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Dinosaur diversity during the transition between the middle and late parts of the Late Cretaceous in eastern Shandong Province, China: Evidence from dinosaur eggshells

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The record of dinosaur eggs from the Upper Cretaceous Wangshi Group in eastern Shandong Province, China shows that the dinosaur species represented by elongatoolithids were present from the middle to the late Late Cretaceous, whereas those represented by the dictyoolithids and spheroolithids became extinct in the middle Late Cretaceous and the new species represented by ovaloolithids appeared in the late Late Cretaceous. Estimated eggshell conductance of water vapor is over 4 to over 115 times higher in spheroolithids and the dictyoolithids than in elongatoolithids and ovaloolithids, indicating that eggs of the first two oofamilies required higher humidity during incubation. Based on the $\delta^{18}O$ record as preserved in eggshell, a change from relatively humid to relatively dry climatic conditions can be assumed to have taken place during the transition between the middle and late parts of the Late Cretaceous. It is reasonable to suggest that the change in climate was the cause of the dinosaur diversity.

dinosaur eggshell, gas conductance, dinosaur diversity, middle-late Late Cretaceous, eastern Shandong Province

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Since the 1980s, there has been considerable progress in research into regional and global biological events. A huge mass of data from the marine strata of Americas, Europe, northern Africa and India indicate that ten major marine biological events took place in the Cretaceous [1], including the Cenomanian-Turonian boundary mass extinction, the Turonian-Coniacian stage boundary bio-events, the Coniacian-Santonian stage boundary bio-events, the Santonian-Campanian stage boundary bio-events, the middle Maastrichtian extinction interval, and finally the Cretaceous-Paleogene boundary mass extinction at the conclusion of the Late Cretaceous. However, the fossil record preserved in Cretaceous continental strata is less complete than its marine counterpart. The Cretaceous-Paleogene dinosaur extinction is well documented in inland western North America [2–7], the Mediterranean coast of Europe [8,9], western India [10] and the Nanxiong Basin, Guangdong Province, China [11–14] in Asia, but evidence from continental settings regarding other biological events that took place in the Cretaceous is very limited.

Upper Cretaceous Wangshi Group in Laiyang-Zhucheng, eastern Shandong Province, yields abundant dinosaur eggs [15–18]. Changes in this dinosaur egg fauna may represent important ecological changes during the transition between the middle and late portions of the Late Cretaceous [17,19,20].

Previous studies published since 1992, and especially since 2010, led us to travel to Laiyang, Jiaozhou and Zhucheng to investigate the Upper Cretaceous Wangshi Group, which yields dinosaur eggs. We collected specimens, and studied the water vapor conductance of different kinds of dinosaur egg from the Wangshi Group using biomechanical methods. In this paper we present the results of this research, and discuss the processes and causes underlying dinosaur diversity patterns in the middle-late Late Cretaceous.

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1 Geological setting and confirmation of the position of the boundary between the middle and late parts of the Late Cretaceous

The Upper Cretaceous Wangshi Group exposed in eastern Shandong Province is a set of continental clastic deposits composed of red conglomerate, sandstone and silty mudstone. The Wangshi Group directly overlies the Lower Cretaceous Qingshan Group, and crops out widely in areas including Laiyang, Jiaozhou and Zhucheng (Figure 1). In the 1920s, Tan [21] investigated in the area around Jiangjunding and Jingangkou in Laiyang County and established the 'Wangshi Series'. In the 1950s, dinosaur eggs [22,23] and some complete dinosaur skeletons including the holotype of the famous *Tsintaosaurus spinorhinus* [24] began to be recovered from the middle and upper parts of the 'Wangshi Series', catching the attention of government agencies whose responsibilities included aspects of geology or paleontology. Subsequently, some of these agencies initiated extensive research on the lithostratigraphy and biostratigraphy of the "Wangshi Series". *Shantungosaurus giganteus* and other dinosaur remains were found in Zhucheng [25]. In 1995, Cheng et al. [26] revised the lithostratigraphic divisions of the "Wangshi Series". The Wangshi Series was described as Wangshi Group and divided into, in ascending order, the Xingezhuang, Jiangjunding and Jingangkou Formations in the Laiyang area.

The Wangshi Group has yielded abundant hadrosaurid dinosaur specimens. Young [24] considered that the hadrosaurs from the Jiangjunding and Jingangkou Formations in the Wangshi Group were distinctive derived forms, and that they indicated a Late Cretaceous age for the Wangshi Group. Hu et al. [25] suggested that the dinosaurian fauna dominated by *Shantungosaurus giganteus* from the Xingezhuang Formation was early Late Cretaceous (corresponding to Cenomanian-Turonian) in age, whereas the dinosaur fauna represented by *Tanius sinensis* from the Jiangjunding Formation was middle Late Cretaceous (corresponding to Coniacian-Santonian) and the dinosaur fauna represented by *Tsintaosaurus spinorhinus* from the Jingangkou Formation was late Late Cretaceous (corresponding to Campanian). Recently, Wang et al. [27] compared and discussed the dinosaur egg faunas and strata of the major Chinese basins in which dinosaur eggs had been found, and also suggested the Jiangjunding and Jingangkou Formations of the Wangshi Group were middle and late Late Cretaceous respectively (corresponding to Coniacian-Campanian). In addition, the Jingangkou Formation has also been interpreted as late Late Cretaceous based on gastropod and ostracod biostratigraphy [28,29].

In modern stratigraphy, boundaries between different units are defined on the basis of two elements: recognizable geological events, and the time equivalence of a given event in different places. The dinosaur egg faunas from the Jiangjunding and Jingangkou Formations can be distinguished from one another with remarkable clarity [12]: the major egg type seen in the Jiangjunding Formation is spheroolithid, and that seen in the overlying Jingangkou Formation is ovaloolithid. Furthermore, the δ^{18}O signatures of

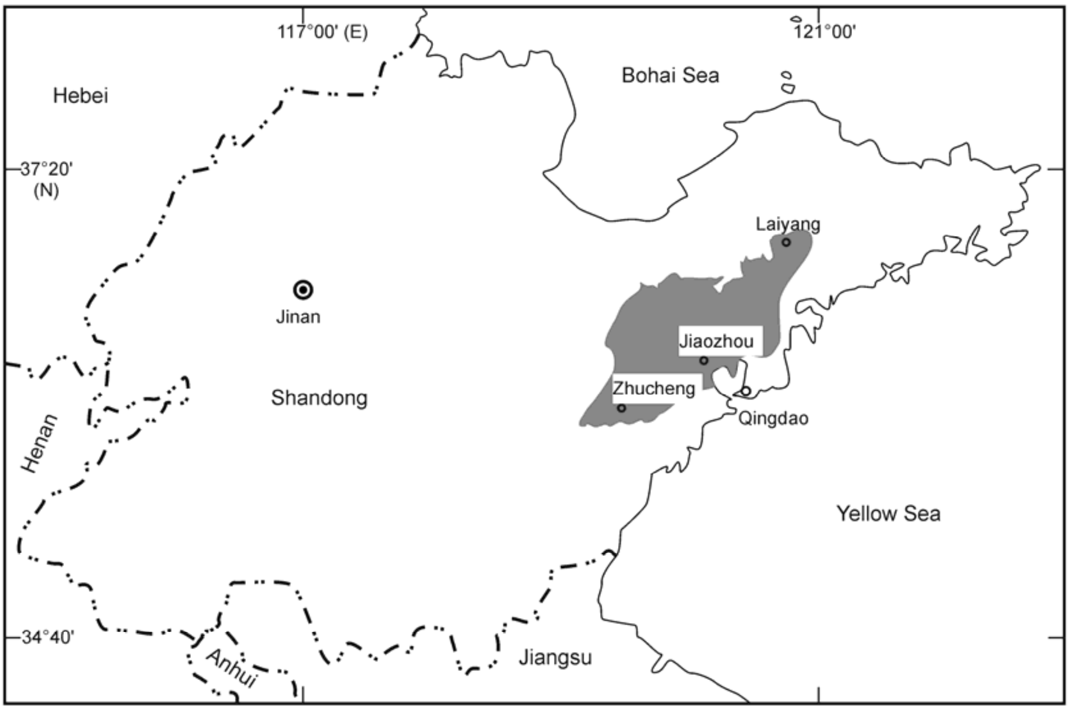

Figure 1 Distribution of the Wangshi Group in eastern Shandong Province.

dinosaur eggshell preserved in the two formations are also very different [20]. Therefore, the stratigraphic boundary between the middle and late parts of the Late Cretaceous in eastern Shandong should correspond to the boundary between the Jiangjunding and Jingangkou Formations.

2 Dinosaur diversity in the middle-late Late Cretaceous in Shandong

The dinosaur egg fauna of the Wangshi Group in eastern Shandong occurs mainly in the Jiangjunding and Jingangkou Formations of Laiyang, Jiaozhou and Zhucheng, and is especially abundant in the Wangshi Group of Laiyang. More than one hundred and twenty complete or nearly complete dinosaur eggs, and numerous eggshell fragments, have been found to date. Eleven oospecies representing five oogenera and four oofamilies (Elongatoolithidae, Spheroolithidae, Ovaloolithidae and Dictyoolithidae) have been erected [18,19,30,31]. Other specimens, especially some that have been collected in the past twenty years, include new types that remained undescribed but can be assigned to Elongatoolithidae, Ovaloolithidae or Prismatoolithidae based on preliminary observations. Since more time will be needed before a formal report can be published, these specimens are not discussed further in this paper.

(1) In total, six oospecies belonging to four oogenera have been recovered from the middle Upper Cretaceous Jiangjunding Formation:

Elongatoolithidae
Elongatoolithus elongatus
Dictyoolithidae
Protodictyoolithus jiangi
Spheroolithidae
Spheroolithus spheroides
S. chiangchiungtingensis
S. megadermus
Paraspheroolithus irenensis

(2) In total, seven oospecies representing three oogenera have been recovered from the upper Upper Cretaceous Jingangkou Formation:

Elongatoolithidae
Elongatoolithus elongatus
Spheroolithidae
Paraspheroolithus irenensis
Ovaloolithidae
Ovaloolithus chinkangkouensis
O. monostriatus
O. tristriatus
O. mixtistriatus
O. laminadermus

Comparisons of eggshell microstructure among the aforementioned oospecies (Figure 2) show that *Protodictyoolithus jiangi*, *Spheroolithus spheroides* and *S. chiangchiungtingensis* have loosely arranged eggshell units and a well developed pore canal system. These oospecies have been found only in the middle Upper Cretaceous Jiangjunding Formation and never in the overlying Jingangkou Formation or other known upper Upper Cretaceous strata located elsewhere in China [11,19,32], suggesting that the dinosaurs whose eggs are represented by these oospecies became extinct in the middle Late Cretaceous. *Paraspheroolithus irenensis* is characterized by tightly arranged eggshell units, with pore canals resembling those of spheroolithids but a

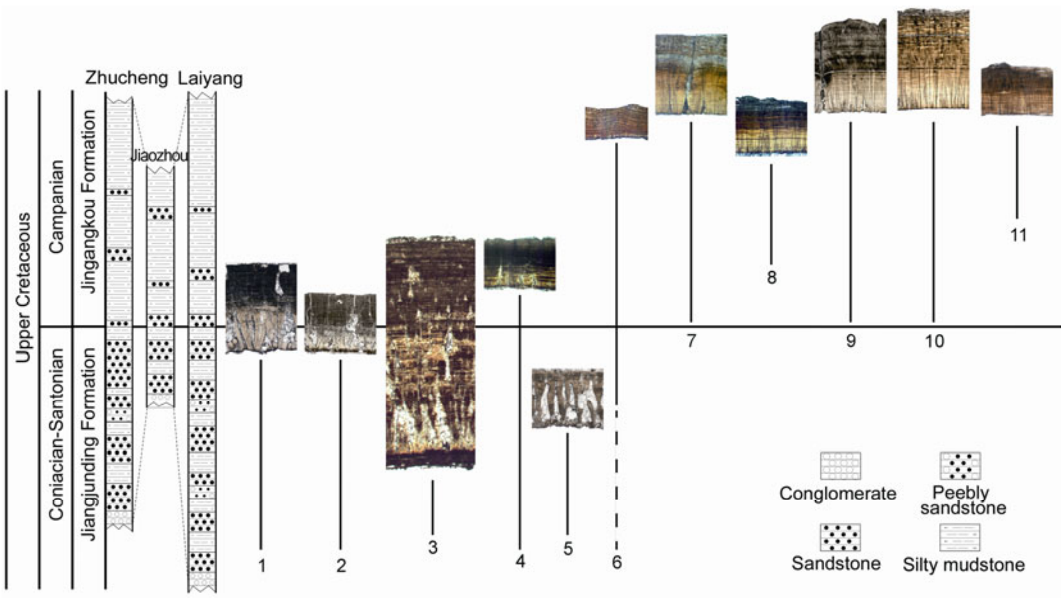

Figure 2 Stratigraphic occurrence of oospecies in eastern Shandong Province. 1, *Spheroolithus spheroides*; 2, *S. chiangchiungtingensis*; 3, *S. megadermus*; 4, *Paraspheroolithus irenensis*; 5, *Protodictyoolithus jiangi*; 6, *Elongatoolithus elongatus*; 7, *Ovaloolithus chinkangkouensis*; 8, *O. monostriatus*; 9, *O. mixtistriatus*; 10, *O. tristriatus*; 11, *O. laminadermus.*

lower pore density. This type of dinosaur egg occurs no lower than the bottom of the Jingangkou Formation. The eggshell microstructure of elongatoolithids and ovaloolithids is basically similar to that of avian eggs, with tightly arranged eggshell units and very low pore density (Table 1). Elongatoolithids have been found in both the Jiangjunding and Jingangkou Formations, but ovaloolithids have only been found in the Jingangkou Formation. Based on available records, all known ovaloolithids have come from upper Upper Cretaceous strata [11,19,32,33], strongly suggesting that a new dinosaur fauna characterized by the production of ovaloolithid eggs evolved in the late Late Cretaceous.

3 Water vapor conductance of dinosaur eggshell and the nest microenvironment

Successful egg hatching must have been a crucial issue for dinosaur reproduction and survival. During incubation, the embryo exchanges gases with the environment through a large number of pores that penetrate the egg surface, dissipating water and carbon dioxide generating by metabolic activity and absorbing oxygen continually. The gas flow rate through the pores is a function of factors including eggshell structure, nest temperature and humidity, and oxygen and carbon dioxide levels. The eggshell's structural fitness for the incubation environment is an essential determinant of the embryo's ability to maintain normal metabolism. Seymour [34] considered that water vapor conductance G_{H_2O}, mg/(d mmHg) values estimated from dinosaur eggshell structural parameters could provide a reliable basis for inferences regarding the nesting environments in which the eggs were incubated.

In order to improve current understanding of the mechanisms responsible for generating dinosaur diversity, we estimated eggshell water vapor conductance for well-preserved specimens of *Elongatoolithus elongatus*, *Ovaloolithus chinkangkouensis*, *Paraspheroolithus irenensis*, *Spheroolithus spheroides*, *Spheroolithus chiangchiungtingensis* and *Protodictyoolithus jiangi* from the Wangshi Group.

Calculating the eggshell G_{H_2O} for a given oospecies requires knowledge of the following macro- and microstructural parameters:

(1) Egg volume (V) and surface area (S). Egg volume can be estimated from the following empirical equation, derived from statistical data on avian eggs by Hoyt [35],

$$V = Kv \times L \times B^2, \quad (1)$$

where L is the long axis of the egg (cm), B is the equatorial diameter (cm), and Kv is the index of volume. For *Paraspheroolithus irenensis*, *Spheroolithus spheroides*, *S. chiangchiungtingensis*, *Ovaloolithus chinkangkouensis* and *Protodictyoolithus jiangi*, the shape of which is similar to that of avian eggs, we use the Kv value 0.507 directly based on Hoyt's calculation [35]. However, Kv must be corrected for *Elongatoolithus elongates* because of its elongated shape.

$$Kv = 0.5228 - 0.1033 \times As + 0.0740 \times Bi, \quad (2)$$

where As, asymmetry, and Bi, bicone, are respectively given by the following equations [36]:

$$As = (Rb - Rp) \times \left(L/B^2\right), \quad (3)$$

Table 1 Macro- and micro-structural parameters and water vapor conductance values for six oospecies from eastern Shandong Province

	Elongatoolithus elongatus	*Ovaloolithus chinkangkouensis*	*Paraspheroolithus irenensis*	*Spheroolithus spheroides*	*Spheroolithus chiangchiungtingensis*	*Protodictyoolithus jiangi*
Length (L, cm)	15.0	8.8	8.5	8.1	8.1	13.7
Equatorial diameter (B, cm)	5.6	6.7	7.0	7.1	7.7	12.3
Volume (V, cm^3)	248.030	199.818	213.478	207.108	243.486	1045.157
Surface area (S, cm^2)	215.16	167.89	174.10	169.46	187.46	497.75
Weight (g)	268	216	230	224	263	1129
Single pore area (mm^2)	0.0024±0.0017 n=27	0.0112±0.0136 n=38	0.0216±0.0303 n=207	0.0180±0.026 n=110	0.0169±0.018 n=56	0.0037±0.0055 n=537
Pore density (per mm^2)	0.831	0.780	1.470	3.113	2.524	45.740
Pore number	17880	13091	25596	52751	47308	2276706
Total pore area (Ap, cm^2)	0.44	1.46	5.53	9.28	7.99	83.97
Effective pore length (L, mm)	0.83	2.0	1.8	1.6	1.5	1.4
Water vapor conductance (G_{H_2O}, mg/d mmHg)	126	176	741	1430	1283	14450
Water vapor conductance for avian eggs of similar weight (G_{H_2O}, mg/d mmHg)	42	35	37	36	42	142
Water vapor conductance ratio for dinosaur egg to avian egg of similar weight	3	5	20	40	30	102

$$Bi = (Rb + Rp) \times (L/B^2) - 1, \quad (4)$$

where *Rb* and *Rp* are the radii of curvature of the egg's blunt and pointed ends, respectively.

Typical lengths and equatorial diameters for *Paraspheroolithus irenensis*, *Spheroolithus spheroides*, *S. chiangchiungtingensis*, *Ovaloolithus chinkangkouensis* and *Protodictyoolithus jiangi* were obtained from the literature [15,16,18]. Length and equatorial diameter values for *Elongatoolithus elongatus* were obtained directly from the well-preserved eggs in the nest IVPP V 734, by averaging the measured dimensions of the individual eggs.

To calculate radii of curvature for the blunt and pointed ends of *Elongatoolithus elongatus*, we imported a photograph of V 734 into drawing software CAXA 2007, and worked out the radii of curvature of the blunt and pointed ends of the well-preserved eggs.

Egg surface area can be calculated according to the following equations [37], once volume has been estimated,

$$S = Ki \times V^{2/3}, \quad (5)$$

$$Ki = 4.393 + 0.394El, \quad (6)$$

$$El = L/B, \quad (7)$$

where *Ki* is the surface-volume index, and *El* is elongation.

(2) Total pore area (*Ap*). Tangential sections were made through the columnar layer of the eggshell for *Paraspheroolithus irenensis*, *Spheroolithus spheroides* and *S. chiangchiungtingensis*, near the outer surface of the eggshell for *Elongatoolithus elongatus* and *Protodictyoolithus jiangi*, and through the upper part of the columnar layer for *Ovaloolithus chinkangkouensis*. Each tangential section was made using an EXAKT 300CP automatic microtome, and photographed through a Leica DMRX microscope. For each tangential section, the number of visible pores was counted and this value was used to calculate pore density by dividing by the total area of the section. The area of each complete pore was measured using AutoCAD 2008, and an average pore area was calculated for each oospecies. Assuming the pores to be evenly distributed on the egg surface, *Ap* is the product of average pore area, pore density and eggshell surface area.

(3) Effective length of pore canal (*Lp*). The eggshell cones of *Spheroolithus spheroides* and *S. chiangchiungtingensis* are arranged loosely, seldom forming complete pores. Therefore, the effective length of each pore canal corresponds to the thickness of columnar layer. In contrast, the eggshell cones of *Paraspheroolithus irenensis*, *Ovaloolithus chinkangkouensis* and *Elongatoolithus elongatus* are arranged in such a way that the pore canals extend to the inner surface of eggshell, making their effective length equivalent to the thickness of the eggshell itself. The eggshell units of *Protodictyoolithus jiangi* are arranged quite loosely, fusing together only near the outer surface of the eggshell to form a very thin even layer. Eggshell units in other parts of the eggshell are isolated from each other, and do not form complete pore canals. Considering that the organic matter that originally filled the irregular lacunae between eggshell units would have blocked the diffusion of water vapor, the effective length of each pore canal can be regarded as equal to eggshell thickness.

Eggshell thickness values for *Paraspheroolithus irenensis* and *Elongatoolithus elongatus* are based on the literature [16,30], whereas those for other taxa were obtained directly from specimens.

Once the aforementioned parameters have been estimated, the water vapor conductance of a given type of eggshell G_{H_2O} [mg/(d mmHg)] under given temperature conditions can be obtained from the following formula [38]:

$$G_{H_2O} = (C/RT) \times D_{H_2O} \times (Ap/Lp), \quad (8)$$

where *C* is a conversion constant 1.56×10^9 (secmg)/(dmol), *R* is the gas constant 6.24×10^4 (cm^3 mmHg)/(mol K), *T* is the absolute temperature in the nest during incubation (K), D_{H_2O} is the binary diffusivity between water vapor and air, 0.292 cm^2/s [34] at 30°C, *Ap* is the total pore area of the eggshell (cm^2), and *Lp* is the effective length of each pore canal (mm).

Structural parameters and estimated conductance values for six oospecies from the Upper Cretaceous Wangshi Group of eastern Shandong are shown in Table 1. Estimated eggshell water vapor conductance for *Spheroolithus spheroides*, *S. chiangchiungtingensis* and *Protodictyoolithus jiangi* at 30°C are 1430, 1283 and 14450 mg/(d mmHg), values that are respectively 40, 30 and 102 times higher than those for avian eggs of similar weight. The estimated eggshell water vapor conductance for *Paraspheroolithus irenensis* is 741 mg/(d mmHg), 20 times higher than that of an avian egg of similar weight; and estimated eggshell water vapor conductance for *Elongatoolithus elongatus* and *Ovaloolithus chinkangkouensis* are 126 and 176 mg/(d mmHg), respectively 3 and 5 times higher than those for avian eggs of similar weight.

Seymour [34] reported that water vapor conductance values were 1203, 17000 and 189 mg/(d mmHg) at 30°C for eggs he considered to have been laid by, respectively, *Hypselosaurus* (Megaloolithidae) from France, a sauropod (Faveoloolithidae) and "*Protoceratops*" (Elongatoolithidae) from Mongolia. He considered these conductance values to be very high, being respectively over 7, 100 and 4 times higher than those of avian eggs of similar weight. Hence, these dinosaur eggs were likely buried in sand or constructed nesting mounds of soil for incubation. The nest microenvironment was humid, with a low concentration of O_2 but a high concentration of CO_2. Mou [39] estimated water vapor conductance values of 136, 120 and 231 mg/(d mmHg) at 30°C for eggs of three elongatoolithid oospecies from the Nanxiong Basin in Guangdong Province, China, values over 2 to over 3 times higher than those for avian eggs of similar weight. These results also indicate that incubation involved burial. Recently, Deeming [40] collected comparable data for eggs of more than 40 oospecies, including spheroolithids, elongatoolithids, megaloolithids, prismatoolithids, dendroolithids and faveoloolithids. Again, calculations demonstrated that these eggs were probably buried in some substrate for incubation.

Because birds usually incubate their eggs in nests built in trees or other ventilated places, water vapor conductance values for avian eggshell are relatively low. Equivalent values for modern non-avian reptiles are comparatively high, because their eggs are incubated in humid environments. In *Alligator mississippiensis*, eggshell water vapor conductance is 5 times higher than in an avian egg of similar weight [41], and conductance is also high in the eggs of modern mound-nesting birds. The water vapor conductance of the eggs of a kind of swallow that burrows in sand banks is 1.42 times higher than that of the eggs of another kind of swallow that nests in the open [42].

Table 1 shows that eggshell water vapor conductance values are 4–115 times higher for *Spheroolithus spheroides*, *S. chiangchiungtingensis*, *Protodictyoolithus jiangi* and *Paraspheroolithus irenensis* than for *Elongatoolithus elongatus* and *Ovaloolithus chinkangkouensis*, indicating that eggs of the former set of oospecies were incubated in more humid environments.

4 The reasons for dinosaur diversity during the transition between the middle and late parts of the Late Cretaceous

Modern avian and non-avian reptile eggs lose a certain amount of water during incubation. The total amount of water typically lost from an avian egg amounts to 14%–18% of the initial weight of the whole egg under normal conditions [43,44]. If the amount of water lost during incubation reaches 25% of the initial weight of the whole egg, the probability of successful hatching will decrease sharply [30]. There is evidence that some reptile eggs absorb water from humid sand during incubation [45].

According to Zhao et al. [20], δ^{18}O values for dinosaur eggshells from the Jiangjunding Formation of the Wangshi Group (previously known as the middle part of the Wangshi Group) are between −7.37‰ and −8.42‰, and average −7.83‰. By contrast, δ^{18}O values of dinosaur eggshells from the Jingangkou Formation of the Wangshi Group (previously known as the upper part of the Wangshi Group) are between −4.47‰ and −5.25‰, and average −4.91‰. This research shows that δ^{18}O values obtained from dinosaur eggshells from the Jiangjunding Formation are relatively low, indicating a warm and humid climate, but whereas δ^{18}O values of dinosaur eggshells from the Jingangkou Formation are relatively high, indicating a dry climate during deposition of the Jingangkou Formation.

Dry climate undoubtedly affected the microenvironment of the nest during dinosaur egg incubation, especially in the cases of the dictyoolithids and spheroolithids. As mentioned above, the most distinctive characteristics of these two types of dinosaur egg are loosely arranged eggshell units, a well-developed pore canal system and very high water vapor conductance. The climate of eastern Shandong was relatively humid in the middle Late Cretaceous, and water loss during incubation would have been correspondingly low. This situation would have been conducive to embryonic development. In the late Late Cretaceous, the climate became drier, and substrates accordingly less moist. The dry conditions would have increased the eggshell water vapor conductance in dictyoolithids and spheroolithids, causing embryos contained in such eggs to die as a result of dehydration. In contrast, the eggs of elongatoolithids and ovaloolithids are basically similar in structure to those of birds. The eggshell water vapor conductance values of these eggs would have been relatively low, because of their tightly arranged eggshell units and very low pore density. Elongatoolithids and ovaloolithid eggs are clearly more structurally refined than those of dictyoolithids and spheroolithids with regard to preventing excessive loss of water.

The above conclusion reinforces the general rule that research on dinosaur eggs from well studied strata using a synthesis of geochemical, biomechanical and histological methods can provide reliable evidence bearing on paleoclimatic and paleoenvironmental changes during continental Cretaceous, as well as issues of dinosaur diversity and dinosaur extinction.

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