The first *Choerolophodon* (Proboscidea, Gomphotheriidae) skull from China

WANG ShiQi[*] & DENG Tao

Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

Here we report the first discovery of a relatively complete skull of *Choerolophodon* from the late early Miocene Dalanggou quarry of Linxia Basin, Gansu Province in China. The skull is low and elongated, with two enamel-less and outward-and-upward curved incisors and the choerolophodont molars. These characters indicate that the new specimen can be assigned to the genus *Choerolophodon,* as it is quite distinct from other common gomphotheres in northern China such as *Gomphotherium*, *Platybelodon*, and *Sinomastodon*. The skull is also primitive in possessing laterally-expanded zygomatic arches, anteriorly-positioned orbits, weakly-developed cheek teeth cement, and retention of a P4. Prior to this discovery, *Choerolophodon* was found primarily from the middle-late Miocene of Africa, Eastern Europe, and western and southern Asia. The discovery of this new material expands the known temporal and spatial distributions of this taxon and helps us better understand the phylogeny, evolution, and adaptive radiation of gomphotheres in early Miocene of China.

gomphotheres, *Choerolophodon*, Linxia Basin, early Miocene, China

The name gomphotheres herein refers to the Gomphotheriidae Hay, 1922. According to Shoshani and Tassy [1], Gomphotheriidae, the main clade of the proboscideans, approximately equals the bunodont trilophodont mastodonts of Tobien [2]. Gomphotheres stemmed from African Elephantiformes Tassy, 1988 (including *Palaeomastodon* and *Phiomia* [1]) from the Oligocene of Fayûm, Egypt. At the beginning of their evolution, gomphotheres were already heavy-built animals conducive to long-distance migration. By the early Miocene, gomphotheres migrated to Eurasia [3] and reached America by the middle Miocene [4]. Gomphotheres adapted to a range of ecologies and diversified into numerous genera and species; thus, they were regarded as excellent biostratigraphic markers.

As a transfer center of the migration of gomphotheres among Africa, Eurasia, and America, the records of fossil gomphotheres in China are abundant after the middle Miocene. However, gomphotheres are rare in the early Miocene. An important discovery was *Platybelodon dangheensis* found in the early Miocene lower Tiejianggou Formation (about 19–20 Ma) from the Subei Mongolian Autonomous County of Gansu Province [5, 6]. Recently, other gomphothere materials were found in the early Miocene Shangzhuang Formation of the Linxia Basin, Gansu Province. Among the collected materials, a relatively complete skull is here referred to *Choerolophodon guangheensis* sp. nov. This genus belongs to a primitive lineage of gomphotheres, which is distinct from the genus *Gomphotherium*. In China, the limited records of *Choerolophodon* sp. include some fragmentary cheek teeth originally assigned to *Gomphotherium* or *Platybelodon* and later reassigned by Tobien

et al. [7]. Therefore, this new material from the early Miocene of the Linxia Basin adds to our knowledge of the adaptive radiation of gomphotheres in China.

Linxia Basin is located at the northeastern corner of the Tibetan Plateau in western China, where the Cenozoic sedimentary sequence from the early Oligocene to early Pleistocene is almost without interruption. The fossil gomphotheres were excavated from a small gully named the Dalanggou quarry (35°26′50.7″N, 103°27′28.5″E; elevation 2060 m; locality No., LX200001; Figure 1) on the south bank of the Guangtong River, southeast of the Maijiaxiang Township, Guanghe County. The section was divided from bottom to top into the early Miocene Shangzhuang Formation, the middle Miocene Dongxiang Formation, the middle Miocene Hujialiang Formation, the late Miocene Liushu Formation, and with the Pleistocene Malan loess overlying these deposits. The Shangzhuang Formation consists of yellowish brown carbonate-cemented medium sandstones and brownish red silty mudstones. The materials described here were found in the upper conglomerate lenses in the red mudstones. The estimated age is late early Miocene, based on an early Miocene fauna of small mammals found in the Shangzhuang Formation of Sigou locality, which is on the north bank of the Guangtong River. The small mammals include *Mioechinus* sp., *Amphichinus* sp., *Sinolagomys ulunguensis*, *Atlantoxerus* sp., *Paracricetulus*? sp., *Hete- rosminthus* sp., *Protalactaga* sp., *Litodonomys* sp., *Sayimys* sp., and *Tachyoryctoides* sp.

The descriptions of occlusal structures of gomphotheriid cheek teeth and the cranial measurements follow Tassy ([8], figures 4 and 5).

Institutional abbreviations: GM-Vm, prefix for specimens of Geological Museum of China, Beijing, China; HMV, prefix for specimens of Hezheng Paleozoological Museum, Hezheng, Gansu, China; IVPP V, prefix for specimens of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; TM, prefix for specimens of Tianjin Natural History Museum, Tianjin, China.

1   Systematic paleontology

Order Proboscidea Illiger, 1811
  Family Gomphotheriidae Hay, 1922
    Subfamily Choerolophodontinae Gaziry, 1976
      Genus *Choerolophodon* Schlesinger, 1917
        ***Choerolophodon guangheensis* sp. nov. (Figures 2–6; Tables 1, 2)**

Holotype: IVPP V17685 is a relatively intact skull with a pair of complete I2; the left zygomatic arch is broken. The specimen is considered a young adult.

Referred materials: IVPP V17686, a fragmented left M2? only with the 3rd loph and talon preserved; HMV1774, a middle segment of right? I2; HMV1775, four fragmented segments of I2; HMV1776, a posterior segment of left I2; HMV1777, a complete left I2; HMV1778, a middle segment of right I2; HMV1779, a complete left I2; HMV1780, a posterior segment of right I2; HMV1822, an anterior segment of right? I2; HMV1823, a right I2; HMV1816-1 and HMV1816-2, both are left I2; HMV1817, a huge block of red mudstone imbedding multiple materials, at least four segments of I2 were referred to the species.
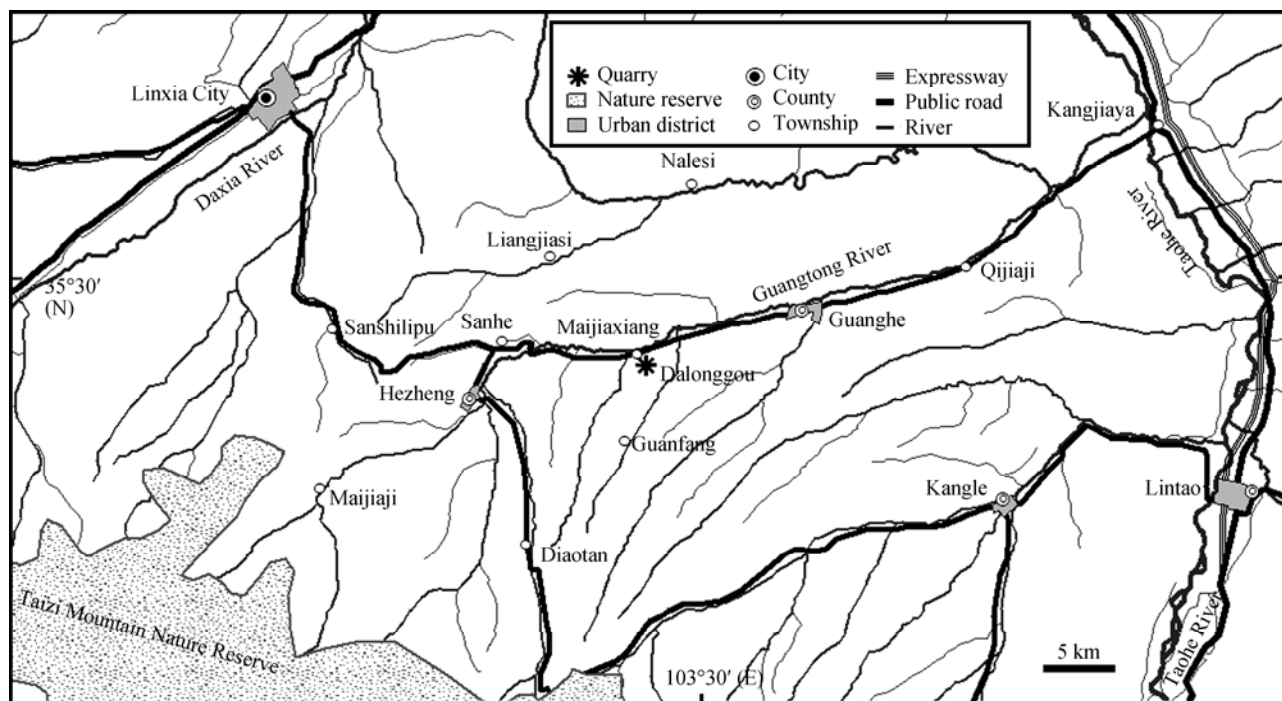

Figure 1   Geographic location map of the Dalanggou quarry.

Table 1 The cranial measurements from *Choerolophodon guangheensis* sp. nov. (IVPP V17685) (mm)[a]

Measurements	1	2	3	4	5	6	7	8	9
Skull	765	398	395	368	63	428	316 (ca.)	352	74
Measurements	10	11	12	13	14	15	16	17	18
Skull	270 (ca.)	94	777	345	192	310	273	115	580
Measurements	19	20	21	22	23	24	25	26	27
Skull	476	63	87	211	84	125	175	570 (ca.)	90 (ca.)
Measurements	28	29	30	31	32	33	34	35	36
Skull	–	45	96	234 (ca.)	468	292	269	401	231

a) The measurements were defined by Tassy ([8], figure 5): 1, maximal length taken from the occipital border; 2, length of cerebral part; 3, length of premaxilla; 4, length of the fossa incisive; 5, length of nasal bones upon the nasal fossa; 6, maximal supra-orbital width; 7, posterior rostral width (taken between the infra-orbital foramina); 8, anterior rostral width; 9, width of nasal bones upon the nasal fossa; 10, width of nasal fossa; 11, minimal cerebral width between temporal lines; 12, maximal length taken from the condyles; 13, length of the zygomatic arch taken from the processus zygomaticus of the maxilla to the posterior border of the glenoid fossa; 14, length of the orbitotemporal fossa taken at the level of the zygomatic arch; 15, palatal length from the anterior grinding tooth to the choanae; 16, length of basicranium from the choanae to the foramen magnum; 17, thickness of processus zygomaticus of the maxilla; 18, maximal cranial width taken at the zygomatic arches; 19, width of the basicranium taken at the lateral borders of the glenoid fossae. 20, maximal width of choanae; 21, internal maximal width of the palate; 22, external maximal width of the palate; 23, internal width of the palate taken at the anterior grinding teeth; 24, minimal palatal width between the interalveolar cristae (maxillary ridges); 25, sagittal height of the occipital; 26, occipital width; 27, height of premaxilla; 28, facial height taken at the anterior grinding tooth; 29, height of the maxilla ventral to the processus zygomaticus; 30, height of the orbit; 31, cranial height taken from the top of cranium to the pterygoid process; 32, length of basicranium from the condyles to the pterygoid process; 33, facial length taken from tip of the rostrum to the pterygoid process; 34, length of the orbitotemporal fossa taken from the squamosal to the anterior border of the orbit; 35, mid-cranial length taken from the external auditory meatus to the ventral border of the orbit; 36, mid-cranial height taken from the pterygoid process to the dorsal border of the orbit.

Table 2 Teeth measurements from *Choerolophodon guangheensis* sp. nov. (IVPP V17685)[a]

	L	W	H	L1	L2	L3	Talon	I
I2 l.	1115*	–	94.5**					
I2 r.	1018*	120**	96**					
P4 l.	37	24	–					64.9
P4 r.	40	–	14					–
M1 l.	72+	49	–	44	49	48		–
M2 l.	97	60	–	57	60	60		61.9
M2 r.	103	63.5	–	63.5	62.5	60		61.7
M3 l.	134	74	51***	74	71	61	43	55.2
M3 r.	130+	79	52.5***	79	–	–	–	–

a) L, length; W, width; H, height; L1, width at the 1st loph; L2, width at the 2nd loph; L3, width at the 3rd loph; talon, width at the talon; Unit: mm. I, index; I=W × 100/L; l., left; r., right. *, length from the tip to the front end of the incisive alveolus; **, taken at the front end of the incisive alveolus; ***, taken at the lateral side of the posttrite of the 1st loph.

Species name: Derived from the county name where the fossils were excavated.

Diagnosis: Relatively small *Choerolophodon*. The neurocranium and the face are flattened and elongated. The premaxillae are particularly long and the convex ledge of the posterior border of the incisive fossa is located behind the tip of the nasal (in-depth of the external nares). The convergence of the temporal lines on the dorsal table of neurocranium is closer than that in *Choerolophodon pentelici*, but not as close as that in *Afrochoerodon chioticus*; the posterior border of the dorsal table of the neurocranium is concave in the middle. The zygomatic arches and the basiocranium are laterally-expanded significantly, and the posterior end of the jugal reaches the antero-lateral border of the glenoid. The posterior palatal border is behind the posterior end of the last functional cheek tooth. The basiocranium (the posterior part of the pterygoid processes) and the palate (the anterior part of the pterygoid processes) are located almost in the same plane. The anterior border of the orbit is located at the 3rd loph of the M2. The upper incisors are extremely robust and long with rounded or oval cross-sections. The P4 is very weak and coexists with M1, M2, and M3. The intermediate upper molars are tri-lophed, and the M3 is triangular shaped with 3.5 lophes. The molars are apparent choerolophodonty and relatively weak ptychodonty; the cement is weakly-developed.

Descriptions: Skull (Figures 2–4): The holotype (IVPP V17685) is deeply weathered showing a squamiform surface.

Dorsal view (Figure 2(a)): The neurocranium and face are narrow and long; the dorsal part of the frontal and parietal of the left side are partially damaged and the left zygomatic arch is not preserved.

The premaxillae are wide and long, and protrude forward horizontally. The incisive fossa is well developed between the two premaxillae with the posterior part transversely ex-
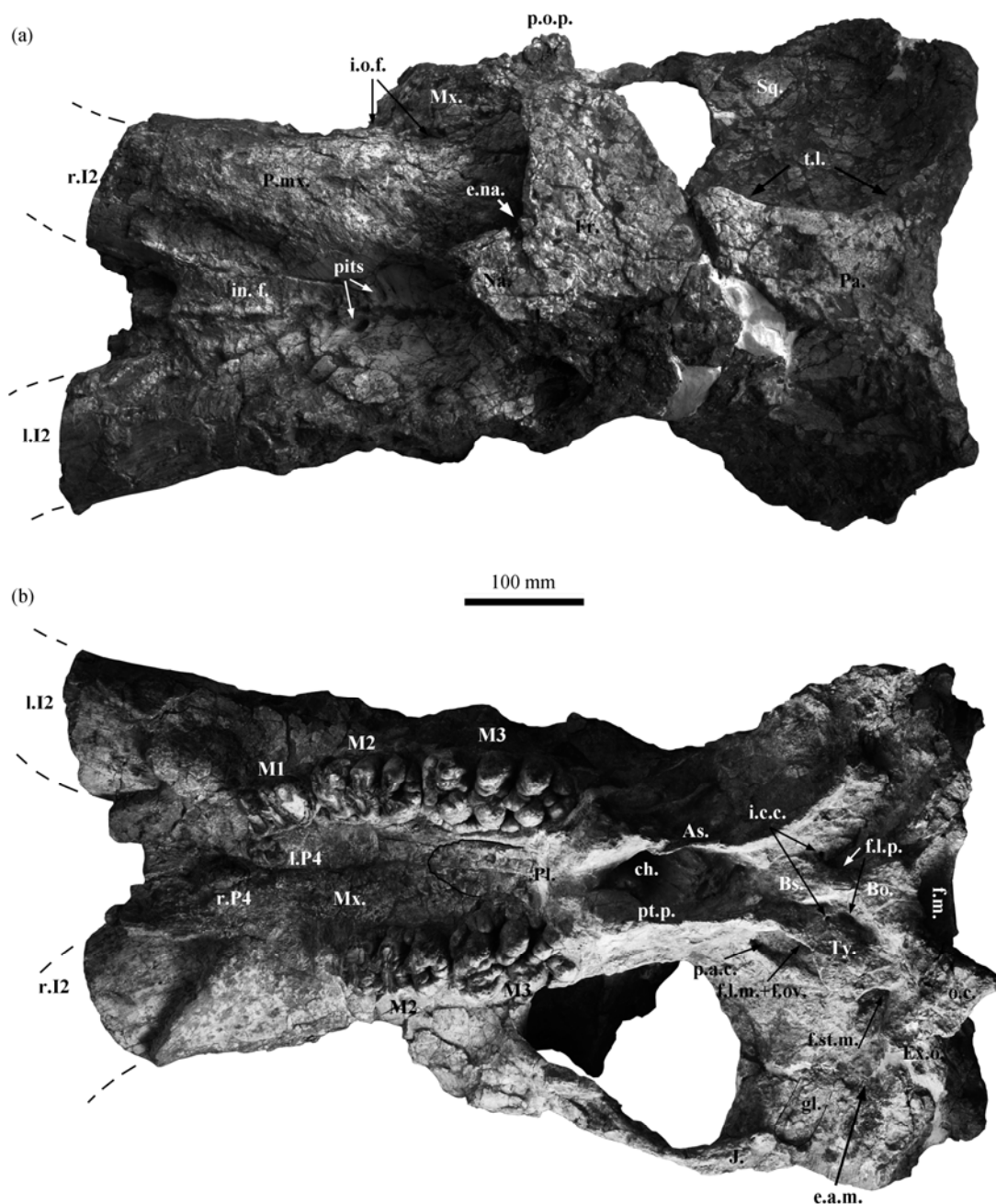
Figure 2 The skull of *Choerolophodon guangheensis* sp. nov. (IVPP V17685). (a) The dorsal view; (b) the ventral view. Abbreviations: As., alisphenoid; Bo., basioccipital; Bs., basisphenoid; ch. choanae; e.a.m., (secondary) external auditory meatus; e.na., external nares; Ex.o., exoccipital; f.l.m., middle lacerated foramen; f.l.p. posterior lacerated foramen; f.m., foramen magnum; f.ov., oval foramen; f.st.m., stylomastoid foramen; Fr., frontal; gl., glenoid; i.c.c., canal for internal carotid artery; i.o.f., infraorbital foramen; in.f., incisive fossa; J. jugal; l.I2, left second incisor; l.P4, left fourth premolar; Mx., maxilla; Na., nasal; o.c., occipital condyle; p.a.c., posterior opening of the alisphenoid canal; P.mx., premaxilla; p.o.p., posterior orbital process; Pa, parietal; Pl., palatine; pt.p. pterygoid process r.I2, right second incisor; r.P4, right fourth premolar; Sq., squamosal; t.l., temporal line; Ty., tympanic bulla.

panded and the anterior part widely open, connected by a narrow neck. The posterior convex ledge of the incisive fossa is located in-depth of the external nares, and at each side of the middle suture of the incisive fossa, there are 5–6 small pits presumably for the attachment of maxillo-labialis. The sockets of the incisive alveoli are extremely robust and separate externally by an angle of about 25°. The front part of the nasal is robust and triangular shaped, although the tip

is slightly damaged. The dorsal part of the frontal is flattened and broad. The temporal lines, which forward and laterally extend to connect the postorbital processes, are parallel in the middle before extending backward and laterally to merge with the occipital crest, making the dorsal part of the parietal form an antero-posteriorly elongated rectangle. The distance between the temporal lines on the parietal part is narrower than that in *Choerolophodon pentelici*, but

wider than that in *Afrochoerodon chioticus*. The posterior border of the dorsal table of the neurocranium is concave in the middle, and the temporal region of the parietal and squamosal bones are laterally expanded.

Ventral view (Figure 2(b)): The left basicranium is partially damaged and the left zygomatic arch is not preserved.

There is a huge triangular notch on the anterior end of the ventral side of each alveolus. The palate between the teeth rows is narrow and flattened, and slightly arched upward. The broad and plate-like zygomatic process protrudes outward horizontally and turns backward with a slightly concave ventral face. The right zygomatic arch is expanded widely. The front part of the palatine is long and triangular, and the anterior end of the palatine is located at the boundary of M2 and M3 with a clear suture. The posterior border of the palatine forms an inclined plane which deflects downward to the choanae.

The front part of the choanae is oval. The outer alisphenoid and inner pterygoid enclose the maxillary process located on the posterior part of each maxilla. The pterygoid process is relatively blunt and the angle between the basicranium (the posterior part of the pterygoid processes) and the palate (the anterior part of the pterygoid processes) reaches 170°, such that they are located almost in the same plane. The posterior opening of the alisphenoid canal is large, oval, and located at the postero-medial part of the alisphenoid.

The sharp crest of the pterygoid process extends backward to connect with the anterior crest of the tympanic bulla; the common opening of the oval foramen and the middle lacerated foramen is located in the deep groove under the crest. The tympanic bulla is diamond-shaped and extends outward-and-backward. There is a small opening on the inner side of the tympanic bulla, which represents the canal of the internal carotid artery. The depression behind the inner side of the tympanic bulla represents the posterior lacerated foramen. The postero-lateral side of the tympanic bulla forms a vertical concave surface; the stylomastoid foramen is located in a deep fossa outside of this surface.

The squamosal is large and extends outward. The anterior portion of the ventral side of squamosal forms a plane that rises upward; the glenoid is located in the middle part, which is relatively flattened and lacking a prominent postglenoid ledge. The posterior end of the jugal reaches the antero-lateral border of the glenoid, and in the posterior part of the ventral side of squamosal is a depressed region representing the secondary external auditory canal. The exoccipital behind the squamosal is raised, extending outward and slightly forward.

Only the right occipital condyle is preserved, which is large and triangular and extends backward and strongly outward. The foramen magnum is dorso-ventrally compressed. The basioccipital is low and triangular in the posterior region, rises to form a cylinder shaft at the middle, and descends to attach to the anterior basisphenoid. The

presphenoid and vomer, which extend into the choanae, have been damaged by pressure.

Front view (Figure 3(a)): The transversely-elliptical opening of the external nares is wide and low; the right orbit is laterally protruded; the developed sockets of the incisive alveoli take up the most part of the faces.

Back view (Figure 3(b)): The occipital surface is very wide, nearly perpendicular to the dorsal and ventral sides of the skull. The ligamentum nuchae fossa is very large (155 mm wide and 120 mm tall) and deep in order to support the huge skull and incisors; it is located in the middle of occipital surface, which possesses straight upper and convex lower borders, and a thin crest, in the middle.

Lateral view (Figures 3(c), 4): The neurocranium and the face are flattened and elongated. The skull is slightly arched with the vertex at the boundary of the frontal and parietal.

The alveolus is particularly elongated with the anterior end thicker than the posterior end. The lateral face of the maxilla is low and elongated. The tip of the nasal is protruded and the upper border of the external nares is located just above the middle of the orbit.

The orbit is relatively large with the anterior border located at the 3rd loph of the M2. A small lachrymal process is located at the middle of the anterior border with a small notch beneath it. The lower infraorbital foramen is relatively large and located just in front of the zygomatic process of the maxilla, and the upper infraorbital foramen is slit-like and located on the antero-dorsal side of the orbit. Both upper and lower infraorbital foramina are irregular because of the breaks of adjacent maxillary bone. The postorbital process is robust. The orbitotemporal crest extends inferoposteriorly and the lower part of the crest forms the front edge of the alisphenoid, which overlaps the posterior part of the maxilla.

The temporal fossa is long and broad. The jugal is slender.

Incisor (Figures 4, 5): The incisors are extremely robust without any vestige of enamel band. In the type specimen, the incisor, which curves upward but not as prominently as that in *Choerolophodon pentelici* and *Ch. corrugatus*, extends outward at the proximal part and converges again at the distal part (Figures 4, 5(a) and (b)). The cross-section of the right incisor at the front end of the alveolus is dorso-ventrally compressed with a flattened dorsal line and a convex ventral line (Figure 5(c)). The shape of the cross-section becomes rounded in the middle segment (Figures 5(d), (e)) and returns to elliptical shape in the front segment, with a flattened ventral line and a convex dorsal line (Figure 5(f)). Besides the type specimen and among other referred materials, the section of the thickest specimen (HMV1816-2) reaches 143 mm on the long axis and 105 mm on the short axis. The longest specimen (HMV1779) with a reliable restoration reaches 1245 mm from root to tip in the straight line.

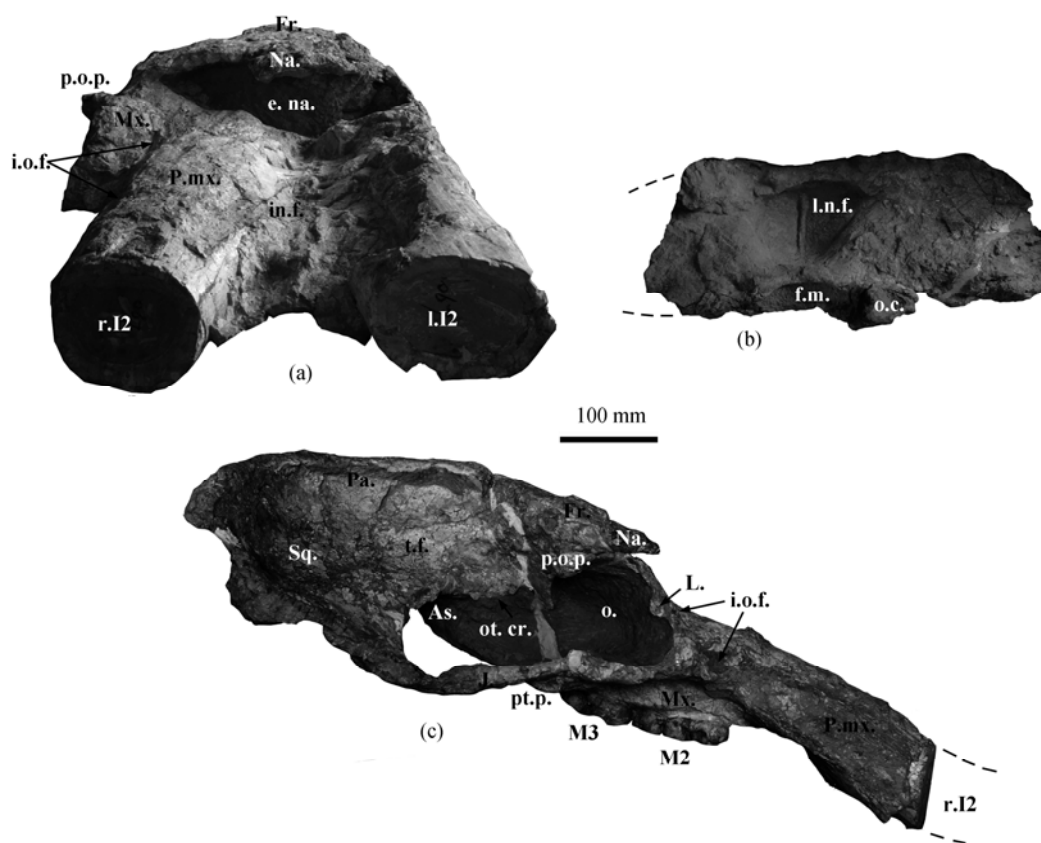Cheek teeth (Figure 6): This series of teeth is very pecu-

Figure 3   The skull of *Choerolophodon guangheensis* sp. nov. (IVPP V17685). (a) The front view; (b) the back view; (c) the lateral view. Abbreviations: L., lachrymal; l.n.f., ligamentum nuchae fossa; o., orbit; ot.cr., orbitotemporal crest; t.f. temporal fossa; other abbreviations are defined in Figure 2.

Figure 4   The sketch of the lateral holomorph for the skull and incisor of *Choerolophodon guangheensis* sp. nov. (IVPP V17685).

liar. The left P4–M3 are present, the right M1 had been shed, but the right P4 is preserved. The P4s are asymmetrical: the left P4 is located on the inner side of the left M1, of which the anterior border is at the middle of the left P4; in the right P4, the crown rotates inward to the middle sagittal surface of the palate and is located entirely in front of the left one. The P4s are small and low-crowned without wear. The crown is oval with two lophs and a posterior talon. The 1st loph is larger; the pretrite and postrite are merged and co-

vered by a thin layer of cement. Both the pretrite and posttrite of the 2nd loph consist of two fissive cones, and two other small talon cones behind them. The cingulum is poorly developed. The development of the tooth indicates that P4 is very regressive in this species.

The right M1 has been shed and the left, of which the root had been highly exposed, would have shed soon. The 3rd loph of the left M1 is more deeply worn than the former two lophs, which may be caused by the constant pushing of
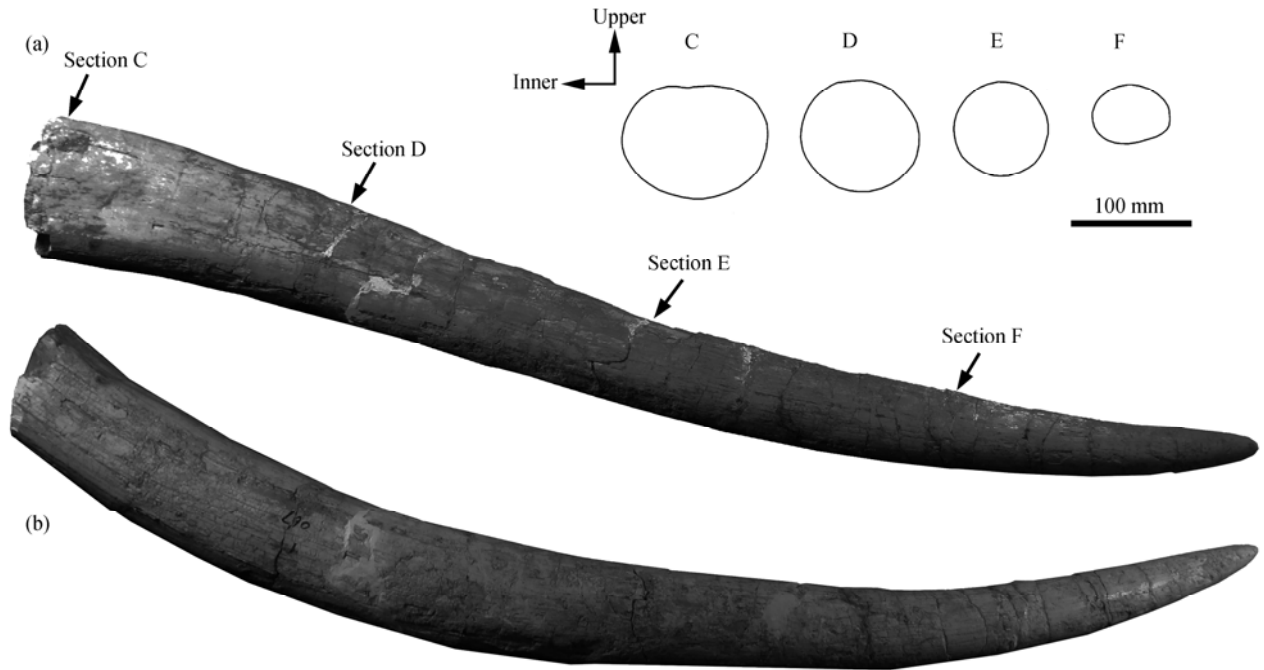
Figure 5 The right I2 of *Choerolophodon guangheensis* sp. nov. (IVPP V17685). (a) The dorsal view; (b) the lateral view. Sections C–F show the contour outline of the cross-section at the end of alveoli (1018 mm from the tip) (C), and the cross-sections at 750 mm (D), 500 mm (E), and 250 mm (F) to the tip of the incisor, from the back view.
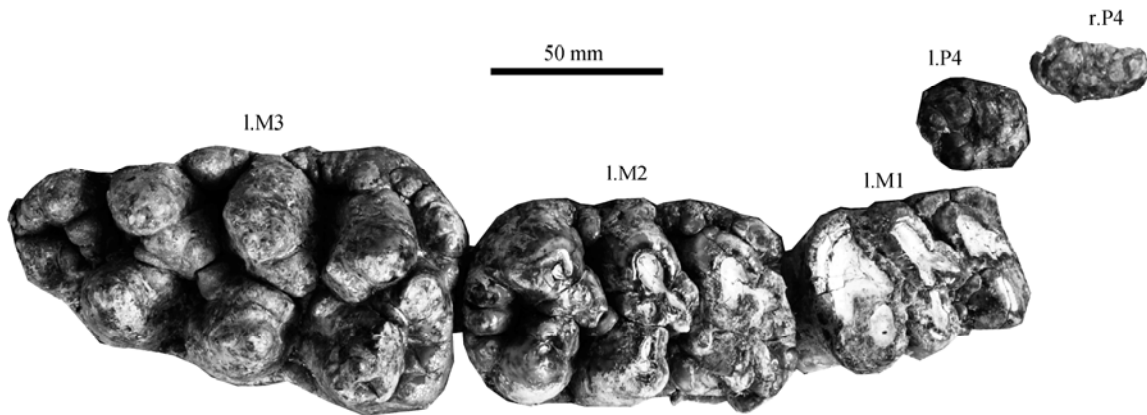

Figure 6 The left P4–M3 dentition and the right P4 of *Choerolophodon guangheensis* sp. nov. (IVPP V17685).

the M2 to raise the rear of the M1 during the growth of teeth. This phenomenon, which may be an intermediate stage in the evolution of horizontal tooth replacement, was also reported in the African genus *Eozygodon* [9]. The rectangular M1 is composed of three lophs. The wear pattern of the pretrite on the 1st loph forms a forward-adaxially tilted trefoil; the mesoconelet is moved forward. The wear pattern of the posttrite forms a transverse ellipse perpendicular to the middle axis and the posterior posttrite central conule is prominent with enamel layers strongly folded at the back wall of the posttrite. A large enamel cusp and other small cones are developed in the 1st ectoflexid (labial side). The 2nd loph is similar to the 1st one. The mesoconelet of the pretrite is fused to the anterior pretrite of the central conule

to form a trefoil pattern, which is more forward-adaxially tilted than that in the 1st loph. The wear pattern of the posttrite also tilts slightly forward-adaxially with the development of mesoconelet and posterior posttrite central conule. The enamel layer of the back wall of the posttrite is also strongly folded. The 2nd interloph has been reduced by the wear from the 3rd loph. The pretrite of the 3rd loph is deeply worn, merging with the talon to form an orthogonal fan shape with an irregular adaxial edge. The wear facet of the posttrite is elliptical and tilts slightly forward-adaxially. The cingulum is developed at the anterior border (although it has been broken) and outside the pretrite of the 1st loph, and poorly developed elsewhere. The cement is very weak.

The rectangular left M2 is composed of three lophs and a

talon, with a relatively rounded posterior end. The 1st loph is moderately worn and the 3rd loph shows only the early signs of wear. The last two lophs are V-shaped with the apices oriented forward. The crown of the tooth is apparent choerolophodonty and partial ptychodonty. The wear pattern of the pretrite of the 1st loph is not a typical trefoil. The large anterior pretrite central conule is linked to the anterior cingulum, and the mesoconelet, separated from the main cone of the pretrite, moves anteriorly to join the anterior pretrite central conule. The enamel layer folds at the back wall. The posttrite of the 1st loph is mostly damaged but the outline shows a strong main cusp and a weaker mesoconelet; a posterior posttrite central conule is developed. A strong cusp is developed at the cingulum of the 1st entoflexid (labial side) in which other small cones are developed, and another strong cusp and some small cones are developed in the 1st ectoflexid (lingual side). The 2nd loph is similar to the 1st one. At the pretrite side which tilts forward-adaxially, in addition to the large anterior pretrite central conule, the posterior pretrite central conule moves anteriorly and is strongly developed. It could not be recognized whether the mesoconelet fuses to the anterior or posterior pretrite central conule. The posttrite titles forward-adaxially. The main posttrite cusp is strong; the mesoconelet is transversely elongated to form a wasp-waisted wear pattern; and a posterior posttrite central conule is developed. A strong cusp is developed on the cingulum of the 2nd entoflexid and the 2nd ectoflexid is narrow. The enamel layer folds weakly at the back wall and furrows develop on the side wall of both the pretrite and posttrite. The main cusp of pretrite of the 3rd loph is strong. The mesoconelet fuses to the strong and serrated anterior pretrite central conule to link to the posterior posttrite central conule of the 2nd loph. The main cusp of posttrite is strong and the mesoconelet is somewhat weaker. The half lophs of both the pretrite and posttrite sides strongly tilt forward-adaxially with furrows developed at the back and side wall of the enamel layer. Three cusps are arranged in an arc, declined in turn, and extended from the very weak posterior pretrite central conule of the 3rd loph, forming the talon. The cingulum is well developed on the anterior border and outside of the labial wall of the 1st loph, but poorly developed elsewhere. The cement is weak. The right M2 is similar to the left one with some damage to its front end.

The long triangular left M3 is composed of three complete lophs, and a developed talon forms the incomplete 4th loph and has been pushed entirely out of the maxillary process but yet had any wear. The crown is apparent choerolophodonty and weak ptychodonty; the 2nd and 3rd lophs are V-shaped with the apices directed forward. The main cusp of the pretrite of the 1st loph is strong and high. A laminar cone is separated from the main cusp, which might be the mesoconelet, and is fused to the strong anterior pretrite central conule, which is serrated and linked to the anterior cingulum. The posterior pretrite central conule is

large. The main cusp and mesoconelet of the posttrite are nearly fused, and both tend to split into fissive cones at the top. The posttrite is attached to the pretrite mesoconelet and the posterior posttrite central conule is well developed. Furrows are developed outside the enamel wall, but the back enamel is poorly folded. The 1st interloph is relatively smooth without prominent small cones. The 2nd loph is similar to the 1st loph. The serrated anterior pretrite central conule is fused to the mesoconelet. The posterior pretrite central conule is absent. Weak furrows are developed outside the enamel wall. The main cusp of the posttrite is nearly fused to the mesoconelet, with some fissive fine cones on its top. The posttrite tilts forward-adaxially, and the central conule of the anterior posttrite is weakly developed. There is a large cusp at the edge of the entoflexid (labial side) of the 2nd loph, and the ectoflexid is smooth. The 3rd loph is similar to the first two, except that the width is narrower and the height of the crown is lower. The main cusp of the pretrite is strong; the mesoconelet is fused to the serrated anterior pretrite central, but the posterior pretrite central conule is absent. The posttrite is very similar to that of the former loph; the talon is well developed to form the incomplete 4th loph. The two main cusps of both the pretrite and posttrite sides are obliquely arranged forward-adaxially to form a V-shape, with the apices pointed forward. Another small cusp is developed at the back of the V-shape to enclose the opening. The entire talon forms a ring of enamel cusps. The cingulum is well developed at the anterior end and outside the labial wall of the 1st loph, but poorly developed elsewhere. The cement is very weak. The right M3 is similar to the left one, but the talon has not been pushed entirely out of the maxillary process.

2   Comparisons and discussion

Choerolophodon was established by Schlesinger [10] who assigned the *Mastodon pentelici* Gaudry et Lartet, 1856 of Pikermi, Greece, to this genus; Gaziry [11] established the Choerolophodontinae, which included the only genus *Choerolophodon*. Besides the genotype *Ch. pentelici*, other species included *Ch. palaeindicus* Lydekker, 1884; *Ch. pygmaeus* Depéret, 1897; *Ch. corrugatus* Pilgrim, 1913; *Ch. kisumuensis* MacInnes, 1942; *Ch. ngorora* Maglio, 1974; *Ch. chioticus* Tobien, 1980, and *Ch. zaltaniensis* Gaziry, 1987; which are distributed mainly in the Miocene of Africa, Eastern Europe, and western and southern Asia [11−18]. Pickford [13, 19] reassigned *Ch. kisumuensis* and *Ch. chioticus* to his new genus *Afrochoerodon* (still belonging to the Choerolophodontinae). Sanders and Miller [20] believed that *Ch. palaeindicus* might also belong to *Afrochoerodon*.

Based on some isolated cheek teeth from the late Miocene or Pliocene of southern China, Zhou and Zhang ([21], pages 31, 32, plate xii) reported three species of *Synconolophus* (Tassy [22] considered it a synonym of *Cho-*

erolophodon), *S. fukienensis* Zhou et Zhang, 1974, *S.* cf. *ptychodus* Osborn, 1951, and *Synconolophus* sp. indet. These species may be directly related to the late Miocene *Ch. corrugatus* of Siwalik. Some materials in China referred to *Gomphotherium* (viz. *Trilophodon*) or *Platybelodon* were reassigned to *Choerolophodon* sp. by Tobien et al. ([7], figures 17–23), including 1) TM-18 902, left M1, *Tr.* cf. *wimani*; 2) TM-18 899, right M2, *Tr. wimani*; 3) GM-Vm503, fragmentary right m3 (m2), *G. elegans*; 4) IVPP V2565, left M1, *G.* cf. *connexus*; 5) IVPP V2680, fragmentary left M3, *G. changzhiensis*; 6) IVPP V3083, fragmentary left m3, *Pl. grangeri*; 7) IVPP V5576, right M1, *Pl. grangeri*. All of these materials are isolated cheek teeth, and thus the assignment to *Choerolophodon* was unreliable. For example, Chen [23] considered that among the above materials, 1) and 2) should be assigned to the genus *Sinomastodon*.

Schlesinger [10] diagnosed *Choerolophodon* as having the following characters: the skull is low and elongated with two enamel-less incisors curved outward-and-upward; the mandibular symphysis is medially long with lower tusks absent; the molars are choerolophodonty. Although the mandible characters are unknown in the new specimen, other diagnostic characters are consistent with the Danglanggou specimen. The enamel-less and up-curved incisors are distinct from the genus *Gomphotherium*, *Platybelodon*, and *Zygolophodon*; the low and elongated skull, as well as choerolophodonty molars are also distinct from the genus *Sinomastodon* and *Anancus*. Therefore the Danglanggou specimen should be undoubtedly assigned to the genus *Choerolophodon*.

Tassy [8] enumerated the revised diagnoses of *Choerolophodon* in: 1) the cranium is narrow, and the zygomatic arches expand far from the skull; 2) the face is relatively long than the cranium; 3) the palate extends behind the last tooth in function; 4) the orbit and the external nares are located behind the last tooth in function; 5) the symphyseal groove is large and deep; 6) the upper incisors turn upward without any enamel bands; 7) the lower incisors are absent; 8) the dp2, P2, P3, p3, P4, and p4 are lost; 9) the meso-conelets of pretrite of dp3 are connected with metacones; 10) the molars are choerolophodonty. Except for characters 5, 7, and 9, which could not be observed, characters 1, 3, 6, and 10 are consistent with the Dalanggou specimen. The new specimen differs in characters 2, 4, and 8: laterally expanded zygomatic arches, anteriorly positioned orbits, and retention of the P4, which are the primitive characters in the Dalanggou specimen.

Schlesinger (ref. [10], tafeln xxiii–xxxi) described three juvenile skulls belonging to the genotype *Choerolophodon pentelici* from the late Miocene of Pikermi; Gaziry ([11], tafeln 5–12) also described *Ch. pentelici* material from the late Miocene of Turkey, including complete skulls. Although there are several common characters that unite species of *Choerolophodon*, there are many differences between *Ch. pentelici* and the Dalanggou specimen: in *Ch. pentelici*, the dorsal portion of the parietal is very broad, almost as wide as the dorsal part of the frontal; the posterior border of the dorsal table of the neurocranium is relatively straight and the length of temporal fossa is short; the lateral expansions of the zygomatic arches and the exoccipital bones are relatively weak; the basioccipital is relatively long and the ligamentum nuchae fossa is small and round; the external nares are relatively narrow and the posterior convex ledge of the incisive fossa is located in front of the tip of the nasal. The orbit of *Ch. pentelici* is located behind the dentition and on the top of the lateral side of the skull. Furthermore, relative to the Dalanggou specimen, the incisors of *Ch. pentelici* are curved upward more strongly, the dental choerolophodonty and cement are more developed, and dental size is slightly greater (Figure 7).

The known materials of the late Miocene *Choerolophodon corrugatus* from the Siwalik locality differ greatly from the Dalanggou specimen ([15], figure 23, tableau xii, planche iv): *Ch. corrugatus* is larger in size, with the lengths of M3 generally measuring over 160 mm and the M2 over 110 mm (Figure 7); the M3 has four lophs plus a talon; the orbit is located behind the last functional tooth; the maxilla is fairly high; and the basicranium and the palate form a steep angle, instead of being located nearly in the same plane. The choerolophodonty, ptychodonty and cement of the cheek teeth in *Ch. corrugatus* are more developed than those of the Dalanggou specimen. The only known materials of early to middle Miocene *Choerolophodon* sp. from the Kamlial Formation of Siwalik are isolated cheek teeth, of which the M3 possesses four lophs and is slightly larger than the Dalanggou specimen ([16], figures 29, 31), suggesting they are related to *Ch. corrugatus*.

The holotype of the late Miocene *Choerolophodon ngorora* from Member E (the top member) of the Ngorora Formation, Kenya, is a fragmentary maxilla preserving M2–M3 dentition [24]. Pickford [13] assigned other specimens from the lower strata of this Formation to the genus *Afrochoerodon*; only the specimens in Member E of the Ngorora Formation were assigned to *Choerolophodon*. *Ch. ngorora* differs from the Dalanggou specimen in that: the cheek teeth of *Ch. ngorora* are larger (Figure 7) with a complete 4th loph of the M3; the lophs are compressed antero-posteriorly and the interlophs are wide; the folds of enamel are prominent and the cement is well developed (ref. [24], plate 100).

There are four obviously primitive characters preserved in the Dalanggou specimen: laterally-expanded zygomatic arches, anteriorly-positioned orbits, retention of the P4, and weakly developed cement on the cheek teeth. These characters-distinguish the Dalanggou specimen from the late Miocene choerolophodonts (although the first two differences of the skull are still unknown in *Choerolophodon ngorora*).

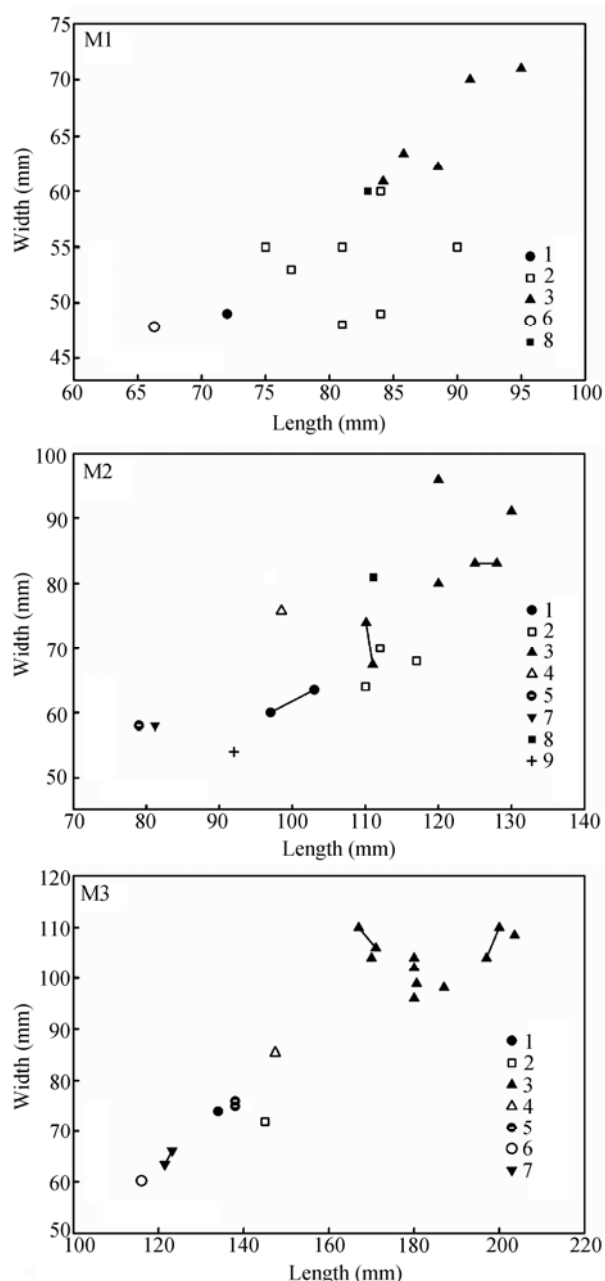Depéret (ref. [26], planche xix) described a fragmentary

Figure 7 Biviate plots of cheek teeth measurements of Choerolophodontinae (mm). Abbreviations: 1, *Choerolophodon guangheensis* sp. nov.; 2, *Ch. pentelici*, data from ref. [11]; 3, *Ch. corrugatus*, data from reference [15]; 4, *Ch. ngorora*, data from ref. [24]; 5, *Ch. zaltaniensis*, data from ref. [12]; 6, *Ch. pypmaeus*, data from ref. [13]; 7, *Afrochoerodon kisumuensis*, data from ref. [19]; 8, *Af. chioticus*, data from ref. [18]; 9, *Ch. palaeindicus*, data from ref. [25]; Paired data points connected by lines represent the same individuals.

gomphotheriid m3 from Kabylie, Algeria. This specimen, named *Mastodon angustidens pygmaeus*, retains three rear lophs with thicker cement. For a long time, there have been different opinions on where to place this isolated specimen phylogenetically. Pickford (ref. [13], plates 1 and 2) described the fossil gomphothere from Member A (the bottom member, middle Miocene, approximately 13 Ma) of the

Ngorora Formation, including upper and lower dentitions, fragmentary incisors and a partial skeleton. Pickford believed that the m3 of these materials is very similar to the m3 described by Depéret (1897) and that these materials are referable to *Choerolophodon*. As a result, he assigned these materials to *Ch. pygmaeus*. This species was also found in South Africa and Namibia [14]. *Ch. pygmaeus* is a dwarf choerolophodont with smaller dental sizes than those of the Dalanggou specimen (Figure 7). *Ch. pygmaeus* shows the following more-derived characters relative to the Dalanggou specimen: the 4th loph of M3 is well developed and followed by a talon; the lophs are somewhat compressed antero-posteriorly with wider interlophs; the cement is well developed.

Gaziry (ref. [12], figure 2) erected the species *Choerolophodon zaltaniensis* based on some cheek teeth and partial mandibles from the late Miocene of Jabal Zaltan, Libya. The M3 of this species is close to the Dalanggou specimen in size (Figure 7); however, it possesses a complete 4th loph, and well developed choerolophodonty and cement of the cheek teeth, characters that are similar to *Ch. pygmaeus*. Pickford [13] presumed that *Ch. zaltaniensis* is a junior synonym of *Ch. pygmaeus* and the size differences of those two are merely caused by sexual dimorphism, but there is no sufficient evidence to support his hypothesis. Regardless, *Ch. zaltaniensis* shows more evolved dental characters than the Dalanggou specimen.

Pickford (ref. [19], plates i–iii) established the new genus *Afrochoerodon* based on the specimens from the middle Miocene Muruyur Formation of Cheparawa, Kenya. He considered these materials very closely related to *Choerolophodon kisumuensis* and reassigned *Ch. kisumuensis* as the genotype of *Af. kisumuensis*. He also reassigned *Ch. chioticus* Tobien, 1980 of Chios, Greece, to this new genus [13, 19]. Pickford considered *Afrochoerodon* as closely related but distinct from *Choerolophodon*, based on the presence of a sharply declined face, closely converged temporal lines, a high and short neurocranium, redressed basicranium, and lateral positions of the pretrite in m3. The weakly developed choerolophodonty and tooth cement, and the remainders of enamel on the tusks indicate that *Afrochoerodon* is more primitive than *Choerolophodon*.

The Dalanggou specimen shares many primitive characters with *Afrochoerodon kisumuensis*. The cement is also poorly developed and the cusps on the lophs of the cheek teeth are relatively blunt and rounded. However, the Dalanggou specimen differs from *Af. kisumuensis* in having a lower and longer cranium, a longer distance between two temporal lines on the dorsal table of neurocranium, a relatively lower face, and more horizontal incisive alveoli. Even the dental size is slightly greater (Figure 7). Similar differences could also be observed in *Af. chioticus* (ref. [18], figure 18.2), but the dental size of *Af. chioticus* is larger than that of the Dalanggou specimen (Figure 7). Because above differences (except dental size) are synapomorphies of

Choerolophodon that are distinct from *Afrochoerodon*, the specimen from Dalanggou is more likely referable to the genus *Choerolophodon* than to *Afrochoerodon*.

The only known materials of early Miocene *Choerolophodon palaeindicus* from Dera Bugti, Pakistan, are isolated teeth: an m3 and a fully worn M2 (ref. [25], page 268, figure 211). The size of the M2 is close to that of the Dalanggou specimen (Figure 7). The m3 of *Ch. palaeindicus* is obviously a choerolophodont but has weakly developed enamel folds and cement, suggesting some similarities with the Dalanggou specimen (although unable to compare the two directly). Sanders and Miller [20] considered that these specimens should probably be referred to *Afrochoerodon* because the simple dental structure is comparable to that of *Af. kisumuensis*. However, *Ch. palaeindicus* was based on very limited material with very obscure properties. It can only be suggested that the Dalanggou specimen is possibly related to *Ch. palaeindicus*.

For the establishment of *Choerolophodon pygmaeus*, Pickford [13] considered that *Choerolophodon* possibly originated in the middle Miocene of Africa, and migrated to Eurasia by the late Miocene. He assigned *Choerolophodon pygmaeus* to *Choerolophodon* based on following dentition characters: well-developed choerolophodonty, ptychodonty and cement. However, these characters are probably the synapomorphies in the late members of Choerolophodontinae; while the cranial characters, which provide more important differential diagnoses of the two genera, have not been known. Pickford did not mention the *Ch. palaeindicus* in southern Asia when discussing the migration of *Choerolophodon* from Africa to Eurasia in the late Miocene; he probably considered *Ch. palaeindicus* as an afrochoerodont. However, the low and elongated skull of the Dalanggou specimen is significantly different from that of *Afrochoerodon kisumuensis*. Although we could not get an direct date for the Dalanggou locality, our estimation suggests it is no younger than 16 Ma. This date is older than the localities of *Ch. pygmaeus*. Therefore, the discovery of the Dalanggou specimen is not consistent with Pickford's hypothesis about the origin and migration of *Choerolophodon*. If it is reliable to assign the Dalanggou specimen to *Choerolophodon*, this species may be closer to the ancestral form of the genus. Thus, the first appearance datum of *Choerolophodon* should be advanced at least to the early Miocene although the origin of the clade is still a mystery, whether it was in Africa or Eurasia.

3 Conclusions

The fossil *Choerolophodon guangheensis* sp. nov. from the Dalanggou quarry was excavated from the early Miocene Shangzhuang Formation. The age is far older than the Member A of the Ngorora Formation in Africa, which yielded *Ch. pygmaeus* (middle Miocene locality [13]). In agreement with their stratigraphic age, *Ch. guangheensis* sp. nov. displays some primitive characters, such as laterally expanded zygomatic arches, anteriorly-positioned orbits, retention of P4, and weakly-developed cement on the cheek teeth. The discovery of the Dalanggou specimen provides strong evidence that choerolophodonts were already well-established in the northern China by the early Miocene. As a result, the discovery of the new Dalanggou specimen is not only an important record of fossil gomphotheres in the early Miocene China, but also important in studying the origin and evolution of the genus *Choerolophodon* and adaptive radiations of gomphotheres in Eurasia. Furthermore, *Choerolophodon* has been considered an amphibious or semi-amphibious animal, especially the species *Ch. pentelici,* because of its flattened skull and high positions of the orbits [14]. The Dalanggou specimen also possesses a flattened skull (but the orbits have lower positions). This suggests that the living habit of *Ch. guangheensis* sp. nov. may also have had an aquatic component. Deng [27] also chronicled the presence of the symbiotic *Aprotodon* sp., which has been considered an amphibious mammal similar to the living hippopotamus [27, 28]. This suggests that at that time, the climate of Dalanggou was fairly humid with a large aquatic environmental component. This is helpful to reconstruct the paleoenvironment of the early Miocene Linxia Basin.

1   Shoshani J, Tassy P. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. Quat Int, 2005, 126-128: 5–20

2   Tobien H. On the evolution of mastodonts (Proboscidea, Mammalia). Part 1: The bunodont trilophodont groups. Notizbl Hess L-Amt Bodenforsch, 1973, 101: 202–276

3   Tassy P. The earliest gomphotheres. In: Shoshani J, Tassy P, eds. The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives. Oxford, New York, Tokyo: Oxford University Press, 1996. 89–91

4   Lambert W D. The biogeography of the gomphotheriid proboscideans of North America. In: Shoshani J, Tassy P, eds. The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives. Oxford, New York, Tokyo: Oxford University Press, 1996. 143–148

5   Wang B Y, Qiu Z X. A new species of *Platybelodon* (Gomphotheriidae, Proboscidea, Mammalia) from early Miocene of the Danghe area, Gansu, China (in Chinese with English summary). Vert PalAsiat,

2002, 40: 291–299

6   Wang B Y, Qiu Z X, Wang X M, et al. Cenozoic stratigraphy in Danghe area, Gansu Province, and uplift of Tibetan Plateau (in Chinese with English summary). Vert PalAsiat, 2003, 41: 66–75

7   Tobien H, Chen G F, Li Y Q. Mastodonts (Proboscidea, Mammalia) from the late Neogene and early Pleistocene of the People's Republic of China. Part I: Historical account: The genera *Gomphotherium*, *Choerolophodon*, *Synconolophus*, *Amebelodon*, *Platybelodon*, *Sinomastodon*. Mainz Geowiss Mitt, 1986, 15: 119–181

8   Tassy P. Les Elephantoidea Miocènes du Plateau du Potwar, Groups de Siwalik, Pakistan. I^re partie: cadre chronologique et géographique, mammutidés, amébélodontidés. Ann Paléontol, 1983, 69: 99–136

9   Tassy P, Pickford M. Un nouveau mastodonte zygolophodonte (Proboscidea, Mammalia) dans le Miocène Inférieur d'Afrique orientale: systématique et paléoenvironnement. Géobios, 1983, 16: 53–77

10   Schlesinger G. Die mastodonten des K. K. naturhistorischen Hofmuseums. Denkschr K K Naturhist Hofm, Geol-paläont, 1917, 1: 181–222

11   Gaziry A W. Jungtertiäre mastodonten aus Anatolien (Türkei). Geol Jb, 1976, B22: 3–143

12   Gaziry A W. New mammals from the Jabal Zaltan site, Libya. Senckenb Leth, 1987, 68: 69–89

13   Pickford M. Partial dentition and skeleton of *Choerolophodon pygmaeus* (Depéret) from Ngenyin, 13 Ma, Tugen Hills, Kenya: Resolution of a century old enigma. Zona Arqueologica: Miscelànea en Homenaje a Emiliano Aguirre, Paleontologia, 2004, 4: 428–463

14   Pickford M. *Choerolophodon pygmaeus* (Proboscidea Mammalia) from the middle Miocene of southern Africa. S Afr J Sci, 2005, 101: 175–177

15   Tassy P. Les Elephantoidea Miocènes du Plateau du Potwar, Groups de Siwalik, Pakistan. IIe partie: Choerolophodontes et gomphothères. Ann Paléontol, 1983, 69: 235–297

16   Tassy P. Nouveaux Elephantoidea (Proboscidea, Mammalia) dans le Miocène du Kenya: Essai de réévaluation systématique. Paris: Cahiers de Paléontologie. E'ditions du Centre National de la Recherche Scientifique, 1986. 56, 65–79

17   Tassy P. Proboscideans (Mammalia) from the late Miocene of Akkaşdağ, Turkey. Geodiversitas, 2005, 27: 707–714

18   Tobien H. A note on the skull and mandible of a new choerolophodont mastodont (Proboscidea, Mammalia) from the middle Miocene of Chios (Aegean Sea, Greece). In: Jacobs L, ed. Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert. Flagstaff: Museum of Arizona Press, 1980. 299–307

19   Pickford M. *Afrochoerodon* nov. gen. *kisumuensis* (MacInnes) (Proboscidea, Mammalia) from Cheparawa, middle Miocene, Kenya. Ann Paléontol, 2001, 87: 99–117

20   Sanders W J, Miller E R. New proboscideans from the early Miocene of Wadi Moghara, Egypt. J Vert Paleontol, 2002, 22: 388–404

21   Zhou M Z, Zhang Y P. Chinese Fossil Elephantoids (in Chinese). Beijing: Science Press, 1974. 31–32

22   Tassy P. Who is who among the Proboscidea. In: Shoshani J, Tassy P, eds. Evolution and Palaeoecology of Elephants and Their Relatives. Oxford, New York, Tokyo: Oxford University Press, 1996. 39–48

23   Chen G F. *Sinomastodon* Tobien et al., 1986 (Proboscidea, Mammalia) from the Pliocene and early-middle Pleistocene of China (in Chinese with English summary). In: Wang Y Q, Deng T, eds. Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology. Beijing: China Ocean Press, 1999. 179–187

24   Maglio V J. A new proboscidean from the late Miocene of Kenya. Palaeontology, 1974, 17: 699–705

25   Osborn H F. Proboscidea: A monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. Volume I: Moeritherioidea, Deinotherioidea, and Mastodontoidea. New York: The American Museum Press, 1936. 268

26   Depéret C. Découverte du *Mastodon angustidens* dans l'étage cartennein de Kabylie. Bull Soc géol Fr, 1897, 3: 518–521

27   Deng T. Neogene rhinoceroses of the Linxia Basin (Gansu, China). Cour Forsch-Inst Senckenberg, 2006, 256: 43–56

28   Deng T. Evolution of the late Cenozoic mammalian faunas in the Linxia Basin and its background relevant to the uplift of the Qinghai-Xizang Plateau (in Chinese with English abstract). Quat Sci, 2004, 24: 413–420