buffetaut *et al.,* 2005; Grellet-Tinner in press) also provide a source of new data for the paleobiology of saurischian dinosaurs (Grellet-Tinner *et al.,* 2006). Investigation of the physiology in fossilized vertebrates seems a doubtful query, as it cannot be observed directly. However, the discoveries of troodontids species in high paleolatitudes (Fiorillo and Gangloff, 2000), or with feathers in Chinese Lagerstätten suggest a metabolism different than the typical reptilian ectothermy. More importantly, recent evidence of an avian behavior in a non-avian dinosaur led to the interpretation that a 130 millions years old basal troodontid (Xu and Norell, 2004) would have already acquired a homeothermic physiology. Independent paleobiological interpretations founded on oological data allowed Grellet-Tinner *et al.* (2006) to unravel the evolution of thermophysiology in saurischians. A concise review of key elements is presented here with new conclusions.

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[1] Museu de Zoologia, Universidade de São Paulo, Caixa Postal 42494-970, CEP 04218-970, São Paulo, SP, Brasil. E-mail: deinonychus@swissinfo.org

Abbreviations

Institutional abbreviations: AMNH, American Museum of Natural History, New York; IGM, Institute of Geology, Mongolia, Ulaan Baatar; MCZ, Museum of Comparative Zoology, Harvard; MOR, Museum of the Rockies; YPM, Yale Peabody Museum of Natural History, New Haven; USC, University of Southern California; LX09XLOZLX00, identification number for US Dept. of Interior.

Technical abbreviations: BSEM, backscattered scanning electron microscopy; CL, cathodoluminescence; DPI, dots per inches; MT, Membrana Testacea; microscopy; PLM, polarized light microscopy; SEM, scanning electron microscope; TLM, transmitted light microscopy.

MATERIALS AND METHODS

Material

Fossil eggs can only be identified taxonomically with certainty either by observing an egg-laying female or by the embryos they contain. In the fossil record, the former requires the rare preservation of a female with eggs in its reproductive system (Sato *et al.,* 2005), the latter is relatively more often recorded (Currie and Horner, 1988; Horner and Weishampel, 1988; Horner and Currie, 1994; Norell *et al.,* 1994, 2001; Horner, 1997; Manning *et al.,* 1997; Mateus *et al.,* 1997; Chiappe *et al.,* 2001a; Schweitzer *et al.,* 2002). These discoveries have also allowed the association of eggs of several extinct dinosaurs to species-specific nest structures (Varricchio *et al.,* 1997; Chiappe *et al.,* 2004) and in some instances, to species-specific nesting behaviors (Norell *et al.,* 1995; Dong and Currie, 1996; Clark *et al.,* 1999; Varricchio *et al.,* 1999; Grellet-Tinner *et al.,* 2006). Nevertheless, taphonomic and taxonomic levels of confidence (two different indices) might differ for a given oological specimen according to its proximity to specific skeletal remains and it's *posteriori* taxonomic identification, thus could foster erroneous phylogenetic and paleobiological interpretations. As such, the highest level of taphonomic confidence in the association of fossil eggs with skeletal remains occurs when diagnostic embryos are found *in ovo* (Norell *et al.,* 1994, 2001; Chiappe *et al.,* 2001a) or when eggs are preserved inside a gravid female (Sato *et al.,* 2005). However, a high taphonomic level does not always correspond to a first level of taxonomic confidence. The identification of the skeletal remains could be uncertain, controversial (Horner, 1997; Manning *et al.,* 1997; Mateus *et al.,* 1997), rebutted (Chiappe *et al.,* 2001b), or at a low taxonomic hierarchical level that does not allow an identification at the species or family level (Schweitzer *et al.,* 2002, Buffetaut *et al.,* 2005), leading to a lower level of taxonomic confidence. Although such occurrences do not by essence discriminate against their use for phylogenetic analyses or paleobiologic interpretations, the descriptions of their discoveries and identifications need to be reported. For descriptions of the various taphonomic and taxonomic levels of confidence assigned to the studied material (Table 1), see Grellet-Tinner *et al.* (2006).

In order to better understand the evolution of eggs, eggshell structures, nesting behaviours, and reproductive patterns in saurischian dinosaurs, crocodilians and modern birds, the two living clades that bracket this group of dinosaurs, need to be considered. This because many aspects of the reproduction, nesting structures, and behaviours of these living clades reflect two radically opposite thermophysiologies (Table 2).

Methods

Eggshell samples were examined under SEM at the AMNH and Field Museum facilities. Additionally, radial thin sections of eggshell were studied using transmitted light (TRM) and polarized light (PLM) microscopy at the AMNH and Earth Sciences Department of USC. Cathodoluminescence (CL) analysis was performed at the Earth Sciences Department of USC to determine possible diagenetic changes of composition or structure.

Readers are referred to Grellet-Tinner *et al.* (2006) for more detailed information.

RESULTS

The saurischian taxa studied (Table 1) by Grellet-Tinner *et al.* (2006) clearly reveal a reproductive evolutionary cline (Fig. 1) from basal archosaurs (as inferred from crocodilians) to modern birds, namely a successive acretion of eggshell structural layers, an monoautochronic ovideposition, the atrophy of one ovary or the evolutionary development of a single functioning ovary, clutch spatial arrangements and nest structures that reflects a change of parental care, which is itself related to a successive and gradual change in thermophysiology in saurischians. Without paraphrasing Grellet-Tinner *et al.* (2006), a brief review of re-

TABLE 1. List of specimens in Grellet-Tinner 2005 analysis.

ITEM	MUSEUM	SPECIMEN	LOCALITY	AGE
Egg and eggshells	MCF-PVPH	titanosaurid nests	Patagonia, Auca Mahuvo	Campanian, Anacleto FM
Egg and eggshells	MCF-PVPH	titanosaurid MT	Patagonia, Auca Mahuvo	Campanian, Anacleto FM
Egg and eggshells	MOR 246	*Troodon formosus*	Montana, Egg island and Egg Montain	Campanian, Two Medecine FM
Eggshells/skull	IGM 100/972	*Byronosaurus jaffei*	Mongolia, Ukhaa tolgod	Campanian-Maastrichtian, Djadokhta FM
Eggshells/nest	IGM 100/974	*Byronosaurus jaffei*	Mongolia, Ukhaa tolgod	Campanian-Maastrichtian, Djadokhta FM
Egg and eggshells	AMNH 3015	*Deinonychus antirrhopus*	Montana. Cashen ranch	Albian, Cloverly FM, V
Eggshells/skull	IGM/978/971	*Citipati osmolka*	Mongolia, Ukhaa tolgod	Campanian-Maastrichtian, Djadokhta FM
Egg and eggshells	IGM 100/979	*Citipati osmolka*	Mongolia, Ukhaa tolgod	Campanian-Maastrichtian, Djadokhta FM
Egg and eggshells	IGM 100/1127/ 973/1002	*Citipati osmolka*	Mongolia, Ukhaa tolgod	Campanian-Maastrichtian, Djadokhta FM
Eggs and eggshells	LACM/7477/149736	Baby Louie	China, Henan-Xixia (Sanlimiao)	Maastrichtian
Eggshell	MUCPv-284, 350, 351	Enantiornithine	Neuquen	Santonian, Rio Colorado FM
Eggshells	YPM 16961	*Lithornis celetius*	Montana, Bangtail, Gallatin National Forest, Park County	Paleocene, Fort Union FM
Eggshells	LACM#	*Lithornis vulturinus*	UK, Isle of Sheppey	Eocene, London Clay FM
Egg clutch	Nanyang Museum	Macroelongatoolithid	China, Henan-Xixia (Sanlimiao)	Maastrichtian
Eggs and eggshells	SK1-1	*incertae sedis*	Phu Phock, Nahkon	Barremian, Sao Khua FM
Egg clutch, Egg and eggshells	LX09XLOZLX0001-2156 and 2151	Troodontid	China, Inner Mongolia	Unknown

productive transformations in the saurischian lineage with explanation of key features is provided below with discussion and new interpretations.

Considering the entire body of oological and nesting evidence, titanosaurid dinosaurs, a clade of saurischian dinosaurs, would have possessed a *quasi* similar reproductive system and nesting behaviours as crocodilians. The similarities include an *en masse* egg laying strategy, symmetrical eggs without air cells, mono-layered eggshell structure, and a very limited nesting parental care (Grellet-Tinner, 2005, Grellet-Tinner *et al.,* 2006). Unlike titanosaurs, the oviraptor *C. osmolskae* IGM 100/979 (Norell *et al.,* 1994, 2001) and other oviraptorid fossils have been found sitting on their nests in an avian posture (Dong and Currie, 1996). In such life assemblages, oviraptors sit atop an egg clutch with their axial skeleton posited in the clutch center that lacks eggs (Clark *et al.,* 1999; Norell *et al.,* 2001), an important feature for the interpretation of nesting parental care. Commonly, the eggs are paired and arranged in a sub-horizontal position forming up to three superposed layers (Clark *et al.,* 1999; Norell *et al.,* 2001). While this type of life assemblage documents a brooding activity, here solely recognized as protective behavior, it falsifies at the same time the possibility of any heat transfer (incubation) by the presence of multiple rows of eggs and the absence of evidence of egg post-partum manipulation (Grellet-Tinner, 2005; Grellet-Tinner *et al.,* 2006). Nevertheless, the oval and elongated eggs of *C. osmolskae* display an avian trend by having a faint polar asymmetry not yet as pronounced as that of extant birds but that still indicates the presence of a small air cell (Grellet-Tinner *et al.,* 2006), a feature that is absent in the symmetrical crocodilian (Iverson and Evert, 1995) and titanosaurids eggs (Grellet-Tinner *et al.,* 2004, 2006). Another feature that characterizes *C. osmolskae* is its paired eggs, a spatial arrangement indicative of two functioning ovaries (Clark *et al.,* 1999; Norell *et al.,* 2001), as titanosaurs and all primitive saurischians. At the same time this advocates for a monoautochronic ovideposition (Clark *et al.,* 1999; Norell *et al.,* 2001, Sato *et al.,* 2005), unlike the *en masse* ovideposition of crocodilians and titanosaurids. In addition to this mosaic of characters, the eggshell of *C. osmolskae* is structurally divided in two layers, an intermediate character between the mono-layered crocodilian (Grellet-Tinner and Chiappe, 2004) and tri-layered avian eggshell structures (Grellet-Tinner, 2000, Grellet-Tinner and Chiappe, 2004, Grellet-Tinner *et al.,* 2006; Grellet-Tinner, 2006). Kamat *et al.* (2000) argued that molluscs achieve a greater mechanical equilibrium by increasing the num-

TABLE 2. Comparison and contrast between crocodilian and avian reproduction

CHARACTERS	CROCODYLIA	AVES
ovideposition	En masse	Monoautochronic
Egg spatial distribution	None	Possibly according to species
ovaries	Two functioning	One functioning
Egg manufacturing	Coeval manufacturing of tissues	In line/sequential manufacturing
Egg rotation in ovary	No	After shelled in shell gland
Egg maximum diameter	NA	Generally not exceed pelvic opening
Hatchlings	Precocial	Precocial or altricial
Egg geometry	Totally symmetrical	Asymmetrical
Sex determination	Temperature dependent	Genotypic
Albumen	One type	Two types
Chalazae	Absent	Present
Air cell	Absent	Present
Eggshell material	Composite (protein + CaCo3)	Composite (protein + CaCo3)
Eggshell crystals	Tabular without acicular precursor	Blade-shape with acicular precursor
Eggshell structural layers	Mono-layered	At least tri-layered
Contact among structural layers	NA	Prismatic for neognaths Aprismatic for paleognaths
Parental care/incubation	None	Mostly thermoregulation by body heat transfer
Post hatching parental care	Present	Present but more developed
Nests	Dug out holes or vegetation mounds	Elaborated and co-varies with species

ber of structural layers of their shell and emphasized that differences in crystallographic orientation among layers enhances this trend, a type of biological plywood. In that respect, it is worth noting that the volume of *C. osmolskae* eggs closely matches that of the Auca Mahuevo titanosaurs but its bi-laminated eggshell is twice as thin and its eggs need to support the weight of overlying eggs and the partial weight of the appendicular skeleton of a brooding adult.

Dozen of small asymmetrical eggs some with embryonic remains *in ovo* have been found in Cretaceous exposures of the Bajo de la Carpa Formation of Neuquén city, Patagonia (Schweitzer *et al.,* 2002). Although the taphonomic level of confidence of this material is extremely high by the presence of embryos *in ovo,* the phylogenetic position of this material has been only bracketed between the Ornithothoraces and Ornithuromorpha avian nodes with a likelihood that it could belong to enantiornithines (Schweitzer *et al.,* 2002). As expected by their phylogenetic proximity to extant birds, the fully asymmetric shape of these ornithothoracine eggs from Neuquén shaped like those of modern galliform birds is indicative of the presence of a fully developed air cell (Grellet-Tinner *et al.,* 2006), and their eggshell bears no surficial ornamentation (Schweitzer *et al.,* 2002; Grellet-Tinner *et al.,* 2006).

Most importantly, these eggs share with modern birds a tri-laminated eggshell structure with prismatic inter layers contacts (*sensu* Grellet-Tinner and Norell, 2002) and short blade-shaped calcite crystals in layer 1. However, the thickness of layer 1 exceeds that of layer 2 (by a ratio close to 1.4) in these enantiornithines (Grellet-Tinner, 2005; Grellet-Tinner *et al.,* 2006) and Phu Phok eggs (Buffetaut *et al.,* 2005). This character is so far unique to these two groups and not recorded in any other positively identified non-avian theropod or modern birds (Buffetaut *et al.,* 2005; Grellet-Tinner *et al.,* 2006). Several eggs in Neuquén were discovered within a limited area but only a few were complete and the rest consists of the halves with a tapered pole (without air cell). This taphonomic feature is entirely congruent with the hatching process in modern seagull colonies where the same egg sections are left intact resting on the ground surface (Hayward *et al.,* 2000). The blunt polar region (with the air cell) and the region immediately adjacent to this pole are often destroyed during the hatching process in modern birds (Hayward *et al.,* 2000). All the oological characters and hatching patterns advocate that basal ornithothoraces would have had a modern avian nesting and hatching behaviors, thus an avian thermophysiology.

In many aspects, troodontids, here phylogenetically bracketed between Oviraptorids and enantiornithines (Hwang *et al.,* 2004; Novas and Pol, 2005), offer intriguing and intermediary characters between *C. osmolskae* and the ornithothoracine eggs from Neuquén. First, the troodontid eggs of *T. formosus* are still elongated but conical and extremely asymmetrical (Figs. 2A, B). One pole is extremely rounded, which offers a greater mechanical stress resistance as it approximates the shape of a sphere (Bain, 1991). This asymmetry is far more pronounced than that of

C. osmolskae and closely resembles the condition commonly observed in ornithothoracines. This feature also suggests that troodontids already possessed an avian-like air cell instead of a small air cell as inferred for oviraptorids and other elongatoolithid eggs (Grellet-Tinner *et al.,* 2006). Second, the short and blade-shaped calcite crystals present in the eggshell structural layer 1 (Figs. 2C, 3C, D) are similar to those observed in known Avialans (Grellet-Tinner, 2000; Grellet-Tinner and Chiappe, 2004) and depart from the acicular crystals (Fig. 3A) observed in this layer of oviraptorid eggshell (Grellet-Tinner *et al.,* 2006) and *Deinonychus*

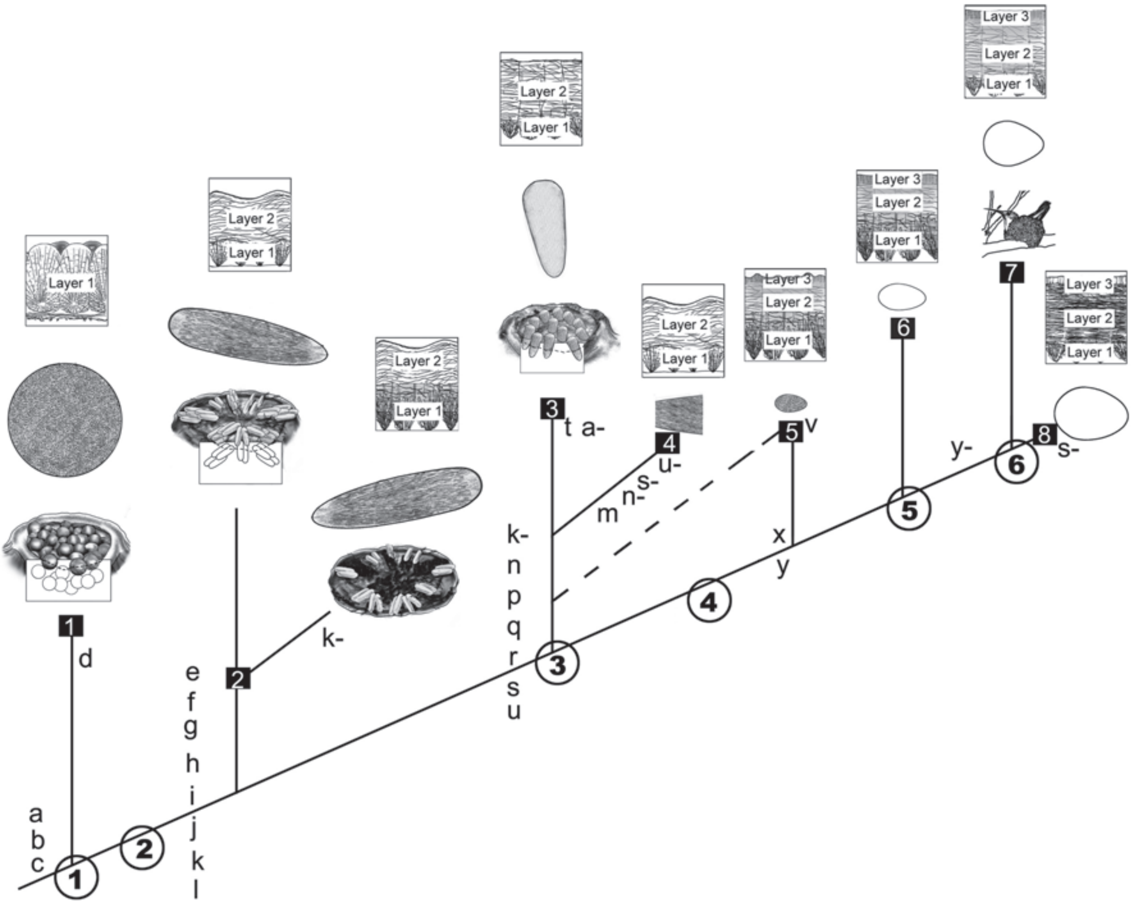

FIGURE 1. Cladogram inspired from Clark *et al.,* 2002 and Buffetaut *et al.,* 2005, and oological analyses from Grellet-Tinner *et al.,* (2006) and Grellet-Tinner and Makovicky *(in press).* Note the coeveal appearance of a change in the architecture of the nest, egg shape, and eggshell structure namely in oviraptorids and at the level of troodontids. All these evolutionary transformation reflect a change of thermophysiology, interpreted as an avian-like endothermy in troodontids. Letters indicate the appearance of synapomorphies and when followed by a negative sign indicate a reversal (homoplasy). The optimization of several of these characters is putative and likely to change when more taxa are described in the future.

Node 1- Sauropoda; Node 2- Maniraptora; Node 3- Paraves; Node 4- Avialae; Node 5- Ornithothoraces; Node 6- Neornithines

Clade 1- Titanosauria; Clade 2- Oviraptorosauria; Clade 3- Troodontidae; Clade 4- Dromaeosauridae; Clade 5- an unidentified coelurosaurid from Phu Phok; Clade 6- possible enantiornithine from Néuquen; Clade 7- Neognathae; Clade 8- Paleognathae

Characters

a. Presence of surficial ornamentation; **b.** Acicular crystals as building blocks of the eggshell structure; **c.** Eggs contained within a rimed nest; **d.** Nodular ornamentation in titanosaurids; **e.** Presence of two and aprismatic layers; **f.** Acicular crystals limited to layer 1; **g.** Linear ornamentation; **h.** Elongated eggs; **i.** Presence of a small-air cell; **j.** Monoautochronic ovideposition as indicated by the eggs arranged in pairs; **k.** Eggs are laid on the perimeters of circles that superposed in 2-3 layers and with an empty space in the center of the clutch; **l.** Presence of brooding behavior; **m.** Differentiation of organic lines within layer 2; **n.** Presence of blade-shaped crystals in layer 1; **o.** Presence of a single circle of eggs; **p.** Presence of a fully developed air cell; **q.** No space devoid of eggs in the center of the clutch; **r.** Reduction from two to one functioning ovary; **s.** Presence of two and prismatic eggshell structural layers; **t.** Eggs are vertically oriented in the substrate with air cell up; **u.** Absence of eggshell surficial ornamentation; **v.** Presence of bi-modial nodular ornamentation; **x.** Presence of three prismatic eggshell structural layers; **y.** Layer 1 wider than layer 2.

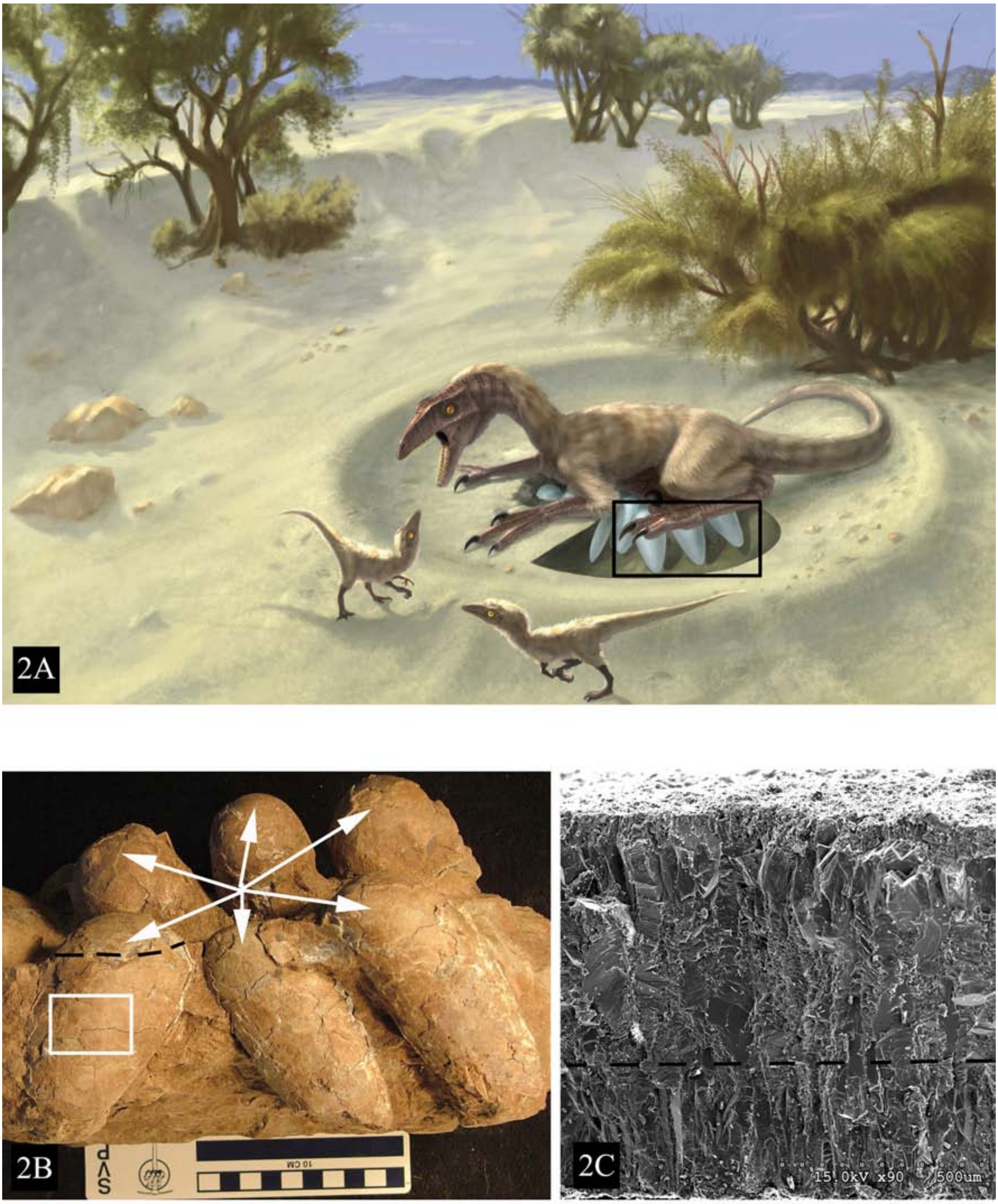

FIGURE 2. A. Incubating troodontid in a desert/semi-desert environment in Asia (rendered by artist Doyle Trankina). Note the position of the incubating parent on the egg clutch as its axial skeleton rests on the vertically/sub-vertically orientated eggs, a position that contrasts with that of oviraptorids where mostly their appendicular skeleton covers the clutch. Furthermore, there is no space without eggs in the clutch center as observed in oviraptorids and unidentified Chinese Macroolithid egg clutches. B. Partial troodontid egg clutch from China (LX09XLOZLX0001-2156). Although not associated with any skeletal remains, taxonomic identification was supported by the eggshell microstructure and egg morphology. Note that the asymmetric shape of these eggs due to the presence of a well developed air cell (arrows) and that the pointed pole faces down with the eggs buried nearly up to the level of the location of the air cell (doted lines). C. SEM of eggshell spared from the region indicated by the white rectangle. Note the presence of two prismatic layers, here separated by a dotted lines, with layer 1 consisting of blade-shaped calcite crystals.

antirrhopus (Makovicky and Grellet-Tinner, 2000 and Grellet-Tinner and Makovicky; in press). Third, in contrast to the aprismatic contact between the two structural layers observed in oviraptorids and *D. antirrhopus* (Fig. 3A) and other well-identified Mesozoic theropod eggshells (per. obs, Lourinhã allosauroid material) and in resemblance to ornithothoracine, the transition between layers 1 and 2 (Figs. 2C, 3C, D) is prismatic (*sensu* Grellet-Tinner and Norell, 2002). Fourth, troodontid eggshells lack surficial ornamentation (Figs. 2C, 3C, D) and fifth, the novel spatial arrangement of troodontid eggs (Fig. 2A, B) mimics that of modern pluvianids (e.g. Grant, 1982; Howell, 1979) by having eggs nearly vertically embedded with their round poles (with air cell) up and barely exposed above the sediment (Figs. 2A, B), a nesting behavior compatible with the hot environments where this troodontid species reproduced (Varricchio, 1993, Loope *et al.,* 1998) and that optimizes the space in the nest (Barta and Szckely, 1997). Lastly, the combined absence of space devoid of eggs in the clutch center (Figs. 2A, B) and the presence of a partial adult skeletal atop the eggs in MOR 748, 750 (Varricchio *et al.,* 1997) fundamentally separate troodontid from oviraptorid nesting behaviors as the axial skeleton of brooding troodontid is in direct contact with eggs placed on a single level. Remarkably, a recently discovered clutch of the Asian troodontid (in prep), *Byronosaurus jaffei,* from the Upper Cretaceous layers of Djadokhta Formation of Ukhaa Tolgod (Mongolia) and clutches of recently acquired troodontid eggs from China (per.obs) corroborates what has been documented in *T. formosus.* Moreover, as for the Neuquén ornithothoraces eggs (Grellet-Tinner *et al.,* 2006), the *B. jaffei* eggs consist of only the tapered halves and adjacent region, indicative of a hatching strategy similar to that of modern birds (Hayward *et al.,* 2000). Above all, Reptilian and avian nests are regarded as microenvironments that optimize egg incubation and hatching (Proctor and Lynch, 1993; Barta and Szckely, 1997). As behaviors of extinct animals are extrapolated from observations of their living relatives, pluvianid nesting and incubating behaviors provide valuable biological clues about the possible nesting behavior and thermophysiology of troodontids. The pluvianid *Pluvianus aegyptius* partially buries its eggs by digging a depression in sandbars (Howell, 1979). Egg Mountain and Egg Island, the two localities where *T. formosus* have been recovered were islands in local lacustrine systems (Varricchio, 1993) and *B. jaffei* paleoenvironments is best described as semi-desertic with sand dunes and oasis. *Pluvianus aegyptius* eggs fill a bowl-like depression without leaving any empty space, are positioned in a sub-vertical position pointed pole down with only the blunt pole of these eggs exposed periodically. Eggs partially buried or buried only a few centimeters below the surface in hot environments could easily reach lethal levels of 40° centigrade for birds but only 28° centigrade for other extant reptiles during the day if not attended by the parents and experience severe cooling periods during the night. The thermoregulation strategy of the parents is to cool down their clutch with water from nearby sources (Grant, 1982) and supply body heat during the cool hours by exposing the rounded pole of their eggs to incubate them. The over all suite of preserved oological and nesting structure in extinct troodontids closely resembles those extant pluvianids and favorably argues that troodontids could possess

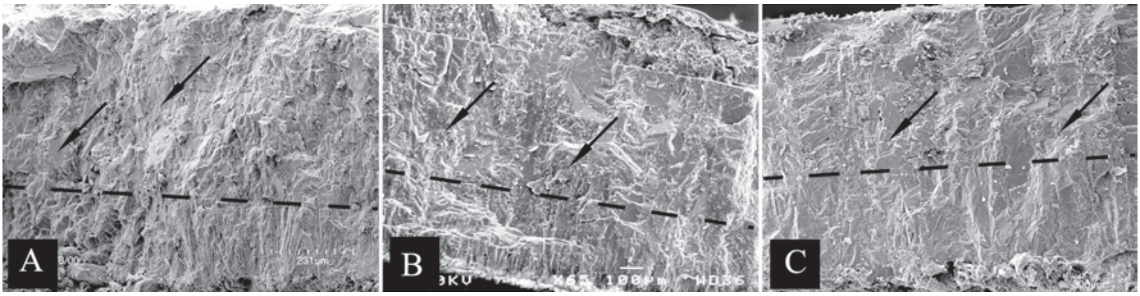

FIGURE 3. A. SEM of an oviraptorid egg (IGM 100/979). Note the bi-layered eggshell structure, with layer 1 consisting of acicular calcitic crystals and where the contact between layers 1 and 2 is aprismatic (dotted line). B and C. SEMs of troodontids *T. formosus* and *B. jaffei.* Note the similarity of the microstructure of the eggshells among these two troodontids and the Chinese egg, clutch LX09XLOZLX0001-2156. Also note the significant difference of crystallization in layer 1 between oviraptorids and troodontids as well as the type of contact between structural layers 1 and 2. The dotted lines denote the border between layers 1 and 2 and arrows the voids in all figures. Arrows in layer two points to voids that are more numerous in this second structural layer than in layer 1. These voids are the mold of protein matter that normally composed 2% of eggshell and were destroyed during the process of fossilization.

similar nesting behaviors. In turn, these reproductive and oological characters highly suggest that the North American and Asian troodontids already acquired an avian-like incubating behaviour, the latter been only feasible by acquiring an endothermic thermophysiology. When considering the total evidence that include oology with the associated nesting behaviour, the discovery of a basal troodontid (Xu and Norell, 2004) preserved with a tuck-in avian posture, other troodontids recovered with feather-like integument, and troodontid remains discovered in high paleolatitudes, it seems parsimonious to argue that troodontid dinosaurs were endothermic and homeothermic. Whether this thermophysiological innovation was limited to this theropod family remains unanswered. Yet, according to Clark *et al.* (2002) Troodontidae is the sister taxon to Dromaesauridae, a clade that contains *D. antirrhopus* (AMNH 3015) a theropod discovered with a partial egg (Makovicky and Grellet-Tinner, 2000; in press). The convex external eggshell surface of AMNH 3015 is apposed to the outer surface of well-preserved gastralia suggesting that, like oviraptorids, this dromaesoraurid would have brooded its eggs. Moreover, the contact of the axial skeleton (gastralia) with the egg, which is similar to troodontids, could be equally interpreted as a heat transfer mechanism, thus suggesting incubation and endothermy in *D. antirrhopus.* In turn, if confirmed, this thermophysiological feature present in both Troodontids and *D. antirrhopus* would be a synapomorphy of Deinonychosauria and have predated the divergence of Avialans.

RESUMO

A origem da endotermia nas aves é uma questão há muito discutida e sua resposta não pode ser encontrada através de observações superficiais. Caracteres oológicos e reprodutivos surgiram como uma nova fonte de dados relevantes tanto para análises filogenéticas quanto para inferências paleobiológicas dos dinossauros Saurischia. Além disso, as observações das tendências evolutivas reprodutivas e oológicas nos dinossauros Saurischia nos levam a inferir que não apenas, como anteriormente a termofisiologia deste grupo de dinossauros tornou-se progressivamente ornítica, mas um posterior reexame nos permitiu concluir que os deinonicossauros, representados aqui por dois troodontídeos e um dromeossaurídeo, provavelmente já haviam desenvolvido uma endotermia semelhante a das aves, anterior, portanto, ao seu surgimento. Estes resultados baseados em características reprodutivas são independentemente corroborados pela descoberta dos dinossauros troodontídeos 1) em altas latitudes, 2) recobertos com penas, no chinês Langerstäten, e, recentemente, 3) fossilizados em posição idêntica à postura de repouso das aves.

PALAVRAS-CHAVE: endotermia, aviano, troodontídeo dinossauro terópodo, oologia, comortamentos reprodutivos.

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