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Dinosaur eggs and dinosaur egg-bearing deposits (Upper Cretaceous) of Henan Province, China: Occurrences, palaeoenvironments, taphonomy and preservation

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Abstract

The Upper Cretaceous dinosaur egg-bearing deposits in Henan Province, central China are divided into three formations in ascending order: Gaogou, Majiacun and Sigou. The Gaogou Formation belongs to alluvial fan deposits containing the fossil dinosaur egg assemblage of *Faveoloolithus*, *Dendroolithus*, *Dictyoolithus*, *Paraspheroolithus* and *Longiteresoolithus*. The Majiacun Formation is interpreted as braided stream to meandering stream deposits with assemblage of *Ovaloolithus, Paraspheroolithus, Placoolithus, Dendroolithus, Prismatoolithus*, rare *Youngoolithus* and *Nanhiungoolithus*. The Sigou Formation is shallow lacustrine/palustrine to low-sinuosity river sedimentary rocks with assemblage of *Macroolithus, Elongatoolithus*, *Ovaloolithus* and *Paraspheroolithus*.

To date, 37 oospecies, 13 oogenera and 8 oofamilies of dinosaur eggs have been distinguished. Autochthonous dinosaur eggs are preserved in the floodplain deposits, whereas allochthonous and parautochthonous dinosaur eggs are preserved in the alluvial fans. This suggests that river floodplains are the best environments for the preservation of numerous autochthonous dinosaur eggs. The preservation of most dinosaur eggs in brown to red calcic palaeosoils, muddy siltstones or mudstones suggests that the paleoclimate of the nesting area was semiarid. The presence of gray and green mudstone and coal layers, however, indicates that there existed an ephemeral subhumid climate during the middle and Late Cretaceous. It is suggested that such a climate was favorable for the development of meandering streams in a vegetated environment.

Keywords: Dinosaur eggs; Upper Cretaceous; Fluvial deposit; Characteristics of taphonomy and preservation; Henan; Central China

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1. Introduction

Although more than 200 sites of dinosaur eggs and eggshells have been identified worldwide [1], studies that focus on dinosaur eggs tend to address morphologic, taxonomic, paleobiologic and biostratigraphic topics [2–6]. Several papers deal with paleoenvironmental or taphonomic aspects with respect to dinosaur eggs [7–11]. Only a limited amount of paleobiological information stemmed from the study of fossil eggs and eggshells [12–14]. More studies on taphonomy and sedimentology of egg-bearing deposits are thus needed in order to further understand the paleoenvironmental and paleoecological aspects of dinosaur nesting sites.

The discovery of dinosaur eggs from Henan Province, central China is one of the significant scientific events in

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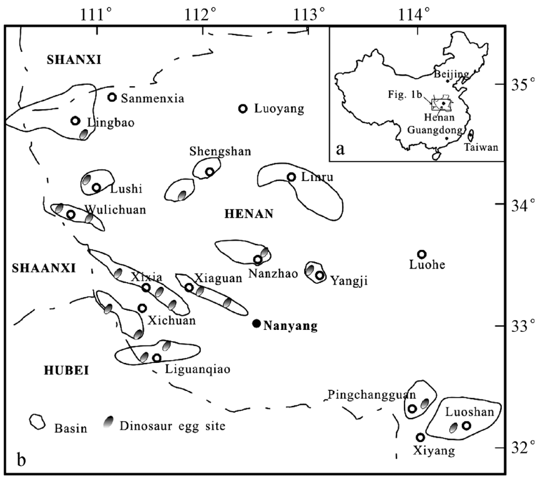

Fig. 1. (a) Location map of the study area and (b) sketch showing the distribution of fossil dinosaur eggs in Henan Province, China. Modified from HNBGMR [18] and Zhou and Feng [19].

China [15,16] by the egg abundance and diversity. The distribution and preservation of dinosaur eggs in Henan Province are almost all in the NW–SE-trending continental basins of the eastern part of the Qinling-Dabie orogenic belt, e.g., Xichuan, Xixia, Lingbao, Nanzhao, Xiaguan and Nanzhao (Fig. 1) with a total area of about 800 km^2 [17]. In addition to the dinosaur eggs, hadrosaur and sauropod bones and tracks, tortoise bones and eggs are found at Taohe, Yangcun, Xiaguan and the northern part of Nanzhao basins in Henan Province. These NW–SE-trending basins provide an ideal opportunity to study the palaeoenvironments of nesting sites of Cretaceous dinosaurs. Here, we describe the occurrences of dinosaur eggs and associated egg-bearing deposits and provide an interpretation of the palaeoenvironment and taphonomic preservation of dinosaur eggs.

During the Cretaceous period, a number of transtensional basins, e.g., Xichuan, Xixia, Nanzhao and Linru, formed in the Henan area, central China [18], in which sedimentation was controlled by regional tectonism, climate and volcanic activity [20]. The Late Cretaceous red strata are divided into three stratigraphic units in ascending order: Gaogou, Majiaocun and Sigou Formations [19,21,22]. The egg-bearing unit consists of a dark red to orange red conglomerate, gravel-bearing sandstone, sandstone or siltstone. It is underlain by the Lower Cretaceous, Paleozoic or Paleoproterozoic strata and overlain by the Neogene deposits [18,19].

The dinosaur egg-bearing basins may have been situated in mid-low latitudes as they are today during the Late Cretaceous [23]. Based on palynological records [18,24,25], calcisol development [21,26], evaporite mineral casts [21], trace elements [27,28] and carbon isotopes of dinosaur eggshells [23], the general palaeoclimatic regime during deposition of the entire Late Cretaceous of central China is interpreted to have been the arid and semiarid of the subtropical zone [25,28].

2. Occurrences

2.1. Dinosaur oospecies

In Henan Province, numerous fossil eggs (Fig. 2) and eggshells have been discovered in the Upper Cretaceous red beds [15,17,28–32] and identified using parataxonomic criteria formalized by Young [33,34] and Zhao [29,35,36]. On those criteria, 37 oospecies have been described [16,29,32,37,38] and allocated to 8 oofamilies and 13 oogenera appear dinosaurian (Table 1). The macrostructural characteristics and the stratigraphical localization of part of the oospecies are described in Table 1.

In the Gaogou Formation, Faveoloolithus, Dendroolithus, Dictyoolithus and Paraspheroolithus are associated with Longiteresoolithus, which is found only in China (Table 2). The assemblage of Ovaloolithus, Paraspheroolithus, Placoolithus, Dendroolithus and Prismatoolithus is frequently found in the Majiacun Formation together with a few Youngoolithus and Nanhiungoolithus, whereas Macroolithus, Elongatoolithus and Ovaloolithus occur in association with Paraspheroolithus in the Siguo Formation (Table 2) [29,38,39]. The co-occurrence of Paraspheroolithus cf. irenensis, Placoolithus cf. taohensis, P. cf. Taohensis and Faveoloolithus indicates the end of the early Late Cretaceous (Turonian to Cenomanian) [40,41], because Prismatoolithus gebiensis, Ovaloolithus chinkangkouensis and Paraspheroolithus irenensis are dominant in the middle Late Cretaceous, and Elongatoolithus andrewis, E. elongates and Macroolithus Yaotunensis characterize the Late Cretaceous (Maastrichtian to Campanian) [15,41].

Studies [29,31,38] of all dinosaur eggs from Xixia, Xichuan, Liguangqiao and Wulichuan basins indicate that dinosaur eggs are layered, generally with 2–10 layers. More egg-bearing beds are found in the Gaogou and Majiacun Formations and less in the Sigou Formation. Dinosaur egg clutches are commonly distributed along a single layer and extend usually 500–1000 m. The clutches tend to occur about 2–20 m apart laterally in a cross-section. Two clutches occur in the same vertical section with a distance of 5–15 cm. The distance between eggs of the clutches is about 1–5 cm [20,29]. Spheroolithid clutches contain up to 55 eggs, whereas macroelongatoolithid clutches contain up to 13 pairs [38]. All clutches consist of eggs of regular and irregular arrangement in a single layer and have been little affected by post-exposure weathering.

The size of dinosaur eggs is variable. The smaller eggs are spheroolithids (Fig. 2a and b, 7–14 cm in diameter), while the larger are macroelongatoolithids (Fig. 2g and h, 34–65 cm in length, 14–27 cm in width) [17,38]. Egg diameter may be related to the age of the dinosaur and its pelvic opening [42], as well as, to the size of the parent [43]. The huge size of *Longiteresoolithus xixiaensis* eggs is, therefore, proportional to the body size of a large dinosaur species as further attested by the sizeable empty space in the clutch center [44].

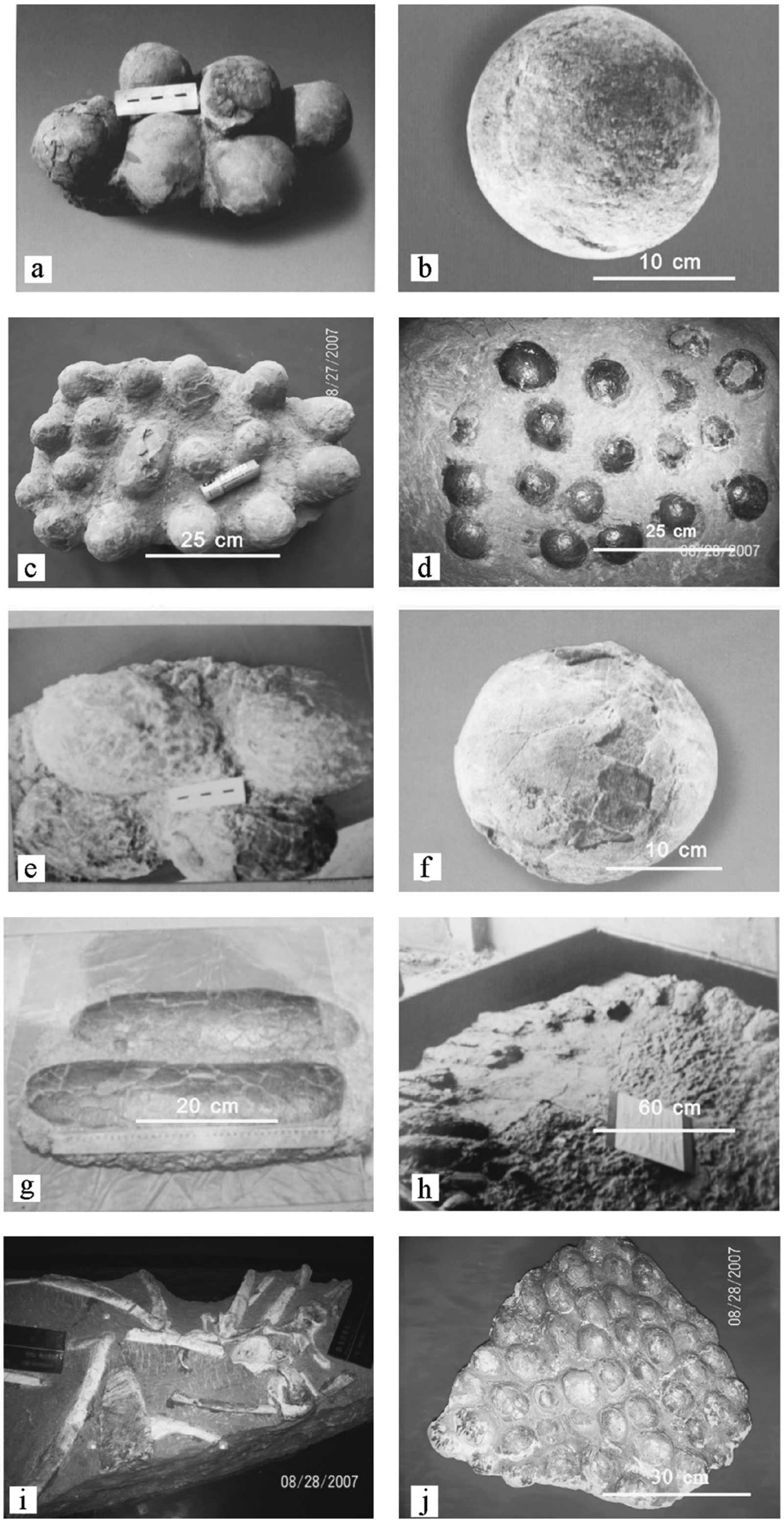

Fig. 2. Photographs of different types of dinosaur eggs and other fossils from Henan Province, China. (a) *Paraspheroolithus irenensis,* the egg clutch preserved in siltstone and sandy mudstone of Majiacun Formation, Yangcheng, Xixia Basin; Majiacun Formation, Xixia. (b) *Sphereoolithus,* preserved in sandy mudstone of Majiacun Formation, Guoyagou, Xixia Basin. (c) *Prismatoolithus gebiensis*, the clutch with 17 eggs is shown upside down. The eggs were laid almost vertically on their pointed end in the nest; Majiacun Formation, Miaoshan, Neixiang, Xichuan. (d) *Dendroolithus*, irregular arrangement, a clutch with 18 eggs, Majiacun Formation, Sanlimiao, Yangcheng, Xixia. (e) *Youngoolithus xiaguangensis*, a clutch with 4 eggs; Gaoguo Formation, Xixia. (f) *Faveoloolithus*, Gaogou Formation, Chimei Neixiang, Xichuan. (g) *Longiteresoolithus xixiaensis*, 2 eggs from Gaogou Formation (Yangcheng, Xixia), which made a parallel arrangement. (h) *Longiteresoolithus xixiaensis*, a clutch from the Gaogou Formation, of at least 13 pairs of eggs that were laid in a large ring of 75 inches in diameter, Fanying, Yangcheng, Xixia. (i) Fossil dinosaur bones (Nanyanggosaur zhugeii), Xiaguan Formation, Upper Cretaceous, Donglinggou, Xiaguan, Neixiang. (j) Tortoise eggs, Majiacun Formation, Xixia.

Table 1
Major type of fossil dinosaur eggs in Henan Province, China.

Serial number	Oofamilies	Oogenera	Oospecies	Occurrences	Locality and horizon
1	*Elongatoolithidae* [35]	*Elongatoolithus* [35]	*E. andrewsi* [35]	Eggshell fragments, incomplete and isolated eggs. Irregular arrangement. Length: 150–260 mm, width: 60–120 mm; its length to width ratio 2–2.4:1. The thickness of the eggshell 1.1–1.5 mm. The outer surface is sculptured by the nodular and catenulate-like structure. Allochthonous burial.	Liguanqiao, Luoshan, Xichuan, Tantou, Pingchuanguan Zhoujiawan Fm.
			E. cf. andrewsi [35]		Hugang Fm. of Sigou Fm.
			E. elongatus [34]	The thickness of the eggshell 0.60–1.12 mm.	
			E. cf. elongatus [34]		
			E. sp. [29]	Eggshell fragments. The eggshell is 1.0 mm thick on average. Irregular worm-like nods are present on the outer surface. The cone layer is 0.18 mm thick.	Wanggou, Shangyegou, Qianjiashan, Xichuan, Fenghuatou, Chujiashan, Taohe. Maojiacun and Sigou Fms.
		Macroolithus [35]	*M. yaotunensis* [35]	Complete egg clutches. The thickness of the eggshell 1.50–1.74 mm.	
			M. cf. yaotunensis [35]		
		Nanhsiungoolithus [35]	*N. chutienensis* [35]	Eggshell fragments. The eggshells are very thin, with a mean thickness of 0.6–0.8 mm, and smooth on the outer surface. The cone layer is 0.15 mm.	Eastern Silugou, Laocheng, Xichuan, Majiacun Fm.
			N. sp		
2	Ovaloolithidae Mikhailov, 1991	Ovaloolithus [15]	*O. cf. chinkangkouensis* [34]		
			O. chinkangkouensis [15]	Complete eggs. Autochthonous burial. The eggs are oval. The thickness of the eggshell is 1.65 mm. Irregular worm-like nods are present on the outer surface.	Shijiawan, Laocheng and Baligang, Jianfanggou, Xichuan. Maojiacun Fm.
			O. sangpingensis [32]		
			O. sp.		
3	*Spheroolithidae* [15]	*Paraspheroolithus* [15] (Fig. 2a)	*P. irenensis* [34]		
			P. cf. irenensis [15]	Complete egg clutches, eggshell fragments. Eggs are subspherical, averaging 70–90 mm in diameter. The outer surface bears weak sagenotuberculate ornament. The eggshell is 1.8 mm thick on average. Autochthonous or allochthonous burial.	Maojiacun Fm. Zhoujiawan, Laocheng, Xichuan; Gaogou Fm. Yangcheng, Majiagou and Wanggou, Xixia
			P. shizuiwanensis [32]		
			P. yangchengensis [31]		
			P. sp		
			P. sp. nov.		
		Sphereoolithus [15] (Fig. 2b)	*S.* sp		

Table 1 (*continued*)

Serial number	Oofamilies	Oogenera	Oospecies	Occurrences	Locality and horizon
4	*Troodontidae* Varricchio et al., 1997	*Prismatoolithus* Zhao [84] (Fig. 2c)	*P. gebiensis* [38]	Egg clutches. Each clutch contains 6–7 eggs. The eggs were preserved standing up, vertically and obliquely in siltstone. Eggshells are very thin and smooth on the outer surface. The thickness of the eggshell is between 0.6 and 0.9 mm. The eggs are 105–116 mm long and 36–48 wide. The shape index is 41.3.	Nanbeizhai, Yangcheng and Miaoshan, Neixiang, Xixia. UU of Gaogou Fm.
5	*Dendroolithidae* Zhao and Li [85]	*Dendroolithus* Zhao and Li [85] (Fig. 2d)	*D.* sp	Intact eggs, clutches	Maojiacun Fm., Gaogou Fm., Zhuyangguan Fm., Haohanpo Fm. Xixia, Majiacun, Taohe, Xichuan
			D. zhaoyingensis [32] *D. furcatus* [32] *D. dendriticus* [32] *D. saniimiaoensis* [32]		
			D. xichuanensis [29]	Eggshell fragments and collapsed eggs. Eggs are oval and 120–160 mm in diameter. Incomplete shell units loosely arranged. The thickness of the eggshell is 1.5–1.8 mm. The outer surface is smooth. Allochthonous burial.	Gaogou Fm. Zhaojiagou, Dashiqiao, Xichuan
		Placoolithus [29]	*P. taohensis* [29]	Complete egg clutches. Eggs are nearly spherical and 110–135 mm in diameter, and disposed at random in the nest. The thickness of the eggshell is 1.7–1.9 mm. The shape index is 97.6. Autochthonous burial.	MU and LU of Maojiacun Fm. Majiacun, Taohe, Xichuan
			P. cf. taohensis [29]	Egg clutches	UU and MU of Gaogou Fm. Xichuan, Xixia
6	*Faveoloolithidae* [40]	*Youngoolithus* [15] (Fig. 2e) *Faveoloolithus* [40] (Fig. 2f)	*Y. xiaguanensis* [15,41] *Y. xipingensis* [32] *Y.* sp ***F.*** sp *F.* sp. nov.		
7	*Dictyoolithidae* Zhao [84]	*Dictyoolithus* Zhao [84]	*D. neixiangensis* Zhao [84] *D. hongpoensis* Zhao [84]		
8	*Macroelongatoolithidae* [38]	*Longiteresoolithus* [38] (Fig. 2g and h)	*L. xixiaensis* [38]	Complete egg clutches. Eggs are long columned. Length 340–610 mm, width 140–270 mm; its length to width ratio is 2.5–2.9:1. The thickness of the eggshell ranges from 1.2 to 3.1 mm. The outer surface is sculptured by irregular worm-like nods or weak sagenotuberculate ornament. Autochthonous burial.	Fanying, Liuying, Zhaoying and Madaya, Yangcheng Xixia, Wangjiaying, Chimei and Chenbeigou, Danshui, Neixiang, Xixia MU and UU of Zoumagang or Gaogou Fm.

Table 2
Representative Late Cretaceous egg-bearing stratigraphic units and dinosaur egg assemblages in Henan Province, China [16–18].

Formations	Sigou Formation or Luyemiao Formation or Hugang Formation	Maojiacun Formation or Zhaoying Formation	Gaogou Formation or Zoumagang Formation
Age span	Maastrichtian to Campanian 65–83 Myr	Santonian to Coniacian 83–88 Myr	Turonian to Cenomanian 88–96 Myr
Lithology and thickness (m)	Purple-red muddy siltstone and gray yellow calcareous sandstone, interbedded with each other, bearing conglomerate and gray pebble to cobble-bearing coarse-grained sandstone in the base and upper. 200–1000 m.	Purple-red to variegated siltstone and fine-grained sandstone in the upper, interbedded with conglomerate or pebble-bearing coarse-grained sandstone; mid-coarse-grained sandstone and conglomerate in the lower, interbedded with gray calcareous sandstone and muddy siltstone. 100–2000 m	Yellow and gray coarse-grained pebble-bearing sandstone, red and purple-red muddy siltstone interbedded with each other in the upper; Purple-red mudstone and gray conglomerate interbedded with each other in the lower. 600–1500 m
Depositional environments	Shallow lacustrine/palustrine to a low-sinuosity river	Braided stream to meandering streams	Alluvial fan
Dinosaur egg assemblages	*Macroolithus, Elongatoolithus*, *Ovaloolithus* and *Paraspheroolithus*	*Ovaloolithus, Paraspheroolithus, Placoolithus, Dendroolithus*, *Prismatoolithus* and a small quantity of *Youngoolithus* and *Nanhiungoolithus.*	*Longiteresoolithus, Dendroolithus, Dictoolithus, Faveoloolithus* and *Paraspheroolithus*
Examples			
Xixia Basin	*Paraspheroolithus* sp., *P*. sp. nov	*Paraspheroolithus* sp., *P*. cf. *irenensis, Dendroolithus* sp., *D. sanlimiaoensis, Ovaloolithus* sp., *Prismatoolithus gebiensis*	*Longiteresoolithus xixiaensis*, Dendroolithus furcatus, *D.* sp.*, D. zhaoyingensi, D. dendriticus, Placoolithus* cf. *taohensis, Youngoolithus xiaguanensis, Y. xipingensis, Faveoloolithus* sp.*, Paraspheroolithus* cf. *irenensis, P.* cf. *yangchengensis, P.* sp., *Dictyoolithus neixiangensis, D. hongpoensis*
Xichuan Basin	*Elongatoolithus* cf. *elongates, E. sp. E.* cf. *andrewsi*	*Ovaloolithus chinkangkouensis, O*. cf. *chinkangkouensis, Paraspheroolithus irenensis, Nanhsiungoolithus chuetienensis, Placoolithus taohensis*	*Dendroolithus xichuanensis*, *Placoolithus* cf. *taohensis*, *Paraspheroolithus* cf. *irenensis*
Liguanqiao Basin	*E. andrewsi, E. elongatus, Macroolithus yaotunensis, M.* cf. *yaotunensis*		
Xiaguan Basin		*Paraspheroolithus* sp., *Ovaloolithus* sp.	*Youngoolithus xiaguanensis*
Wulichuan Basin		*Paraspheroolithus shizuiwanensis, P.* sp., *Ovaloolithus* sp.*, O. sangpingensis, Youngoolithus xiaguanensis*	*Faveoloolithus* sp., *Spheroolithus* sp., *Dendroolithus* sp.
Lingchangguan Basin	*Elongatoolithus andrewsi, E. elongates, Macroolithus* cf. *yaotunensis, M. yaotunensis*		
Luoshan Basin		*Paraspheroolithus* sp., *Ovaloolithus* sp.	
Zhaobei Basin		*Dendroolithus* sp.	
Lingbao Basin	*Macroolithus* cf. *yaotunensis,*		
Tantou Basin	*Elongatoolithus* sp.		
Yangji Basin		*Paraspheroolithus* sp.	

2.2. Dinosaur bones and other fauna and flora associated with dinosaur eggs

It is significant that the bones of the hadrosaur, tyrannosaur, lizard and troodontid dinosaurs have been found in the Majiacun Formation at Taohe in Xichuan, Yangcheng in Xixia, Xiaguan in Neixiang (Fig. 2i) and northern Nanzhao basins [15,19,45]. Dinosaur bones were discovered in the overlying and underlying egg-bearing beds and observed rarely in the egg-bearing units except that tyrannosaur bones were found together with *Longiteresoolithus xixiaensis* and *Youngoolithus xipingensis* at Neixiang in the Xiaguan Basin [19]. A partial hadrosaur skeleton (*Nanyanggosaurus zhugeii*) and sauropod bones were ever collected from the purple-red muddy siltstone of the lower part of the Xiaguan Formation (equivalent of the Gaogou Fm., Xixia Basin) in the Xiaguan Basin (Fig. 2i) [45]. Thousands of dinosaur eggs (*Youngoolithus xiaguanensis*, *Paraspheroolithus* sp., *Ovaloolithus* sp.) also have been discovered and collected at this site [15,19,45]. However, the association of dinosaur bones and dinosaur eggs does not prove that the eggs have been laid by those dinosaurs. Only embryos within eggs are unquestionable proof [4,42,46]. Although the prismatoolithid eggs from the Xixia Basin contain no embryonic remains, the similarity of their eggshell structure and the pattern of the egg arrangement in the clutches (Fig. 2c) suggest that the same type of troodontids or closely related species had laid these eggs

[30]. Based on the discovery of eggs containing embryos and of eggs associated with adult hadrosaur skeletons, spheroolithid eggs from the Xiaxia and Xichuan basins were confirmed to have been laid by hadrosaurids [47].

In addition to dinosaur bones, dinosaur tracks, tortoise bones, tortoise eggs, sporomorphs and charophytes are also discovered in almost all egg-bearing beds [15,19,25]. In the sporomorph composition, fern sporomorphs occupy a dominant position, while the pollen of gymnosperms and angiosperms hold the second. Charophytes consist mainly of *Porochara anluensis*, *Porochara jingshanensis* and occasionally of *Songliaochara* [18]. Footprints of dinosaurs (sauropods) occur within the dinosaur eggs or directly on dinosaur eggs [15]. A lot of trace fossils are found in the fluvial-lacustrine sediments, including *Skolithos linearis, Cylindricum ichno* sp. and *Palaeophycus tubularis* [48]. Fossil tortoises are found with dinosaur eggs in a piece of calcareous fine-grained sandstone (Fig. 2j).

2.3. Burial types of dinosaur eggs

On the basis of the occurrence of dinosaurs and the peculiarities of distribution of eggs or egg clutches, the burial of dinosaur eggs can be divided into three types [49]: autochthonous, allochthonous and parautochthonous (Fig. 3).

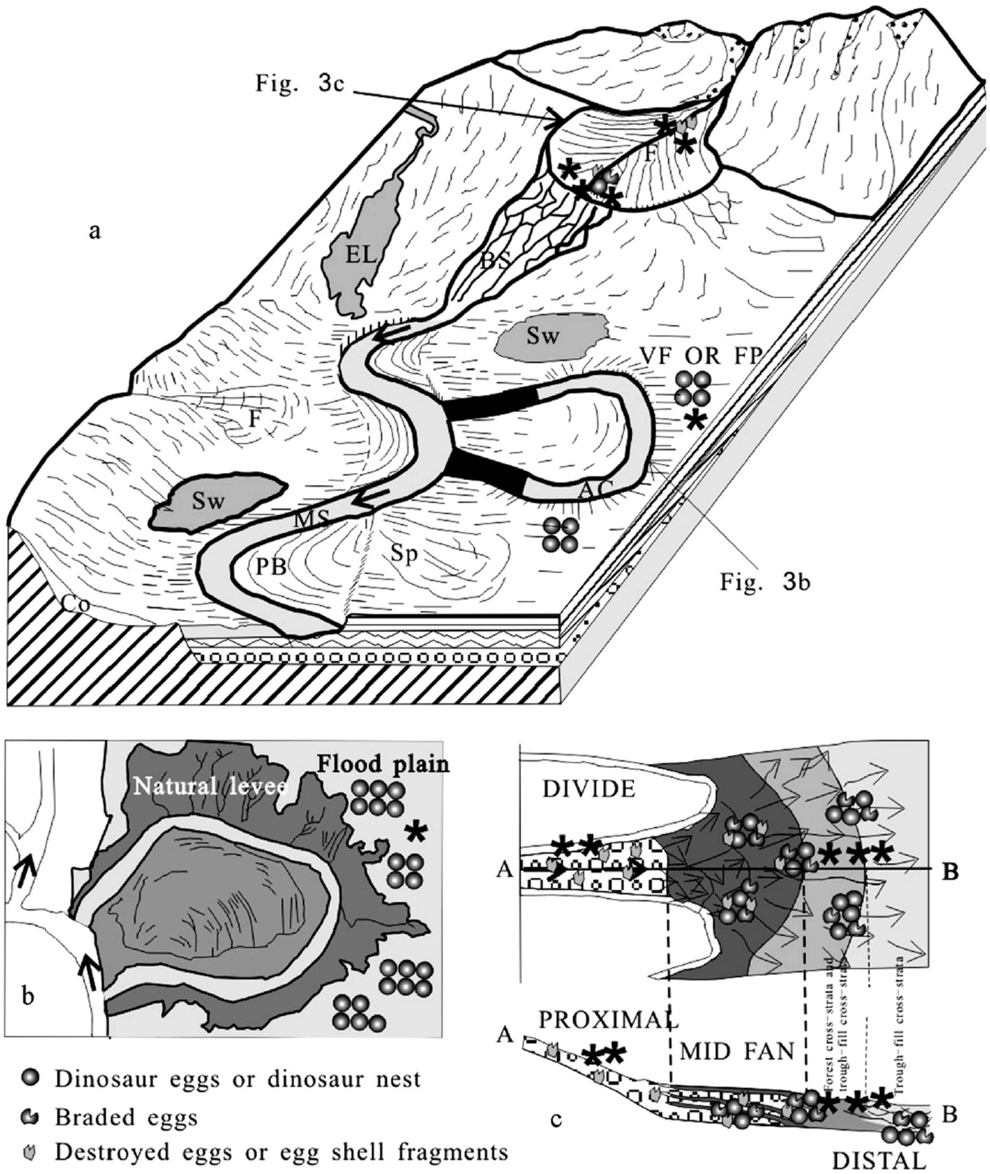

Fig. 3. Schematic diagram of one edge of an alluvial plain, which developed braided and meandering streams [50,51] and the outcrop distribution positions of different burial types of dinosaur eggs. Tributary stream at the left and top has built fan (F) onto the alluvial plain. Insets b and c (see Fig. 3a for location) are enlargements of the flood plain [52] and alluvial fan [53]. AC = abandoned channel (now an ox-bow lake and filling with fine sandstones); BS = braided stream; EL = ephemeral lake; FP = flood plain; MS = meandering stream; NL = natural levee; PB = point bar; Sp = splay deposit; Sw = swamp; VF = valley floor. * autochthonous burial, ** allochthonous burial and *** parautochthonous burial.

The autochthonous type is mostly distributed in the silt and soil deposits of the floodplain (Fig. 3a and b). When dinosaurs laid eggs, the environment was relatively stable, and eggs were buried rapidly at primary spots and were not destroyed by regional tectonism after deposition. Autochthonous eggs with complete shape and regular arrangement formed in the place where found and were preserved in an initial state, as seen at Shanlimiao, Xixia, Neixiang and Xiaguan.

The allochthonous type is observed in the alluvial proximal fan coarse clastic deposits (Fig. 3a and c), such as conglomerates and pebble-bearing sandstones. After dinosaurs laid eggs, the eggs and egg clutches were moved a long distance and, sometimes, were destroyed due to unstable environments with strong hydrodynamic processes. Broken egg pieces were scattered in rocks, or distributed as a thin bed, as seen at Xiping and Manlirong of the Xixia Basin and in the eastern Xiaguan Basin. Eggshell density shows generally some vertical and horizontal variation within the coarse-grained clastic rocks but no clear patterns emerge. In some parts of the outcrop, eggshell fragments form a significant component of the rock.

The parautochthonous type is seen in the alluvial mid fan and distal fan coarse- to very coarse-grained sandstones, rarely in floodplain deposits (Fig. 3a and c). Being transported only a small distance, eggs and egg clutches of this type are not in situ. However, the original integrity of eggs or egg clutches were almost maintained, and egg bodies were only slightly abraded or destroyed in these settings, as observed at Toumen, Yangcheng and Qiyu of the Xixia Basin and in the Wulichuan and Xiaguan basins.

2.4. Arrangement of dinosaur eggs

Statistics [31,35,54] indicates that the spatial arrangement of dinosaur eggs can be divided into four modes: circular or oval radial, cross-parallel, multi-bed parallel and irregular (Fig. 4).

Elongatoolithus, Macroolithus and *Longiteresoolithus* eggs are arranged in regular oval or circular arrangement (Fig. 4a). Eggs dip inward with an angle of 10–15°. The distance between eggs is increasing outwardly. The angle between the long axes of two adjacent eggs is generally 13–40° [47], sometimes the axes are almost parallel to one another. This suggests either that both oviducts have laid the eggs, or that a single oviduct has laid the eggs in two phases [55,56]. Dinosaur eggs occur commonly in one bed, or occasionally in two or three continuous beds, where the upper bed is gradually diminished relative to the lower.

Ovaloolithus, Paraspheroolithus and *Dendroolithus* eggs are in a parallel arrangement as across mode (Fig. 4b). Two or more rows of dinosaur eggs are in a parallel arrangement as across mode not only in the horizontal plane but also in the vertical section (Fig. 4b). Vertically egg-bearing beds can be parallel to or overlap each other. Mostly, one egg-bearing bed is found, but 2–4 egg-bearing beds can also be observed. The distance between two rows in a bed and two egg-bearing beds is about 1–10 cm and 5–15 cm, respectively, while the distance between eggs in a row is mostly 1–5 cm.

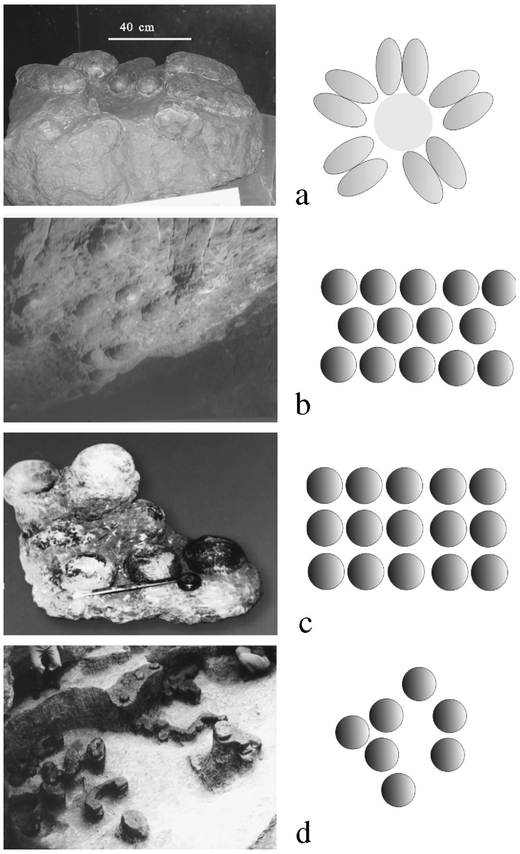

Fig. 4. Outcrop photograph (left) and sketch map (right) of the different types of arrangement of dinosaur eggs. (a) Circular or oval type; *Macroelongatoolithus xixiaensis*, a clutch from the Gaogou Fm. (Xixia), of at least 5 pairs of eggs that were laid in a small ring about 40 cm in diameter (two of which are destroyed). (b) Cross-parallel type; *Dendroolithus* showing cross-parallel arrangement, Majiacun Fm., Sanlimiao, Xixia. (c) Multi-bed parallel type; *Dendroolithus* showing multi-bed parallel arrangement in the vertical section, Majiacun Fm., Sanlimiao, Xixia. (d) Irregular type; *Dendroolithus* egg clutch showing irregular arrangement, Majiacun Fm., Sanlimiao, Xixia.

Faveoloolithus and part of *Ovaloolithus, Paraspheroolithus* and *Dendroolithus* make a multi-bed parallel arrangement (Fig. 4c). Eggs are parallel to each other on the same plane and are distributed equidistantly. When two or three beds contain eggs, they are also almost parallel to each other in the vertical and horizontal direction and form a regular network. The distance between eggs is mostly 5–10 cm, the distance between ranks is 3–15 cm, and the distance between egg-bearing beds is 1–10 cm.

Prismatoolithus and a small quantity of *Ovaloolithus, Paraspheroolithus, Dendroolithus* and *Elongatoolithus* show an irregular arrangement (Fig. 4d) including irregular across, curving and vertical or standing modes. Eggs occur commonly in a sandstone or siltstone bed, occasionally in two beds. The distance between eggs varies from 3 to 20 cm.

3. Dinosaur egg-bearing deposits

Dinosaur egg-bearing strata include (in ascending order) the Gaogou, Majiacun and Sigou Formations in the Xixia, Xichuan basins (Fig. 5a and b) [21] or equivalent formations (such as Zoumagang, Xiaguan or Zhuyangguan and Hugang or Qiupa Formations) in other basins (e.g., Liguanqiao, Xiaguan, Wulichuan, Pingchangguan, Zhaobei, Tantou and Lingbao; Fig. 5c, d and e) [19]. Here, the detailed stratigraphic and sedimentologic features of the Upper Cretaceous of the Xixia Basin, an example of dinosaur egg-bearing basins, are represented as follows.

The Gaogou Formation is mainly exposed in the western and northern (such as Zoumagang, Yangcheng and Chimei) Xixia Basin. Zhou et al. [21] estimated the Gaogou Formation to be approximately about 900–1500 m thick based on the distribution of exposures in the basin (Fig. 5a). Historically, the Gaogou Formation has been divided into three fining-upward stratigraphic units based on lithological differences visible in the Tumenya-Gangding, Qiyu-Xiaoliying or Danshui-Tangou outcrops (Fig. 5a): (1) the lower unit, up to 460 m thick, is composed of gray or black massive polygenetic conglomerate, imbricate conglomerate, thin-bedded conglomerate and rare red medium-bedded mudstone or silty mudstone (Fig. 6a and b); (2) the middle unit, up to 440 m thick, is characterized by the presence of gray or red imbricate conglomerate, thin-bedded conglomerate, pebbly sandstone and red medium-bedded silty mudstone containing calcareous nodules and marlstone lenticles (Fig. 6c, d and e), where the dinosaur eggs and bones are concentrated, such as *Longiteresoolithus xixiaensis*, *Dendroolithus dendriticus*, *Youngoolithus xiaguanensis, Faveoloolithus* sp., *Paraspheroolithus* cf. *irenensis*, *Dictyoolithus neixiangensis* and ornithopod bones [19]; (3) the upper unit, up to 230 m thick, consists of gray or purple-red medium-bedded conglomerate, pebble-bearing coarse-grained sandstone, thin- to medium-thick-bedded siltstone and thick-bedded mudstone (Fig. 6f, g and h) and contains, locally, calcareous nodules, tuffs and palynoflora fossils, such as *Schizaeoisporites* sp*.*, *S. palaeocenicus, S. cretacius, S. certus* and *Classopollis annulatus* [18,25]. Most of the conglomerates of the Gaogou Formation are very poorly sorted and matrix supported. Red mudstone lenticules were frequently found in the gray black and brown-red conglomerate beds of the lower unit of the Gaogou Formation (Fig. 6a). Planar bedding and cross-bedding are common in the pebbly sandstones and mudstones (Fig. 6e and g) with palaeocurrents oriented towards the southwest [57]. The bones of sauropod and ornithopod (*Nayangosaurus zhugeii*) dinosaurs have been found in the pebble-bearing sandstone and sandstone of the lower part of the Xiaguan Formation at the neighbor-

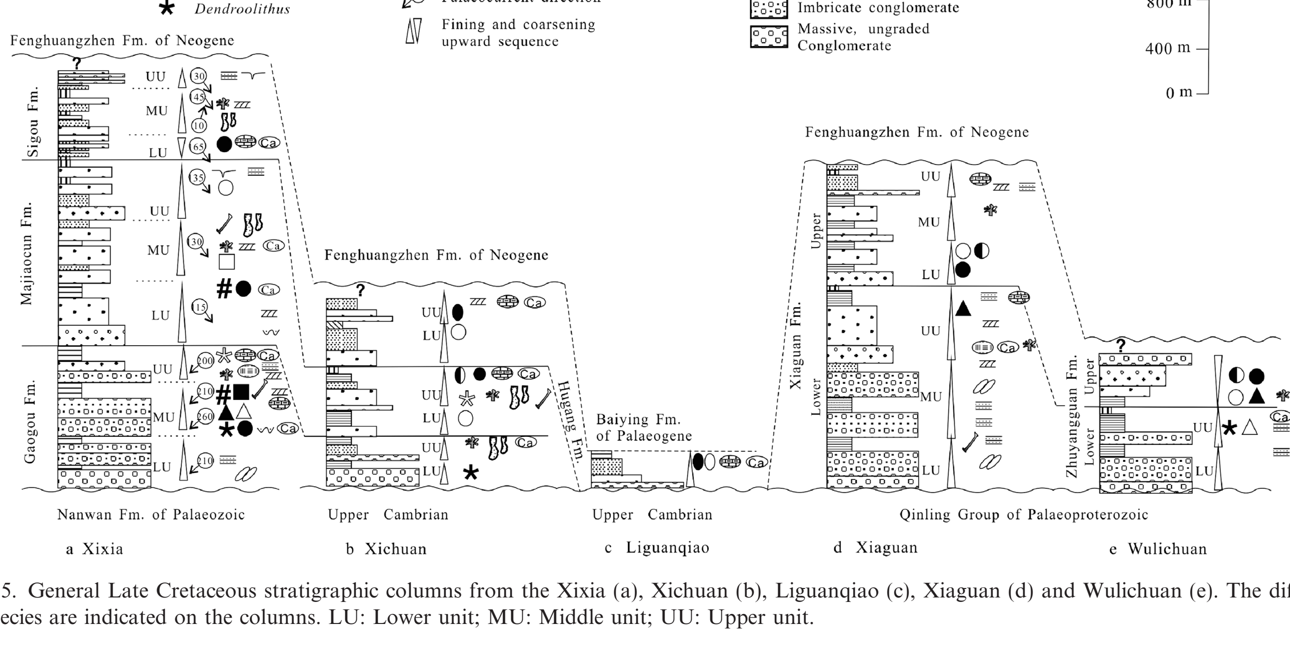

Fig. 5. General Late Cretaceous stratigraphic columns from the Xixia (a), Xichuan (b), Liguanqiao (c), Xiaguan (d) and Wulichuan (e). The different oospecies are indicated on the columns. LU: Lower unit; MU: Middle unit; UU: Upper unit.

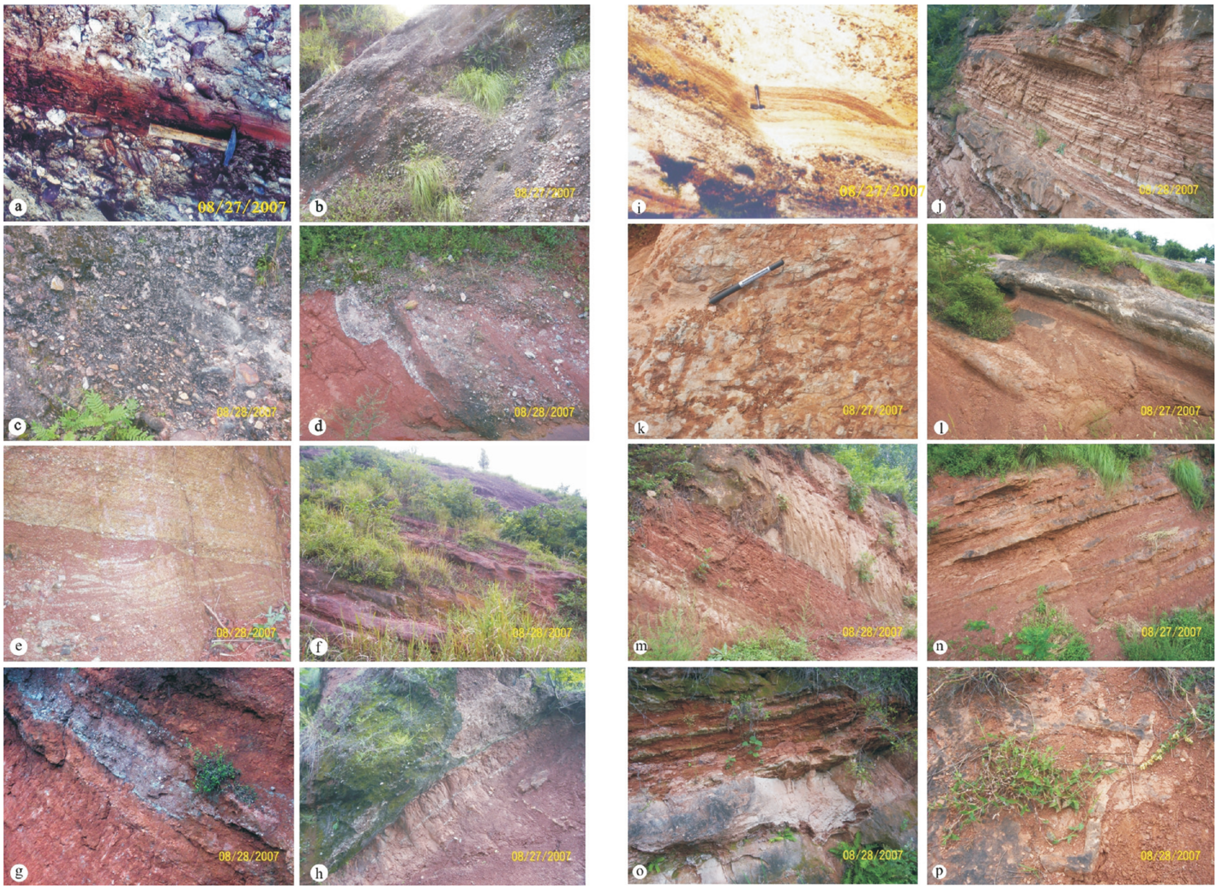

Fig. 6. Outcrop photographs of sedimentary and tectonic structures from Late Cretaceous rocks of the Danshui-Tangou (a, b, i, k, l, n) and Qiyu-Xialiying (c, d, e, f, g, h, j, m, o, p) sections, Xixia Basin. (a) Gray black and brown-red massive polygenetic conglomerates containing red mudstone lenticules, the lower unit of Gaogou Fm. (b) Gray imbricate and thin-bedded conglomerate, the lower unit of Gaogou Fm. (c) Gray imbricate conglomerate, the middle unit of Gaogou Fm. (d) Gray imbricate conglomerate and sandstone on erosive base, the middle unit of Gaogou Fm. (e) Gray, yellow and red sandstone and pebbly sandstone with cross-bedding, the middle unit of Gaogou Fm. (f) Red pebbly sandstone, thin- to medium-thick-bedded siltstone and thick-bedded mudstone, the upper unit of Gaogou Fm. (g) Thin-bedded conglomerate, pebbly sandstone, muddy siltstone with erosive base, the upper unit of Gaogou Fm. (h) Sandstone, pebbly sandstone and siltstone with calcareous nodules, the upper unit of Gaogou Fm. (i) Cross-bedding formed in the coarse-grained sandstone, the lower unit of Majiacun Fm. (j) Interbedded gray sandstone, red siltstone and mudstone with trough cross-bedding, the middle unit of Majiacun Fm. (k) Sandstone-filled burrows within siltstone or mudstone, the middle unit of Majiacun Fm. (l) Trough cross-stratified gravel-bearing coarse-grained sandstone, horizontally stratified siltstone, interbedded fine sandstone and sandy mudstone, the upper unit of Majiacun Fm. (m) Coarsening-upward sequences of fine-grained sandstone–siltstone–claystone, fine-grained low-angle cross-bedded sandstone, the lower unit of Sigou Fm. (n) Interbedded fine-grained sandstone and siltstone with parallel lamination and small-scale cross-lamina, the middle unit of Sigou Fm. (o) Interbedded red pebbly sandstone, sandstone, red siltstone and gray mudstone, the upper unit of Sigou Fm. (p) Polygonal desiccation cracks observed in the mudstone, the upper unit of Sigou Fm.

ing Xiaguan Basin [45]. In addition, dinosaur footprints have been reported in the area [15,19].

The Majiacun Formation is mainly exposed in the central (such as Huiche, Danshui and Huangping) Xixia Basin and is represented by a 800–1300 m thick repetitive succession of brown and red sandstones interbedded with purple to green or brown to red muddier intervals (Fig. 5a). These beds form stacked fining-upward units: laterally extensive sandstone ledges, consisting of calcite- and silica-cemented arenites, fining-upward into muddy sandstones and mudstones in the nonledge-forming interval [57]. It can be subdivided into three stratigraphic units. The lower unit, up to 600 m thick, is made up of trough cross-stratified gravel-bearing coarse-grained sandstone, large- through small-scale planar cross-stratified sandstone, ripple horizontally laminated sandstone and rare red medium-bedded mudstone containing calcareous nodules (Fig. 6i). The middle unit, about 500 m thick, is composed of sandstone, siltstone and mudstone (Fig. 6j). The sandstones are yellow to purple-red, fine-grained to very coarse-grained and feldspathic to arkosic sandstones. The finer-grained sandstones are characterized by ripple cross-laminations, horizontal laminations and flame structures. The coarser-grained sandstones exhibit trough cross-beds and horizontal laminations. Numerous eggs and eggshells are frequently found in the muddy siltstone (Table 2). Most mudstones are bioturbated (Fig. 6k) and contain gastropod shells. Pedogenic features, such as carbonate nodules, redoximorphic features (i.e., mottles), slickensides, and clay and iron oxide coatings, are developed to various degrees within mudstones. The upper unit, up to 550 m thick, is characterized by the presence of trough cross-stratified gravel-bearing coarse-grained sandstone, horizontally stratified siltstone, interbedded fine sandstone and sandy mudstone and structureless mudstone (Fig. 6l). Lateral accretion architectures are present, and coals are also, locally, common. Dinosaur eggs (*Paraspheroolithus* cf. *irenensis*) occur in the top. Thin, nodular, calcareous horizons are locally present [20,21]. In addition, Ornithopod bones and palynoflora fossils (such as *Schizaeoisporites* sp., *Cicatruicosisporites* sp., *Lygodiumsporites* sp., *Cyathidites* sp., *Osmundacidites* sp. and *Pagiophyllumpollenites* sp.) have been identified in the mudstone and siltstone of the upper unit of the Majiacun Formation in the area [18,25].

The Sigou Formation, up to 700 m thick, is mainly exposed in the southern (Qiyu-Xi'ao) Xixia Basin and is also subdivided into three stratigraphic units (Fig. 5a). The lower unit comprises coarsening-upward sequences, varying up to 220 m in total thickness. The sequences are vertically arranged as stacks of coarsening-upward sequences of fine-grained sandstone–siltstone–claystone, fine-grained low-angle cross-bedded sandstone and muddy conglomerate (Fig. 6m). Sandstone contains current ripple cross-lamination and horizontal lamination and is commonly fine to medium-grained and moderately sorted. Dinosaur eggs (*Paraspheroolithus* sp.) have been found in the muddy siltstone. The middle unit, up to 370 m thick, mainly consists of gray, yellow and red fine-grained sandstone, siltstone, carbonaceous claystone, marlstone, rare limestone and coal (Fig. 6n). The external geometry of these beds is commonly sheetlike [58]. Parallel lamination and small-scale cross-lamina are the dominant physical sedimentary structures within the sandstone and siltstone beds, with palaeocurrents oriented towards the southeast or northeast by north [57]. The laminated and fine-grained sandstones are associated with siltstone and gray siltstone calcareous claystone. The organic-rich claystone beds display massive to poorly laminated structure, and locally contain gastropod, lamellibranch and ostracode and plant material fossils [18]. Massive marl beds always occur as interbeds in gray organic-rich laminated claystone. Numerous palynoflora fossils (such as *Schizaeoisporites* sp., *S. cretacius*, *S.* cf. *certus*, *S. longus*, *S. laevigataeformis*, *S. evideus*, *Lygodiumsporites* sp. and *Aquilapollenites*) occur in the gray green muddy siltstone of the middle part [18,25]. The upper unit, more than 100 m thick, is composed of purple-red mudstone, calcareous siltstone and muddy siltstone in its lower part and fining-upward cycles of gray or gray yellow stratified conglomerate, planar cross-bedded conglomerate, planar-trough cross-bedded pebble-bearing sandstone, and medium-coarse-grained sandstone, interbedded with red siltstone, mudstone and rare gypsum in the upper part (Fig. 6o). It is generally not well exposed. The conglomerates are laterally discontinuous and have slightly scoured bases. The planar cross-bedded conglomerate is interbedded with planar cross-stratified and stratified sandstone. Trough cross-bedded sandstones commonly grade laterally and vertically into conglomerates. Fine-grained sandstone and siltstone occur as laterally continuous beds having flat bases. Red mudstone is the most abundant of all deposit facies in the study area. The mudstones are closely associated with horizontally laminated fine-grained sandstone. Mudcracks and rain prints are common in the mudstone of the unit (Fig. 6p). Evaporites are very rare; however, gypsum is observed. In addition, traces of evaporate minerals including halite and sulphate are common in the deposits of the unit.

4. Discussion

4.1. Palaeoenvironments, taphonomy and preservation

The absence of marine fossils and the common development of the Upper Cretaceous nonmarine-red terrigenous clastics interbedded with argillaceous strata within the egg deposits indicate that they are continental [21,50], and the abundance of channel deposits with erosive bases and carbonate and gypsum suggest that fluvial and lake actions were involved in their deposition [9,57]. The upward-fining units, which occur in repetition within egg deposits, may form in various fluvial and lake environments such as the alluvial fan, braided river, floodplain or meandering river and shallow lake [53,59–61].

During the deposition of the Gaogou Formation, the deposits are represented by fining-upward sequences comprising massive polygenetic conglomerate (C1), imbricate conglomerate (C2), thin-bedded conglomerate (C3), pebble-bearing coarse-grained cross-stratified sandstone (S1) and red medium- to medium-thick-bedded mudstone (M1) and thick-bedded mudstone (M2). The physical characteristics of the muddy conglomerates are diagnostic of debris flow deposition [61,62]. The sandstones and mudstones associated with the debris flows were deposited by fluvial processes. The mudstones with conglomeratic lags directly above the conglomerates represent reworking of the muddy conglomerates by waning flood stages of the same event that initiated the debris flow or by later normal discharge events [63]. The overall vertical succession of stacked conglomerates, sandstones and mudstones is similar to the models developed for alluvial fan deposition. Facies C1, C2 and C3, which represent the deposits of the lower part of the Gaogou Formation, are interpreted as alluvial proximal fan deposits [58,64]. Facies C2, C3 and M1, which occurred in the middle part of the Gaogou Formation, characterize alluvial mid fan deposits, while facies C3, S1, M1 and M2, which represent the deposits of the upper part of the Gaogou Formation, are interpreted as alluvial distal fan deposits [62,65].

During the deposition of the Majiacun Formation, alluvial fan deposits have gradually been replaced by the deposits of braided streams and meandering streams [20,57]. The lower unit of the Majiacun Formation is composed of trough cross-stratified gravel-bearing coarse-grained sandstone, large- through small-scale planar cross-stratified sandstone, ripple horizontally laminated sandstone and red medium-bedded mudstone, which characterize braided stream to sheetflood deposits. These are similar to those in modern alluvial fan and sheetflood deposits [66,67]. The middle unit is characterized by thin basal pebble layers, fine- to coarse-sandstone bodies, with horizontal laminations, ripple cross-laminations and trough cross-beds, and mudstones or siltstones, which separate sand bodies locally. The thin basal pebble layers that are associated with these sandstones in some localities represent channel bottom lags [51]. The horizontal laminations were either formed as plane beds on longitudinal bars or as upper flow regime plane beds in shallow channels. The trough cross-beds were formed by migrating dunes in the broad channel networks. The ripple cross-laminations in the finer grained sands represent lower flow regime deposition during waning stages or low discharge periods. The mudstones, which separate sand bodies locally, probably represent suspension deposition in inactive or abandoned channels [62,65,68]. The overall facies relationship suggests deposition in a braided fluvial system [68]. The upper unit of the Majiacun Formation consists of stratified conglomerate, trough or planar cross-stratified gravel-bearing coarse-grained sandstone, horizontally stratified muddy siltstone, laminated mudstones with sandstone and structureless mudstone characterizing a low to moderate sinuosity river [50]. Lateral accretion architectures in the upper unit indicate the development of meandering river systems, and the fines and coal measures construct the overbank elements. Vertical stacking of fining-upward cyclothems resulted from the migration of channels and the contemporaneous subsidence of the basement. The calcareous nodular zones may represent palaeosoils [69].

The Sigou Formation is characterized by the presence of pebble-bearing sandstone, fine-grained low-angle cross-bedded sandstone, red siltstone, carbonaceous claystone, marlstone, rare limestone, gypsum and coal. The lower unit of the Sigou Formation is represented by interbedded fine-grained gray sandstone–siltstone–claystone and low-angle cross-bedded sandstone, which are interpreted as crevasse-splay deposits [70]. The middle unit is composed of gray, yellow and red fine-grained sandstone, siltstone, carbonaceous claystone, marlstone and rare nonmarine fossiliferous limestone, which are interpreted as a shallow lacustrine/palustrine environment associated with marshes and swamps. Coal layers overlying the flora-bearing mudstone are autochthonous and were deposited in a swamp/mire environment [58]. Purple-red mudstone, calcareous and muddy siltstone, which are present in the lower part of the upper unit of the Sigou Formation, characterize alluvial plain facies. Interbedded stratified conglomerate, planar cross-bedded conglomerate, planar-trough cross-bedded pebble-bearing sandstone and cross-bedded medium-coarse-grained graded sandstone, which are laterally and vertically interbedded with red mudstone and siltstone in the upper part of the upper unit of the Sigou Formation, are interpreted as low-sinuosity river deposits [59,68,71].

Alluvial fans and braided streams commonly occur in arid environments, mountainous terrain or in valleys having steep profiles in the interiors of continents at some distance from the sea, while meandering streams and lakes spread out in semiarid or humid environments, low-relief in the interiors of continents or in low-relief coastal plains [51]. The expansion of an arid flora into eastern Asia from the Cenomanian to the Maastrichtian [72] suggests an arid palaeoclimatic condition during the Late Cretaceous in the Henan Province, central China [25]. The preservation of the dinosaur egg clutches in calcic palaeosoils indicates that the palaeoclimate of the nesting area was semiarid and seasonal with regard to water availability [73]. The presence of hematite-coated grains, gypsums in the calclithite and mudcracks supports a semiarid palaeoclimatic condition [25,74]. However, there may be ephemeral climatic changes in the period of Late Cretaceous. Mudcracks can form under any climate: they just reflect that mud dried, not an arid climate. In the Gaogou Formation and lower unit of the Majiacun Formation, brown to red palaeosoils are clearly most abundant, but gray and light green palaeosoils are found in the middle to upper unit of the Majiacun Formation and lower unit of the Sigou Formation [18]. The various colors of palaeosol horizons reflect the concentration of iron and manganese compounds present in the matrix, which is controlled in part by the predominant palaeoenvironmental and palaeoclimatic conditions [75]. The red coloration of palaeosoils is produced by the abundance of iron oxides, primarily hematite, accompanied by a low organic content. The red and brown colors are formed under oxidizing conditions and represent well-drained environments. In contrast, the gray and light green colors are formed under deoxidizing conditions and represent impeded drainage setting. Of course, gray and green paleosoils do not necessarily indicate a humid climate. They may represent poorly drained floodplain conditions, a condition independent of climate. Changes in paleosoil types may reflect a change in drainage conditions, especially when changes in the fluvial system are also observed. During the deposition of the upper unit of the Majiacun Formation to the middle unit of the Sigou Formation, the combination of fluvial style and the absence of desiccation features within the muddy floodplain and channel deposits point towards perennial flow, probably in a relatively subhumid climate without significant periods of drought. The geochemical composition of egg-bearing mudstones and palaeosoils also suggests that a strongly seasonal subhumid climate prevailed during the periods of mid-late Late Cretaceous [76]. This situation would have benefited the development of meandering streams in vegetated environments and was also suggested to be a prerequisite for the development of stable mixed-load and suspended-load meandering streams in the late Cretaceous.

Fossil dinosaur eggs in Henan Province are widely distributed. Eggs with complete shapes and regular arrangements (autochthonous type) are mostly distributed in floodplain surfaces whereby they were buried by sheetflood deposits, while destroyed or incomplete dinosaur eggs (allochthonous and parautochthonous type) were situated on unstable proximal and mid fans that were buried by debris deposits. Rapid burial is a basic condition for the preservation of integrated dinosaur eggs [9,11]. In the Late Cretaceous, the climate in the study area was commonly dry and hot, and intermittent flooding could easily take place, thus providing conditions for the development of alluvial fans and river floodplains. River floodplains or "overflow events" have been documented as the best environments for the preservation of dinosaur eggs because the proximity of nests to a body of water can result in their rapid burial [1,7,20]. Based on the sedimentology, the Henan dinosaur clutches were also located close to channels and could be buried readily by flooding [20]. The development of calcic palaeosoils, however, indicates that flooding was infrequent [10,57]. After burial, the calcic soil or siltstone condition likely contributed to the preservation of eggs [28]. Calcic palaeosoils also served as sites of egg preservation in the Upper Cretaceous of Argentina [77], Korea [11], inner Mongolia and Guangdong, China [35,78]. Moreover, a relatively stable tectonic setting has caused full clutches of eggs to be preserved. However, alluvial fans or "alluvial events" have been documented as the worst environments for the preservation of dinosaur eggs, because the eggs were destroyed and transported by the deposits of debris flow, which may be caused by left-lateral strike-slip movements along the Xiguanzhuang-Chibi Tectonic Line.

4.2. Habits of living of dinosaurs

Evidence for the dinosaur mode of life is rarely found in the fossil record, and thus habitat hypotheses have been supported by indirect arguments [55]. The discovery of various dinosaur eggs, bones and tracks in the Upper Cretaceous fluvial-lake deposits of the Xixia, Xichuan and Xiaguan basins, provides insight into the mode of life of some dinosaurs.

During the Late Cretaceous period, the Xixia, Xichuan and Xiaguan basins were distributed at the southern part of the east Qinling-Dabie orogenic belt and went into the nonmarine back-arc and inner forearc sedimentary environment [79]. These sedimentary basins provided the stage for dinosaur activities in a continental setting [80]. The Late Cretaceous strata were deposited in nonmarine environments in response to the post-orogenic collapse of the eastern Qinling-Dabie orogenic belt [57,79]. All the fossil dinosaur eggs, bones and tracks are found in the terrestrial deposits (alluvial fans, floodplains, paleosoils, abandoned channel-fill deposits and shallow-lake deposits) [45]. Sauropod and hadrosaur tracks have been reported not only in the Xixia and Xichuan basins, Henan Province [15], but also in others of China (such as Anhui, Shandong, Hunan, Yunnan and Sichuan provinces) [81]. In addition to the studies of dinosaur eggs, bones and tracks, plant and invertebrate fossils also provided evidence of the Late Cretaceous terrestrial ecosystem in the fluvio-lacustrine Xixia and Xichuan basins. These support terrestrial habits for some dinosaurs such as hadrosaurs and sauropods [82,83]. This view of terrestrial habits is now largely accepted by most dinosaur palaeontologists [60,81,83].

5. Conclusions

(1) The dinosaur eggs and eggshells found in the Xixia, Xichuan, Xiaguan and Liguanqiao basins have approximately been classified into over 37 oospecies allocated to 8 oofamilies and 13 oogenera. The arrangement of dinosaur eggs includes circular or oval radial, cross-parallel, multi-bed parallel and irregular. The burial of dinosaur eggs can be divided into three types: autochthonous, allochthonous and parautochthonous, which were preserved in the alluvial proximal fan, alluvial mid and distal fan, and floodplain, respectively.

(2) Dinosaur egg-bearing deposits of the Upper Cretaceous are divided into the Gaogou, Majiacun and Sigou Formations and are interpreted as alluvial fan, braided and meandering stream, and shallow-lake deposits, respectively.

(3) Dinosaur eggs are mostly preserved in brown to red calcic palaeosoils, muddy siltstones or mudstones, indicating that the palaeoclimate of the nesting area was semiarid. However, the presence of rare gray and little green mudstone and coal layers suggests that there existed an ephemeral subhumid climate during the Late Cretaceous period.

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