Statistical Approach for Classification of Dinosaur Eggs from the Heyuan Basin at the Northeast of Guangdong Province

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Abstract: The Zhutian and Dafeng formations (Upper Cretaceous) of the Heyuan Basin in northeastern Guangdong Province, China, have produced thousands of dinosaur eggs. Macromorphological features (egg diameter, egg shape, outer surface texture, and shell thickness) of 461 eggs were analyzed using non-destructive techniques and subjected to statistical analyses in order to assess their diversity and taxonomic affinities. Three types (1, 2 and 3) of eggs were discerned based on shape and outer surface morphology. Type 1 eggs are spherical to ellipsoidal in shape and have a rough surface. Three subtypes (Type 1-A-1, 1-A-2, and 1-B) are apparent from scatter plots and cluster analyses of egg diameters and shell thickness. Type 2 eggs are elongate with linear ornamentation on the surface, and are comparable to eggs that belong to the oofamily Elongatoolithidae. Type 3 eggs are elongate with a smooth surface, and are assigned to the oofamily Prismatoolithidae. Macromorphological features of the various egg types suggest that Type 1 could have been laid by ornithischian, sauropod or therizinosaur dinosaurs, Type 2 by oviraptorids, and Type 3 by troodontids. This study represents the first comprehensive statistical analysis of macrofeatures of dinosaur eggs, and reveals taxonomic diversity in the dinosaurs that were laying eggs in the Upper Cretaceous Heyuan area heretofore unrecognized in skeletal remains.

Key words: dinosaur egg, Nanxiong Group, Late Cretaceous, Heyuan Basin, Guangdong, China

1 Introduction

Fossil eggs have been classified parataxonomically using various features of the eggs, including eggshell structure, ornamentation, pore shape, eggshell thickness, and egg shape (for review see Mikhailov, 1991; Mikhailov et al., 1996; Zelenitsky et al., 1996; Zelenitsky and Hirsch, 1997). Although both quantitative and qualitative features have been used to establish new oospecies or assign specimens to existing ootaxa, few studies have incorporated statistical analyses of these features in order to establish or classify ootaxa. Some researchers have used statistical methods as a means of differentiating ootaxa among eggshell fragments using shell thickness or various micromorphological features (e.g., shell unit width) (Panadés I Blas, 2002; Panedés I Blas, 2005). However, no study has used statistical analyses of macromorphological features (e.g., egg dimensions and eggshell thickness) to classify ootaxa, which is likely due to limited sample sizes of well-preserved fossil eggs from most localities.

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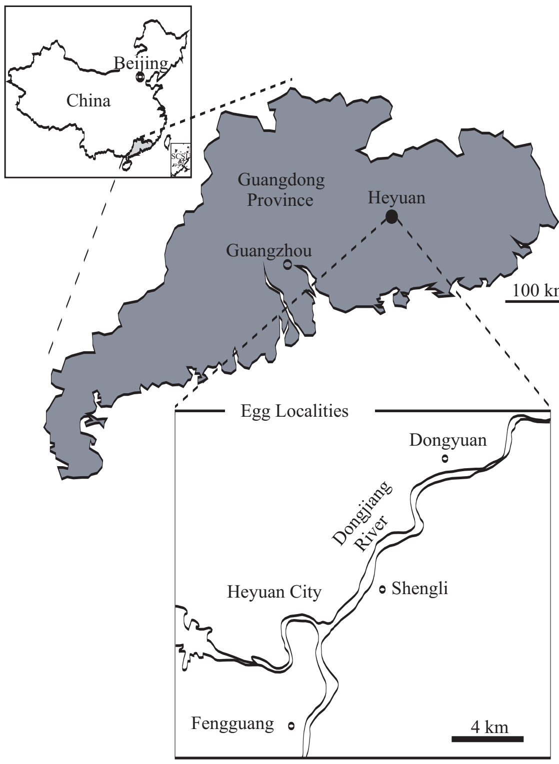
The Heyuan Basin in northeastern Guangdong Province, China (Fig. 1) has produced thousands (>12000) of complete or nearly complete fossil eggs from Upper Cretaceous rocks (Dafeng and Zhutian formations) of the Nanxiong Group (see Lü, 2005; Huang, 2006). Five ootaxa (*Paraspheroolithus sanwangbacunensis*, *Dendroolithus fengguangcunensis*, *Macroolithus yaotunensis*, *Elongatoolithus elongatus,* and *Prismatoolithus heyuanensis*) have been identified so far from the region, based primarily on studies of the eggshell microstucture (Fang et al., 2005; Lü et al., 2006). Although a large number of well-preserved eggs are known from Heyuan, statistical analysis of egg characteristics have yet to be used to classify these fossils.

A



B

System	Series	Group	Formation
Paleogene	Eocene	Danxia Gr.	
	Paleocene		Shanghu Fm.
Cretaceous	Upper	Nanxiong Gr.	Zhenshui Fm.
			Zhutian Fm.
			Dafeng Fm.
Jurassic	Lower		Jinji Fm.

Fig. 1. Locality map and stratigraphic position of Heyuan eggs: A, localities of eggshells (samples are collected from Dongyuan, Shengli, and Fengguang areas); B, stratigraphic positions of the Zhutian and Dafeng formations with fossil eggs (modified from Lü, 2005).

In the present study we examine a large number of eggs and use statistical procedures to classify over 450 eggs from Heyuan, based on egg shape, egg size, outer surface texture, and shell thickness. We also discuss the egg morphotypes recognized using our statistical methods and compare them to those ootaxa previously recognized based on microscopic features.

Abbreviations: **D**, diameter of egg; **N**, number; **SD**, standard deviation; **ST**, eggshell thickness.

2 Materials and Methods

Four hundred and sixty-one complete and partial eggs, housed at the Heyuan Museum and given tentative specimen numbers (except HYMV-20), were examined. Most eggs are broken, crushed or covered by matrix, and the insides of the eggs are matrix-filled. Some eggs are preserved as partial clutches (clutch number 01–11), whereas all the other eggs are isolated. Non-destructive methods were used to document features of the eggs, including ornamentation type, shell thickness, and egg dimensions. Dimensions of the eggs were taken as: maximum length (D1), maximum breadth at equator (D2), and the breadth at equator of eggs, which intersects D2 at right angles (D3) (Fig. 2). Eggshell thickness was mostly measured from the equatorial region, or from regions between the equator and the poles; some were taken from around polar regions due to poor preservation of specimens. Among 461 eggs, three dimensions were measured in 24 eggs, two dimensions were measured in 136 eggs, one dimension was measured in 140 eggs, and only shell thickness was measured for the remainder of the eggs. Egg dimensions were measured using a Mitutoyo digital caliper, model # CD-20CX (accuracy of ± 0.02 mm), and thickness was measured using calipers or a Mitutoyo digital micrometer, model # CPM30-25MJ (accuracy of ±2 μm). Ornamentation was observed using a hand lens.

Statistical analyses were conducted based on the measurements of the three dimensions and shell thickness. In order to assess if there were significant differences between two egg populations and to classify the various egg samples, the measurement data were subject to statistical analyses, including independent samples T-test and cluster analyses, using SPSS software for Windows 11.01J (SPSS Inc. Chicago, IL, USA). Cluster analyses were performed on the data using three (D1, D2, and ST) and four (D1, D2, D3, and ST) variables. Eleven combinations were used for the cluster analyses: Euclid

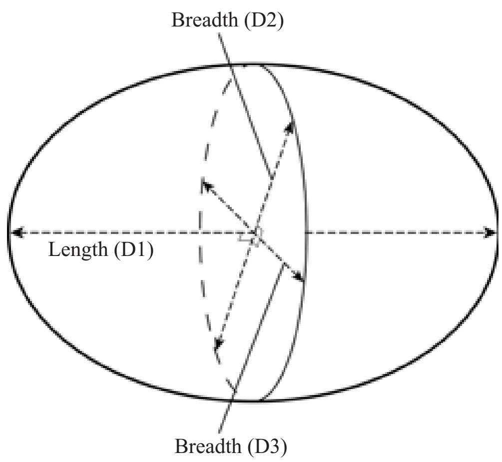


Fig. 2. Illustration of three axes in one egg (length (= D1) ⊥ maximum breadth (= D2) ⊥ another breadth (= D3)).

distance + Average Linkage (Between Groups), Average Linkage (Within Groups), Single Distance, Complete Linkage, Squared Euclid distance + Average Linkage (Between Groups), Average Linkage (Within Groups), Single Distance, Complete Linkage, Centroid, Median, and Ward methods.

3 Results

The eggs are categorized into three types, based on egg shape and outer surface morphology: Type 1, spherical to sub-spherical eggs with a rough surface texture; Type 2, elongate ellipsoidal eggs with linear ornamentation on outer surface; Type 3, elongate ellipsoidal eggs with a smooth surface (Fig. 3). Only Type 1 eggs were subject to statistical analyses because of the large number of samples, and the wide range of egg size and shell thickness.

3.1 Type 1: spherical to sub-spherical eggs

Spherical to sub-spherical eggs are from the Shengli or

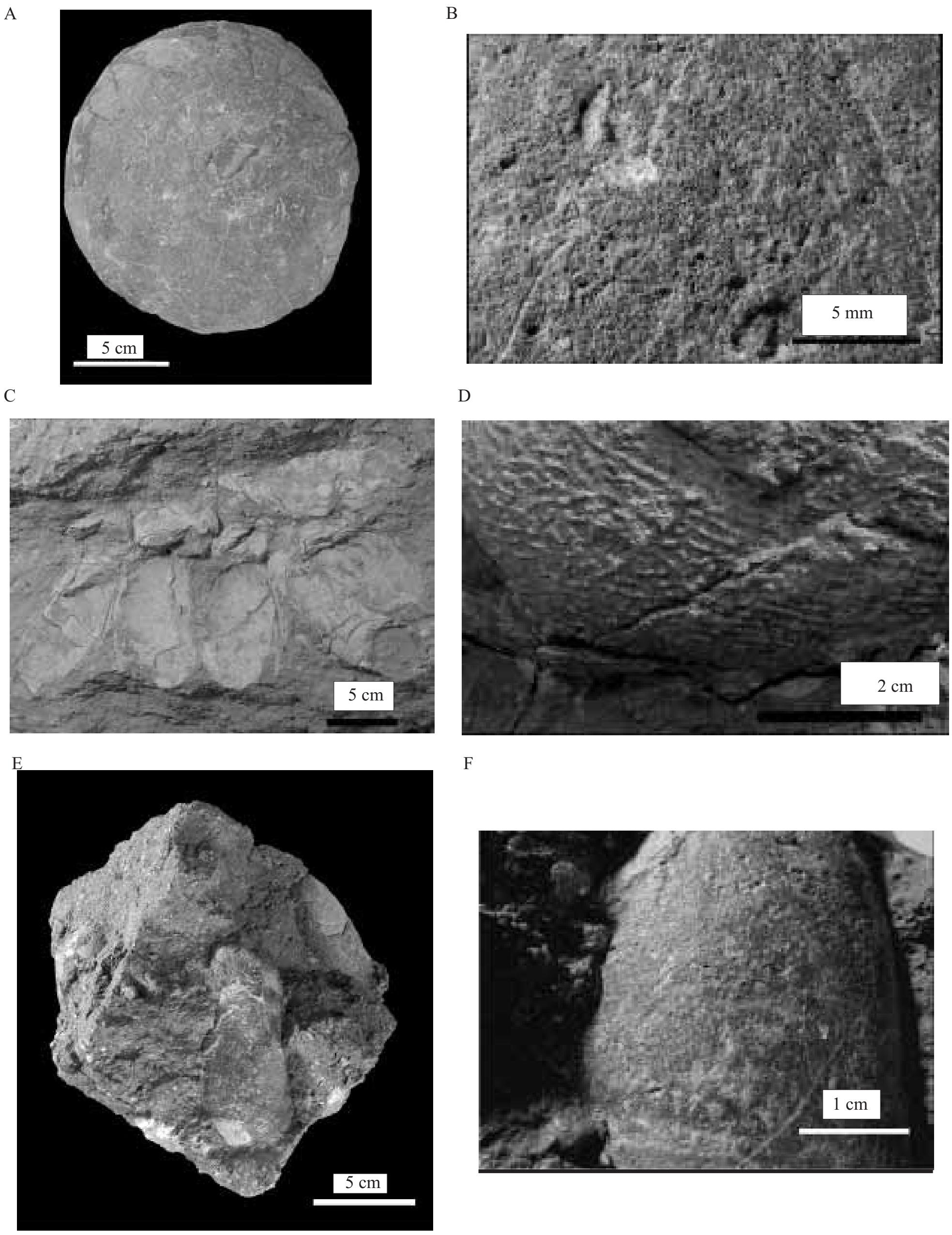


Fig. 3. Photographs of fossil eggs collected from Heyuan area: A, round to elliptical eggs with rough surface (Type 1); B, magnification of outer surface (Type 1); C, elongate eggs with linearituberculate ornamentation (Type 2); D, magnification of outer surface (Type 2); E, elongate eggs with smooth surface (Type 3; *Prismatoolithus heyuanensis*, HYMV-20); F, magnification of smooth outer surface (HYMV-20-1).

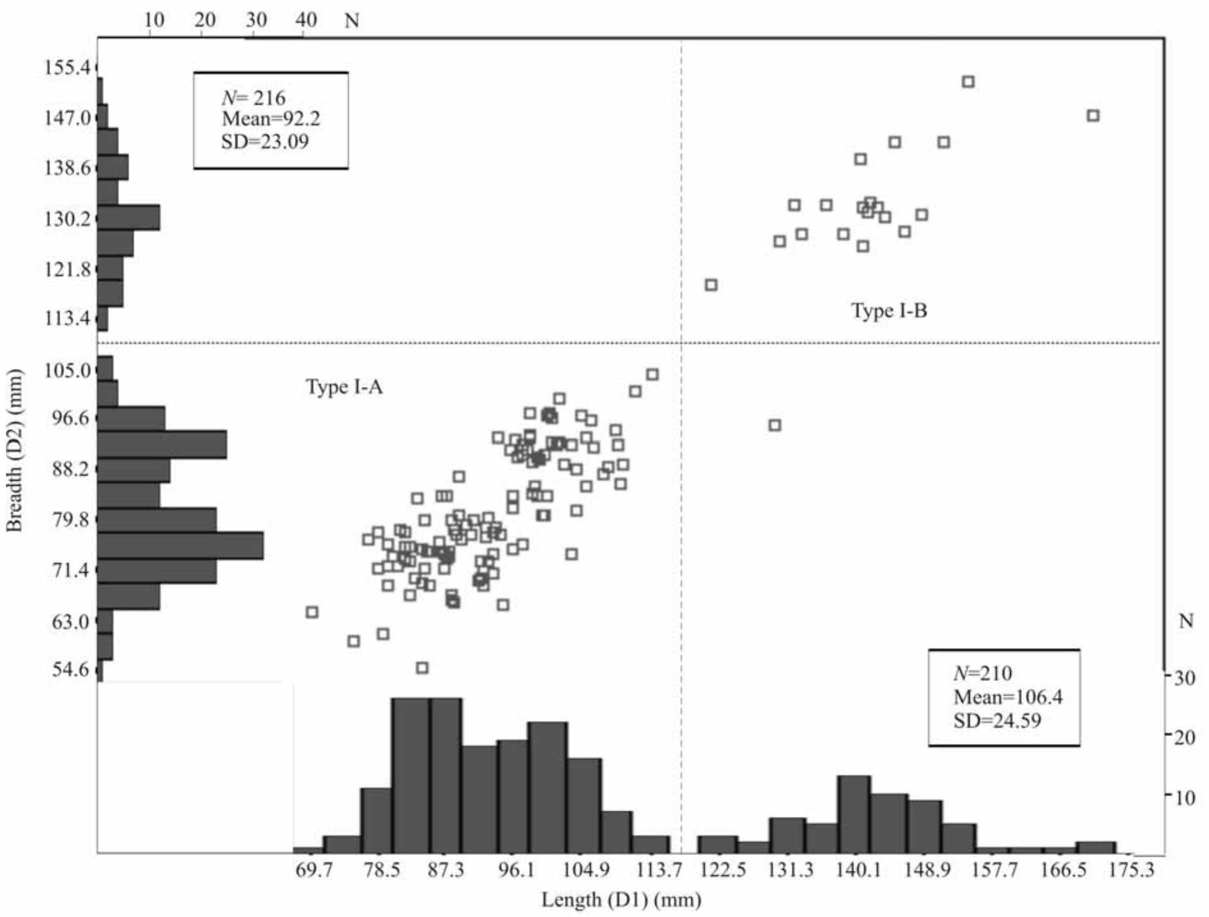


Fig. 4. Histograms and a scatter plot of length and width in Type 1 eggs, showing two peaks for Type 1-A and Type 1-B.

Fengguang areas of the Dafeng Formation (Huang, 2006) (Fig. 1), and represent the bulk of the eggs collected for this study (*n*=443) (Fig. 3A). The outer surface of these eggs is rough and lacks distinct ornamentation (Fig. 3B). This type contains a wide range of egg sizes (70–170 mm in length and 50–150 mm in breadth) and shell thicknesses (0.5–3.0 mm).

Histograms and scatter plots of egg length and breadth, along with independent samples T-test, shows that there are two significantly different populations for Type 1 eggs, indicating two different groups (Fig. 4; Table 1): (1) Type 1-A (*n*=204) is characterized by small eggs (about 70–120 mm in length and 50–110 mm in breadth) with a wide range of shell thickness (about 0.5–3.0 mm); and (2) Type 1-B (*n* = 86) is characterized by large eggs (about 120–170 mm in length and 110–150 mm in breadth) with a narrower range of shell thickness (about 0.5–1.5 mm) (Fig. 5).

Eggs of the group Type 1-A were subject to cluster analyses using four (D1, D2, D3, and ST) (*n* = 21) and three variables (D1, D2, and ST) (*n*=114), which revealed two major clusters (clusters of smaller eggs with thin eggshell and larger eggs with thick eggshell) in four-variable cluster

Table 1 Results of Independent T-test: A, descriptive statistics of Types 1; B, results of Independent T-test for Type 1, showing significant differences between Type 1-A and Type 1-B.

A

	Type	N	Mean	Standard error	Standard error of the mean
Length	Type 1-A	152	92.547	9.564	0.776
	Type 1-B	57	142.997	10.796	1.430
Breadth	Type 1-A	168	81.052	10.547	0.816
	Type 1-B	48	130.776	9.147	1.320

B

	T value	Degree of freedom	p
Length	−32.769	207	<0.001
Breadth	−32.035	86.225	<0.001

analyses (Fig. 6; Table 2). This result is supported by all 11 combinations: each dendrogram bifurcates and diverges smaller branches. In the three-variable cluster analyses (*n* = 114), eight combinations support two major clusters, but the results of other three combinations lack clear divisions (Table 2). Two major clusters are adopted by majority rule, and members of each cluster are concordant in the eight combinations (Fig. 7). As a result, Type 1-A can be further divided into two types: (1) Type 1-A-1 (Cluster 1) (*n*=58) is

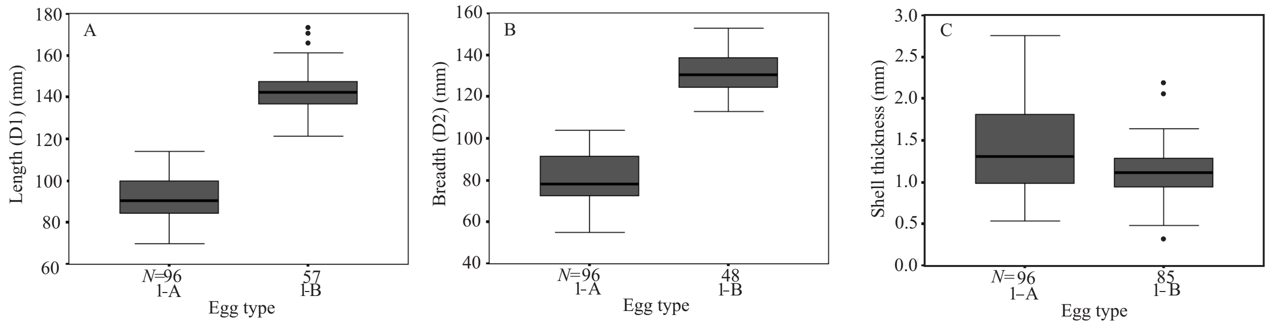
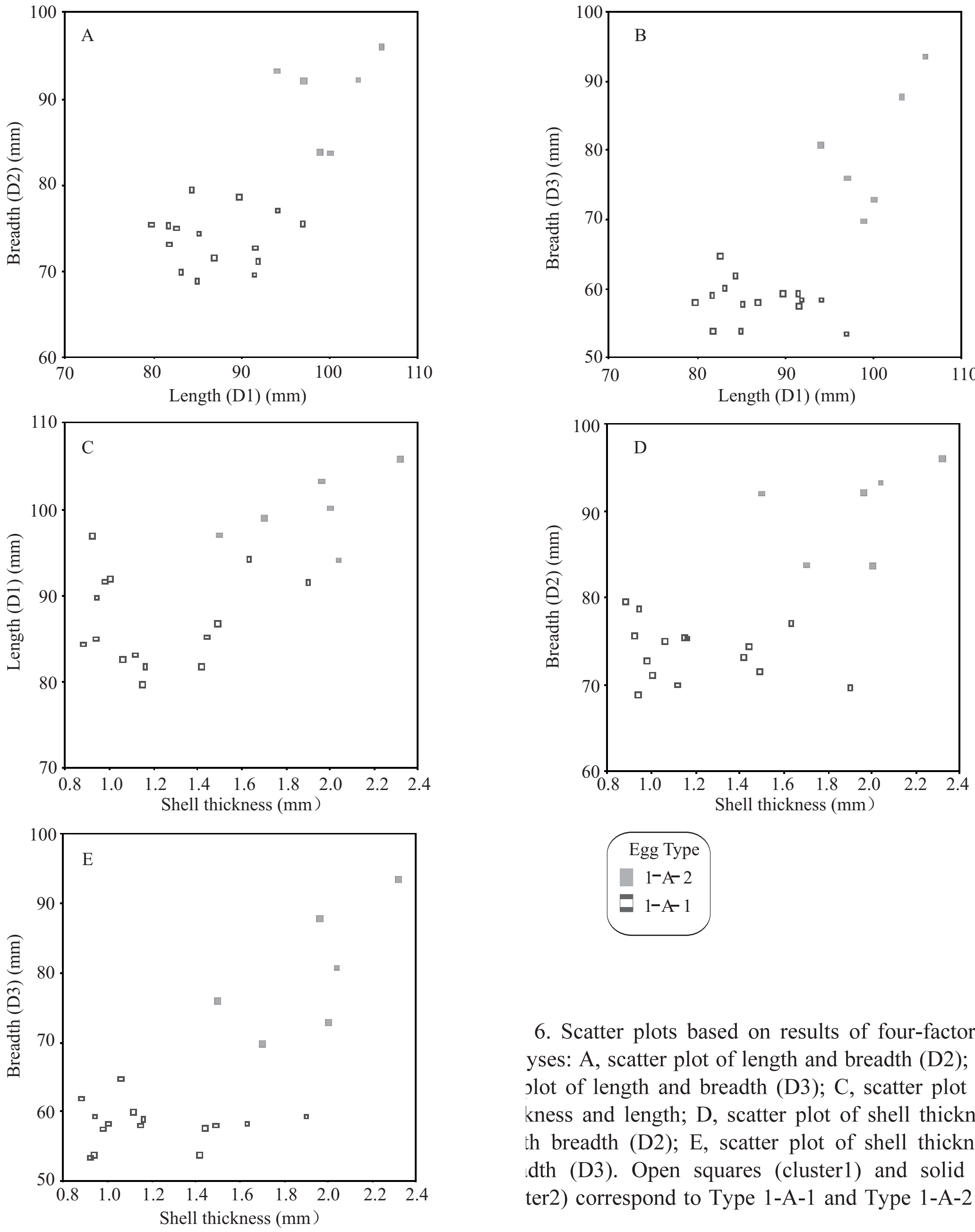


Fig. 5. Boxplots of Type 1-A and 1-B eggs, showing each type exhibits different length and breadth (D2), but Types 1-A and 1-B have the similar range of shell thickness: A, boxplot of length; B, boxplot of breadth (D2); C, boxplot of shell thickness. Black dots represent outliers.



6. Scatter plots based on results of four-factor cluster yses: A, scatter plot of length and breadth (D2); B, scat- plot of length and breadth (D3); C, scatter plot of shell kness and length; D, scatter plot of shell thickness and th breadth (D2); E, scatter plot of shell thickness and dth (D3). Open squares (cluster1) and solid squares ter2) correspond to Type 1-A-1 and Type 1-A-2 respec-

Table 2 Coefficients of two clusters derived from two cluster analyses using 11 combinations of methods, showing the distance of both clusters.

	4 factors cluster analysis coefficients	3 factors cluster analysis coefficients
Euclid distance		
Average linkage (between groups)	31.145	23.563
Average linkage (within groups)	18.9	16.43
Single linkage	14.131	×
Complete linkage	52.706	59.236
Squared euclid distance		
Average linkage (between groups)	1063.152	621.916
Average linkage (within groups)	520.781	365.914
Single linkage	199.687	×
Complete linkage	2777.919	3508.943
Centroid linkage	911.717	509.681
Median method	1048.118	×
Ward method	5207.809	20674.159

characterized by smaller eggs (about 70–100 mm in length and 55–85 mm in breadth) with thin eggshell (averaging 1.10 mm); and (2) Type 1-A-2 (Cluster 2) (n = 38) is characterized by larger eggs (about 95–115 mm in length and 80–105 mm in breadth) with thick eggshell (averaging 1.85 mm). Box plots show that each of the three types has different means and ranges of length and breadth. Type 1-A-2 has thicker shells than the other two types (Types 1-A-1 and 1-B) (Fig. 8). The ranges of variation around the mean for length and for breadth are similar between Types 1-A-1 and 1-A-2, whereas those of Type 1-B are greater than the former two types. These ranges of variation are comparable to those of known ootaxa with similar size and shape (e.g., *Spheroolithus*, *Ovaloolithus*, and *Megaloolithus*) (Young, 1954, 1965; Khosla and Sahni, 1995; Mohabey, 1998). The range of variation about the mean for eggshell thickness is comparable among these three types. In summary, statistical analyses reveal three morphotypes among the Type 1 eggs: (1) small eggs with thin eggshell (Type 1-A-1); (2) medium eggs with thick eggshell (Type 1-A-2); and (3) large eggs with thin eggshell (Type 1-B).

There are 10 partial clutches of Type 1 eggs (Fig. 9; Table 3). Two of the 10 clutches belong to Type 1-A-1 and four belong to Type 1-B. Type 1-A-2 eggs have not been identified among the clutches, and are only known from

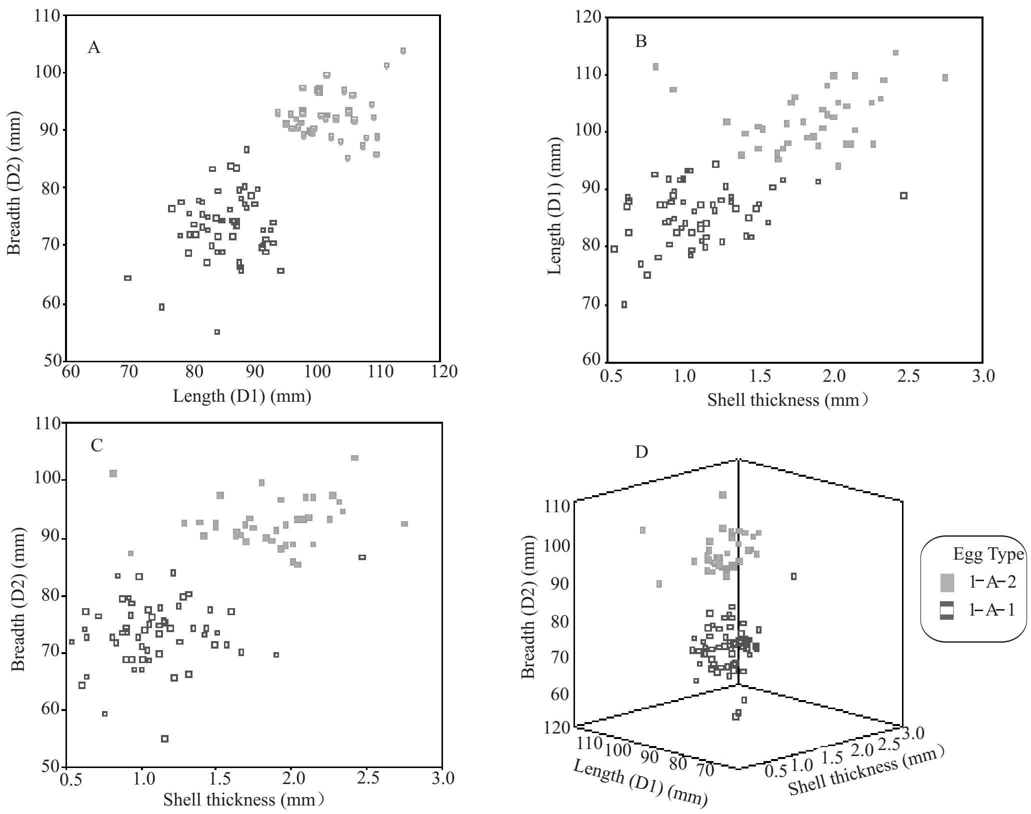


Fig. 7. Scatter plots based on results of three-factor cluster analyses: A, scatter plot of length and breadth (D2); B, scatter plot of shell thickness and length; C, scatter plot of shell thickness and breadth (D2); D, scatter plot of shell thickness, length and breadth (D2). Open squares (1-A-1) and solid squares (1-A-2) correspond to Type 1-A-1 and Type 1-A-2 respectively.

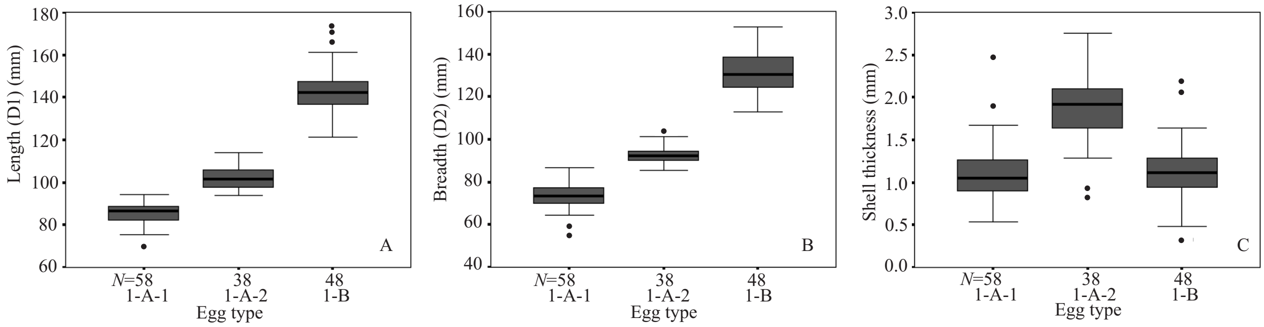


Fig. 8. Boxplots of Type 1-A-1, 1-A-2, and 1-B eggs, showing each type exhibits different length, breadth (D2), and shell thickness, but Types 1-A-1 and 1-A-2 have the similar ranges of variation around the mean for length and for breadth (D2), narrower than that of Type 1-B, whereas all three types have the similar range of variation around the mean for shell thickness: A, boxplot of length; B, boxplot of breadth (D2); C, boxplot of shell thickness. Black dots represent outliers.

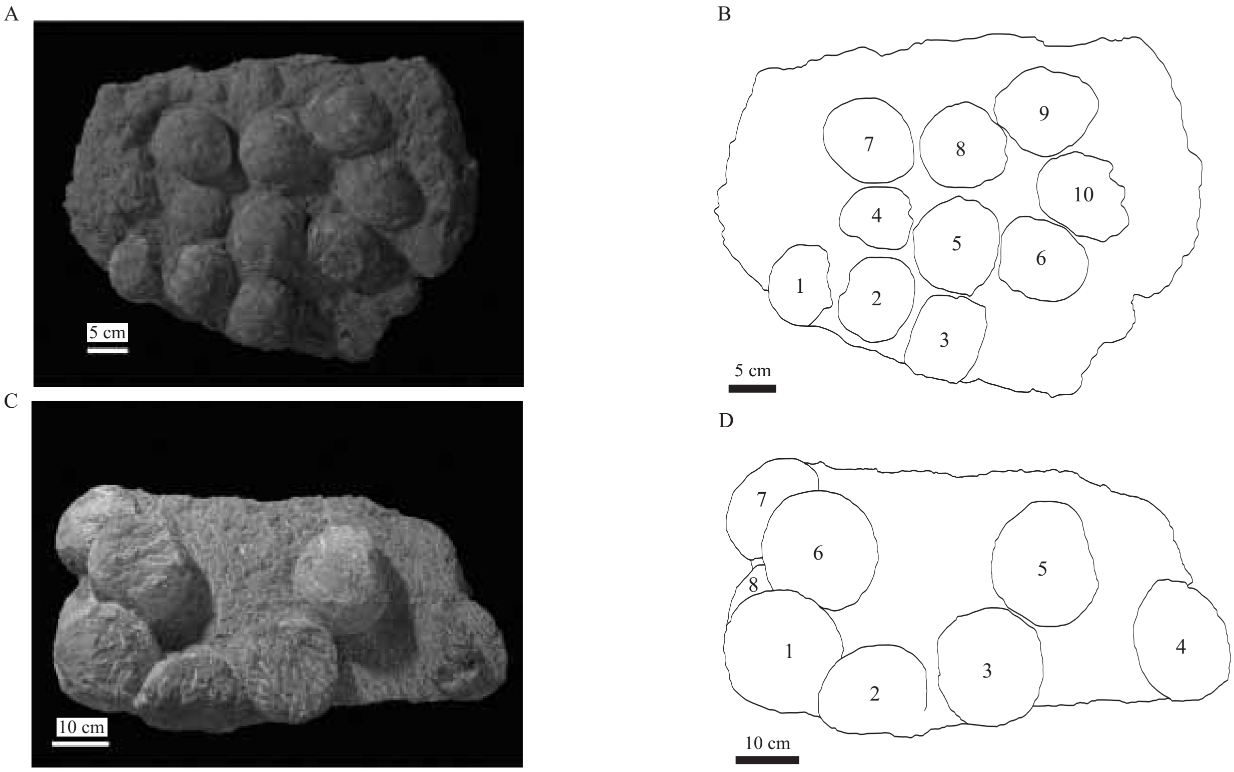


Fig. 9. Examples of round-egg clutches, showing randomly packing: A, a photograph of Type 1-A-1 egg clutch (Clutch02); B, a line drawing of Clutch02; C, a photograph of Type 1-B egg clutch (Clutch06); D, a line drawing of Clutch06.

isolated eggs. Clutches of Types 1-A-1 and 1-B contain at least 10 and eight eggs, respectively. Eggs are randomly arranged in a single layer. Shell thickness varies within a single clutch (Table 3) by up to a factor of two in some clutches of Type 1-A-1 (Clutch02 and Clutch04). The difference between the thickest and thinnest eggshells in most clutches of Type 1-B eggs (Clutch06, Clutch07, and Clutch08) is within 0.5 mm, and in Clutch09 of Type 1-B is up to 0.8 mm.

3.2 Type 2: elongate eggs with linear ornamentation

Elongate eggs in the Heyuan Basin were collected from the Dongyuan area of the Zhutian Formation (Huang, 2006) (Fig. 1). Fifteen eggs, most of which were partially broken and compressed, were examined. Twelve eggs are in a partial clutch (Clutch11) consisting of two circular layers, which are compressed vertically (Fig. 3C). Two other isolated eggs (specimen numbers g1 and g2) are oval-shaped and appear to have a broad and a narrow pole. Type 2 eggs have an average length of 160 mm, average breadth

Table 3 A list of Type 1 egg clutches, showing numbers of containing eggs, egg arrangement, and range of shell thickness in eggs laid by same parent (species).

Clutch No.	Egg No.	Type	Containing eggs	Arrangement	ST (mm)
Clutch01	10034-1–14	1	14*	Irregular?	0.85–1.48
Clutch02	a167–176	1-A-1	10	Irregular?	0.80–2.06
Clutch03	FG8449–8455	1	7*	Irregular?	0.55–1.29
Clutch04	FG8021–8026	1-A-1	6	?	0.54–1.22
Clutch05	9651–9654	1	4	?	0.95–1.60
Clutch06	c134–141	1-B	8	Irregular?	0.89–1.36
Clutch07	FG5216–5218	1-B	3	?	0.90–0.94
Clutch08	c142–147	1-B	3?	Irregular?	1.06–1.33
Clutch09	c148–154	1-B	7	Irregular?	0.74–1.51
Clutch10	96HC1-1–8	1	7	Irregular?	0.78–1.47

*Including a fragment.

of 60 mm, and average shell thickness of 0.95 mm (n=15). The eggshell thickness varies, depending on position in an egg (equatorial regions are thicker than polar regions), and the range of shell thickness in this type is relatively wide (0.67–1.26 mm). The outer surface of the eggs exhibits linearituberculate ornamentation (Fig. 3D), which consists primarily of linear ridges in the equatorial region and of nodes in the polar regions.

3.3 Type 3: elongate eggs with smooth ornamentation

Prismatoolithus heyuanensis was collected from the Upper Cretaceous Dongyuan Formation (equivalent to the upper part of the Dafeng Formation to the lower part of the Zhenshui Formation: Fang et al., 2005) of Fengguang area (Fig. 1). Three partial eggs were described previously as *Prismatoolithus heyuanensis* (HYMV-20). The eggs are smooth on the outer surface, 0.52 mm in shell thickness (n=3), elongate (~50 × 95 mm in diameter), and asymmetrical about the equator as described by Lü et al. (2006) for the holotype of *Prismatoolithus heyuanensis* (Fig. 3E, F).

4 Discussion

Previous studies of dinosaur eggs from Heyuan described two oospecies of elongatoolithid eggs (*Elongatoolithus elongatus* and *Macroolithus yaotunensis*), two oospecies of spherical eggs (*Dendroolithus fengguangcunensis* and *Paraspheroolithus sanwangbacunensis*), and one oospecies of prismatoolithid (*Prismatoolithus heyuanensis*) (Fang et al., 2005; Lü et al., 2006), some of which are comparable to the eggs studied here. Our quantitative and qualitative analyses of egg shape, egg size, outer surface morphology, and shell thickness of 461 eggs from Heyuan reveals these eggs can be classified into five different types (Fig. 10; Table 4). Type 1-A-1 and 1-B eggs are similar in egg size, shell thickness, and surface texture to. *P. sanwangbacunensis* (50 mm × 70 mm in size and 1.5 mm in shell thickness) and *D. fengguangcunensis* (150–170 mm in diameter and 1.6 mm), respectively. Type 1-A-2 have much thicker shells than *P. sanwangbacunensis* and *D. fengguangcunensis,* and are intermediate in size between these two ootaxa, and thus may represent an additional oospecies from this area. Type 2 eggs may also represent an additional oospecies that is intermediate in size to *Elongatoolithus elongatus* (144–149 mm × 61–67 mm; 0.7–1.1 mm in shell thickness) and *Macroolithus yaotunensis* (176–208 mm × 67–94 mm; ~1.6 mm), based on the values provided by Young (1965) and Zhao (1975). Type 3 eggs are the specimens of the holotype *P. heyuanensis* and differ from the other egg types in that they are elongate with a smooth outer surface and thin shells. Based on our analyses of 461 eggs, there may be as many as seven oospecies from the Heyuan area, five of which have been previously assigned to ootaxa. Although eggshells were not available for microscopic analysis for this study, such analyses may help verify the number of oospecies.

The taxonomic affinity of the three types of eggs can be determined based on various features. Macromorphological features, including egg shape and outer surface texture, indicate that Type 1 eggs could have been laid by

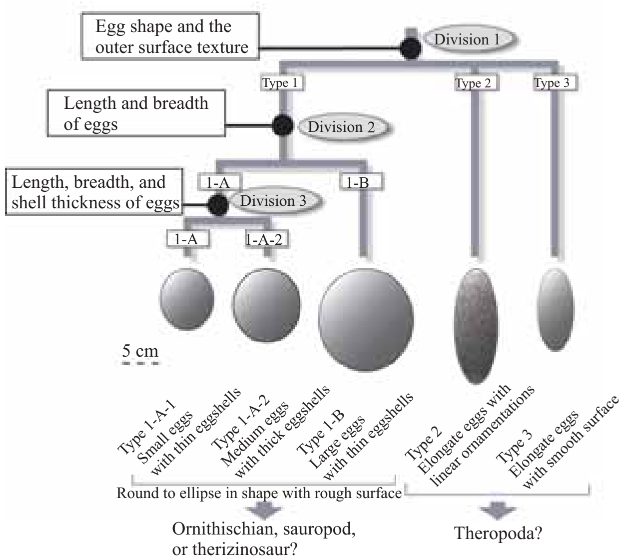


Fig. 10. Summary of fossil egg types at Heyuan area, showing five different types.

Table 4 Five types of fossil eggs from the Heyuan area.

Type	N	Shape	Outer surface ornamentation	Length (mm)	Breadth (mm)	Shell thickness (mm)
1-A-1	58	Round to ellipse	Rough	69.90–94.38 (Mean 85.57) (*N*=58)	55.03–86.77 (Mean 73.37) (*N*=58)	0.54–2.47 (Mean 1.10) (*N*=58)
1-A-2	38	Round to ellipse	Rough	93.99–113.98 (Mean 102.44) (*N*=38)	85.25–103.90 (Mean 92.67) (*N*=38)	0.82–2.76 (Mean 1.85) (*N*=38)
1-B	86	Round to ellipse	Rough	121.39–173.04 (Mean 143.00) (*N*=57)	112.98–152.72 (Mean 130.78) (*N*=48)	0.32–2.19 (Mean 1.12) (*N*=85)
2	15	Elongate	Linear ridges	About 160	About 60	0.67–1.26 (Mean 0.95) (*N*=15)
3	3	Elongate	Smooth	More than 95	More than 50	0.42–0.63 (Mean 0.52) (*N*=3)

ornithischian, sauropod or therizinosaur dinosaurs; the study of the microstructure of these eggs may further aid their identification (Mikhailov, 1991; Zelenitsky, 2004). Elongate eggs (Types 2 and 3) are assigned to theropods due to a combination of characters (elongate shape and linearituberculate ornamentation or smooth surface), features that are generally present in the eggs of more derived theropods (e.g., troodontids, oviraptorids) (e.g., Norell et al., 1994; Dong and Currie, 1996; Varricchio et al., 1997, 1999, 2002; Sato et al., 2005; Zelenitsky, 2006; Cheng et al., 2008; Zelenitsky and Therrien, 2008). The elongate shape and the linearituberculate ornamentation of the Type 2 eggs are comparable to elongatoolithid eggs, which are generally thought to belong to oviraptorosaurs since many such eggs are associated with their skeletal remains (Norell et al., 1994, 1995; Dong and Currie, 1996; Sato et al., 2005; Cheng et al., 2008; Weishampel et al., 2009; Fanti et al., 2012). The smooth-shelled, elongate eggs of *Prismatoolithus heyuanensis*, herein designated Type 3, are comparable to eggs assigned to troodontid theropods (Lü et al., 2006). Our study reveals taxonomic diversity in the dinosaurs laying eggs in the Upper Cretaceous Heyuan area beyond that recognized from skeletal remains, as only oviraptorids have been reported from the area thus far (Lü, 2002, 2005).

This study shows that otherwise similar dinosaur egg may be discriminated into multiple types using statistical analyses, provided a sufficiently large number of samples are available. These methods are useful for analysis of both micromorphological (Panadés I Blas, 2002; Panedés I Blas, 2005) and macromorphological features (this study). In spite of discoveries of abundant complete or nearly complete dinosaur eggs in China (e.g., Heyuan and Nanxiong basins in Guangdong Province, Xixia Basin in Henan Province, and Laiyang-Zhucheng Basin in Shangdong Province; Young, 1965; Zhao and Jiang, 1974; Cultural Relics Administrative Bureau of Henan Province, 1998; Huang, 2006), eggs are usually classified without resort to statistical methods. Because some egg types within a single morphotype show similar quantitative values for features (Mikhailov et al., 1996), statistical approaches may provide a more accurate classification for dinosaur eggs.

5 Conclusions

The Heyuan eggs could be clearly divided into three types (Types 1, 2, and 3) based on egg shape and outer surface texture of the eggshells. Type 1 eggs are spherical to sub-spherical with a rough surface, and are subdivided into three subtypes (Types 1-A-1, 1-A-2, and 1-B), based on length, breadth, height, and shell thickness. Type 2 eggs are elongate with linear ornamentation on the outer surface, and Type 3 eggs are elongate with a smooth surface. Based on the macromorphological features, Type 1 eggs could have been laid by ornithischian, sauropod or therizinosaur dinosaurs, Type 2 eggs by oviraptorids, and Type 3 eggs by troodontids. This study indicates a greater taxonomic diversity in the dinosaurs laying eggs in the Late Cretaceous Heyuan area, which is heretofore unrecognized from skeletal remains.

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References

Cheng, Y.N., Qiang, J., Wu, X.C., and Shan, H.Y., 2008. Oviraptorosaurian eggs (Dinosauria) with embryonic skeletons discovered for the first time in China. *Acta Geologica Sinica* (English edition), 82(6): 1089–1094.

Cultural Relics Administrative Bureau of Henan Province, 1998. *The research on the groups of fossil dinosaur eggs in Henan Province*. Henan Science and Technology Publishing House, Zhengzhou (in Chinese with English summary).

Dong, Z.M., and Currie, P.J., 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*, 33(4): 631–636.

Fang, X., Zhang, Z., Zhang, X., Lu, L., Han, Y., and Li, P., 2005. Fossil eggs from the Heyuan basin, Guangdong, China. *Geological Bulletin of China*, 24(7): 682–686 (in Chinese with English abstract).

Fanti, F., Currie, P.J., and Badamgarav, D., 2012. New specimens of Nemegtomaia from the Baruungoyot and Nemegt formations (Late Cretaceous) of Mongolia. *PLoS ONE*, 7(2): e31330. doi:10.1371/journal.pone.0031330

Huang, D., 2006. Brief introduction to vertebrate fossils from the Heyuan Basin, Guangdong Province. In: Lü, J.C., Kobayashi, Y., Huang, D., and Lee, Y.-N. (eds.), *Papers from the 2005 Heyuan International Dinosaur Symposium*. Beijing: Geological Publishing House, 1–9 (in Chinese with English abstract).

Khosla, A., and Sahni, A., 1995. Parataxonomic classification of Late Cretaceous dinosaur eggshells from India. *Journal of the Palaeontological Society of India*, 40: 87–102.

Lü, J.C., 2002. A new oviraptorid (Theropoda: Oviraptorosauria) from the Late Cretaceous of Southern China. *Journal of Vertebrate Paleontology*, 22(4): 871–875.

Lü, J.C., 2005. *Oviraptorid dinosaurs from Southern China*. Beijing: Geological Publishing House.

Lü, J.C., Azuma, Y., Huang, D., Noda, Y., and Qiu, L., 2006. New troodontid dinosaur eggs from the Heyuan Basin of Guangdong Province, Southern China. In: Lü, J.C., Kobayashi, Y., Huang, D., and Lee, Y.-N. (eds.), *Papers from the 2005 Heyuan International Dinosaur Symposium*. Beijing: Geological Publishing House, 11–18.

Mikhailov, K.E., 1991. Classification of fossil eggshells of amniotic vertebrates. *Acta Palaeontologica Polonica*, 36(2): 193–238.

Mikhailov, K.E., Bray, E.S., and Hirsch, K.F., 1996. Parataxonomy of fossil egg remains (Verterovata): principles and applications. J*ournal of Vertebrate Paleontology,* 16(4): 763–769.

Mohabey, D.M., 1998. Systematics of Indian Upper Cretaceous dinosaur and chelonian eggshells. *Journal of Vertebrate Paleontology*, 18(2): 348–362.

Norell, M.A., Clark, J.M., Demberelyin, D., Barsbold, R., Chiappe, L.M., Davidson, A.R., McKenna, M.C., Altengerel, P., and Novacek, M.J., 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science*, 266: 779–782.

Norell, M.A., Clark, J.M., Chiappe, L.M., and Dashzeveg, D., 1995. A nesting dinosaur. *Nature*, 378: 774–776.

Panadés I Blas, X., 2002. Does diversity of dinosaur eggshells means diversity of dinosaurs? *Journal of Vertebrate Paleontology*, 22(suppl. 3): 94A.

Panadés I Blas, X., 2005. Diversity versus variability in Megaloolithid dinosaur eggshells. *PalArch's Journal of Vertebrate Paleontology*, 2(1): 1–13.

Sato, T., Cheng, Y.N., Wu, X.C., Zelenitsky, D.K., Hsiao, Y.F., 2005. A pair of shelled eggs inside a female dinosaur. *Science*, 308: 375.

Varricchio, D.J., Jackson, F., Borkowski, J.J., and Horner, J.R., 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature*, 385: 247–250.

Varricchio, D.J., Jackson, F., and Trueman, C.N., 1999. A nesting trace with eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology*, 19(1): 91–100.

Varricchio, D.J., Horner, J.R., and Jackson, F.D., 2002. Embryos and eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology*, 22(3): 564–576.

Weishampel, D.B., Fastovsky, D.E., Watabe, M., Varricchio, D., Jackson, F., Tsogtbaatar, K., and Barsbold, R., 2009. New oviraptorid embryos from Bugin-Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *Journal of Vertebrate Paleontology*, 28(4): 1110–1119.

Young, C.C., 1954. Fossil reptilian eggs from Laiyang, Shantung. *Scientia Sinica*, 2(4): 371–388 (in Chinese).

Young, C.C., 1965. Fossil eggs from Nanhsiung, Kwangtung and Kanchou, Kiangsi. *Vertebrata PalAsiatica*, 9(2): 141–170. (Chinese 141–159; English 159–170)

Zelenitsky, D.K., 2004. *Description and phylogenetic implications of extant and fossil oologic remains* (Ph.D. dissertation), University of Calgary, Calgary, Alberta, Canada.

Zelenitsky, D.K., 2006. Reproductive traits of non-avian theropods. *Journal of Paleontological Society of Korea*, 22(1): 209–216.

Zelenitsky, D.K., and Hirsch, K.F., 1997. Fossil eggs: identification and classification. In: Wolberg, D.L., Stump, E., and Rosenberg, G. (eds.), *Dinofest International: A Symposium Held at Arizona State University*. Philadelphia: Academy of Natural Sciences, 279–286.

Zelenitsky, D.K., and Therrien, F., 2008. Phylogenetic analysis of reproductive traits of maniraptoran theropods and its implications for egg parataxonomy. *Palaeontology*, 51(4): 807–816.

Zelenitsky, D.K., Hills, L.V., and Currie, P.J., 1996. Parataxonomic classification of ornithoid eggshell fragments from the Oldman Formation (Judith River Group; Upper Cretaceous), southern Alberta. *Canadian Journal of Earth Sciences*, 33(12): 1655–1667.

Zhao, Z.K., 1975. The microstructure of the dinosaur eggs of Nanxiong, Guangdong and the problems in dinosaur egg classification. *Vertebrata PalAsiatica*, 13(2): 105–117 (in Chinese).

Zhao, Z., and Jiang, Y.K., 1974. Microscopic studies on the dinosaurian eggshells from Laiyang, Shangdong Province. *Scientia Sinica*, 17(1): 73–83.