Morphology and taxonomy of Gazella (Bovidae, Artiodactyla) from the Late Miocene Bahe Formation, Lantian, Shaanxi Province, China (Postprint)

Authors: ZHANG Zhao-Qun, YANG Rui

Date: 2017-11-07T00:00:00+00:00

Abstract

Fossil gazelles have been widely distributed in Eurasia and Africa during the late Neogene. They are key elements of "Hipparion" faunas with prominent biochronologic and ecological significance. However, no pre-Baodean age gazelle previously reported from China. We describe here in detail materials found from the Bahe Formation, Shaanxi Province, which include by far the most complete skulls and postcranials. The first fossil gazelle skeleton is mounted based on the new findings. Morphology and measurements show the similarity with Gazella lydekkeri from Dhok Pathan Formation of middle Siwaliks, different from the most common species G. gaudryi, G. paotehensis, and G. dorcadoides from Baodean age and other gazelles from Europe. Ecomorphology and measurements of long bones indicate the Lantian species, Gazella cf. G. lydekkeri, is possibly a fast runner, adapted to an open environment in Bahean age. The open environment was also suggested by faunal composition, sedimentological analysis and isotope data.

Full Text

Preamble

Vertebrata PalAsiatica, Vol. 54, No. 1, January 2016, pp. 1—20, figs. 1—6

Morphology and taxonomy of Gazella (Bovidae, Artiodactyla) from the Late Miocene Bahe Formation, Lantian, Shaanxi Province, China

ZHANG Zhao-Qun[1], YANG Rui[1],[2]
(1 Key Laboratory of Vertebrate Evolution and Human Origins, Chinese

Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, zhangzhaoqun@ivpp.ac.cn)
(2 University of Chinese Academy of Sciences, Beijing 100049)

Abstract

Fossil gazelles have been widely distributed across Eurasia and Africa during the late Neogene. They represent key elements of "Hipparion" faunas with prominent biochronologic and ecological significance. However, no pre-Baodean age gazelles have been previously reported from China. We describe here in detail materials recovered from the Bahe Formation, Shaanxi Province, which include by far the most complete skulls and postcranial elements. The first fossil gazelle skeleton has been mounted based on these new findings. Morphology and measurements demonstrate similarity with *Gazella lydekkeri* from the Dhok Pathan Formation of the middle Siwaliks, and differences from the most common species *G. gaudryi*, *G. paotehensis*, and *G. dorcadoides* from Baodean age deposits and other gazelles from Europe.

Ecomorphology and measurements of long bones indicate that the Lantian species, *Gazella* cf. *G. lydekkeri*, was likely a fast runner adapted to an open environment during the Bahean age. This open environment is also suggested by faunal composition, sedimentological analysis, and isotope data.

Key words Lantian, Shaanxi; Late Miocene; Bahe Formation; gazelles

Citation Zhang Z Q, Yang R, 2016. Morphology and taxonomy of *Gazella* (Bovidae, Artiodactyla) from the Late Miocene Bahe Formation, Lantian, Shaanxi Province, China. *Vertebrata PalAsiatica*, 54(1): 1—20

1 Introduction

The genus *Gazella* (Bovidae, Artiodactyla) is one of the most common taxa in "Hipparion" faunas, widely distributed across Eurasia and Africa. The earliest gazelle fossils include *Gazella* sp. from Fort Ternan of the Middle Miocene (14 Ma) and *Gazella pregaudryi* from Bou Hanifia (10 Ma), Algeria (Arambourg, 1959; Gentry, 1970, 2010). Gentry (2010) also mentioned the occurrence of Middle Miocene *Gazella* from the Siwaliks.

The study of Chinese gazelles has a long history, pioneered by Schlosser (1903) on specimens from drugstores without detailed provenance, followed by Bohlin (1935, 1939) on the Lagrelius Collection housed in Uppsala, Sweden, and by Teilhard de Chardin and Young (1931) and Teilhard de Chardin and Trassaert (1938) on specimens from the Yushe Basin. Chen (1997) conducted a systematic revision of fossil gazelles from the Yushe Basin based on the Sino-American project collection and Licent's collection in the Tianjin Natural History Museum.

However, all *Gazella* species previously described from China are recorded from Baodean and younger ages (Chen and Zhang, 2009), leaving a significant temporal gap in our understanding of gazelle evolution in East Asia.

The ecological significance of gazelles was first noted by Schlosser (1903) and greatly advanced by Kurtén (1952), who emphasized the importance of two species—*G. gaudryi* and *G. dorcadoides*—as representatives of eastern wet forest and western dry steppe faunas in North China, respectively. The paleodiets and habitats of these species were later corroborated by stable carbon isotope evidence (Passey et al., 2007).

During 1997-2001, the Sino-Fennic joint project yielded a large collection of fossil bovids, particularly gazelles from the Bahe Formation, Lantian, Shaanxi Province (Zhang et al., 2002, 2013; Zhang and Liu, 2005). Among the 52 localities, Loc.31 yielded exceptionally well-preserved *Gazella* specimens, including five skulls and nearly all postcranial elements, providing an unprecedented opportunity to understand the skeletal morphology and taxonomy of this taxon. This paper provides a detailed description of these specimens and discusses their taxonomy, with brief comments on the ecological environment.

Terminology for skull and teeth follows Chen (1997), Gentry (1966, 1970), and Gray (1977). Measurement methods follow Pilgrim (1937), Yang et al. (2005), and Xia et al. (2005). Comparative materials were examined from the Natural History Museum, London; Evolution Museum of Uppsala University; Paleontological Museum of Athens University; and IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences).

2 Systematic Paleontology

Artiodactyla Owen, 1848
Bovidae Gray, 1821
Antilopinae Baird, 1857
Gazella de Blainville, 1816
Gazella cf. *G. lydekkeri* Pilgrim, 1937 (Figs. 1-6)

Specimens Five almost complete skulls with lower jaws (IVPP V 15246-V 15250); associated with skull V 15246 are four cervicals (C1-C4, V 15246.1-4) and other postcranial elements tentatively assembled as a complete skeleton (V 15246.5-76); eight vertebrae (C5-T2, T3-T7, V 15251.1-8); five lumbar vertebrae, one sacrum, and one caudal vertebra (V 15252.1-7); nine vertebrae (two axes, one C5/C6, six lumbars, V 15253.1-9); three broken scapulae (V 15254.1-3); four pelves (V 15255.1-4); one partial sternum (V 15256); seven humeri (three complete, two proximal and two distal parts, V 15257.1-7); two broken ulnae (V 15258.1-2); one complete and four partial radii (V 15259.1-5); three proximal and one distal femur fragments (V 15260.1-4); two proximal and two distal tibia parts (V 15261.1-4); one complete juvenile metacarpal, four proximal and three distal partial metacarpals (V 15262.1-8); three complete adult and one juvenile metatarsals, two proximal parts (one articulated with naviculo-cuboid and cuneiform) (V 15263.1-6); four complete articulated tarsals (V 15264.1-4); eight carpal bones (one with scaphoid, lunar, cuneiform, and pisiform articulated, one scaphoid, two magnums, and one unciform) (V

15265.1-5); four first phalanges, three second phalanges (V 15425.1-7).

Locality and stratigraphic horizon Loc.31 (N34°11 04 ; E109°15 04), named Snake Locality, discovered by our colleagues Dr. Liu Liping and Prof. Mikael Fortelius after encountering a poisonous snake and stumbling upon the fossils. Stratigraphically, this locality lies in the middle part of the Bahe Formation. Magnetostratigraphic data indicate an age of 8.9 Ma, Bahean age (Zhang et al., 2013).

Measurements See Tables 1-3.

Description

A total of five skulls were recovered from the locality, all well-preserved with lower jaws. Skull IVPP V 15246 is the least distorted, only slightly compressed on the right side, with the right parietal, right zygomatic arch, and right lower jaw missing. V 15247 is more laterally distorted, with the upper part of the horn cores and left zygomatic arch lost, though the lower jaws are well-preserved. V 15248 is also compressed, lacking the right zygomatic arch, but with the pterygoid preserved; the lower jaws are in good condition. The anterior part of V 15249 is laterally compressed, with the pterygoid lost, but the lower jaws are well-preserved. V 15250 is strongly distorted, with the zygomatic arch and pterygoid lost, though the lower jaws are well-preserved. V 15246 and V 15247 possess horn cores and are likely males. V 15248, 15249, and 15250 lack horn cores and represent female individuals. All five skulls are adult, with V 15248 being the oldest based on tooth wear.

V 15246 has nearly complete horn cores. The horn cores are long and slender, with a long oval cross-section, and maximum thickness positioned posterior to the midpoint. No keel is developed. The horn cores insert on the frontals above the orbits at an angle greater than 60°. Divergence is moderate at the base (on V 15247, the long axes of the horn cores form an angle of about 40° measured from the base) and becomes less angled upward. Curvature is moderate. The horn cores taper gradually toward the tip. The inner side is relatively more convex than the outer side. No torsion is observable. Moderately deep postcornual fossae are present.

All five skulls are similar in size without sexual dimorphism (Tables 1-2) and share similar morphology except for the presence of horns in males. The skulls are medium-sized, long and slender in general appearance. The facial region is narrow and long despite taphonomic distortion. The maximum skull width occurs at the posterior ridge of the orbits. The cranial portion behind the orbit is also long and narrow, making the skull appear elongated and slender. The braincase is bent downward, with the cranial axis angled approximately 30° to the facial axis.

Dorsal view The nasals are narrow and domed with parallel sides anteriorly, widened at the midpoint, then tapered between the developed nasal processes of the frontals (Fig. 1A [Figure 1: see original paper]). The posterior end of the nasal extends to the level of the frontal edge of the orbit. The anterior part of the frontal is slightly depressed, and the posterior part is elevated along the suture. The supraorbital foramina are located at the base of the horn core in males and above the orbital roof in females, with anteroposteriorly extended surrounding pits. The dorsal orbital rim is wide (Fig. 2A [Figure 2: see original paper]). The parietal-frontal suture is straight and wide. The parietal narrows posteriorly with observable temporal ridges on both sides leading to the minimum distance at the parietal-interparietal suture. The interparietal is narrow anteriorly and contacts the mastoid posterolaterally via posterior extension. The occipital face has a prominent median crest, which makes each side of the occipital surface face lateroposteriorly.

Lateral view The premaxilla is a thin, narrow plate-like structure, strongly inclined and contacting the nasal at a vertical level slightly anterior to P2 (Fig. 1A). The maxillae narrow anteriorly in front of the tooth rows and widen posteriorly to maximum width at the level of the maxillary tuberosities. The preorbital fossa is moderately deep with a well-developed lacrimal bone. An ethmoidal fissure exists between the lacrimal and nasal bones. The infraorbital foramen opens anteriorly, situated above P2 at a low position (Fig. 1C). The maxillary tuberosity above M1 is moderate in size. The orbital fossa is round-shaped with well-developed upper and lower ridges. The upper orbital ridge is lower than the highest point of the skull, which is positioned at the posterior part of the frontals. The anterior ridge of the orbit is level with the M3 paracone. The zygomatic arch posterior to the orbit is short. The zygomatic process of the squamosal is long and wide with a saddle-like morphology for articulation with the coronoid process dorsally and the condylar process ventrally. A large postglenoid foramen is present. The tympanic bulla is large and round in lateral view with a short acoustic meatus. The oval foramen is large, round, and opens laterally at the posterior end of the lateral plate of the pterygoid (Fig. 1B). The jugular process extends downward, tightly enclosing the posterior surface of the tympanic bulla (Fig. 2C), and contacts the mastoid anterodorsally, which is visible in lateral view.

Ventral view No incisive foramen is preserved on any of the five skulls. The palatal ridges in front of the tooth rows approach but do not touch. The palatine foramen is located at the level of the posterior lobe of M2 (Fig. 1B). The maxilla width reaches maximum at the level of M2 and diminishes greatly forward from P4. The median palatine indentation (choana) is anterior to the lateral ones, especially in female individuals (Fig. 2B). The basioccipital is long and quadrate in shape, with weakly developed and laterally extended posterior tuberosities in male individuals; the anterior tuberosities are even weaker, and the groove between them is extremely shallow. In female individuals, the basioccipital is slightly narrower with slightly larger anterior tuberosities. The tympanic bulla length does not exceed that of the basioccipital.

The mandibular ramus is also long and slender (Fig. 2D). The inner side is flat, and the outer side is outbowed, with the thickness of the horizontal ramus increasing posteriorly. The symphysis is short, extending to the level of the mental foramen. The mental foramen is long oval-shaped, posterior to the canine. The diastema is longer than the molar row. The coronoid process is high and curved posteriorly, with a slightly concave inner side and flat outer side. The condyle is below the highest point of the coronoid process, separated by a deep notch (Fig. 2D). The angular process extends slightly away from the posterior edge of the vertical ramus.

The premolar row is relatively short (Fig. 3 [Figure 3: see original paper]; Table 1). P2 is very small; the paracone is large with a rib. P3 is very similar to P2 but shorter. P4 has a triangular occlusal surface. The paracone is large. A parastyle is present; however, the metastyle is weak. The protocone is located along the midline, with anterior and posterior ridges forming a triangular shape together with the labial cusps. The molars are basically quadrate in shape, increasing in size from M1 to M3. On M1–2, small lingual basal pillars are present. Labial styles are developed, with the mesostyle being the largest. The rib between the parastyle and mesostyle is more developed than the posterior rib.

The i1 is shovel-shaped, with a straight medial side and flanged distal side. The i2 is long rectangular and much smaller than i1. Only the root of i3 is preserved on V 15249. The canine is represented by its root, extending anteriorly in the direction of the root, possibly having an incisor-like shape. The p2 is small with a simple occlusal structure. The protoconid is the main cusp, and the paraconid is much lower and not well separated from the protoconid. The p3 is significantly larger than p2. Its paraconid is well separated from the protoconid and not connected with the parastyle and metaconid. The metaconid extends posterolingually but does not contact the entoconid. The protoconid is slightly more anterior than the metaconid, and the hypoconid is not enlarged. The p4 has rather derived characters: the metaconid extends anteriorly and connects with the paraconid in later wear stages, and posteriorly connects with the entoconid. The hypoconid is prominent, with a furrow separating it from the protoconid on the labial side. A hypoconulid is present, connecting with the entoconid. The paraconid extends posterolingually and is well separated from the parastyle.

Lower molars have basal pillars on buccal sides, which are more developed in males than in females. The basal pillar decreases from m1 to m3. Goat folds are almost indistinguishable. The m3 has a large, labially offset third lobe and a developed anterior cingulum.

Associated with skull V 15246 are four cervical vertebrae in situ. The other four skulls each have an atlas attached. The atlas is trapezoid in outline, with a narrower proximal and wider distal side (Fig. 4A [Figure 4: see original paper]). The articular fossae for the occipital condyles are deep and laterally bounded, separated by a shallow, wide notch dorsally and a wider, deeper U-shaped notch ventrally. Two separate depressions are developed, separated by a central ridge at the anterior one-third of the dorsal arch. The ventral arch presents a median tubercle. The transverse processes are thin plate-like, extending posterolaterally to form a sharp spike. The alar foramen is round without a groove in dorsal view.

The axis (Fig. 4B) is longer than wide, with a high, plate-like spinous process dorsally, while the body is not well developed, about half the length of the axis. The odontoid process is C-shaped, surrounded by a well-developed saddle-like articular facet. The transverse process flanges posterolaterally. The ventral ridge extends cranially but does not reach the level of the collar. The vertebral artery foramen opens obliquely; posteroventral to it, a smaller foramen opens anteriorly.

The third cervical (C3) is slightly shorter but stronger than the axis. The transverse processes are thin plate-shaped, longer than the body, with lateral flanges protruding posterolaterally. The ventral ridge in the middle of the surface extends completely across the body. The dorsal arch is rectangular with four equally sized articular processes. The fourth cervical (C4) is similar to the third in morphology and size, except the dorsal arch is wider with stronger articular surfaces, and the transverse processes are not confluent anteroposteriorly.

C6 has a more slender spinous process, pointed anteriorly, with more constrained lateral sides of the dorsal arch and rod-like transverse processes positioned more anteriorly. Unlike the previous cervical vertebrae, C7 has a well-developed spinous process with the same basal length as the dorsal arch, becoming triangular from mid-height. The caudal width across the posterior articular processes is narrower and shorter than in the preceding cervical vertebrae.

The first thoracic (T1) is characterized by a saber-shaped dorsal spine and the presence of anterior articular processes that are smaller than those on the cervicals. Inferior to the transverse process, a saddle-like articular facet for the rib tubercle is developed. The transverse processes and facets become smaller in posterior thoracic vertebrae. The last thoracic (T13) is more like a lumbar vertebra, except for having anterior costal pits and triangle-shaped transverse processes.

Lumbar vertebrae are similar in structure, tightly articulated with hook-like articular processes and flat, wing-like transverse processes. From the first to the last lumbar (L7), the body and dorsal arch become shorter and wider, transitioning from rectangular to more square-shaped. The posterior articular surface of the body becomes wide and oval-shaped to fit the anterior articular surface of the sacral body.

The sacrum consists of four sacral elements (Fig. 4D). It has larger, more anteroposteriorly elongated hook-like articular surfaces with the lumbar vertebrae. The wing is roughly round-shaped, facing posterolaterally. The sacral width narrows sharply posterior to the wing, reaching a minimum at the third sacral bone. The medial ridge is well united and forms a wall-like plate with a slightly enlarged dorsal roof.

Ribs are not well preserved due to their slenderness. The first rib is slightly curved, with a large tubercle articulating tightly with the saddle-like facet of the first thoracic vertebra. The head is almost horizontally oriented with a long neck. The rib body becomes flatter and wider distally.

A partial sternum is also preserved, which is flat and plate-like with a long, rod-shaped xiphoid process (Fig. 4F).

The scapula (Fig. 4C) is triangular in shape. The spine is prominent, located anteriorly, with the central part curved. The glenoid fossa is round without an obvious notch. The articular surface is at the same level as the acromion.

In lateral view, the humerus shaft is moderately curved, with the proximal portion posteriorly and the distal portion anteriorly oriented (Fig. 5A [Figure 5: see original paper]). The deltoid tuberosity is low and ridge-like. The humeral head is large and round. The greater tubercle is prominent and much higher than the lesser tubercle, and the intertubercular sulcus between them is wide and shallow. The distal end of the humerus extends laterally, with a developed trochlea. The lateral epicondyle is larger than the medial epicondyle. The olecranon fossa is deep, bounded by developed epicondylar ridges.

The ulna is almost fused with the radius at the proximal end, with space remaining downward in the middle of the shaft. The proximal part above the trochlear notch is a thin, rectangular plate in lateral view with a slightly curved posterior edge.

The radius is also moderately curved in lateral view, like the ulna. The posterior surface of the shaft becomes flat or slightly concave in the middle part. The proximal head is short and wide, extending laterally with the medial part slightly longer than the lateral end. At the distal part, two dorsal low ridges exist that are parallel to each other.

The carpal bones are tightly articulated in situ and not separated (Fig. 4I). The scaphoid is rectangular in medial view, anteroposteriorly longer than high, articulating proximally with the medial end of the radius. The lunar is located between the scaphoid and cuneiform, articulating with the lateral end of the radius and both the magnum and unciform distally.

The metacarpal is about the length of the radius (Table 3), and the shaft is slightly curved in lateral view. A developed, wide groove exists on the plantar surface. On the dorsal surface at the distal part, there is a slight vascular groove. The proximal articular surface is triangular, with a developed metacarpal tuberosity. Two articular surfaces with a sagittal ridge are separated by a deep intertrochlear notch.

The pelvis is almost complete with only slight loss at the iliac wing (Fig. 4E). The articular surface with the sacrum is flat. The ventral side of the ilium body is straight and ends with a deep fossa anterior to the acetabulum, which is located in the middle of the ilium and ischium. The greater sciatic notch is obtusely incised. The lesser sciatic notch is very shallow. Three tubercles are developed at the posterior end of the ischium, with the lateral one being the largest. The obturator foramen is long oval-shaped. The pubis is L-shaped with a ridge developed along the pelvic symphysis.

The femur (Fig. 5B) head is round and bulky in the medial part, and the articular surface becomes narrower and more constrained laterally toward the level of the midline of the femoral shaft. The greater trochanter is rectangular plate-like in lateroposterior view, and its proximal end is higher than the femoral head. The notch between them is narrow. The lesser trochanter is moderately developed and connected with the greater trochanter by a crest, which encloses the deep trochanteric fossa. The femoral shaft is slightly curved in lateral view. The medial trochlear ridge is thicker and higher than the lateral ridge and extends more proximally. The trochlear ridges extend obliquely relative to the long axis of the shaft at an angle of about 20°. The lateral condyle is more robust than the medial one, and both are obliquely elongated, but with a reversed direction relative to the trochlear ridges.

The tibia is the longest limb bone (Fig. 5C). The proximal part is stronger with a developed tibial tuberosity and a high crest extending downward to one-third of the shaft length. The medial side of the crest is flat, and the lateral side is concave. The cross-section of the shaft near the proximal part is triangular and becomes rectangular distally. With the developed tuberosity, the proximal articular surface forms a sharp triangle, incised laterally by the extensor groove. The intercondylar tubercles are prominent. The lateral articular surface with the femur is spike-like and protrudes downward, articulating with the medial surface of the astragalus.

The calcaneum is robustly built with a mediolaterally compressed body. The calcaneal tuberosity is prominent dorsally and triangular, while ventrally there is a trochlear-shaped groove. The anteroposterior length of the calcaneal body becomes longer, reaching maximum below the sustentaculum. The articular surface with the medial malleolus has similarly sized proximal convexity and distal concavity (Fig. 4G, H).

The metatarsal is about 20% longer than the metacarpal. The cross-section of the shaft is subrectangular, with width slightly less than length (Fig. 5F). A wide, deep groove exists on the dorsal surface of the shaft. The proximal articular surface is pentagonal. The distal end consists of two similarly sized articular trochleae.

The phalanges of the hand and foot in bovids are very similar in shape and size (Sisson, 1914). Pending further analysis, we describe them together as phalanges. The first phalanx is the longest, with a slightly convex lateral surface and flat medial side. The proximal articular surface is divided into two parts by a deep central groove, with the lateral part larger than the medial part. The first and second phalanges have similar distal morphology, centrally separated into two articular surfaces. The second phalanx is about two-thirds the length of the first phalanx. The third phalanx is triangular, diminishing distally (Fig. 4J).

Based on the described materials, we mounted a complete skeleton using casts of the specimens (Fig. 6 [Figure 6: see original paper]), with only some ribs and tail elements reconstructed by reference to living goats.

3 Comparison

All five skulls with jaws are similar in size (Tables 1–2) and morphology, except for the presence of horns in males. One-way ANOVA analysis of tooth measurements confirms no significant differentiation. Hence, they can readily be attributed to a single species.

The specimens described here are similar in size to the female skull of *Dorcadoryx orientalis* (IVPP V 14423) from the same formation (Chen, 2005: fig. 1B); however, their cheek teeth are proportionally smaller than in that species. Although dorsoventrally distorted, V 14423 shows shallow preorbital fossae and a wider snout due to less forward narrowing at the premolar rows. The horn cores from the frontlets of *Dorcadoryx orientalis* are also larger and taper more rapidly upward.

The morphology of the Lantian species exhibits characters of the most common bovid genus *Gazella* as listed by Gentry (2010): small size with moderately long horn cores; maximum mediolateral width positioned slightly behind the anteroposterior midpoint; absence of keels or torsion; oval-shaped cross-section with the lateral surface flatter than the medial; moderately upright insertions; backward curvature; placement behind the orbits; presence of postcornual fossa; absence of sinuses within the frontals; braincase not shortened; occipital surface with each half facing partly laterally as well as backward; large tympanic bullae; and m3 with a large third lobe.

Fossil gazelles are abundant in "Hipparion" faunas, with more than a dozen species recorded. From the Chinese Late Miocene, three species (*Gazella gaudryi*, *G. dorcadoides*, and *G. paotehensis*) are the most common and have been studied in detail (Bohlin, 1935; Teilhard de Chardin and Young, 1931). Table 4 shows comparisons with these species based on observation of specimens in the Lagrelius collection. Although many similarities exist, differences between the Lantian species and these three species are obvious.

The Lantian specimens are, however, more similar to *Gazella lydekkeri*, described by Pilgrim (1937) from the Dhok Pathan Formation of the middle Siwaliks. They share many characters: females lack horn cores; long and slender skull with deep preorbital fossa and narrow face; premaxilla extending back to the level of P2; braincase longer than wide; face bent down on the cranial axis at about 35°; occipital surface not flat, with a prominent median crest terminating above in a knob-like swelling with flattened depressions on either side; tympanic bulla laterally flattened; horn cores with relatively flat lateral side and convex median side; cross-section basically oval or subtriangular; molars with basal pillars; p4 with hypoconulid separated from entoconid in early wear stages; and third lobe of m3 offset labially. However, the Lantian specimens show some different characters: braincase more heavily bent down; horn cores more compressed laterally, more divergent and less inclined, and relatively less closely set; lower mandible more slender; molars with less developed goat folds; ribs on upper and lower molars less developed, especially on P4 and last molars; premolar row relatively shorter; and less prominent basioccipital tuberosities with no groove between them. Considering the unknown individual variation of *Gazella lydekkeri*, we tentatively assign the Lantian specimens as *Gazella* cf. *G. lydekkeri* herein.

The Lantian species is distinct from *Gazella capricornis* from Pikermi, Greece, in having less robust and more mediolaterally flattened horn cores and relatively larger teeth. Compared with *G. deperdita* from Cucuron, France, the Lantian species has longer horn cores with anteroposterior length decreasing gradually from base to tip, more straight insertion above the orbit, and differs from *G. deperdita* which has strong posteriorly narrow horn cores. The Lantian species differs from the Samos species *G. mytilini* in the latter having the hinder half of the orbit situated beneath the horn core, horn cores parallel to each other, more hypsodont teeth, and basal pillars on molars wholly lacking. Different from *G. pilgrimi*, the Lantian species has more curved horn cores, a relatively shorter premolar row, and more developed basal pillars on molars.

4 Discussion and Conclusion

Bovid fossils from the Chinese Middle Miocene are relatively rare and less diversified than those from the Late Miocene. Only three genera—*Eotragus* of Bovinae, *Kubanotragus* of Hippotraginae, and *Turcocerus* of Urmiatheriinae—have been documented previously (Chen and Zhang, 2009). The gazelle fossils from the Bahe Formation represent the earliest records of Antilopinae in China.

A systematic study of all *Gazella* species is still pending and beyond the scope of this paper. Nonetheless, it is difficult to relate the Lantian species to all later-occurring species from China, given some seemingly derived characters: short premolar row, enlargement of metaconid on p4, compressed oval-shaped cross-section of horn core, and long, bent-downward braincase.

Kurtén (1952) analyzed "Hipparion" faunas from the Chinese Late Miocene, highlighting the ecological significance of the high-crowned *Gazella dorcadoides* and low-crowned *G. gaudryi*, representing western dry and eastern humid realms in North China, respectively. Based on tooth crown height, the Lantian species is intermediate between these two species, showing no strong dietary preferences.

However, the Lantian species' slim and elegant body plan may indicate good running ability. The femur has a long, horizontal neck of the femoral head, a deep notch between the head and greater trochanter, wide distal articulation, and an anteriorly projected median ridge. The tibia has prominent tubercles on the proximal articular surface and two sagittally oriented deep trochlear grooves separated by a central ridge at the distal end. The metatarsal and metacarpal both have same-sized and parallel articular trochleae. The proximal articular surface of the first phalanx is divided into two parts by a deep central groove. All these characters indicate adaptation for fast forward running without much turning flexibility (Gentry, 1970). The length ratios of radius/humerus and tibia/femur are roughly 120%, also suggesting fast running ability (Osborn, 1929). This fast-running lifestyle likely indicates an open environment during their time period, consistent with the ecological pattern of the Bahean Fauna (Zhang et al., 2002; Zhang, 2006), based on sedimentological study (Kaakinen and Lunkka, 2003) and isotope data (Kaakinen et al., 2006).

The bovid assemblage from the Bahe Formation, together with *Shaanxispira baheensis*, *Dorcadoryx orientalis*, and *Lantiantragus longirostralis* (Zhang, 2003; Chen, 2005; Chen and Zhang, 2004), contrasts sharply with the much more diversified assemblage of Baodean age (Chen and Zhang, 2009). The turnover of the bovid assemblage across the Bahean/Baodean boundary fits the climatic and ecological change scenario suggested by Kaakinen et al. (2006) and Zhang et al. (2013).

Acknowledgements The authors sincerely thank all participants in the Lantian project for the discovery and excavation of the fossils described in this paper. Professor Chen Guanfang from IVPP provided critical comments and suggestions that greatly improved the manuscript. ZZQ appreciates help from his senior colleague and mentor, Dr. Alan Gentry, during his visit to the Natural History Museum, London in 2002 as a newcomer. He is also indebted to Dr. Solweig Stunes, recently deceased curator of the Evolution Museum of Uppsala University, for hosting his visits and study of the Lagrelius collection.

New Record of a Haplocyonine Amphicyonid in Early Miocene of Nei Mongol Fills a Long-Suspected Geographic Hiatus

WANG Xiao-ming[1],[2], *WANG Hong-jiang*[3], *JIANGZUO Qi-gao*[2],[4]
(1 Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California 90007, USA; Corresponding author: xwang@nhm.org)
(2 Key Laboratory of Vertebrate Evolution and Human Origins, Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China)
(3 Administration Station of Cultural Relics of Xilinguole League, Xilinhaote 026000, Nei Mongol, China)
(4 University of Chinese Academy of Sciences, Beijing 100049)

Abstract We report a newly discovered amphicyonid (beardog) upper molar from the Early Miocene Lower Red Mudstone Member of the Aoerban Formation in central Nei Mongol. This molar is highly diagnostic of European haplocyonines or North American temnocyonines, two subfamilies of beardogs long known from those continents but notably absent from Asia. The new molar is strikingly similar to *Haplocyonoides mordax* and *Temnocyon percussor* in its dumbbell-shaped M1 outline, reduced parastyle, protocone isolated by a surrounding cingulum, and extreme reduction of pre- and postprotocristae. Given the limited material, we tentatively refer the new Chinese fossil to the European *Haplocyonoides* cf. *H. mordax* based on similar size and age relationships. If this identification is correct, our new record fills a large gap in the geographic distribution of haplocyonines and represents an excursion of this rare subfamily from Europe.

Key words Aoerban, Nei Mongol; Early Miocene; Amphicyonidae; zoogeography

Citation Wang X M, Wang H J, Jiangzuo Q G, 2016. New record of a haplocyonine amphicyonid in Early Miocene of Nei Mongol fills a long-suspected geographic hiatus. *Vertebrata PalAsiatica*, 54(1): 21–35

1 Introduction

Straddling between Europe to the west and North America to the east, Asia has long been suspected to be either a source of certain Cenozoic mammals that, thus far, are only found in Europe and/or North America, or at the very least, must have served as a "jumping board"to and from destination continents during dispersal events. When taxa are found in both Europe and North America, their absence in Asia fuels speculation of Holarctic continuity, with the expectation that filling the Asian gap may be only a matter of time. Temnocyonine and haplocyonine amphicyonids represent such a long-suspected geographic hiatus waiting to be filled.

Temnocyoninae and Haplocyoninae are peculiar lineages of amphicyonids, or beardogs, with hypercarnivorous dentitions and, in some species, digitigrade posture (Hunt, 2011). Members of these groups typically possess a very trenchant lower molar battery that aligns their main cusps in a single row to facilitate shearing function, accompanied by a narrow, high-crowned premolar series (e.g., Bonis, 1973; Hunt, 2011; Peigné and Heizmann, 2003). Asian records of amphicyonids have generally lagged behind those of Europe and North America, partly due to a shorter history of field exploration associated with a late start of scientific enterprise in most Asian countries. Occasionally, Asian field records do catch up, and we have the satisfaction of reporting a new fossil record of haplocyonines from the Early Miocene of Nei Mongol (Inner Mongolia) that confirms, once again, that Asia has much to offer for our understanding of Holarctic zoogeography.

Abbreviations ACM, Amherst College Museum of Natural History, Amherst, Massachusetts; AMNH, Division of Paleontology, American Museum of Natural History, New York; F:AM, Frick Collection, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; IM, IVPP fossil localities from Nei Mongol; LACM, Natural History Museum of Los Angeles County, Los Angeles; NM, Northwest Museum, Portland State University, Portland, Oregon; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt; TRO, Timberlane Research Organization, Lake Wales, Florida; UCMP, Museum of Paleontology, University of California, Berkeley; UNSM, Vertebrate Paleontology, University of Nebraska State Museum, Lincoln; USNM, Department of Paleobiology, Smithsonian Institution, Washington, D.C.; YPM-PU, Princeton Collection, Peabody Museum, Yale University, New Haven.

2 Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Amphicyonidae Haeckel, 1866
Subfamily Haplocyoninae Bonis, 1966
Genus Haplocyonoides Hürzeler, 1940
Haplocyonoides cf. *H. mordax* Hürzeler, 1940

Referred specimen IVPP V 22639, an isolated left M1. Collected by X. Wang on August 8, 2015.

Locality, stratigraphy, and age IVPP IM1530 locality (XWIM04), N43°20’ 34’ ‘, E113°54’ 30’’ , elevation 1050 m, Sonid Zuoqi, Xilinhot League, central Nei Mongol (Fig. 1 [Figure 1: see original paper]). Locality IM1530 is stratigraphically positioned at the boundary between the Lower Red Mudstone and Middle Green Mudstone members of the Aoerban Formation (Fig. 2 [Figure 2: see original paper]). Locally, the two members transition into each other, possibly due to diagenetic effects of the green coloration. IVPP V 22639 thus belongs to the uppermost Lower Aoerban Fauna (Wang et al., 2009). Based on small mammal biochronology, Qiu et al. (2013a) estimated that the upper part of the Lower Aoerban Fauna was approximately 19 Ma, corresponding to the late Xiejian or possibly early Shanwangian Chinese land mammal ages (see Qiu et al., 2013b).

Description With the exception of missing roots, IVPP V 22639 is almost perfectly preserved, lacking only the anterior rim of enamel at the waist. Fresh breakage at the base of the roots indicates they were broken after re-emergence from sediment encasement during erosion. V 22639 shows only minor wear at the apex of the metacone, representing a young adult.

V 22639 is almost twice as transversely wide as anteroposteriorly long (see measurements in Table 1). Overall, it is dumbbell-shaped with a distinctly constricted waist at the junction of the protocone on the lingual side and the paracone-metacone on the labial side. In occlusal view, the paracone and metacone are about the same size, although the paracone is taller—especially when viewed from the lingual side, but less so from the labial side. A parastyle is poorly developed, indicated by a slightly thickened and higher cingulum surrounding the parastyle. A distinct notch separates the paracone and metacone.

Both paracone and metacone have anterior and posterior ridges aligned in a single line and are completely encircled by a thin cingulum.

The protocone has a rounded base and is located slightly anterior to the paracone-metacone notch. The low-crowned protocone is about half as tall as the metacone and about one-third the height of the paracone. An extremely faint preprotocrista is present on its anterolabial face, pointing to the narrowest point (anterior waist) of the tooth. A postprotocrista is slightly more distinct than the preprotocrista, anteroposteriorly oriented and ending posteriorly at the posterior cingulum. Both paraconule (protoconule) and metaconule are absent, giving the protocone an isolated appearance. The protocone is nearly completely encircled by a cingulum of varying thickness. Lingually, this cingulum forms an almost perfect half-circle with similar crown heights throughout the protocone. However, the cingulum thickens toward the posterolingual aspect of the protocone, becoming more than twice as thick as its anterior segment, and along the medial and posterior sides of the protocone, the cingulum has some minor wrinkles on its crest.

In anterior and posterior views, V 22639 has a distinctly concave appearance (Fig. 4A, C [Figure 4: see original paper]) due to a deep trigon basin that occludes with a high-crowned m1 hypoconid. The high-crowned paracone-metacone crest shears with the labial face of the m1 hypoconid.

3 Comparisons

Despite the meager material from Aoerban, there is no doubt that V 22639 belongs to Amphicyonidae, although a dumbbell-shaped M1 is found in other similar-sized carnivorans, such as *Enhydrocyon* and *Paraenhydrocyon* of hesperocyonine canids (Wang, 1994), *Megalictis* of basal musteloids (Matthew, 1907), and *Eomellivora* of mellivorine mustelids (e.g., Valenciano et al., 2015). However, in all three of the latter cases, a prominently developed M1 parastyle dominates the labial half of the tooth with a much larger paracone and very reduced metacone, in sharp contrast to the more evenly developed paracone and metacone (with a more quadrate outline for the labial half of the tooth) in most amphicyonids.

The Aoerban tooth is easily distinguished from all known amphicyonids in Asia. Excluding small, primitive forms from the Late Eocene through Early Miocene, such as *Guangxicyon sinoamericanus* from the Late Eocene of Guangxi Province (Zhai et al., 2003), unnamed species from the Late Eocene of Mongolia (Egi et al., 2009), *Cynodictis elegans* from the middle Oligocene of Nei Mongol (Huang, 1982), and the questionable *Ictiocyon* cf. *I. socialis* from the Early Miocene of Gansu (Wang et al., 2005), almost all Asian Miocene forms are large amphicyonine amphicyonids. Well-known examples include the Early Miocene *Amphicyon confucianus* and *Ysengrinia* sp. from Shanwang, Shandong Province (Qiu and Qiu, 2013; Qiu et al., 1986; Young, 1937), Middle Miocene *Ysengrinia* sp. from Japan (Kohno, 1997; Kohno et al., 1997), Middle Miocene *A. tairumensis* from

Nei Mongol (Colbert, 1939) and Gansu (Deng et al., 2013), Middle Miocene *A. ulungurensis* from Xinjiang (Qi, 1989), and Late Miocene *A. palaeoindicus* and *Vishnucyon* cf. *V. chinjiensis* from Yunnan Province (Qi, 2006), although caution must be exercised in some of these generic assignments because many Asian taxa of large size, often based on fragmentary materials, tend to be tentatively placed in *Amphicyon* (Hunt, 2003). From Southeast and South Asia, several taxa are assignable to amphicyonines, such as Middle Miocene *Maemohcyon potisati* from Thailand (Peigné et al., 2006), Late Miocene *Amphicyon* from Myanmar (Egi et al., 2010; Sein and Thein, 2011), and *A. sindiensis*, *A. palaeoindicus*, *A. pithecophilus*, *Arctamphicyon lydekkeri*, and *Vishnucyon chinjiensis* from Early to Late Miocene Siwalik strata of India and Pakistan (Colbert, 1935; Lydekker, 1884; Pilgrim, 1932). The M1 in *V. chinjiensis* has a markedly narrowed lingual half with a constricted appearance, but its protocone retains distinct pre- and postprotocristae (Pilgrim, 1932: plate II, fig. 9 [Figure 9: see original paper]). When present, the M1s in these Asian forms have triangular outlines with distinct pre- and postprotocristae typical of amphicyonines and are easily distinguishable from the dumbbell-shaped Aoerban M1. Even without an upper molar, these taxa have reduced, low-crowned lower premolars or basined lower molars, in contrast to the high-crowned premolars and trenchant molars in haplocyonines and temnocyonines.

Aktaucyon brevifacialis from the Early Miocene of Kazakhstan shows a hint of waist constriction in M1 (Kordikova et al., 2000). However, its pre- and postprotocristae are still distinct, and it has a large M2 relative to M1, features suggesting that its M1 constriction may be convergent. The Middle Miocene *Gobicyon macrognathus* from Nei Mongol (Colbert, 1939; Zhai, 1964), and possibly also from Xinjiang (Wang et al., 1998) and Gansu (Deng et al., 2013), may be an aberrant form of haplocyonines because of its high-crowned, piercing premolars, although its fragmentary m1 talonid appears not quite as trenchant as its European relatives (Hunt, 1998:208). Unpublished upper M1s from the Hezheng area, Gansu Province, also exhibit a dumbbell shape (Qiu Zhanxiang pers. comm.). A Serbian (formerly Yugoslavian) partial mandible previously referred to *G. macrognathus* by Pavlovic and Thenius (1959) has since become the basis of a new species *Haplocyonoides serbiae* (Ginsburg, 1999a), although its diagnostic characters remain in dispute (Peigné and Heizmann, 2003).

The distinctly constricted waist with a dumbbell outline in V 22639 is the most salient feature of this specimen, seen only in European haplocyonines and North American temnocyonines. Haplocyoninae is a lineage of hypercarnivorous amphicyonids from the Late Oligocene to middle Miocene of Europe, commonly including genera such as *Haplocyon*, *Haplocyonoides*, and *Haplocyonopsis* (Ginsburg, 1999a; Peigné and Heizmann, 2003). Dentally, it is characterized by high-crowned premolars and highly trenchant lower molars that may lose metaconids and entoconids (Bonis, 1966, 1973; Helbing, 1928; Peigné and Heizmann, 2003; Rothausen, 1988). Most haplocyonine species with known M1s (including *Haplocyon crucians*, *Haplocyon elegans*, *Haplocyon dombrowskii*, *Haplocyonopsis crassidens*, *Haplocyonoides mordax*, *Haplocyonoides suevicus*) tend to be somewhat more primitive than V 22639 in having a stronger parastyle, larger paracone relative to metacone with a more acute angle between the labial border of M1 and that of P4, M1 protocone with at least a remnant pre- and postprotocristae, and a not very constricted waist area.

Advanced haplocyonines may have dumbbell-shaped upper M1s, such as in *Haplocyonoides mordax* (Hürzeler, 1940). However, published figures of the only M1 of *H. mordax* (SMF-M1653e; Hürzeler, 1940: figs. 3–5) from the type locality in Hessler, Mainz Basin show several differences from V 22639: a relatively larger protocone, narrow cingulum surrounding the protocone, and a stronger preprotocrista with a distinct paraconule at its end (see Fig. 4F [Figure 4: see original paper]). Peigné and Heizmann (2003), however, referred a second M1 (SMF-M6000) from Budenheim, Rhineland-Palatinate, Germany, which has never been figured. S. Peigné graciously provided a photograph of this specimen, permitting a much-needed assessment of variation (Fig. 4G, H [Figure 4: see original paper]). This referred specimen is strikingly similar to V 22639 in its much-reduced protocone resulting from a widened surrounding cingulum, greatly reduced pre- and postprotocristae, and nearly complete loss of a paraconule. Consequently, the lingual half of SMF-M6000 assumes a distinct appearance of an isolated protocone, not only because of its smaller protocone footprint relative to the broad surrounding cingulum but also its isolation from the trigon basin due to reduction of pre- and postprotocristae. Details on the labial half of this tooth are also remarkably consistent with those of V 22639. The labial side of SMF-M6000 is almost symmetrical with nearly identical paracone and metacone sizes, making it difficult to determine tooth side without associated P4 or M2. Nevertheless, judging by the slightly higher-crowned paracone and parastyle (Fig. 4H [Figure 4: see original paper]), we interpret this tooth as a right M1, which, if correct, would be slightly more derived than V 22639 due to the general morphocline among European haplocyonines toward decreased parastyle and symmetrical paracone and metacone.

Minor differences between the European and Chinese forms include a more anteriorly located protocone, a slightly more bulging parastyle, and a less distinct (not very ridge-like) lingual cingulum in V 22639.

Haplocyonoides mordax was initially established from Hessler near Wiesbaden in the Mainz Basin, Germany, in the Early Miocene (MN2) based on isolated upper and lower teeth (Hürzeler, 1940) that may or may not belong to a single individual (Rothausen, 1988). Bonis (1973: pl. 4, fig. 5) referred an additional right maxillary fragment with P4–M1 from Laugnac (MN2, Lot-et-Garonne) as ?*H. mordax*, although he noted that its M1 lacks a median constriction. More recently, Ginsburg (1999b:119) also listed *H.* cf. *H. mordax* from "faluns of Anjou (MN3 or 5)" in addition to recognizing a new species, *H. serbiae* (formerly *Gobicyon macrognathus* by Pavlovic and Thenius, 1959), plus the previously described *H. ponticus* (Kuss, 1960). While describing a new German species, *H. suevicus*, Peigné and Heizmann (2003: appendix) provided a complete hypodigm for *H. mordax*. In addition to materials from the type locality and Laugnac mentioned above, they included one specimen from Weisenau (MN1) and three specimens from Budenheim (MN2), both from the Mainz Basin in Rhineland-Palatinate, Germany. Furthermore, they (Peigné and Heizmann, 2003:68) listed several sites from the MN3 of France and M2 of Spain, but preferred to treat *Haplocyonoides mordax huerzeleri* (Rothausen, 1988) as a nomen dubium and cast doubt over generic assignments of *H. serbiae* and *H. ponticus*.

V 22639 is also quite comparable to some North American temnocyonines, which share considerable similarities with European haplocyonines, interpreted as convergences by Hunt (2011). In several respects, temnocyonines have become even more hypercarnivorous than haplocyonines, with short and robust crushing P4 in advanced forms, M1 protocone isolated by a flat platform of surrounding cingulum, substantial reduction of M2 and loss of M3, and digitigrade posture (Hunt, 2011). M1 morphology is particularly diagnostic for temnocyonines, with clear trends observable to help delineate lineages. The smallest and most basal species, *Temnocyon altigenis*, has an enlarged parastyle, a protocone at the beginning stage of isolation but still with a preprotocrista connecting to a small paraconule, and a lingual cingulum slightly widened. Successively larger and more derived species, such as *T. subferox* and *T. ferox*, have a more isolated protocone, lost preprotocrista (in *T. subferox* but not in *T. ferox*) and paraconule, and more expanded lingual cingulum. *T. fingeruti*, apparently a side branch from the main chronospecies series (*T. altigenis-subferox-ferox*) (Hunt, 2011: fig. 70 [Figure 70: see original paper]), does not quite follow this same trend, such as retaining strong pre- and postprotocristae and lacking middle constriction. Large, bone-crushing genera, *Mammacyon* and *Delotrochanter*, further elaborate this theme by widening the cingulum surrounding the protocone, among other specializations.

In light of the above trends within the main *Temnocyon* chronospecies series (Hunt, 2011: fig. 70 [Figure 70: see original paper]), V 22639 falls somewhere close to *T. subferox* and *T. ferox* both in metric plots (Fig. 5 [Figure 5: see original paper]) and some qualitative characters. The Chinese form has extremely reduced pre- and postprotocristae, not quite the complete loss seen in *T. subferox* (Hunt, 2011: fig. 10A [Figure 10: see original paper]) but certainly exceeding that condition in *T. ferox* (Hunt, 2011: fig. 12B [Figure 12: see original paper]). However, neither of these two North American species has reduced their parastyles to the extent seen in V 22639. The degree of protocone area enlargement in V 22639 is also somewhat more pronounced than in the above two American species. We also note that some characters are not strictly in a linear sequence, such as the precocious reduction of pre- and postprotocristae in *T. subferox*, although current knowledge about intraspecific variation is too limited to permit evaluation of morphological outliers.

A poorly known large species, *Temnocyon percussor* Cook, 1909, is also intriguingly close to V 22639. An isolated M1 (AMNH 81047) from the type locality (Cook Quarry, Anderson Ranch Formation, Sioux County, Nebraska, late Arikareean) was referred to this species (Fig. 4I [Figure 4: see original paper]). As described by Hunt (2011), this tooth is remarkably similar to V 22639. Its large size aside, AMNH 81047 has almost identical morphology to V 22639 in its protocone area enlargement: widening of lingual cingulum, reduction of pre- and postprotocristae, and reduction of parastyle. The only subtle difference is a slightly more convex labial border, compared to a very faint concave border in V 22639.

Although we cannot completely rule out the new Aoerban material being related to the North American temnocyonine, the balance of evidence, as shown by this single M1, seems to tip toward something close to *Haplocyonoides mordax*. In favor of such an assignment is the relatively closer age relationship between the Chinese and European forms (see Zoogeographic remarks below). If this taxonomic assessment is correct, future discoveries of more complete materials of this Nei Mongol species should bear additional haplocyonine characters.

4 Zoogeographic Remarks

In his study of Aquitanian mammals, Bonis (1973) commented on the striking morphological similarities between European haplocyonines and North American temnocyonines, as also noted earlier by Viret (1929). Bonis regarded these similarities as parallel developments by groups confined to their respective continents, a conclusion also maintained by Hunt (1996, 1998, 2011), who further explicitly derived his Temnocyoninae from within an early stock of Haplocyoninae (Hunt, 1998: fig. 11 [Figure 11: see original paper].3). Additionally, European haplocyonines and North American temnocyonines seem to have had independent evolutionary trajectories and chronological sequences, at least in the case of more derived temnocyonines (Fig. 5 [Figure 5: see original paper]). If that is the case, it implies a single immigration event during the Early Oligocene that brought a primitive haplocyonine to North America to give rise to the temnocyonines, as postulated by Hunt (1998). However, *Haplocyonoides mordax* is much too late and too derived to be ancestral to temnocyonines.

If Peigné and Heizmann' s (2003) concept of *Haplocyonoides mordax* is followed, the age range for *H. mordax* extends to European Neogene mammal zones 1-3. If we take this at face value—a species range as long as ~5 million years (23–18 Ma)—the later part of the European records would be equivalent in age to the new Nei Mongol record. However, based on actual M1s from MN2 of Germany that we can compare, the Chinese form likely represents an eastward expansion of this lineage. If so, the Aoerban form would be the first occurrence of this lineage in Asia, possibly followed by later *Gobicyon* in the Middle Miocene.

Acknowledgements We have benefited greatly from discussions with Robert M. Hunt, Jr., who has been unstinting in sharing his vast knowledge of European and North American amphicyonids. We also greatly appreciate exchanges with Stéphane Peigné, who generously provided unpublished photos critical to the formulation of ideas in this paper. Discussion with Louis de Bonis was also helpful for fossil identification. We thank Naoki Kohno for providing relevant reprints and a cast, and Naoko Egi for furnishing photos of Myanmar amphicyonid materials. We appreciate careful reviews by Qiu Zhanxiang and Zhang Zhaoqun; their comments and suggestions greatly improved this paper. We gratefully acknowledge the hard work of our 2015 field crew: Deng Tao, Yuri Kimura, Li Yikun, Sun Danhui, as well as our drivers Feng Wenqing and Gao Wei. Funding for fieldwork during the past 20 years was provided by: Chinese National Natural Science Foundation (No. 41430102), Strategic Priority Research Program of the Chinese Academy of Sciences (XDB03020104), Chinese Academy of Sciences Outstanding Overseas Scholar Fund (KL205208), National Science Foundation (US) (EAR-0446699, 0444073, 0958704, 1227212 to XW), and National Geographic Society (NGS 5527-95 to XW).

Restudy of the Late Oligocene Dormice from Northern Junggar Basin

Wu Wen-Yu[1], **Meng Jin**[1],[2], **Ye Jie**[1], **Ni Xi-Jun**[1], **Bi Shun-Dong**[1],[3]

[1]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
[2]Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA
[3]Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705, USA

Abstract

A new glirid genus and species, *Gliruloides zhoui*, is named based on specimens from the Late Oligocene Tieersihabahe Mammal Assemblage Zone I (Tie-I zone) of the northern Junggar Basin, Xinjiang. The new genus is diagnosed by the following features: medium-sized dormouse; concave occlusal surface of cheek teeth; upper and lower cheek teeth dominantly with nine transverse ridges; the anterotrope(id) and posterotrope(id) well developed and extending almost the full length of corresponding valleys; transverse ridges of upper cheek teeth usually free-ended labially; M1/2 with V- or narrow U-shaped trigon; the precentroloph not connected to the endoloph that is incomplete or nearly complete; the endolophid in lower cheek teeth discontinuous or continuous; labial end of the anterolophid curving slightly distally but not connected with the protoconid; root number of p4, m1-3, P4 and M1-3 being 2, 2, 3 and 3 respectively. We discuss the differences of *Gliruloides* from *Glirulus* and *Vasseuromys* and assign the Anatolian *Vasseuromys duplex* and *Vasseuromys aff. V. duplex* from the Early Miocene of Turkey to *Gliruloides.* It is posited that *Gliruloides* and *Glirulus* may share a common ancestor similar to *Glis guerbuezi* from the Lower Oligocene of Thrace, Turkey. *Gliruloides* might live in a relative wet and warm biotope.

Key words northern Junggar Basin, Late Oligocene, Tieersihabahe Mammal

Assemblage Zone I, dormouse

Citation Wu W Y, Meng J, Ye J et al., 2016. Restudy of the Late Oligocene dormice from northern Junggar Basin. *Vertebrata PalAsiatica*, 54(1): 36−50

Our study on earliest Chinese dormice (Wu et al., 2000) was based on specimens collected in 1998 from the Late Oligocene Tieersihabahe Formation in northern Junggar Basin of Xinjiang. Only four teeth, among which three were assigned to *Glirulus* sp., were available at the time. An additional 11 teeth were collected by screenwashing at the same level of the same locality (XJ 98024) and other nearby localities (XJ 98035, XJ 200209 and XJ 20004) in four field seasons from 1999 to 2002. All teeth but one right M3 (IVPP V 18113) are almost identical to the specimens described by Wu et al. (2000). Undoubtedly, they belong to the same taxon. Since the work of Wu et al. (2000), we have realized that these teeth show high similarities to *Vasseuromys duplex* from the Early Miocene of Anatolia (Ünay, 1994), and therefore cited *Vasseuromys* sp., instead of *Glirulus* sp., in fauna lists of our successive papers (Meng et al., 2001, 2006; Ye et al., 2001a,b; 2003a,b) but without further explanation. The present paper restudies the Late Oligocene Junggar dormouse based on all material available to us and reinterprets its taxonomic position.

Our study reveals that the specimens of the Late Oligocene Junggar dormouse are more similar to *Vasseuromys duplex* than to any other dormouse and that *V. duplex* differs considerably from other European *Vasseuromys* species and *Glirulus*. Thus, we name a new genus, *Gliruloides*, for the Junggar dormouse and assign the Anatolian species, *Vasseuromys duplex* and *Vasseuromys aff. V. duplex*, to this genus.

In describing the tooth morphology, we use a modified terminology derived from de Bruijn (1966) and Freudenthal (2004), which is convenient and unambiguous for description of the extra ridges of the dormice cheek teeth (Fig. 1). The SEM photographs were taken by Meng Jin, using the Hitach S-4700 scanning electron microscope at the American Museum of Natural History in 2005.

Fig. 1 Dental terminology of Gliridae (Modified from de Bruijn (1966) and Freudenthal (2004))

Family Gliridae Thomas, 1897

Subfamily Dryomyinae de Bruijn, 1967

Genus *Gliruloides* gen. nov.

Etymology *glirulus* + *oides*, indicates that the dormouse is morphologically similar to genus *Glirulus* but should not be *Glirulus*.

Type species *Gliruloides zhoui* gen. et sp. nov.

Diagnosis Medium-sized dormouse with concave occlusal surface of the cheek teeth. The upper and lower cheek teeth possess dominantly nine transversal ridges. The anterotrope(id) and posterotrope(id) of the upper and lower cheek teeth are well developed and extend almost the full length of the corresponding positioned valleys. The trigon of M1-2 is V- or narrow U-shaped, and the endoloph of upper cheek teeth is incomplete or nearly complete. The main ridges of the upper cheek teeth are labially free-ended. The endolophid of the lower cheek teeth is discontinuous or continuous. The labial end of the anterolophid of the lower molars slightly curves distally, but is not connected to the protoconid. Lower cheek teeth are two-rooted.

Differential diagnoses
1) *Gliruloides* differs from *Glirulus* in having a V-shaped or narrow U-shaped trigon on M1-2, the endoloph incomplete or nearly complete on upper cheek teeth, the lingual end of the precentroloph not connected to the endoloph, and main ridges in the upper cheek teeth free-ended labially. In contrast, the upper molars of *Glirulus* have wide U-shaped trigon, complete endoloph, and the precentroloph that connects lingually to the endoloph (except for geologically older representatives in which the endoloph may be incomplete and the precentroloph unconnected to the endoloph, refer Ünay, 1994). In *Glirulus* the main tooth ridges usually connect with each other labially and form the anterior and posterior loops (see Fig. 4D).
2) *Gliruloides* differs from *Vasseuromys* mainly in having nine ridges on most upper and lower molars, in having the developed anterotrope and posterotrope on the upper cheek teeth, and the usually regular and continuous extra ridges. In *Vasseuromys*, however, the anterotrope and posterotrope outside the trigon of the upper cheek teeth are absent or weak, and the extra ridges of the cheek teeth are usually irregular and interrupted (see Fig. 4B).

Included species *Gliruloides duplex* (Ünay, 1994) from Early Miocene (MN2) of Anatolia, localities Harami 1-3, Turkey. *Gliruloides aff. G. duplex* (Ünay, 1994) from Early Miocene (MN1) of Anatolia, localities Kilçak 0, Kilçak 0" and Kilçak 3A-3B.

***Gliruloides zhoui* gen. et sp. nov.**

Glirulus sp., Wu et al., 2000
Vasseuromys sp., Ye et al., 2001a, b, 2003a, b; Meng et al., 2001, 2006

Etymology In honor of the late Dr. Zhou Mingzhen (Minchen Chow), an academician of the Chinese Academy of Sciences and the pioneer paleomammalogist in China.

Holotype Left M2, IVPP V 18110.1 (Fig. 2C).

Paratype One left M3 (IVPP V 18110.2), one right m1 and one left m1 (V 18110.3-4), and one right m3 (V 18110.5) (Fig. 2D, H, J, K).

Type locality and horizon Locality XJ 98035, Tieersihabahe of northern Junggar Basin, Xinjiang; Tieersihabahe Mammal Assemblage Zone I; Late Oligocene.

Referred specimens One left P4 (IVPP V 18111.1, Fig. 2A), two right p4 (V 18111.2-3, Fig. 2F-G), one right m1 (V 18111.4, Fig. 2I) from XJ 98024. One left M1/2 (V 18112, Fig.2B) from XJ 200209.

The specimens described in 2000 include one right M2 (IVPP V 11812.1), one left M3 (V 11812.2) and one left m1 (V 11812.3) from XJ 98024 (Wu et al. 2000: pl. 1, figs. 1-3, 5).

All specimens listed above were from Tieersihabahe of northern Junggar Basin; Tieersihabahe Mammal Assemblage Zone I; Late Oligocene.

One right M3 (V 18113, Fig. 2E), collected from XJ 20004 at Saerduoyila of northern Junggar Basin. The stratum producing the specimen is correlative to that of Tieersihabahe.

Diagnoses The p4 possesses eight transverse ridges. The anterotropid on the lower cheek teeth is usually single. The endoloph on upper cheek teeth is nearly complete, whereas the endolophid of lower cheek teeth is interrupted. The protoconid and mesoconid of the lower molars are hook-like. The metalophid extends slightly distally to the labial side and then turns abruptly mesiolabially.

Differential diagnoses *Gliruloides zhoui* differs from the Anatolian species *G. duplex* and *Gliruloides aff. G. duplex* in having 1) nearly complete endoloph on M1/2, 2) hook-like protoconid and mesoconid of the lower molars, 3) the metalophid almost always extends slightly distolabially and then turns abruptly mesiolabially and 4) possibly the rare presence of doubled-anterotropid on the lower molars. In contrast, *G. duplex* and *Gliruloides aff. G. duplex* normally have incomplete endoloph on M1/2 and rarely have hook-like protoconid and mesoconid. In both forms, the metalophid usually extends mesiolabially and a doubled-anterotropid is common on the lower molars.

Measurements (length × width in mm)
P4 (V 18111.1) 0.87 × 1.05; M2 (V 18110.1) 1.05 × 1.25; M1/2 (V 18112) 1.03 × 1.09; M3 (V 18110.2) 0.92 × 1.05; M3 (V 18113) 0.77 × 0.98; p4 (V 18111.2) 0.86 × 0.68; p4 (V 18111.3) 0.84 × 0.67; m1 (V 18110.3) 1.17 × 1.05; m1 (V 18111.4) 1.16 × 1.09; m1 (V 18110.4) 1.13 × 1.06; m3 (V 18110.5) 1.11 × 1.00 (Except P4 is larger and m3 is slightly longer than in *G. duplex*, the other teeth are approximate to those of *G. duplex* in size.

Description
The occlusal surface of all cheek teeth is concave. All the upper cheek teeth have usually nine transverse ridges, including the six main ridges (anteroloph, protoloph, metaloph, posteroloph, precentroloph and postcentroloph) and three extra ones (anterotrope, prototrope and posterotrope). Both the anterotrope and posterotrope extend almost the full length of the valleys where they locate. The labial ends of the main ridges are free or lightly connected. The lingual wall of the endoloph on upper cheek teeth is well decorated. All upper cheek teeth have three roots (one major lingual and two minor labial ones).

P4

The left P4 (V 18111.1; Fig. 2A) is suboval-shaped in occlusal view. Its occlusal surface is strongly concave. The anteroloph has its labial end separated from the protoloph and the lingual end touched the protoloph but not the endoloph. The lingual end of the posteroloph is weakly in contact with the endoloph and labially connects to the metaloph. The protoloph is labially free and lingually connects to the endoloph; it is interrupted midway by the U-shaped anterotrope-prototrope connection. The anterotrope extends to the labial border and stays free, whereas the prototrope is half long the anterotrope. The precentroloph ends free labially, but lingually it bifurcates to join the protoloph and metaloph, respectively. The postcentroloph is short and situated in the middle of the valley, with both ends being free. The metaloph is convex distally and interrupted near its lingual end. The posterotrope is long, filling nearly the whole length of the corresponding valley. The trigon is V-shaped.

M1/2

Two M2 and one M1/2 are in the collection. The identification of specimen V 18112 (Fig. 2B) as M1 or M2 cannot be certain so that we denote it as M1/2 (but is probably M1 because of its V-shaped trigon). The holotype M2 (V 18110.1) is moderately worn and almost identical to the specimen V 11812.1 reported by Wu et al. (2000: pl. 1, fig. 1). The occlusal surface is wider than long. The paracone and metacone are prominent. The anteroloph is labially weakly connects to the paracone with a shallow furrow in between and lingually joins the endoloph. The paracone connects the labial end of the precentroloph loosely. The metacone is separated anteriorly from the postcentroloph and posteriorly from the posteroloph by a narrow and very shallow furrow, respectively. The precentroloph is long, extending to the point near the endoloph. The trigon is narrowly U-shaped and contains the long prototrope, precentroloph and postcentroloph. The lingual wall of the endoloph is well decorated. Specimen V 18112, a left M1/2 is slightly worn and closely similar to the holotype, but differs from the latter in being wider anteriorly than posteriorly, the V-shaped trigon, precentroloph being labially far separated from the paracone and curving backwards to the metacone, the anteroloph being labially free from the paracone, and loosely contacting with the protocone lingually to form a nearly complete endoloph. The anterotrope and posterotrope on all three specimens extend the whole length of the corresponding occupied valley.

M3

There are three M3 specimens (V 11812.2, V 18110.2 and V 18113), which are characterized by a trapezoid-shape, being much wider anteriorly than posteriorly. M3 has usually the same number of ridges as M1/2 but the precentroloph is much shorter than the postcentroloph. Specimen V 18110.2 is well worn. The labial side of the paracone was slightly damaged but it seems in connection with the anteroloph and protoloph. The precentroloph is much shorter than the postcentroloph and extends labially to the labial margin of the tooth and has no contact with both the paracone and metacone. The postcentroloph extends lingually and almost reaches the endoloph; its labial end is weakly connected with the metacone. The prototrope is absent, instead is a metatrope present inside the trigon. The metatrope is short, only a half width of the valley, and locates labially. Both metaloph and posteroloph are interrupted by a narrow gap at the midway. It seems that the endoloph is separated from the lingual end of the anteroloph before the tooth was worn. The specimen V 11812.2 (Wu et al., 2000: pl. 1, fig. 2) is highly similar to V 18110.2. There is, in addition to the anterotrope, an extra ridge between the anterotrope and protoloph. Both prototrope and metatrope are present. The specimen V 18113 (Fig. 2E) from XJ 20004 is similar to specimen V 11812.2, but its ridges are more slender and the anterotrope is weaker and shorter. We tentatively assign this tooth to this species.

The p4

Both p4 are round trapezoid in shape, wider posteriorly than anteriorly (Fig. 2F, G). The anterolophid is convex mesially and connected distally to the metalophid to form a closed loop. The centrolophid is thin and long, connected lingually to the metaconid weakly, and extends to the labial border. The labial end of the mesolophid turns abruptly mesially along the labial border on one specimen (V 18111.2) but becomes well-swollen labially on the other (V 18111.3); the mesolophid connects lingually to the posterolophid at the entoconid, and labially connected to or separated from the posterolophid. The anterotropid and posterotropid are well developed, and the mesotropid is short or long. The metatropid is absent in both teeth so that p4 is eight-ridged.

The m1

Four specimens are in the collection, including the one described by Wu et al. (2000: pl. 1, fig. 3). They are quite monotonous morphologically and generally trapezoid-shaped with the anterior end being slightly narrower than the posterior end. The m1 usually has nine transverse ridges, including five main ridges (anterolophid, metalophid, centrolophid, mesolophid and posterolophid) and four extra ridges (anterotropid, metatropid, mesotropid and posterotropid). All four extra ridges are well developed, of which the anterotropid and posterotropid extend nearly the entire length of the located valleys. However, specimen V 11812.3, described by Wu et al. in 2000, remains an exception because it has an additional secondary extra ridge between the anterotropid and metalophid. For all specimens of m1, the anterolophid is slightly concave mesially, labial end slightly curved distally and free-ended; its lingual end slightly curved distally too, and gradually merges into the metaconid lingually.

The metalophid is lingually connected to the metaconid and extends slightly distolabially, with its labial end turning abruptly mesially to form a hook-like protoconid that is not connected to the anterolophid. The centrolophid is long and extends labially near the mesoconid but does not reach to the labial border of the tooth. Lingually the centrolophid is either separated from or connected with the metaconid. The mesolophid is slightly convex distally and extends mesiolabially where, like the metalophid, it turns abruptly mesially and forms a hook-like mesoconid that is separated from the protoconid mesially and from the hypoconid distally. The posterolophid joins the mesolophid lingually at the entoconid. An endolophid is absent.

The m3
This tooth is mesially much wider than distally. The anterolophid is slightly convex mesially. Except for the four extra ridges seen in m1, there are two more secondary extra ridges: one mesial and the other distal to the posterotropid, respectively. Furthermore, a very small and weak enamel bulge but not ridge is present between the anterolophid and anterotropid.

All lower cheek teeth have two roots, but the mesial root of m1 (V 11812.3) shows a trend of bifurcation at the end.

Several teeth display distinctive striations of abrasion in mesiolingual-distolabial direction on the occlusal surface (Fig. 3), which we record here. We think this information should be useful for further study of this animal in masticatory movement, dietary, and perhaps taxonomy.

Fig. 3 Occlusal view of the lower and upper cheek teeth of *Gliruloides zhoui*. Arrows indicate the direction of striations caused by wear on the concave crown surface.

Comparisons and Discussions

As mentioned above, the Junggar glirid, represented by three specimens at the early time, was first assigned to *Glirulus* (Wu et al., 2000) because it is similar to *Glirulus* in having usually nine ridges on both upper and lower cheek teeth, with well-developed anterotrope and posterotrope in upper cheek teeth and the anterotropid and posterotropid in lower cheek teeth. However, additional specimens collected subsequently made us reconsider the taxonomic assignment of the Junggar glirid. We have listed above several features that differentiate the Junggar form from *Glirulus* in the differential diagnoses. At the same time, we noted that the Junggar form is quite similar to the Turkish Lower Miocene dormouse, *Vasseuromys duplex*, in both upper and lower molars. Thus, we considered that the Junggar glirid should not be assigned to *Glirulus* and have referred it to *Vasseuromys* in several of our papers (Meng et al., 2001, 2006; Ye et al., 2001a, b; 2003a, b) without explaining the reason until this study.

Vasseuromys was established by Baudelot and de Bonis (1966) based on the type species *V. rugosus* from the Lower Miocene of Laugnac, France. The only material of this species was a mandible with p4-m2. The original generic diagnosis states (translated from French by Daams and de Bruijn, 1995:50): "Medium-sized Gliridae. Cheek teeth with concave occlusal surface. Lower molars characterized by a centrolophid reaching the labial border and by a longitudinal prolongation of the labial cusps that form a nearly continuous ectolophid."

Based on additional specimens of upper cheek teeth from the type locality de Bonis (1973:54) emended the diagnosis of the genus as: "Vasseuromys characterized by multiplicity of the extra ridges and by the upper molars with a continuous endoloph (translated from French)."

The upper cheek teeth referred in the work of de Bonis (1973) consisted of one P4, one M1/2, and two M3. While working on the dormice from Austria and Spain, Daxner-Höck and de Bruijn (1981) and Alvarez Sierra et al. (1990) have independently visited the collections of *Vasseuromys rugosus* housed at the University of Utrecht; all the specimens are from the type locality. The two research teams noticed that there were several upper molars of *V. rugosus* with incomplete endoloph. Alvarez Sierra et al. (1990) wrote: "Although de Bonis (1973) characterizes this species as having a continuous endoloph (on the basis of one worn specimen), several M1,2 without endoloph are present in the collections of the University of Utrecht. The specimens from the Utrecht collections have a long anteroloph whose lingual end descends toward the base of the protocone." Daxner-Höck and de Bruijn (1981) further provided figures of the upper and lower molars of *V. rugosus*, which show the V-shaped or narrow U-shaped trigon and incomplete endoloph in the upper molars (Daxner-Höck and de Bruijn, 1981: fig. 1-h,r,s,t,u; fig. 2-m,n,o,p) (see Fig. 4B).

Up to now ten species have been included in this genus (ref. Daams and de Bruijn, 1995; Ruiz-Sánchez et al., 2012a, b; 2014):

Vasseuromys rugosus Baudelot & de Bonis, 1966; type locality and type level: Laugnac of France, MN2B, Early Miocene.
V. priscus de Bonis, 1973; type locality and type level: Moissac 1 of France, MN1, Early Miocene.
V. pannonicus (Kretzoi, 1978); type locality and type level: Budapest, Freshwater Limestone of the Széchenyi hill; MN10?, Late Miocene (Synonym: *V. thenii* Daxner-Höck & de Bruijn, 1981).
V. autolensis (Cuenca, 1985); type locality and type level: Autol, La Rioja, Spain; MN1, Early Miocene.
V. bacchius (Martínez-Salanova, 1987); type locality and type level: Fuenmayor 2, Autol 1, La Rioja, Spain; MN2B, Early Miocene.
V. elegans Wu, 1993; type locality and type level: Stubersheim 3, Germany, MN3, Early Miocene.
V. duplex Ünay, 1994; type locality and type level: Harami 1, Turkey; MN2, Early Miocene.
V. cristinae Ruiz-Sánchez et al., 2012; type locality and type level: Pico del Fraile 2, Ebro Basin, Spain; MN4/5, Miocene.
V. rambliensis Ruiz-Sánchez et al., 2012; type locality and type level: Pico del Fraile 1, Ebro Basin, Spain; Upper Ramblian, MN3, zone A, Early Miocene
V. bergasensis Ruiz-Sánchez et al., 2014; type locality and type level: Bergasa, Ebro Basin, Spain; MP30, Late Oligocene (ref. Lacomba, 1988).

Apart from the above listed species, *Nievella mayri* Daams, 1976 from the Early Miocene of Cetina de Aragón, the early Late Miocene *Ramys multicresatus* (de Bruijn, 1966) and *Myolidus* may belong to *Vasseuromys*, as so suggested by Agusti et al. (2011).

The taxonomy, phylogeny and biostratigraphy of the known species of *Vasseuromys* are beyond the scope of this study. Our focus is on whether the Junggar form belongs to *Vasseuromys*, a potential assignment we have indicated in our previous studies (Meng et al., 2001, 2006; Ye et al., 2001a, b; 2003a, b).

After intensive survey of the literatures about *Vasseuromys*, we realized that, in general, all European species have features in common with the type species *V. rugosus* and differ from those of the Turkish *V. duplex* and *Vasseuromys aff. V. duplex*. We recognize the fundamental difference between them as representing two dental patterns of *Vasseuromys* cheek teeth, primarily reflected in the upper cheek teeth, which are differentiated below:

In European species of *Vasseuromys*, the anterotrope and posterotrope outside the trigon are usually absent; if present, they are short and weak; the ridges are rugose and asymmetrically arranged.

In *V. duplex* and *Vasseuromys aff. V. duplex* from Anatolia of Turkey, the anterotrope and posterotrope outside the trigon are always present and long; they extend almost the full length of the corresponding valleys they are in; the ridges are regular and symmetrically arranged.

In fact, Ünay (1994:470) already noted that "The striking features of Turkish *Vasseuromys* are the ever present long extra ridges in the anterior and posterior valleys outside the trigon on the M1/2···different from all European species." We found that the pattern of the anterotrope and posterotrope is present not only on M1/2 but also on P4 and M3 of Turkish *Vasseuromys* (Ünay, 1994). Because of the distinct morphological differences between the Turkish and European *Vasseuromys* species, we think that *V. duplex* should be inevitably assigned to a different genus. The Junggar and Turkish forms are also different from *Glirulus*, as we discussed above.

In addition to the tooth crown structures, we have compared the root number of various species of *Glirulus* (Paraglirulus included), *Gliruloides* and *Vasseuromys* (Table 1). All upper cheek teeth of the three genera are triple-rooted except that *Glirulus* (Paraglirulus) *werenfelsi* has a double-rooted P4. However, the available data show that the lower cheek teeth of all *Glirulus* species are double-rooted except that p4 of *Glirulus* (P.) *agelaki* from Aliveri is single-rooted and *Glirulus japonicus* has double-rooted p4 and triple-rooted lower molars. *Gliruloides* has also double-rooted lower cheek teeth except that the m3 of *Gliruloides aff. G. duplex* is occasionally triple-rooted. Species of *Vasseuromys*, where the root condition is known, however, have a single-rooted p4 and double or triple-rooted lower molars. Table 1 shows that the Junggar form is similar to *G. duplex* not only in their tooth crown structures but also in the root number. However, it should be noted that only the m3 root number (two or three roots) of *Gliruloides aff. G. duplex* was provided by Ünay (1994), whereas the root number of m1/2 was not provided. With the survey of the root number distributions among relevant species, we consider the root condition to be of taxonomic information for species of the three genera in question, although more data are needed to verify this consideration.

In short, given that the Junggar and Turkish forms share some distinctive dental features but differ from the *Vasseuromys* and *Glirulus* in various features, we think they should be placed in the same genus; thus we establish the new genus *Gliruloides* to include the Junggar and Turkish forms.

Gliruloides currently includes three species: *G. zhoui*, *G. duplex* and *Gliruloides aff. G. duplex* and tentatively assigned to the subfamily Dryomyinae because of several diagnostic features, such as the concaved surface, basically symmetrical upper molar, and some teeth with nearly complete endoloph.

The Origin of *Gliruloides*

The Early Oligocene (ca. MP25) *Glis guerbuezi* from Thrace of Turkey (Ünay-Bayraktar, 1989) is, to our knowledge, the earliest known dormouse that displays considerable resemblance to *Gliruloides* in dental pattern. *G. guerbuezi* has at most nine transverse ridges in either upper or lower molars (see Fig. 4C). On certain M1/2s of *G. guerbuezi*, besides four main ridges, there are precentroloph, postcentroloph and prototrope inside the trigon, and anterotrope and posterotrope outside the trigon. In addition to four main ridges and centrolophid, the anterotropid and posterotropid are developed in m1 and m2, with incipient metatropid and mesotropid present in m2. M1/2 of *G. guerbuezi* also has V-shaped or narrow U-shaped trigon and an incomplete endoloph, and the anterolophid is labially isolated in lower molars. It is probable that *Gliruloides* was derived from a *Glis guerbuezi*-like ancestor, although we are not able to illustrate their detailed evolutionary process because of the limited knowledge available to us. Together with *Gliruloides duplex* and *Gliruloides aff. G. duplex*, Ünay (1994) also described two species of *Glirulus*: *G. ekremi* of MN3 (from Keseköy) and *Glirulus aff. G. ekremi* of MN2 (from Harami 1, associated with *V. duplex*) from Anatolia. We have noticed that the Turkish *G. ekremi* has an incomplete endoloph in 27.50% of M1/2 specimens and a precentroloph connected to the endoloph in only 19.2% of M1/2s, and the lower molars of *G. ekremi* are morphologically very similar to those of the Turkish "Vasseuromys" . Thus, identification of those teeth is not always unquestionable. It is also reasonable to infer that *Glirulus* may also be derived from the same *Glis guerbuezi*-like ancestor so that *Gliruloides* and *Glirulus* share a most recent common ancestor but evolved in different directions as two lineages. The fact that the root number of the most *Glirulus* species is same as that of *Gliruloides*, as shown in Table 1, could be another evidence for their common origin.

Ecology

According to Walker (1975: volume 2:979) the living *Glirulus japonicus* inhabits mountain forests from about 400 to 1800 meters in elevation, with the highest recorded elevation being 2900 meters. This animal' s diet includes fruits, seeds, insects and bird' s eggs. All fossil specimens of *Gliruloides duplex*, *Gliruloides aff. G. duplex* and two species of *Glirulus* Ünay (1994) described were from Lower Miocene lignite containing sections (de Bruijn and Saraç, 1991) of Anatolia (from localities Keseköy, Harami 1-3 and Kilçak 0, 0" , 3A, 3B). The morphological similarity of teeth in *Gliruloides* and *Glirulus* from Turkey could be attributed to a similar ecological environment (ecotope) and diet. The presence of lignite in the sections probably indicates wet biotopes (de Bruijn and Saraç, 1991; Ünay, 1994). *Gliruloides zhoui* is a member of the Late Oligocene Tieersihabahe-I zone fauna, collected from the same localities (XJ 20004 and XJ 98024) as the giant rhino *Paraceratherium sui* (Ye et al., 2003a) but was discovered from the level immediately above the level where rhinoceros located. Three rhino localities were found in Ulungur River area, which arrange in a west-east extending line with the largest distance of ca. 57 kilometers. *Paraceratherium sui* was discovered from the fluvial sediments at the base of Tieersihabahe Formation. Ye et al. (2012:1530) inferred that the presence of this giant rhino, at the time of ca. 25 Ma, is an implication of a temperature rise in the course of global cooling and aridification that begins from the Early Oligocene, which is coincided with the time of "Late Oligocene warming" (Zachos et al., 2001: fig. 2). *Gliruloides zhoui* might still have lived in a relatively wet and warm transitional time somewhat later than *Paraceratherium sui*. We have mentioned above that *Gliruloides* could be derived from the *Glis guerbuezi*-like form. The latter came from the Turkish late Early Oligocene localities situated in the Lignite-Sandstone Formation (Ünay-Bayraktar, 1989:10). The sediments could also indicate that wet and forest environment existed during that period in this regional area.

Acknowledgements
We thank Dr. Ruiz-Sánchez from Department of Geology, Division of Paleontology, University of Valencia of Spain for providing us important literatures about Spanish *Vasseuromys*. Thanks are also due to the American Museum of Natural History, New York for permission to use the scanning electron microscope. We are grateful to Su Jianfen and Wu Shaoyuan for their hard work in the field and to Yue Qiwan for sorting the miniscule teeth from the concentration of screenwashed samples. We also thank many local peoples who helped us in collecting, transporting and screenwashing dirt samples under the baking sun of the desert. This research has been supported by the Strategic Priority Research Program of Chinese Academy of Sciences (CAS, XDB03020501) and National Basic Research Program of China (2012CB821904).

Female Preference Promotes Asynchronous Sex Evolution in Elephantiformes

Wang Shi-Qi[1,2,3], **Deng Tao**[1,2]

[1]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
[2]CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China

[3]Key Laboratory of Economic Stratigraphy and Palaeogeography, Chinese Academy of Sciences (Nanjing Institute of Geology and Palaeontology), Nanjing 210008, China

Abstract

Sexually dimorphic characters are usually thought to enhance copulatory success by intraspecific competition; for example, larger body size and stronger tusks are sexually dimorphic characters in fossil and extant male proboscideans. Here, we show that some sexually dimorphic characters in fossil Elephantiformes, the largest group of proboscideans, are strongly correlated with the evolution of this group rather than direct sexual competition. In Miocene *Platybelodon grangeri* and *Gomphotherium angustidens*, males tended to initially possess evolutionarily more derived characters than females, and females then evolved similar variation. This phenomenon may have occurred as a result of female preference. During the early evolutionary stage (thriving stage) of Elephantiformes, sexual selection pressure promoted development of more prominent derived characters in males than females. However, during their late evolutionary stage (declining stage), sexual selection pressure seems to have weakened; thus, the asynchrony between the two sexes diminished. This new discovery may help explain a common mechanism of large ungulate evolution and extinction, because substantial sexual dimorphism is often displayed in thriving groups, such as Cervidae and Bovidae, in contrast to little sexual dimorphism in declining groups, such as extant taxa of Equidae, Rhinoceridae, and Giraffidae.

Key words Elephantiformes, sexual dimorphism, female preference, evolution

Citation Wang S Q, Deng T, 2016. Female preference promotes asynchronous sex evolution in Elephantiformes. *Vertebrata PalAsiatica*, 54(1): 51−66

1 Introduction

Since Darwin, sexual selection has been considered the key factor that influences secondary sexually dimorphic character development within a species (Darwin, 1874; Fisher, 1930; Andersson, 1994). As a result, these characters are thought to improve male copulatory success by intraspecific competition. However, the relationship between sexual dimorphism and evolution is not fully understood. For example, in Elephantiformes (Tassy, 1988), sexual dimorphism has been observed in Oligocene *Phiomia*, Miocene *Platybelodon grangeri*, *Gomphotherium angustidens*, *?Stegotetrabelodon* sp. (Matsumoto, 1924; Osborn and Granger, 1932; Lambert, 1992; Tassy, 1996, 2013; Bibi et al., 2012; Wang et al., 2013), and extant elephants (Nowak, 1999; Roth and Shoshani, 1988; Kurt et al., 1995; Douglas-Hamilton et al., 2006; Lee and Poole, 2011). In *G. angustidens* there is sexual dimorphism not only of body size and tusk characteristics but also of other characters that have not been fully understood (Tassy, 1996, 2013). Furthermore, in large ungulates, substantial sexual dimorphism is often exhibited in early evolutionary stage (thriving) groups, such as Cervidae and Bovidae; however, little sexual dimorphism appears in late evolutionary stage (declining) groups, such as extant taxa of Equidae, Rhinoceridae, and Giraffidae. Therefore, the mechanism underlying sexual dimorphism and evolution in this group should be studied further.

Recently, a population of fossil *P. grangeri* was discovered from the Middle Miocene Zengjia locality, Guanghe County, Gansu Province, China (Fig. 1). This population included a large number of crania and mandibles (Wang et al., 2013), and therefore provided a good model to study sexual dimorphism in Miocene Elephantiformes and evaluate the relationship between elephantiforme sexual dimorphism and evolution.

Fig. 1 Map showing the Zengjia locality (N 35°26’ 23.1” , E 103°26’ 37.6” , H 2150 m) yielding the population of *Platybelodon grangeri*

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; BPV, Beijing Natural History Museum, Beijing, China; HMV, Paleozoological Museum, Hezheng, Gansu, China; MNHN, Muséum National d’ Histoire Naturelle, Paris, France.

2 Materials and Methods

Specimens

All of the *Platybelodon grangeri* specimens from the Zengjia locality are housed in HMV, and a total of 32 specimens were analyzed: HMV 0014-0020, 0022-0039, 0042, 0043, 0939, 0940, 1836, 1841, and 1842. The ontogenetic ages of the specimens range from Dental Age XVIII to XXI (Tassy, 2013), which means all of the specimens were adults (as determined based on functioning m3 and/or M3) with similar ontogenetic ages. *P. grangeri* from Tunggur are AMNH 26408, 26460, 26462, 26469, 26472, and 26490 (Dental Ages from XVIII to XX). These specimens are from the Platybelodon Quarry and Wolf Camp localities because they were found in the same horizon (Wang et al., 2003). *Loxodonta africana* specimens are four adult females (AMNH 32732, 42469, 51949, and 88404) and four adult males (AMNH 32734, 39083, 51939, and 113819). Two *Gomphotherium angustidens* crania are MNHN Si37 (male, Dental Age XIX) and MNHN SEP185 (female, Dental Age XXI). An adult skull with an associated mandible (probably a male) of *Platybelodon danovi* is BPV 2000 (Dental Age XX). All of the specimens belong to the museum collections and are open to scientific research.

Locality and age

All of the *P. grangeri* specimens that were considered part of the same population were collected from the Zengjia locality (N 35°26 23.1 , E 103°26 37.6 , H 2150 m, No. LX200002, Fig. 1) of the Linxia Basin, Gansu Province, China. The fossil bearing strata belong to the Middle Miocene Hujialiang Formation, which consists of grayish-yellow fine conglomerates and sandstone rocks, which indicate fluvial strata (Deng et al., 2013). The fauna is also composed of a typical Middle Miocene mammalian community, including *Castor* sp., *Alloptox* sp., *Pseudaelurus* sp., *Gomphotherium* cf. *G. subtapiroideum*, *G. wimani*, *Zygolophodon* cf. *Z. gobiensis*, *Chalicotherium* sp., *Anchitherium gobiensis*, *Hispanotherium matritense*, *Listriodon* sp., *Kubanochoerus* sp., and Cervidae indet. (Deng et al., 2013).

Fig. 2 The cranial measurements of Elephantiformes, after Tassy (1996: fig. 11.1, slightly revised), not scaled. A. dorsal view; B. ventral view; C. lateral view; D. posterior view.

Measurements

Cranial and mandibular measurements of elephantiforme specimens were based on those described by Tassy (2013); a total of 36 cranial measurements (Fig. 2, indicated by "C") and 24 mandibular measurements (Fig. 3, indicated by "M") were taken. There was one minor change to the measurement protocol: M1 was taken from the anterior border of the incisive alveolus instead of from the lower tusk, which we did not analyze in the present article, to the mandibular condyles.

Fig. 3 The mandibular measurements of Elephantiformes in lateral (A) and dorsal (B) views. After Tassy (1996: fig. 11.1, slightly revised), not scaled.

Measurement inclusion

In multivariate sex assessment, measurements that reflect little sexual dimorphism and have substantial variation may affect the results. Therefore, the only measurements used in analysis are those for which the coefficient of variation is less than 15. The included measurements consist of a total of 21 cranial measurements, C1-4, 6-8, 10-12, 14, 15, 18, 19, 22, 30, 31, and 33-36, and 18 mandibular measurements, M1-10, 12, 13, 17.

Data prediction and modification

In the multivariate sex assessment analysis, a complete data set is ideal but not available because of the incompleteness of specimens. Therefore, we used a linear regression method (Wang and Deng, 2010) to predict the missing measurements. For the analyzed material, some measurements were questionable because of substantial deformation or unreliable restoration. In these cases, the questionable data were considered missing. Then, the data were weighted based on the mean of the raw data and the predicted data. The weighted measurement values were calculated as follows: where w is the weight, p is the predicted datum, and m is the original measured value (1 -w is assigned as the weight for predicted data). Complete pseudo data sets were constructed using this procedure.

Data normalization

We estimated the total length, or size factor (SF), of each specimen based on the C1 and M1 values. In the complete pseudo data set, data were divided by each SF to produce a size-normalized pseudo (SNP) data set to obtain shape information. Then, the SNP data set was logarithmically transformed, because each measurement was of equal importance for morphological discrimination and should be analyzed on the same scale. The following formula was used: where Mi was an SNP value of a certain measurement of specimen i and was the mean of the SNP values for all specimens. This new data set was defined as the size-normalized logarithmic pseudo (SNLP) data set for multivariate analyses.

Fig. 4 Bivariate scatter plot of upper tusks in male and female *Platybelodon grangeri*. Solid triangles, male; open triangles, female.

Sex assessment

Before sex assessment, only the length of upper incisor could be directly used for sexual discrimination (< ca. 300 mm for females and > ca. 300 mm for males, Fig. 4). These typical adult crania were first selected to form the SNLP data sets (males and females were considered two different groups) and examined by principal component analysis (PCA). The resulting principal components (PCs), of which the cumulative variance contribution rate exceeded 95%, were selected as new variables for Fisher' s discriminant function analysis (DFA), and the first discriminant function (DF1) was calculated. Then, the remaining crania of uncertain sex were examined using the DF1 (Appendix 1) and we preliminarily determined the sex for each cranium. Then, these crania were divided into two groups based on inferred sex, and two more SNLP data sets were constructed then re-examined in a new PCA-DFA cycle. If a cranium clustered into the opposite sex group in DFA, we changed the cranium' s sex assignment and began another PCA-DFA cycle. Cycles did not stop until the data clustered appropriately based on sex assignment. After several PCA-DFA cycles, an optimal sex assessment was obtained for each cranium.

No sex assignment was proposed based on mandibular characters or measurements. The specimens with long symphyses were considered male, because some were associated with male crania (HMV 0939 and 0940). Consequently, those mandibles with short symphyses were considered female. The same PCA-DFA cycles were performed on the mandibles as on the crania until all of the mandibles had optimal sex assessments.

Univariate analyses

Univariate analyses were carried out on individual characters in both sexes. Only the originally measured or modified values were used in analyses, and those specimens missing original measurements were not included. For each measurement (including M3 and m3 measurements), the mean, standard deviation (s.d.), coefficient of variation (c.v.), and maximal and minimal values were calculated. Two-tailed Student' s t-tests were performed between the two sexes, and p-values less than 0.05 were considered significant.

Bivariate scatter plots and histograms

DF1 from the last PCA-DFA cycle and normalized length from crania and mandibles, length and width from M3 and m3, and length and maximal width of mandibular symphyses were depicted in bivariate scatter plots; the 95% confidential eclipses for both sexes were calculated and also included in the plots. C2/C1, C34/C31, and M11/M2 measurements of each specimen were calculated and their statistics were performed. The mean + s.d. of the results were shown in histograms. Two-tailed Student' s t-tests were performed between the two groups, and p-values less than 0.2 were considered significant.

Simpson' s ratio diagrams

The formula for Simpson' s ratio is as follows: where m is a measured value in an object group, s is the corresponding value in the standard group, and r is the resultant Simpson' s ratio. Both m and s are available from individual specimens and the mean of the specimens. Simpson' s ratio diagrams were used to compare both sexes of *Platybelodon grangeri*, *Gomphotherium angustidens*, and *Loxodonta africana*.

The results show that there is significant sexual dimorphism in the population of fossil *P. grangeri* (Figs. 5A, B, and Appendix 1). In addition to larger and more robust upper tusks, which are beneficial for direct combat, other craniomandibular sexually dimorphic characters in males include: 1) a higher-arched but shorter temporal fossa (C34/C31); 2) more posteriorly positioned nasal bones, which indicates a more developed trunk (C2/C1) (Figs. 6A, B, and I); and 3) a longer mandibular symphysis (M11/M2) (Figs. 6C, D, I, and Fig. 7). The p-values of C34/C31 (0.1775) and C2/C1 (0.1233) indicate that these ratios are significant because they are under the significance level of 0.2. This relatively high significance level is acceptable for two reasons. First, male and female individuals are in the same population of the same species. Therefore, the measurement ratios should not substantially differ. Second, the sample size is relatively small. However, the p-value of M11/M2 (0.0058) is under the significance level of 0.05 (as in the univariate analysis); this is important because we used symphysis length to initially determine sex.

Fig. 5 Bivariate scatter plots showing sexual dimorphism in *Platybelodon grangeri* from the Zengjia locality. Cranium (A) and mandible (B) are examined in PCA-DFA cycles for sex-assessment and the final results are shown in normalized length-DF1 plane. As a result of sex-assessment, measurements from M3 (C) and m3 (D) are also shown on length-width plane. Two sexes are represented by solid (male) and open cycles (female), respectively, with 95% confidential ellipses denoting their distributions (solid-lined ellipses for male and dash-lined ellipses for female).

Fig. 6 Sketches showing sexual dimorphism in crania (A, B, E-H) and mandibles (C, D) of *Platybelodon grangeri* (A-D), *Loxodonta africana* (E, F), and *Gomphotherium angustidens* (G, H). A. HMV 0940; B. HMV 0023; C. HMV 0031; D. HMV 0042; E. AMNH 51939; F. AMNH 88404; G. MNHN Si37; H. MNHN SEP185; I. histograms show sexual dimorphism in three evolutionary significant characters (C2/C1, C34/C31, M11/M2) with the form mean + s.d. , male; , female. Measurements are illustrated on the sketches. The number in each bar represents the sample size n and the number near each pair of bars represents the p-value of the t-test.

In addition to the above craniomandibular sexually dimorphic characters, males also possess narrower and longer M3 and m3. Note that the molar measurements, which were not used for sex assessment, are independent variables; thus, this is an independent verification of our sex assessment (Figs. 5C and D). In the Simpson’ s ratio diagrams, the slopes of C1 & C2, C31 & C34, and M2 & M11 differ between male and female *P. grangeri*, which also indicates sexual dimorphism in these characters (Fig. 8). However, Student’ s t-tests for single measurements primarily produce large, non-significant p-values (Tables 1 and 2), which indicates a relatively large amount of overlap in variation of these characters between the two sexes. These sexually dimorphic characters are often obscured by difficulty in sex determination and the incompleteness of specimens unless more elaborate methods are used, such as the one presented in this article.

The above sexually dimorphic characters were also observed in *P. grangeri* from Tunggur. In a female cranium (AMNH 26462), the upper border of the nostril aperture is located in line with postorbital processes (Osborn and Granger, 1932). In contrast, a possible male (AMNH 26480) has more posteriorly positioned nostril aperture, although the incisors were broken. There are also two types of mandibular symphyses, short and long, which may represent females and males, respectively (Fig. 7). However, juvenile individuals exhibit width/length ratios that are intermediate between adult males and females (Fig. 7). Furthermore, these sexually dimorphic characters were also observed in Middle Miocene *G. angustidens.* In male crania, the temporal fossa is higher but short, and the nasal bones are more posteriorly positioned (Figs. 6G, H, I, and Fig. 8; Tassy, 1996: fig. 11.4).

Sexual dimorphism in ancestral *Phiomia serridens* and derived *Loxodonta africana* has also been studied (Matsumoto, 1924; Roth and Shoshani, 1988; Lee and Poole, 2011). In *P. serridens*, there appears to have sexual dimorphism with regard to size but only slight sexual dimorphism with regard to symphyseal morphology. For instance, *P.* “*osborni*” Matsumoto, 1922 differs from *P.* “*wintoni*” (Andrews, 1905) in more posteriorly positioned proximal edge of mandibular symphysis (Matsumoto, 1924). However, these two species now have been considered junior synonyms of *P. serridens* (Shoshani and Tassy, 1996: appendix C2). However, in extant *L. africana*, although size difference is still prominent (Roth and Shoshani, 1988; Lee and Poole, 2011), the high-arched cranium, extremely posteriorly positioned nostril aperture, and stout mandibles are highly homomorphic in both sexes (Figs. 6E, F). In the Simpson’ s ratio diagram, the shapes of polylines that represent the two sexes of *L. africana* are almost identical, which means that individuals of the two sexes display highly similar cranial shapes (Fig. 8).

Fig. 7 Bivariate scatter plot of length vs. maximal width of mandibular symphysis in *Platybelodon grangeri.* , male; , female.

Fig. 8 Simpson’ s ratio diagrams showing the cranial and mandibular sexual dimorphism between two sexes in Elephantiformes. A skull of *Platybelodon danovi* (BPV 2000) is shown as the standard (the black lines). Measurements see Figs. 2 and 3.

4 Discussion

We analyzed sexual dimorphism in four different elephantiforme taxa covering its entire known evolutionary range (Oligocene *Phiomia*, Miocene *Gomphotherium*, *Platybelodon*, and extant *Loxodonta*). These taxa are closely related and represent key nodes in the evolution of Elephantiformes. Previous phylogenetic analyses revealed that *Phiomia* is the sister group of all other taxa of Elephantiformes, except the contemporary *Palaeomastodon* (Shoshani and Tassy, 2005; Gheerbrant and Tassy, 2009). Therefore, *Phiomia* is an ideal primitive elephantiforme model. *Gomphotherium* is considered the most important representative of the group trilophodont gomphotheres s. s., which is derived from *Phiomia* and sister to Elephantoidea; thus, *Gomphotherium* represents an intermediate stage between primitive *Phiomia* and derived elephants. *Platybelodon* (a member of Amebelodontinae), which is also derived from *Phiomia*, is a close relative of trilophodont gomphotheres s. s. and includes the group trilophodont gomphotheres s. l. Moreover, as one of the two representatives of extant elephant genera, *Loxodonta* is representative of elephantiforme terminal taxa.

Many sexually dimorphic characters differ among these taxa. However, larger and stronger upper tusks in males were observed in all taxa. These sexually dimorphic characters are clearly associated with male social behavior, such as combat. However, it is difficult to interpret the role of other sexually dimorphic characters in sexual competition, such as C34/C31, C2/C1, M11/M2, and length/width of M3 and m3 in *Platybelodon* and the sexually dimorphic characters C34/C31 and C2/C1 in *Gomphotherium*. Nevertheless, these characters have strong evolutionary significance in Elephantiformes (Andrews, 1906; Maglio, 1972). The nostril aperture is anterior to the orbit in *Phiomia*, the same level as the orbit in *Gomphotherium* and *Platybelodon*, and posterior to the orbit in *Loxodonta*, which indicates gradual elongation of the trunk in the evolutionary history of Elephantiformes. The brain case is flat and anteroposteriorly elongated in *Phiomia*, slightly arched and shortened in *Gomphotherium* and *Platybelodon*, and strongly arched and shortened in *Loxodonta*; this represents gradual vertical orientation of m. temporalis, which indicates that masticatory function shifted from grinding shearing to horizontal shearing (Maglio, 1972). Therefore, an arched brain case and posteriorly positioned nostril aperture are derived characters in Elephantiformes. Furthermore, the mandibular symphysis is short in *Phiomia* but long in *Platybelodon*, and m3 and M3 are wide in *Phiomia* but narrow in *Platybelodon* (narrowness of m3 and M3 is a diagnostic feature in Amebelodontinae; Tassy, 1986). Therefore, at least in Amebelodontinae, a long symphysis and narrow m3 and M3 are derived characters.

Based on the sexual dimorphism analysis, we can draw two conclusions. First, four evolutionarily significant characters were sexually dimorphic in Miocene *Gomphotherium* or *Platybelodon* and perhaps other members of the trilophodont gomphotheres s. l. group, but were not sexually dimorphic in the primitive taxon *Phiomia* and terminal taxon *Loxodonta*. Second, in *Gomphotherium*, *Platybelodon*, and perhaps other members of the trilophodont gomphotheres s. l. group, if a character was sexually dimorphic, males always possessed evolutionary more derived character states than females. This issue is of interest with regard to elephantiforme evolutionary history, because the two sexes show asynchronous evolution. This asynchrony might have evolved in primitive *Phiomia*, become exaggerated in the Miocene trilophodont gomphotheres, and ceased in extant elephants. It appears as though character variation in males slightly preceded similar variation in females, and eventually the females evolved similar character variation (Fig. 9). However, at present, it is not entirely clear why this phenomenon occurred.

It is difficult to determine the mechanism underlying the production of the sexually asynchronous morphological variations in the evolution of Elephantiformes at genetic and ontogenetic levels. We hypothesize that this asynchrony may reflect female preference; that is, in the evolution of a sex-related character in a group, female choice plays a key role (Fisher, 1930; Anderson, 1994). For example, in a population of *Gomphotherium* or *Platybelodon*, genetic variation (possibly sex-linked gene(s)) produces variation in a sexually dimorphic character, such as trunk length variation in males. The individuals with a longer-than-average trunk, which was determined when there was a more posteriorly positioned nostril aperture (values less than C2/C1), were more attractive to females; this could be because a longer trunk enhances survival of both the males and their offsprings. Similar cases could also be made for the characters C34/C31 and M11/M2. Therefore, this sexual selection pressure may have promoted the prevalence of the sex-linked allele or alleles that code for a longer trunk in the population and produced the sexual dimorphism we observed in *Gomphotherium* and *Platybelodon*.

This "runaway selection" process (Fisher, 1930) represents the first step of the asynchronous sex evolution; the derived male character variation slightly preceded similar variation in females. Because the newly developed character in males was also advantageous in females, the longer trunk allele(s) were gradually fixed as non-sex-linked gene(s). Finally, as determined by similar C2/C1 values for both sexes, extant female Elephantiformes also have longer trunks, as can be observed in extant *Loxodonta*. Moreover, sexual selection pressure also weakened, and it was not necessary for males to have longer trunks than females. This process represents the second step of the asynchronous sex evolution: the females evolved similar traits to those of the males. This two-step hypothesis is plausible for explaining the sexual asynchrony observed in elephantiforme evolution and describing the development of this newly derived character within Elephantiformes.

Fig. 9 Schematics showing asynchronous evolution between two sexes in Elephantiformes. The gray scales in the background represent relatively greater (relatively darker) or smaller (relatively lighter) sexual-dimorphism, not to scale. , male; , female. Sketches of *Phiomia* after Andrews (1906).

This asynchronous sex evolution in Elephantiformes appears to be correlated with thriving and declining groups. Miocene *Gomphotherium* and *Platybelodon* show more prominent sexual dimorphism than primitive *Phiomia* and terminal *Loxodonta*. The Miocene is a thriving period for Elephantiformes, who had a broad geological distribution and diverse taxa; in contrast, there are only three extant species of elephants, which are confined to tropical areas in Asia and Africa (Shoshani and Tassy, 1996). One possible reason for this correlation with asynchronous sex evolution is that females became less selective of these traits in males and sexual selection pressure consequently decreased, which led to extant elephantiforme females and males possessing similar derived characters. For example, females seem very picky in copulation and often refuse to mate with males they dislike (Douglas-Hamilton et al., 2006). Furthermore, relationships between sexual dimorphism and evolution were also observed in other groups of large ungulates. For example, thriving groups, such as Cervidae and Bovidae, often exhibit substantial sexual dimorphism, whereas declining groups, such as extant members of Equidae, Rhinoceridae, and Giraffidae (Janis, 1982), often exhibit little sexual dimorphism. However, some extinct taxa of Equidae and Rhinoceridae, such as *Hyracotherium* and *Chilotherium*, have strong sexual dimorphism during their thriving period (Gingerich, 1981; Chen et al., 2010).

The patterns observed in this study may be related to the relationship between male competition and female preference. As Darwin (1874) and Fisher (1930) have discussed, both factors contribute to animals' mating behaviors. In most cases (especially in the thriving groups), the two factors do not contradict each other. A male elephant does compete and defeat competitors to gain copulatory priority, because female elephants are often attracted to and want to mate with the winner. However, in some cases (appears more frequently being in declining groups), even the winner in male competitions may not successfully attract females. A previous study showed that female elephants may refuse males' mating attempts (Douglas-Hamilton et al., 2006). As in humans, males can attract females by various direct or indirect competitions with other males, but the ultimate decision is often up to the female.

The second issue is that the variation in males is less than that in females. The 95% confidential eclipses of females take up a larger area in Fig. 5A, B, and most standard deviations from female measurements are greater than those of male measurements (Tables 1 and 2). This phenomenon has also been noticed in other larger ungulates, such as extant *Equus hemionus* and fossil *Chilotherium wimani* (Chen et al., 2010; Wang, 2010), and even observed in some birds, reptiles, anurans, and invertebrates (Johnston, 1966; Stamps and Gon III, 1983). This phenomenon could occur if males are opportunists and would be willing to mate with a wide range of females, however females are picky because of their greater sexual investment in fewer gametes (Fisher, 1930; Anderson, 1994). This mechanism may also have been involved in the observed asynchronous sex evolution and would be helpful for preserving potential variation in the genomes of the species to maintain evolutionary potential, which facilitates rapid response to dramatic environmental changes.

5 Conclusions

In this paper, we studied sexual dimorphism in a fossil population of *Platybelodon grangeri* from the Middle Miocene Zengjia locality in China. In this population, males possess larger and stronger upper tusks than females. However, several other morphological characters also slightly differ between the sexes, and males have: 1) slightly more arched brain cases, 2) slightly more posteriorly positioned nostril apertures; 3) longer mandibular symphyses; and 4) narrower m3 and M3. The slightly more arched brain cases and slightly more posteriorly positioned nostril apertures are also observed in Miocene *Gomphotherium* but not in primitive *Phiomia* and terminal *Loxodonta*. By comparing these data with previously determined elephantiforme evolutionary data, we observed asynchronous evolution between males and females. In the thriving period of Elephantiformes, males possessed more derived characters than females; however, in the declining period, females and males possessed similar derived characters. This type of asynchronous sex evolution should be studied further because it might also have occurred in other large ungulates.

Acknowledgements
We thank P. Tassy, U. Göhlich, M. Pickford, Z. X. Qiu, J. Ye, Y. G. Zhang, Q. Q. Shi, S. K. Chen, S. K. Hou, H. B. Lü and Y. N. Zhang for discussions and advice on this work; and W. He, S. Q. Chen, P. Tassy, J. Meng, J. Galkin, E. Westwig, Y. G. Zhang, and Z. H. Zeng for preparing the specimens.

A New Hadrosauroid Dinosaur from the Late Cretaceous of Tianzhen, Shanxi Province, China

Xu Shi-Chao[1], You Hai-Lu[2]*, Wang Jia-Wei[3], Wang Suo-Zhu[1], Yi Jian[1], Jia Lei[1],[2]

[1]Shanxi Museum of Geology, Taiyuan 030024, China
[2]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
[3]Faculty of Geology, Lomonosov Moscow State University, Moscow 119991, Russian Federation

Abstract

A new non-hadrosaurid hadrosauroid dinosaur (*Datonglong tianzhenensis* gen. et sp. nov.) is reported. The new taxon is recovered from the Upper Cretaceous Huiquanpu Formation of Tianzhen County, Shanxi Province in northern China, and represented by an almost complete right dentary with dentition. Different from all other hadrosauroids, *Datonglong* possesses two functional teeth in each alveolus, and the pattern of ridge development on the lingual surface of its dentary crown shows a unique combination of character states (for example: distally offset primary ridge; well-developed secondary ridge; no additional ridge(s); slightly distally curved apical half of primary ridge). Comparative studies indicate advanced non-hadrosaurid hadrosauroids experienced a complex pattern in the evolution of their dentary, especially dentary dentition. Derived hadrosaurid features occurred frequently in these taxa, such as high height/width ratio of tooth crown in *Bactrosaurus*, one primary and one faint ridges in *Gilmoreosaurus*, median placed primary ridge in *Zhanghenglong*, rostrally inclined coronoid process in *Nanningosaurus*, and two functional teeth in each alveolus in *Datonglong*. This implies incredible diversities and attempts close to the origin of Hadrosauridae and difficulties to elucidate their phylogenetic relationships.

Key words Tianzhen, Shanxi; Late Cretaceous; dinosaur, hadrosauroid

Citation Xu S C, You H L, Wang J W et al., 2016. A new hadrosauroid dinosaur from the Late Cretaceous of Tianzhen, Shanxi Province, China. *Vertebrata PalAsiatica*, 54(1): 67—78

1 Introduction

The Huiquanpu Formation was established by the Regional Geological Survey Team of Hebei Province in 1959. It refers to the over 200 meter thick terrestrial deposits bounded by the pre-Cambrian rocks and the Miocene basalts, and is distributed in an area of about 150 km^2 around the boundary of Tianzhen County of Shanxi Province and Yangyuan County of Hebei Province in northern China, with an age assignment of Eocene. Liu (1983) and Chen et al. (1983) reassigned its age to Late Cretaceous based on discoveries of dinosaurs, especially Hadrosauridae dinosaurs. In 1989 and 1991—1994, Shijiazhuang Economic University of Hebei Province excavated over 2300 dinosaur specimens mainly in the Kangdailiang Quarry of Tianzhen County, Shanxi Province (Pang et al., 1996), and two new dinosaurs have been established, namely an ankylosaur *Tianzhenosaurus youngi* Pang & Cheng, 1998, and a sauropod *Huabeisaurus allocotus* Pang & Cheng, 2000. In 1998, another ankylosaur *Shanxia tianzhenensis* Barrett et al., 1998 was also reported from the Wujiashan Quarry of Tianzhen County, about 7 km northeast of the previous Kangdailiang Quarry. These two ankylosaurs may be distinct from each other (Upchurch and Barrett, 2000; Thompson et al., 2012), or represent the same taxon (Sullivan, 2000); while *Tianzhenosaurus* may be synonymous with *Saichania* (Sullivan, 1999). Recent restudy of *Huabeisaurus allocotus* shows this taxon is probably a member of the Cretaceous East Asian endemic clade of Euhelopodidae (D’ Emic et al., 2013).

Pang et al. (1996) and Pang and Chen (2000, 2001) also mentioned the existence of theropod cf. *Szechuanosaurus campi* Young, 1942 and hadrosaurid cf. *Shantungosaurus* sp. in the Huiquanpu Formation. The former has been regarded as a nomen dubium (Carrano et al., 2012); while the assignment of fragmentary material to cf. *Shantungosaurus* sp. is based on observation of their tibia similarity (Pang and Cheng, 2000, 2001).

Here we report a new hadrosauroid specimen recovered from the Kangdailiang

Quarry by the Shanxi Museum of Geological and Mineral Science and Technology (now Shanxi Museum of Geology, SXMG) in 2008 (Fig. 1). Although the specimen is represented only by a right dentary with dentition, it provides numerous important anatomical features to depict its taxonomic status and systematic relationship. Based on our anatomical observation and taxonomic comparison, the new specimen is distinct from all previous known hadrosauroid dinosaurs, represents a new taxon (*Datonglong tianzhenensis* gen. et sp. nov.), and belongs to an advanced non-hadrosaurid hadrosauroid.

Fig. 1 Locality of *Datonglong tianzhenensis* gen. et sp. nov. (SXMG V 00005). A. Shanxi Province in China; B. Tianzhen County in Shanxi Province.

Institutional abbreviations AMNH, American Museum of Natural History (New York City, New York); LPM, Liaoning Paleontological Museum (Beipiao, Liaoning); NHMG, Natural History Museum of Guangxi Zhuang Autonomous Region (Nanning, Guangxi); SBDE, Sino-Belgium Dinosaur Expedition, Inner Mongolia Museum (Hohhot, Nei Mongol Autonomous Region); SXMG, Shanxi Museum of Geology (Taiyuan, Shanxi); XMDFEC, Xixia Museum of Dinosaur Fossil Eggs of China (Xixia, Henan).

2 Systematic Paleontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ornithopoda Marsh, 1881
Iguanodontia Dollo, 1888 sensu Sereno, 2005
Ankylopollexia Sereno, 1986 sensu Sereno, 2005
Styracosterna Sereno, 1986 sensu Sereno, 2005
Hadrosauriformes Sereno, 1997 sensu Sereno, 1998
Hadrosauroidea Sereno, 1986 sensu Sereno, 2005
Datonglong gen. nov.

Datonglong tianzhenensis sp. nov.

Holotype SXMG V 00005, almost complete right dentary with dentition.

Etymology The generic name "Datong" is after "Datong City" , and Tianzhen is a county belonging to it; "long" means "dragon" in Chinese. The specific name "Tianzhen" is after "Tianzhen County" , where the current material is discovered.

Locality and horizon Kangdailiang Quarry, Tianzhen County, Datong City, Shanxi Province, China. Huiquanpu Formation, Upper Cretaceous.

Differential diagnosis (for genus and species by monotypy) Advanced non-hadrosaurid hadrosauroid with one autapomorphy (two functional teeth in each alveolus along at least the mid- and caudal dentary occlusal plane) and the following unique combination of character states in the pattern of ridge development on the enameled lingual surface of dentary tooth crown: 1) distally offset primary ridge, 2) well-developed secondary ridge, 3) no additional ridge(s), 4) slightly distally curved apical half of primary ridge.

3 Description

The dentary is rectangular in lateral view, with roughly parallel dorsal and ventral margins, 14 cm high at the mid portion with the occlusal plane or 10.5 cm high without it (Fig. 2A). The tooth row (28 cm long) ends caudally right medial to the caudal margin of the coronoid process (Fig. 2B). The 8 cm high coronoid process is almost perpendicular and slightly caudodorsally-directed to the ramus, and the dentary height along it is 17 cm. Although the tip of the coronoid process is not preserved, its dorsal portion is expanded at least rostrally as evidenced by its broken contour, and its craniocaudal width at base is 4.8 cm. Its lateral surface bulges slightly, while the medial one is flat, bearing a faint vertical ridge limiting its caudal two fifths with further ridges on it. In dorsal view, the caudal half of the ramus curves laterally, with caudally increasing distance between the tooth row and the lateral surface of the ramus, ending in an about 3 cm wide horizontal shelf separating the coronoid process and the caudal end of the tooth row (Fig. 2C). In caudal view, a triangular fossa is bounded by the coronoid process (Fig. 2D). The fossa extends ventrally to the mandibular adductor fossa. Rostral to the adductor fossa, the Meckelian groove is deep and long, and progressively decreases its dimensions toward the preserved rostral end.

Fig. 2 Photos of right dentary of *Datonglong tianzhenensis* gen. et sp. nov. (SXMG V 00005). A. lateral view; B: medial view. C: dorsal view; D. caudal view; E. close-up of partial dentition in B; E is not in scale.

The tooth row is largely preserved, with 17 alveoli full of teeth plus five successive most caudal alveoli bearing several scattered teeth. At least another five alveoli exist rostral to the above 22 alveoli judging by the preserved length and the existence of two broken teeth in this portion. Therefore, a total of at least 27 alveoli are expected for this animal; and the actual number is probably less than 30 based on the general alveolar contour, which reduces its depth rapidly rostrodorsally. In medial view, a row of neurovascular foramina slightly extends caudodorsally along the mid-caudal portion of the ramus, and in this portion about three quarters of the dorsoventral depth of the dentary ramus is occupied by the alveoli. The partial septum dividing the fourth and fifth most caudal alveoli is exposed, and it is straight and relatively thick (2 mm).

The teeth are best exposed in the mid-caudal portion of the tooth row. In medial view, two or three teeth are vertically aligned in each alveolus (Fig. 2B). In lateral view, each alveolus bears two functional teeth, of which the upper one is large and obviously the same as the uppermost one seen medially, while the lower one should be the remaining worn facet of the earlier functional tooth (Fig. 2A). Therefore, three or four teeth are held in each alveolus. Both worn surfaces in each alveolus are slightly concave, and in some alveoli the upper one is not continuous with the lower one, with the latter placed more medially.

The teeth are large, and their morphology can be best shown in the tenth functional and eleventh replacement positions counting from the caudal (Fig. 2E). A distally offset primary ridge exists on the enameled lingual side in teeth, and is accompanied by a well-developed secondary ridge in the mesial half of the crown. These two roughly parallel ridges divide the lingual crown surface into three zones, without evidence of any subsidiary ridges on it. The ventral halves of these two ridges are vertical, while the dorsal halves curve slightly caudodorsally. The unerupted tooth is diamond-shaped, with the height of 5.5 cm and maximum width of 2.0 cm, a ratio of 2.75. One scattered tooth attached to the third last alveolus exposes its mesial margin, where small mammillated papillae occur apically.

4 Comparison

In the evolution from non-hadrosaurid hadrosauroids to hadrosaurids, their dentaries acquired several key innovations. In all hadrosaurids, the tooth row ends caudally to the caudal margin of the coronoid process (Xing et al., 2014: character 56) and the coronoid process inclines rostrally (Xing et al., 2014: character 48). In addition, the dentary dental battery bears more than 30 alveoli (Xing et al., 2014: character 1), and the unworn crown in the mid-tooth row is elongate lanceolate with a height/width ratio greater than 3.1 (Sues and Averianov, 2009). All these features are not present in *Datonglong*. Therefore, *Datonglong* does not belong to Hadrosauridae, and our comparison will focus on non-hadrosaurid hadrosauroids, especially those from the Late Cretaceous of China. Based on Wang et al. (2013), Xing et al. (2014), and Tsogtbaatar et al. (2014), 15 Late Cretaceous non-hadrosaurid hadrosauroid genera have been reported, with eight from China (*Tanius* Wiman, 1929; *Bactrosaurus* Gilmore, 1933; *Gilmoreosaurus* Brett-Surman, 1979; *Nanyangosaurus* Xu et al., 2000; *Shuangmiaosaurus* You et al., 2003; *Nanningosaurus* Mo et al., 2007; *Yunganglong* Wang et al., 2013; *Zhanghenglong* Xing et al., 2014), three from North America (*Claosaurus* Marsh, 1890; *Eolambia* Kirkland, 1998; *Protohadros* Head, 1998), two from Europe (*Telmatosaurus* Nopcsa, 1903; *Tethyshadros* Dalla Vecchia, 2009), one from Central Asia (*Levnesovia* Sues & Averianov, 2009), and one from Mongolia (*Plesiohadros* Tsogtbaatar et al., 2014). Among these eight Chinese taxa, three (*Tanius*, *Nanyangosaurus*, and *Yunganglong*) do not preserve comparable parts with *Datonglong*.

Nanningosaurus, recovered from the Upper Cretaceous red beds of Guangxi in southern China, was originally reported as a lambeosaurine hadrosaurid (Mo et al., 2007). Recently, it was recovered as a non-hadrosaurid hadrosauroid (Xing et al., 2014). A left dentary and an isolated dentary tooth are included in the holotype (NHMG 8142). It has a high coronoid process that inclines slightly rostrally and ends slightly caudal to the coronoid process, definitely derived features typical for hadrosaurids and different from the conditions in *Datonglong*. However, two ridges are present on the lingual crown of dentary tooth as in *Datonglong*. The primary ridge is sinuous as seen in *Tsintaosaurus*.

An isolated left dentary (LPM 0166) is referred to *Shuangmiaosaurus gilmorei* (You et al., 2003a). In *Shuangmiaosaurus*, the coronoid process inclines caudodorsally and the tooth row ends in a position medial to the middle of the coronoid process. Moreover, the dorsal edge of the dentary ramus slightly bows dorsally and the 27 alveoli clearly incline caudodorsally. All these features are not present in similar-sized *Datonglong*.

Bactrosaurus was originally studied by Gilmore (1933) based on material from a bonebed in Quarry 141 (Johnson' s Quarry) collected by Central Asiatic Expeditions of the American Museum of Natural History. AMNH 6553 is designated as the holotype, and it contains more than one individual including left and right dentaries. Based on Gilmore (1933), 12 dentaries have been collected in this bonebed, and more than half of them pertain to juveniles. However, Gilmore' s description of dentary seems to be based on AMNH 6353 (a right dentary), with a drawing of its medial and dorsal views. The length of adult dentary is 222 mm, and the length of the longest tooth row is 152 mm with 23 alveoli. Each alveolus holds one replacement tooth, and at most two functional teeth. A large unworn tooth crown has a ratio of 3.3 (33/10 mm).

Prieto-Marquez (2011) studied the ontogeny of *Bactrosaurus*. He notices that in the adult dentary (AMNH 6553: 23 cm long) there are as many as three teeth per alveolus arranged dorsoventrally at mid-length of the dental battery with two functional teeth. The tooth crowns have a height/width ratio of 3.1–3.2 as in juvenile specimens; in contrast to 2.75 in *Datonglong* (55/20 mm). The position of the primary ridge is slightly or modestly offset from the midline.

Godefroit et al. (1998) studied *Bactrosaurus* from another bonebed excavated by SBDE in 1995, within 1 km to AMNH Quarry 141. It contains several hundred bones of at least four hadrosaur individuals, including a left dentary (SBDE 95E5/12). Godefroit also demonstrated that all hadrosauroids in Quarry 141 belong to *Bactrosaurus* as Gilmore originally suggested. SBDE 95E5/12 is about the same size as the holotype dentary (AMNH 6553), and bears 20 alveoli. In contrast, around 30 alveoli have been estimated for *Datonglong*; however, the length of dentary in *Datonglong* is about 1.5 times as that in adult *Bactrosaurus*. Godefroit et al. (1998) described that each alveolus is composed of one functional tooth and at least two replacement teeth. However, based on the illustration, two or three teeth can be seen medially, and two functional teeth are visible laterally in the preserved mid- and caudal portion of the tooth row. Here, based on our observation in *Datonglong*, the lower functional tooth should be from the earlier worn facet, but not from any tooth can be seen medially. Therefore, in both *Bactrosaurus* and *Datonglong*, at most two replacement and two functional teeth are present in one alveolus. However, two functional teeth seem to persist along the entire tooth row in *Datonglong*, but not in the rostral portion of the tooth row in *Bactrosaurus* as shown in AMNH 6553. As in *Datonglong*, *Bactrosaurus* also has two ridges, one primary and one relatively well developed secondary ridge on the lingual tooth crown;

however in *Bactrosaurus* there are evidence of other faint ridges in the adults, and a third caudal ridge appears in caudal most teeth. The primary ridges may curve slightly caudally in *Bactrosaurus* as in *Datonglong*. Therefore, the crown ratio, the number of alveoli, and the condition of functional teeth in rostral portion of tooth row are different between *Bactrosaurus* and *Datonglong*. The details of ridge development pattern in the dentary tooth crown are also different.

Prieto-Marquez and Norell (2010) redescribed the second hadrosauroid *Gilmoreosaurus mongoliensis* from the Iren Dabasu Formation in Irenhot. This species is represented by at least four individuals from quarries 145 and 149. Among the material, only a partial right dentary (AMNH FARB 30654) and an isolated dentary tooth (AMNH FARB 30661) are preserved. The dentary mainly consists of the rostral and middle portion without the coronoid process and dentition (295 mm long and 71 mm high), and it is hard to tell definite diagnostic differences between it and *Datonglong*, although the latter seems to be more robust. In contrast, the worn half crown of an isolated dentary tooth possesses only one ridge that lies off center, different from the condition in *Datonglong*, which has two ridges. *Gilmoreosaurus* probably possesses one primary and one faint ridges on its dentary tooth crown (personal communication with Xing Hai).

Zhanghenglong is a recently described hadrosauroid from the Santonian Majiacun Formation of Xixia Basin, Henan Province in central China (Xing et al., 2014). Its holotype (XMDFEC V0013) preserves an incomplete, disarticulated cranium, including a right dentary with dentition. In *Zhanghenglong*, the tooth row bows dorsally and its long axis is nearly parallel to the lateral side of the dentary ramus, unlike the horizontal and diverged condition in *Datonglong*. The 26 alveoli bear one functional tooth at the rostral and caudal portions, two in the midsection, and even three in the 17th tooth alveolus; while in *Datonglong*, two functional teeth seem to persist along the entire tooth row. In *Zhanghenglong*, the primary ridge is situated median (about 40%) or distally offset on the lingual crown of the dentary, a clear secondary ridge is on the mesial half, and additional faint ridge(s) may appear close to the mesial edge; in contrast in *Datonglong*, all primary ridges are placed in the distal halves, and no additional ridge(s) are evident besides the secondary one. The dentary tooth crown has an approximate height/width ratio of 2.36 in *Zhanghenglong*, and less than 2.75 as in *Datonglong*.

The latest reported non-hadrosaurid hadrosauroid is *Plesiohadros djadokhtaensis* from the Campanian of Mongolia (Tsogtbaatar et al., 2014). *Plesiohadros* preserves a left dentary with dentition. The dentary is relatively slender with a straight ramus in occlusal view, while that of *Datonglong* is relatively robust with a laterally curved ramus. Besides the primary and mesial secondary ridges, a distal secondary ridge occurs in some teeth in *Plesiohadros*, while only two ridges exist in *Datonglong*.

5 Conclusion

Datonglong tianzhenensis is a new non-hadrosaurid hadrosauroid from the Upper Cretaceous Huiquanpu Formation of Tianzhen County, Shanxi Province, northern China. It is represented by an almost complete right dentary with dentition. The new taxon is diagnosed by a unique combination of characters: two functional teeth in each alveolus along at least the mid- and caudal dentary occlusal plane; distally offset primary ridge; well-developed secondary ridge; no additional ridge(s); and slightly distally curved apical half of primary ridge. Comparative studies indicate that advanced non-hadrosaurid hadrosauroids experienced a complex pattern in the evolution of their dentary, especially dentary dentition. Derived hadrosaurid features occurred frequently in these taxa, which implies incredible diversities and attempts close to the origin of Hadrosauridae and difficulties to elucidate their phylogenetic relationships.

Acknowledgements
We thank the crew of Shanxi Museum of Geology for collecting the specimen. We also thank Zhang Xing for discussion on the anatomy of hadrosauroid dentaries. This research was supported by the Hundred Talents Program of Chinese Academy of Sciences, National Natural Science Foundation of China (41472020), and Department of Land and Resources of Shanxi Province.

A New Type of Dinosaur Eggs from the Early Cretaceous of Gansu Province, China

Xie Junfang[1], Zhang Shukang[2]*, Jin Xingsheng[1], Li Daqing[3], Zhou Lingqi[3]

[1]Zhejiang Museum of Natural History, Hangzhou 310014
[2]Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044
*Corresponding author: zhangshukang@ivpp.ac.cn
[3]Gansu Geological Museum, Lanzhou 730030

Abstract The Early Cretaceous strata in Gansu Province have yielded abundant dinosaur skeletal remains and footprints, but no egg fossils have been reported to date. Based on eggshell fossils discovered in the Lower Cretaceous Hekou Group of the Lanzhou-Minhe Basin, we establish a new oogenus and oospecies of dinosaur eggs, which we assign to a new oofamily: Polyclonoolithidae. The newly discovered egg fossil specimen differs from all known types of dinosaur eggs in its unique combination of microstructural features: the branched eggshell units extend outward to the outer surface of the eggshell without fusing into a layer near the outer surface; tangential sections show interconnected or isolated multi-angular eggshell units; and the pore canals are irregular. Dinosaur egg fossils from China mostly come from Upper Cretaceous strata, with only occasional reports from the Lower Cretaceous in Liaoning Province, northeastern

China. This new discovery expands the geological and geographical distribution of dinosaur egg fossils in China and may provide new insights into the origin of the eggshell microstructures of spheroolithid eggs.

Keywords Lanzhou-Minhe Basin, Gansu; Early Cretaceous; Polyclonoolithidae; dinosaur egg

1 Introduction

Compared to those from Upper Cretaceous deposits, fossil eggs from the Lower Cretaceous worldwide are relatively rare. They have been recovered from China, Mongolia, Thailand, Korea, Japan, Spain, and North and South America, including elongatoolithids, macroelongatoolithids, prismatoolithids, spheroolithids, faveoloolithids, dendroolithids, reptilian eggs belonging to turtle and crocodile, as well as eggs whose parataxonomic positions are still unknown (Nessov and Kaznachkin, 1986; Kurzanov and Mikhailov, 1989; Kohring, 1990; Bray, 1998; Zelenitsky et al., 2000; Azuma, 2003; Buffetaut et al., 2005; Buscalioni et al., 2008; Kim et al., 2009; Canudo et al., 2010; Grellet-Tinner et al., 2012; Moreno-Azanza et al., 2009, 2014a, b). In China, fossil eggs from the Lower Cretaceous were only reported in Liaoning Province, assigned to the oofamily Elongatoolithidae (Zhao and Zhao, 1999). Most of the ootaxa mentioned above were also recovered from Upper Cretaceous deposits.

The Lower Cretaceous Hekou Group in the Lanzhou-Minhe Basin of Gansu Province is very rich in dinosaur bones and tracks (Qi and Yu, 1999; Zhang et al., 2006; You et al., 2005, 2006, 2008), whereas discoveries of dinosaur eggs are rare. In 2009, the Chinese Academy of Geological Sciences discovered some fossil eggshell fragments in Zhongpu, a town in Lanzhou Basin. However, this discovery remains unpublished, possibly because of uncertainty about the locality and formation that yields the fossil material. In November of 2012, fossil eggshells were again discovered in the Lanzhou-Minhe Basin. Here, we provide a detailed description of the new discovery of dinosaur egg and associated eggshell fragments from Gansu Province. Based on the unique microstructure of the eggshell, we established a new oogenus and oospecies, within a new oofamily. The new discovery has important implications for understanding the diversity and the geological and geographical distribution of Early Cretaceous dinosaur eggs in China, as well as the evolution of dinosaur eggshell structure.

2 Material and Methods

The incomplete egg (ZMNH M1849) was collected from the Lanzhou-Minhe Basin by a work team from Gansu Geological Museum (GGM), Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP), and Institute of Geology, Chinese Academy of Geological Sciences (IGCAGS) during field investigation. Laboratory preparation included removal of sediment from the eggshell with small hand tools. The poorly preserved egg exhibits varying degrees of weathering. Therefore, the least weathered fragments were selected for examination, using a Nikon SMZ1000 stereomicroscope to view the outer surfaces. The eggshell fragments were prepared as standard radial and tangential petrographic thin sections (0.03 mm thick) and studied under a Nikon Eclipse polarized light microscope (Nikon eclipse LV100POL, PLM). Additional eggshells were coated in gold (10 nm), mounted on aluminum stubs, and imaged by a Hitachi S-3700N Scanning Electron Microscopy (SEM) at 20 kV. Structural attributes (eggshell thickness, eggshell unit width) were measured and analyzed with Java image processing software and a digital caliper. The eggshell fragments and the eggshell thin sections are catalogued at the Zhejiang Museum of Natural History (ZMNH).

3 Locality and Geological Setting

**Polyclonoolithus yangjiagouensis* oosp. nov. (Figs. 1, 2)

Etymology: Yangjiagou, locality of the fossil egg in Gansu Province.

Holotype: An incomplete and highly fragmented egg (ZMNH M1849), housed in ZMNH.

Locality and horizon: Yangjiagou Town, border region of Lintao and Yongjing counties, Gansu Province, China; Lower Cretaceous Hekou Group.

Diagnosis: 1.9 mm thick on average, branched eggshell units and obvious horizontal accretion lines. Eggshell units typically fused towards the outer surface, but lacking a compact layer. Multi-angular eggshell units are interlocked or isolated in tangential sections. Pore canals irregular in shape with large cavities near the inner surface of the eggshell.

Description: The eggshell fragments are surrounded by calcareous sandstone and partly cemented to the matrix, whereas in other areas the eggshells separated easily from sandstone (Fig. 1A). The poor condition provides little information about the egg shape other than it may be less than 10 cm in diameter. Because of extensive weathering, the outer surface of ZMNH M1849 is strongly sculptured, which facilitates identification of eggshell units and the pore openings in hand sample (Fig. 1B).

The eggshell thickness ranges between 1.84 and 2.05 mm, with an average of 1.9 mm (Fig. 2A). The closely arranged cones at the inner surface of the eggshell show radiating structure under PLM and SEM (Fig. 2A-B). The height of the cones is about 1/7 of the eggshell thickness. The highly recrystallized portion of the eggshell above the cones represents about 1/4 of the eggshell thickness. The margins of the eggshell units are rather vague in this area. However, the upper 3/5 of the eggshell is well preserved. Eggshell units branch 2-4 times, displaying a sweeping extinction under cross-polarized light. Each eggshell unit typically has more than five branches. The parallel horizontal accretion lines are distributed evenly throughout the eggshell units. Pore canals between eggshell units or the branches of eggshell units are irregular in shape, gradually narrowing towards the outer eggshell surface. The branches of eggshell units are smaller and more closely spaced near the outer surface of the eggshell (Fig. 2A). Tangential sections of the inner surface show multi-angular eggshell units that are tightly packed together (Fig. 2C). There are about 45 cones per square millimeter. In the middle portion of the eggshell, multi-angular eggshell units are separated by large rimiform pore canals, whereas most branches of eggshell units are fused near the outer surface of the eggshell (Fig. 2D-E).

Comparison: With the exception of the oofamilies Dendroolithidae Zhao & Li, 1988, Dictyoolithidae Zhao, 1994, and Similifaveoloolithidae Wang et al., 2011, ZMNH M1849 can be easily distinguished from all other oofamilies by the presence of branched eggshell units.

Compared with eggs of the Dendroolithidae, the eggshell units of ZMNH M1849 are not totally fused together near the outer surface of the eggshell; however, we cannot exclude the possibility that this is a result of weathering. A significant difference between ZMNH M1849 and dendroolithid eggs is that the branches of the eggshell units of *Polyclonoolithus yangjiagouensis* are gradually narrowing towards the inner surface of eggshell, probably indicating that these branches are independent eggshell units. Perhaps because of recrystallization, radially arranged calcite crystals are absent in the upper portion of the eggshell under SEM. In contrast to ZMNH M1849, the diameters of branches of the eggshell units are relatively constant in radial sections of dendroolithid eggs. On the other hand, dendroolithid eggs' eggshell units are round or worm-like in tangential sections (Zhao and Li, 1988; Zhao and Zhao, 1998), differing from the multi-angular eggshell units of ZMNH M1849.

Eggs of the Dictyoolithidae are remarkable for their superimposed branched eggshell units (Zhao, 1994; Wang et al., 2013). But the arrangement of the eggshell units is very irregular, forming a reticulate structure, which is not seen in ZMNH M1849. In tangential sections, the shapes of eggshell units of dictyoolithid eggs are similar to those of dendroolithid eggs, which can be easily distinguished from those of ZMNH M1849.

Eggshell microstructure of similifaveoloolithid eggs in radial sections resembles that of dendroolithid eggs. The diameters of branches of eggshell units are also constant in radial sections. Tangential sections show numerous, evenly distributed pores with irregular shapes. Adjacent eggshell units fuse together to form the walls of pore canals (Wang et al., 2011). Both radial and tangential eggshell microstructures differ from those of ZMNH M1849.

According to these comparisons, we erect a new oofamily Polyclonoolithidae based on the features of ZMNH M1849.

5 Discussion

In China, abundant dinosaur eggs from the Upper Cretaceous have been divided into several dinosaur egg faunas, showing a general process of evolution of dinosaur eggs. The dinosaur egg fauna from the Tiantai Basin, Zhejiang Province, mainly consists of faveoloolithid, dictyoolithid, and macroelongatoolithid eggs, which represents a group that retains primitive structural attributes. The age of this dinosaur egg fauna is 98-91 Ma, corresponding to the early Late Cretaceous (Cenomanian-Turonian) (Wang et al., 2012). Another primitive dinosaur egg fauna is reported from the Xixia Basin, Henan Province, which primarily includes dendroolithid and macroelongatoolithid eggs. Although the absolute age of these dinosaur eggs is unknown, they are believed to come from Late Cretaceous strata based on the studies of other fossils (Wang et al., 2012).

According to the comparison above, ZMNH M1849 likely shares a close relationship to the oofamilies Dendroolithidae, Dictyoolithidae, and Similifaveoloolithidae. Considering the horizon of ZMNH M1849 (Lower Cretaceous), it may represent a more basic type of dinosaur egg than the aforementioned oofamilies, which had become extinct in the Late Cretaceous. The discovery of this new oofamily possibly indicates that there is an unknown dinosaur egg fauna preserved in the Early Cretaceous strata of China.

According to the branched eggshell units and irregular pore canals, ZMNH M1849 should have the same eggshell formation mechanism as dendroolithid, dictyoolithid, and faveoloolithid eggs (Zhao, 1993). Interestingly, the multi-angular eggshell units are somewhat similar to the eggshell units in the tangential sections near the inner surface of eggshells of spheroolithid eggs (*Spheroolithus spheroides*, *S. chiangchiungtingensis*, and *S. megadermus*) (Zhao and Jiang, 1974; Liu et al., 2013), possibly suggesting that this new type of dinosaur egg has some relationships with spheroolithid eggs. If the hypothesis is true, the eggshell formation mechanism of spheroolithid eggs may be the same as that of ZMNH M1849. The "columnar layer" of spheroolithid eggs, which is composed of superimposed eggshell units, probably evolved from the branches of eggshell units of the new oofamily Polyclonoolithidae; otherwise, it may indicate that the branches of eggshell units are actually superimposed eggshell units.

6 Conclusions

The fossil egg ZMNH M1849 from Gansu, China is referable to a new oofamily Polyclonoolithidae based on the following diagnosis: branched eggshell units without a compact layer near the outer surface, interlocked or isolated multi-angular eggshell units in tangential sections, and irregular pore canals. The discovery of the new material expands the diversity and distribution of Early Cretaceous dinosaur eggs in China. The new oofamily Polyclonoolithidae should represent a very basic ootaxon among known oofamilies. Furthermore, ZMNH M1849 has the same eggshell formation mechanism as that of dendroolithid, dictyoolithid, and faveoloolithid eggs, and shows some relationships with spheroolithid eggs. It may reveal the origin of eggshell microstructures of spheroolithid eggs.

Ackgments

The authors would like to thank Ji Shu-An from IGCAGS, You Hai-Lu from IVPP, and Yang Jing-Tao from China University of Geosciences (Beijing) for field work and explaining the stratigraphic information of the Lanzhou-Minhe Basin. We thank Frankie D. Jackson from Montana State University for improving the English text.

Note: Figure translations are in progress. See original paper for figures.