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# The first cranium of *Postschizotherium* (Pliohyracidae, Hyracoidea) from the Lower Pleistocene of China

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**Abstract**

Pliohyracidae, a group of large-bodied hyracoids, successfully colonised Eurasia during the late Cenozoic. However, their cranial morphology has remained poorly understood due to the scarcity of complete specimens in East Asia, particularly for *Postschizotherium*. This study presents the first nearly complete cranium of *Postschizotherium* cf. *intermedium* from the Early Pleistocene Longdan locality in Gansu Province, China. The cranium exhibits several distinctive features, including an exceptionally laterally projecting orbit, a massive maxillary sinus that significantly invades the orbital fossa, and a highly developed pre-orbital fossa system. These morphological traits, especially the first one, suggest that *Postschizotherium* is closely related to *Pliohyrax* and *Kvabebihyrax*, both being large pliohyracids from the upper Cenozoic of East Europe and West Asia. The morphology also suggests that *Postschizotherium* likely occupied semi-aquatic habitats, similar to those of extant hippos, with a diet primarily consisting of grasses. The discovery of this species at Longdan also provides evidence for a relatively humid palaeoenvironment in the region during the earliest Pleistocene, contributing to our understanding of the palaeoenvironmental conditions and evolutionary history of pliohyracids in Eurasia.


*Keywords:* *Postschizotherium*; Early Pleistocene; Longdan; Pliohyracidae; palaeoenvironments

## 1. Introduction

Living hyraxes, small herbivores comparable in size to hares, currently occur only in Afro-Arabia. This group comprises six species in three genera (Hoeck, 2011; Oates et al., 2022). The fossil record reveals that hyracoids were previously highly diverse, particularly during the Paleogene in Africa (Rasmussen and Gutiérrez, 2010). Their body sizes varied from small to large, and their cheek tooth morphology ranged from bunodont, bunoselenodont, to lophodont (Rasmussen and Simons, 1988; Pickford et al., 1997; Rasmussen and Gutiérrez, 2010). During the Paleogene, hyracoids occupied a wide array of ecological niches similar to those of perissodactyls and artiodactyls of Laurasia. The diversity of African hyracoids included four families and over 30 species (Rasmussen and Gutiérrez, 2010). However, this rich diversity began to decline following the closure of the Tethys Sea in the Early Miocene. The arrival of true ungulates in Africa led to increased

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competition, causing many hyracoid species to decline (Sun et al., 2023). Today, only the family Procaviidae Thomas, 1892 survives, often inhabiting marginal ecological areas (Hoeck, 2011). Interestingly, during the Middle to Late Miocene, a group of hyracoids, the Pliohyracidae Osborn, 1899, evolved into larger forms and successfully invaded Eurasia (Fig. 1), including *Kvabebihyrax* Gabunia and Vekua, 1966, *Sogdohyrax* Dubrovo, 1978, *Pliohyrax* Osborn, 1899, *Hengduanshanhyrax* Chen, 2003, and *Postschizotherium* von Koenigswald, 1932, encompassing nearly ten species (Pickford and Fischer, 1987, Pickford et al., 2021). Although not very diverse and in a relatively low abundance, pliohyracids successfully thrived across mid-latitude Eurasia, from the Middle Miocene to the Middle Pleistocene (Pickford et al., 1997; Heissig, 1999; Qiu et al., 2002). It is hypothesised that these animals occupied semi-aquatic niches, much like modern hippos (Vekua, 1972; Gabunia and Vekua, 1974; Heissig, 1999).

*Postschizotherium*, the largest and most recent genus among the pliohyracids, was previously known only from China (Teilhard de Chardin and Licent, 1936; Teilhard de Chardin, 1939; Qiu, 1981; Qiu et al., 2002) (Fig. 1). However, recent discoveries have extended its range to the Baikal region of Russia (Kalmykov, 2013) (Fig. 1). Currently, it is documented from the Pliocene and Pleistocene epochs, but preliminary evidence from China suggests it may have a longer evolutionary history than previously thought (unpublished material). Initially, *Postschizotherium* von Koenigswald was misclassified as a chalicotheriid, as the generic name implies (*Schizotherium* Gervais, 1876, belonging to Chalicotheriidae Gill, 1872), based on some isolated teeth (Teilhard de Chardin and Licent, 1936). However, more comprehensive material, including upper and lower jaws, has confirmed its classification within Hyracoidea Huxley, 1869 rather than Chalicotheriidae (Tong and Huang, 1974; Qiu, 1981). Key diagnostic features supporting attribution to Pliohyracidae include a complete tooth formula with premolar-like canines, as well as tusk-like incisors (I1, i1, and i2). Some pliohyracid genera, such as *Pliohyrax* and *Kvabebihyrax*, known from relatively complete skulls, exhibit highly specialised cranial morphologies (Forsyth Major, 1899; Vekua, 1972; Pickford et al., 2021). This raises intriguing questions about whether *Postschizotherium* also possessed a specialised cranium. Until now, this has remained a long-standing mystery, which the current report aims to address by presenting the first nearly complete cranium of *Postschizotherium* cf. *intermedium* von Koenigswald, 1932 from the Longdan locality.

The Longdan site, located on the northeastern edge of the Tibetan Plateau in Dongxiang Nationality Autonomous County, Gansu Province (Fig. 1), is famous in palaeomammalogy for yielding the earliest Pleistocene fauna from the Wucheng loess, dated to approximately 2.6–2.0 Ma (Qiu et al., 2004). Qiu et al. (2004) published a detailed monograph on this significant locality, covering comprehensive geological backgrounds that we will not reiterate here. In recent years, ongoing excavations at

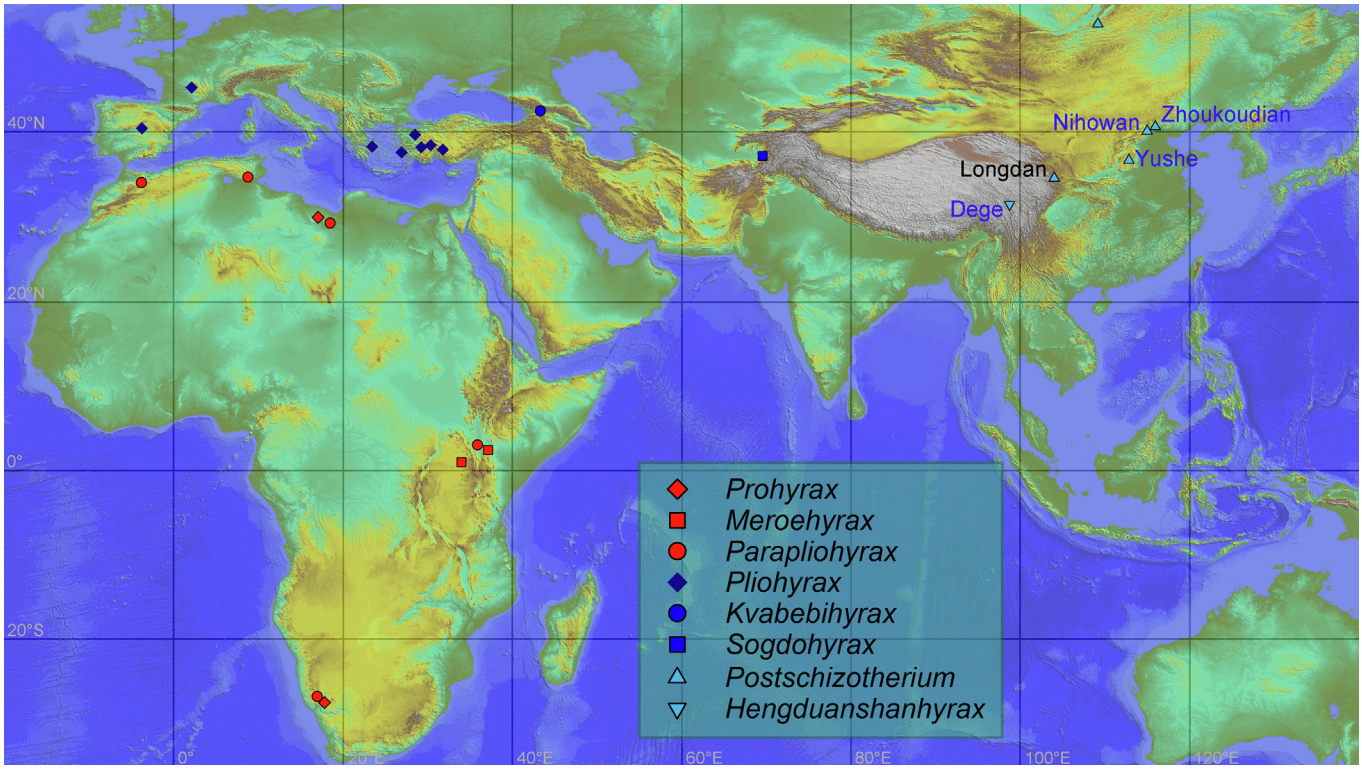



Fig. 1. Map showing the distribution of genera of Pliohyracidae.

Longdan have revealed an increasing number of taxa, including some unexpected forms. Among these is *Postschizotherium* cf. *intermedium*, which we describe in detail herein.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NMB, Naturhistorisches Museum Basel; THP, Tianjin Natural History Museum; TYFT, Chongzhou Tianyan Museum, Chengdu, China.

## 2. Material and methods

The described cranium is housed in the TYFT, and the comparative materials are housed in the IVPP and THP.

The terminology of hyracoid teeth follows Rasmussen and Simons (1988) and some terms to describe perissodactyl teeth were also adopted (Qiu and Wang, 2007) (Fig. 2). The terminology of cranial anatomy follows Pickford et al. (1997), Rasmussen and Gutiérrez (2010), and Pickford et al. (2021). Measurements were taken with Vernier calipers with a precision of 0.1 mm. 3D surface scanning was done using an Artec Spider handheld scanner, providing high-resolution images that highlight intricate morphological details.

## 3. Systematic palaeontology

Order Hyracoidea Huxley, 1869
Family Pliohyracidae Osborn, 1899

Genus *Postschizotherium* von Koenigswald, 1932
**Type species:** *Po. chardini* von Koenigswald, 1932.
**Included species:** *Po. intermedium* von Koenigswald, 1966.
**Amended diagnosis:** Medium-sized to large pliohyracids; orbit cylindrical, protruding strongly laterally and slightly rostrally, elevated above the top of the cranium; braincase short with moderately developed sagittal crest; zygomatic arch laterally expanded; choanae rostrally aligned with the distal tooth row; facial part with complete pre-orbital fossa system; nasal bones potentially retracted; rostrum slightly widened; maxillary sinus (or palatine pocket) extremely developed, caudally compressing the orbital fossa; mandibles lacking internal chamber, only with a shallow inframedial fossa. Complete dental formula with tusk-like I1, i1 and i2; diastemata present between the incisors, incisors single rooted, poorly premolarised; canine premolarised, P4 molarised, premolars tending to become smaller, upper molars moderately to highly unilaterally hypsodont, m3 possessing a well-developed third lobe.
**Differential diagnosis:** Differs from all genera (if cranium available) in the presence of a huge maxillary sinus, and from all genera except for *Pliohyrax graecus* (Gaudry, 1860) in the more laterally projecting orbit (status unknown in *Sogdohyrax* and *Hengduanshanhyrax*), and greater degeneration of premolars; differs from *Sogdohyrax*, *Kvabebihyrax*, *Pliohyrax*, *Prohyrax* Stromer, 1922, and *Meroehyrax* Whitworth, 1954 in the presence of a diastema between I2 and I3; differs from *Hengduanshanhyrax* by its greater dimensions and the absence of I3–Canine diastema; differs from *Parapliohyrax* Lavocat, 1961, *Prohyrax*, and *Meroehyrax* by its larger dimensions and tooth hypsodonty; differs from *Sogdohyrax*, *Kvabebihyrax* and *Pliohyrax* by the slightly widened rostrum; differs from *Kvabebihyrax* and *Pliohyrax* by the presence of complete pre-orbital fossa system with a large, rostrocaudally elongated nasomaxillary foramen; differs from *Kvabebihyrax* by the anteriorly positioned choanae; differs from *Parapliohyrax* by the absence of an internal mandibular chamber.

*Postschizotherium* cf. *intermedium* von Koenigswald, 1966 (Figs. 3, 4; Tables 1, 2)

**Amended diagnosis:** Small *Postschizotherium* with moderate unilateral hypsodonty; sexual dimorphism prominent.
**Differential diagnosis:** Differs from *Po. chardini* by its smaller dimensions, less-developed unilateral hypsodonty, weak cementum, less molarised P4, larger premolars; and lower mandibular symphysis.
**Type specimen:** IVPP RV 33001 (THP 14293), a middle portion of an upper jaw carrying P4–M3, and an associated rostral portion of mandible (Qiu et al., 2002).
**Type locality and horizon:** Qingyangping (46 Locality), Yushe region, from the Lower Pleistocene Haiyan Formation (Qiu et al., 2002).
**Specimen attributed in the present article:** TYFT030, a nearly complete female cranium, from the Longdan locality (2.6–2.0 Ma) of the Early Pleistocene, Gansu Province, China. The presence of DP4 and incompletely erupted M3 indicate a sub-adult status for this individual.
**Age and geographic distribution:** Late Pliocene to early Early Pleistocene, from Mazegouan to the early Nihewanian, approximately 3.6–1.8 Ma; ranging from northern China (Yushe and Tianzheng, Shanxi Province, Nihewan, Hebei Province, and Longdan, Gansu Province).

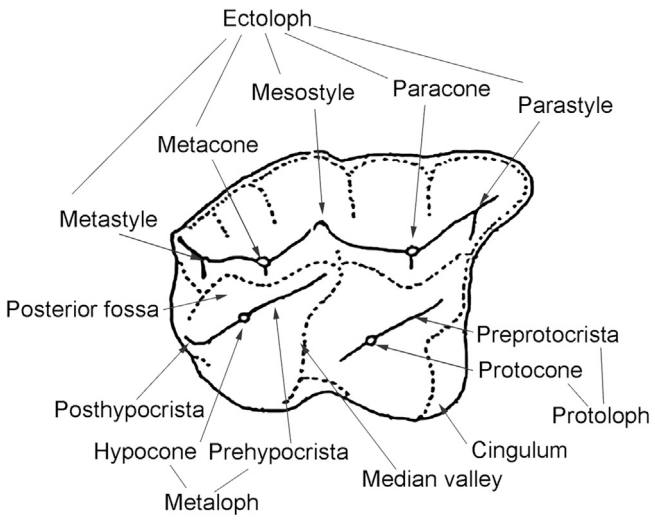
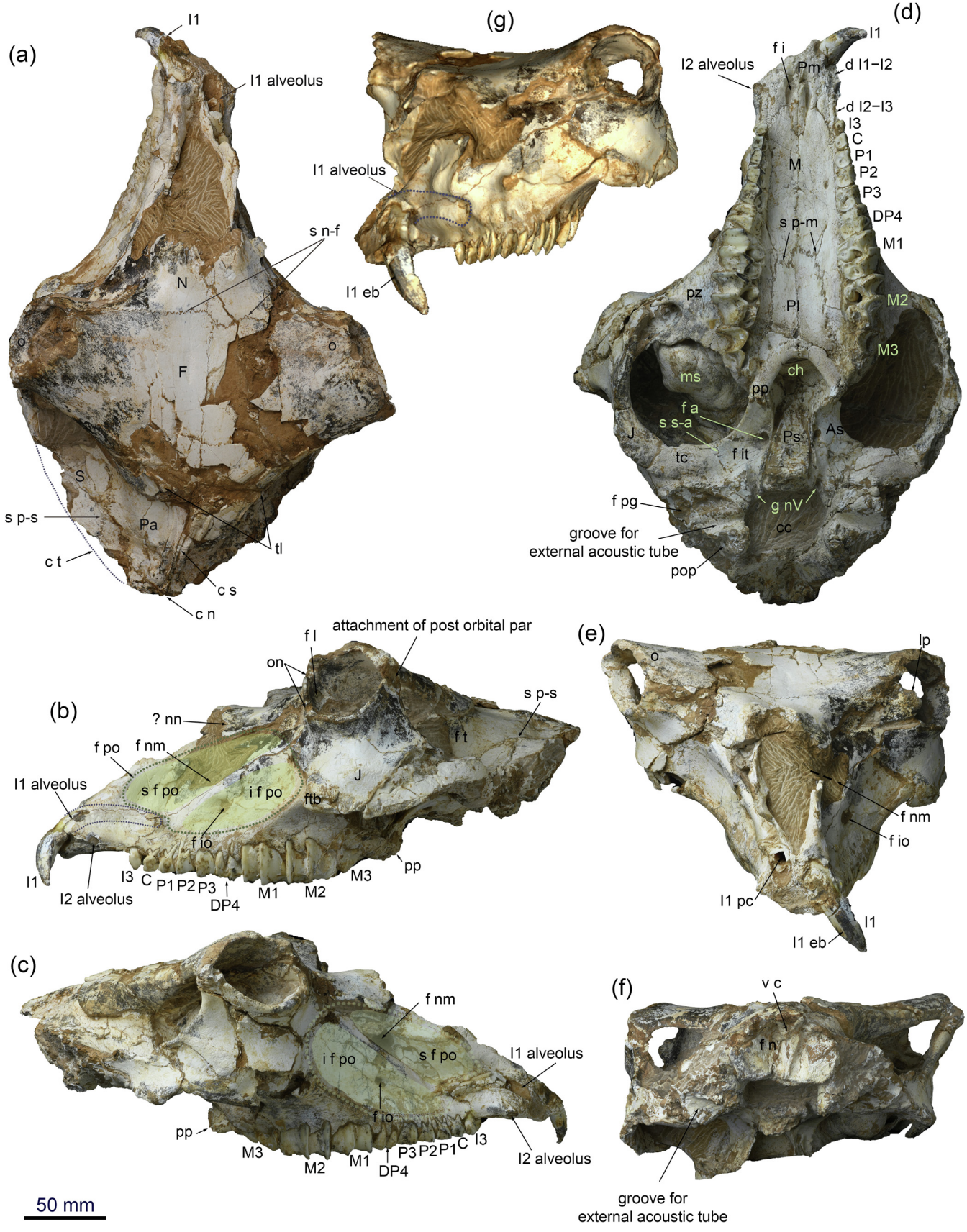



Fig. 2. Nomenclature of hyracoid right upper cheek teeth, modified from Rasmussen and Simons (1988) (not to scale).


(a)
I1
I1 alveolus
s n-f
N
o
o
F
S
s p-s
Pa
t l
c t
c s
c n
(g)
I1 alveolus
I1 eb
(d)
I1
f i
I2 alveolus
Pm
d I1–I2
d I2–I3
I3
C
P1
P2
P3
DP4
M1
M
s p-m
M2
M3
pz
Pl
ms
ch
pp
f a
s s-a
J
Ps
As
tc
f it
f pg
g nV
groove for
external acoustic tube
cc
pop
(b)
attachment of post orbital par
f l
on
s p-s
? nn
f t
f po
f nm
J
I1 alveolus
s f po
i f po
ftb
f io
pp
I1
I3
C
P1
P2
P3
M1
M2
M3
I2 alveolus
DP4
(e)
o
lp
f nm
f io
I1 pc
I1
I1 eb
(c)
f nm
i f po
s f po
I1 alveolus
f io
pp
M3
M2
M1
P3
P2
P1
C
I3
I2 alveolus
(f)
v c
f n
groove for
external acoustic tube
50 mm

**Description of TYFT030:** Cranium (Fig. 3): Most of the cranium is in good condition, with only the basioccipital and petrosal bones missing. The distal portion of the nasal bones and the surrounding areas have sustained damage. Due to dorsoventral compression, the entire cranium is slightly tilted to the right side.

In dorsal view (Fig. 3a), the cranium exhibits a lozenge shape with strong laterally protruded orbits in the middle. The rostrum is characterised by its narrowness and significant forward protrusion. Unfortunately, most of the distal portion of the nasal bones is fractured, making it impossible to determine their exact length. The sutures connecting the nasal and frontal bones are nearly straight, running perpendicular to the cranial sagittal axis, and aligned with the anterior margin of the orbits. The frontal surface of the skull is notably broad and displays a slight concavity. The orbits are prominently laterally extended, featuring a rough lateral edge (Fig. 3e, g). The area of the calvarium posterior to the orbits tapers markedly, resulting in a narrow and short braincase. It should be noted that the sutures between the frontal and parietal bones are damaged. The temporal lines on the skull converge significantly along the midline of the braincase, giving rise to a pronounced sagittal crest. In contrast, the nuchal crest appears relatively narrow, while the temporal crest is extensively flared, extending to connect with the zygomatic arch.

In lateral view (Fig. 3b, c), the cranium displays a posteriorly inclined lozenge shape. The orbit is positioned at the midline of the skull, occupying the highest point. It is characterised by its circular form and a thick, coarse orbital margin. Notably, two deep notches are present on the anterior edge, resulting in a prominent lachrymal process. A round lachrymal foramen can be found on the inner wall of this process. The post-orbital bar of the frontal bone meets the dorsal process of the jugal bone, but they do not fully fuse. Beneath the orbit, the zygomatic arch is high, featuring a pronounced facial tuberosity. Posterior to the orbit, the jugal bone descends steeply. The temporal fossa is elongated with an oval outline, and the parietal-squamosal suture runs through its center. Although the lateral edge of the temporal region is damaged, a deep notch hosting the external acoustic tube can still be observed.

Several fractures caused by compression are evident in the bones of the facial part, making it difficult to distinguish the sutures between the lachrymal, jugal, and maxillary bones. Nevertheless, the face exhibits considerable depth, primarily occupied by a large pre-orbital fossa. This fossa extends from the anterior border of the facial tuberosity and terminates rostrally at the level of the I3. Its ventral border closely follows the tooth row, while the dorsal border reaches the fissure between the nasal and premaxillary bones. A blunt ridge subdivides the pre-orbital fossa into two parts: a narrow dorsal portion is termed the superior pre-orbital fossa and a broader ventral section referred to as the inferior pre-orbital fossa. It appears that the superior pre-orbital fossa may communicate with the nasal cavity by a large, rostrally elongated nasomaxillary foramen (Pickford, 1994), although this area is poorly preserved. In contrast, the infraorbital foramen, which is circular in shape, is clearly visible at the center of the inferior pre-orbital fossa, aligning with the DP4. The premaxillary and maxillary sutures originate from the root of the I3 and extend dorsally through the superior pre-orbital fossa. The rostrum, composed of the premaxilla, houses the upper tusk (I1), which horizontally traverses the rostrum before bending ventrally when emerging from the alveolus. A shallow depression exists between the tusk socket and the interalveolar crest. The nasal notch was possibly caudally retreated as in *K. kachethicus* Vekua, 1972.

In ventral view (Fig. 3d), the cranium is likewise lozenge shaped. As previously mentioned, the basioccipital and petrosal bones are not preserved. The supraoccipital bone exhibits a strong caudal extension, housing a large fossa for the nuchal ligament. A prominent vertical nuchal crest divides this fossa along its midline (Fig. 3e). The cranial cavity appears small and is hexagonal in outline (Fig. 3d). The paroccipital process is robust and triangular when viewed from below. A deep groove, accommodating the external acoustic tube, runs obliquely across the rostral border of the paroccipital process. A triangular region, situated between this groove and the glenoid area, is identified as the post-glenoid fossa, which communicates with the temporal canal. The temporal condyle of the glenoid is slightly ventrally elevated, adjacent to a shallow infra-temporal fossa on its medial side. The squamosal-alisphenoid suture extends anteroposteriorly through the infra-temporal fossa. The alisphenoid bone is relatively narrow, bordered by a sharp alisphenoid crest. A narrow groove, located at the mediocaudal corner of the alisphenoid, represents the channel that houses the mandibular

Fig. 3. Cranium of *Postschizotherium* cf. *intermedium*, TYFT030, from Longdan, lowest Pleistocene. (a) Dorsal view. (b) Left lateral view. (c) Right lateral view. (d) Ventral view. (e) Rostral view. (f) Caudal view. (g) Rostrolateral view. Abbreviations: As, alisphenoid; C, canine; cc, cranial cavity; c f, facial crest; ch, choanae; c n, nuchal crest; c p, pterygoid crest; c t, temporal crest; d I1–I2, diastema between I1 and I2; d I2–I3, diastema between I2 and I3; DP4, 4$^{th}$ upper deciduous molar; eb, enamel band; f i, incisive fossa; i f po, inferior pre-orbital fossa; f a, alar foramen; f io, infraorbital foramen; f it, infra-temporal fossa; f l, lacrimal foramen; f n, nuchal fossa; f nm, nasomaxillary foramen, the dashed line representing the communication to the nasal cavity; f po; pre-orbital fossa; f pg, post-glenoid fossa; f p m, foramen of post-maxillary canal; f p p, post palatine foramen; f t, temporal foramen; ftb facial tuberosity; g nV, groove for nerves V; I1–3, 1$^{st}$–3$^{rd}$ upper incisors; J, jugular; lp, lacrimal process; M, maxilla; M1–3, 1$^{st}$–3$^{rd}$ upper molars; ms, maxillary sinus; N, nasal; o, orbit; on, orbital notch; nn nasal notch; P1–3, 1$^{st}$–3$^{rd}$ upper premolars; Pa, parietal; pc, pulp cavity; Pl, palatine; Pm premaxilla; Ps, presphenoid; pp, pterygoid process; pop, paroccipital process; S, squamosal; s f po, superior pre-orbital fossa; s n-f, suture between nasial and frontal; s p-m, suture between the palatine and maxilla; s p-s, suture between the parietal and squamosal; s s-a, suture between the squamosal and alisphenoid; pz, zygomatic process; tc, temporal condyle; tl, temporal line; v c, vertical nuchal crest.

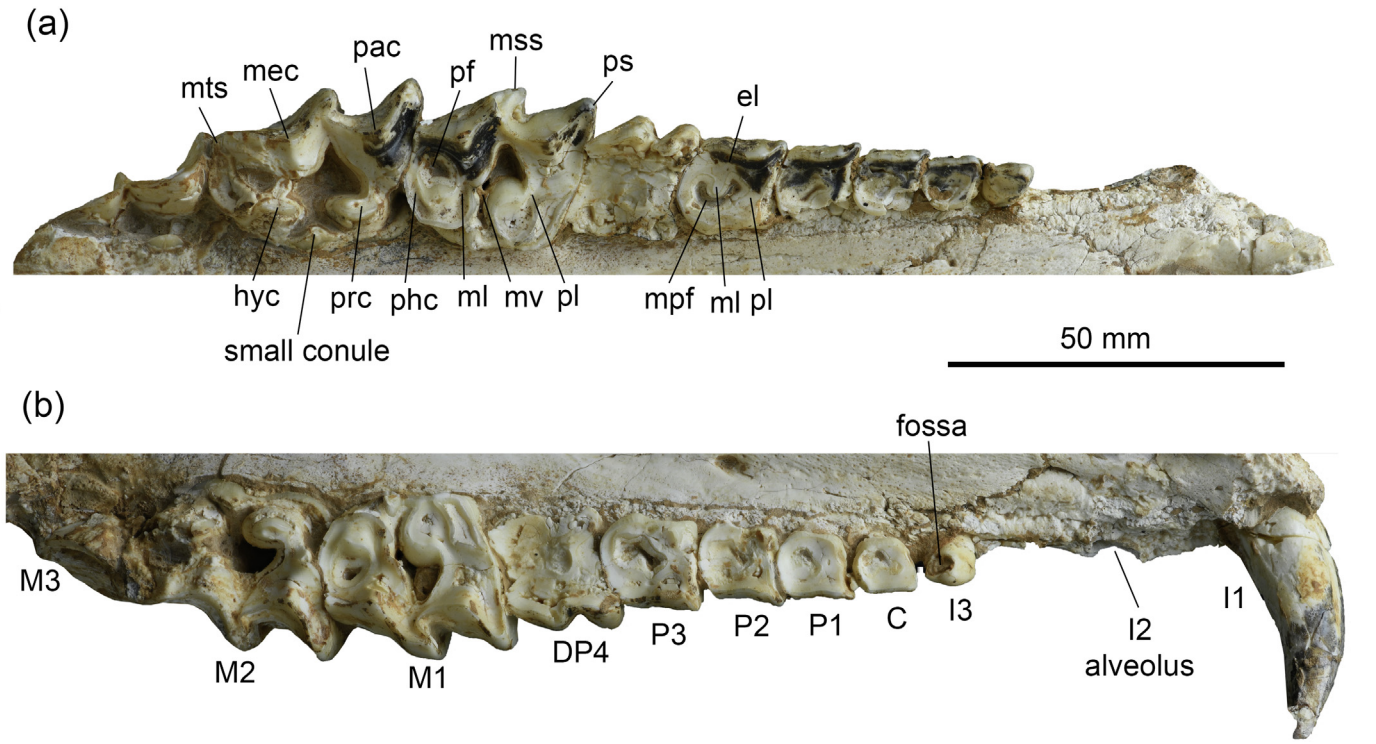



Fig. 4. Upper teeth of *Postschizotherium* cf. *intermedium*, TYFT030, from Longdan, earliest Pleistocene, in occlusal view. (a) Right tooth row. (b) Left tooth row. Abbreviations: C, canine; DP4, 4th upper deciduous molar; el, ectoloph; hyc, hypocone; I1–3, 1st–3rd upper incisors; M1–3, 1st–3rd upper molars; mec, metacone; ml, metaloph; mpf, median-posterior fossa; mss, mesostyle; mts, metastyle; mv, median valley; P1–3, 1st–3rd upper premolars; pac, paracone; pf, posterior fossa; phc, posthypocrista; pl, protoloph; prc, protocone; ps, parastyle.

branch of the trigeminal nerve, connecting it to the cranial cavity. In the middle of the alisphenoid, close to the alisphenoid crest, lies a circular alar foramen. The thick pre-sphenoid bone compresses the medial wall of the alisphenoid crest, tapering rostrally and extending into the choanae.

The palate descends from the ventral surface of the infra-temporal region (i.e., the glenoid region's surface), leading to a prominent pterygoid process. The rostral border of the choanae is rounded, extending to the middle of the erupting M3. The palatine bone exhibits a significant forward protrusion, with its anterior border at the level of M1 being deeply indented. The palate itself is relatively narrow, slightly concave dorsally, and bordered laterally by the tooth rows. Nutrient foramina are present along the lateral margin of the palate. Anterior to the third incisor (I3), the rostrum displays slight lateral expansion. There are diastemata between I1 and I2 and between I2 and I3. The palatine fissure is well defined.

The zygomatic process of the maxillary bone is triangular and connects posteriorly to the robust jugal bone. This specimen presents an unusual feature: the maxillary sinus is highly developed, forming a huge, irregularly shaped bulge that extends posteriorly and occupies most of the anterior portion of the temporo-orbital fossa (ms in Fig. 3d). This structure is only preserved on the right side, while on the left side the bony surface is damaged. While an enlarged maxillary sinus is commonly observed in pliohyracids (Rasmussen and Gutiérrez, 2010), it appears that *Postschizotherium* uniquely possesses a maxillary sinus morphology that occupies a significant part of the temporo-orbital fossa.

Teeth (Fig. 4): *Postschizotherium* exhibits a complete dental formula (Qiu et al., 2002), consistent with primitive placental mammals. The right I1 and both of the I2s are broken. The M3 is in the process of erupting, while the DP4 remains.

The preserved left I1 has a tusk-like form (Fig. 4b). It is relatively slim, suggesting that it may represent a female individual. Approximately two-thirds of the tusk's length is embedded within the alveolus, beginning from the premaxillary-maxillary suture at the level of the boundary between the canine and the P1 (Fig. 3b, c, e). In lateral view, the tusk displays a pronounced ventral and posterior curvature, and it projects slightly laterally in rostral view. At the opening of the alveolus, the cross-section of the tusk is triangular, characterised by a long caudomedial edge and a blunt rostral angle. Apically, the tusk is sharpened due to wear. An enamel band is visible on the labial side of the tusk (I1 eb in Fig. 3e). The right I1 is damaged, with only one-third of its length remaining in the alveolus. This fragment shows an oval cross-section and a prominent pulp cavity (I1 pc in Fig. 3c).

The I2 is also broken but retains a single root (Fig. 4). The diastema between I1 and I2 measures 13.5 mm (left side), while that between I2 and I3 is longer, measuring 17 mm (left side).

Table 1
Cranial measurements (in mm) of *Postschizotherium* cf. *intermedium*, TYFT030.

| | |
|---|---|
| Maximal length (from rostral tip to nuchal crest) | 347.4 |
| Length of rostrum (anterior to the Cs) | 57.4 |
| Width of rostrum (anterior to I3s) | 47.5 |
| Width of rostrum (across I2s) | 51.8 |
| Length of palate (from choanae to rostral tip) | 191.5 |
| Inner palatal width (between the DP4s) | 49.6 |
| Outer palatal width (outside the DP4s) | 87.8 |
| Post-palatal width (posterior to the tooth rows) | 68.3 |
| Width across facial tuberosities | 190.7 |
| Width at the roots of nasal bones | 74.6 |
| Width across pre-orbits | 181.3 |
| Width across post-orbits | 227.2 |
| Width of the braincase | 74.8 |
| Width of the nuchal crest | 24.4 × 2 |
| Width across jugals | 210.3 |
| Length of the zygomatic process (from facial tuberosity to postglenoid process) | 112.9 |
| Height at the canines | 61.1 |
| Height anterior to the orbit | 96.4 |
| Height at the posterior end of the presphenoid | 90.3 |
| Diameter of the orbit | 49.9 |
| Height of the jugal under the orbit | 45.4 |

Table 2
Measurements (in mm) of upper teeth of *Postschizotherium* cf. *intermedium*, TYFT030. L, length; W, width; *, measured at the alveoli.

| Tooth | Measurement | Left | Right |
|---|---|---|---|
| I1 | L | 11.8 | – |
| | W | 13.6 | – |
| I2* | L | 7.0 | 6.9 |
| | W | 5.3 | 6.1 |
| I3 | L | 7.5 | 7.4 |
| | W | 5.7 | 5.4 |
| C | L | 8.0 | 9.1 |
| | W | 8.7 | 8.2 |
| P1 | L | 10.6 | 10.7 |
| | W | 10.0 | 9.7 |
| P2 | L | 11.7 | 10.9 |
| | W | 12.2 | 11.1 |
| P3 | L | 12.7 | 12.8 |
| | W | 13.0 | 13.8 |
| DP4 | L | 17.4 | 17.6 |
| | W | 19.4 | 18.9 |
| M1 | L | 27.6 | 27.2 |
| | W | 24.5 | 24.1 |
| M2 | L | 32.1 | 33.7 |
| | W | 25.2 | 24.7 |

The I3 has an olive-shaped profile in lateral view, with a sharp apex (Fig. 4). The distolingual surface features a shallow fossa that resembles the median fossa, indicating a nascent stage of premolar-like development.

The canine is in moderate wear, exhibiting a premolar-like form (Fig. 4), supported by three roots. Its occlusal surface is sub-square, with a flat buccal surface and a rounded distolingual angle. A shallow median-posterior fossa is located near the distolingual border. In lateral view, the occlusal edge appears straight, closely resembling the morphology of P1 through P3. There are no diastemata in front of and behind the canine.

The moderately worn P1–P3 exhibit identical morphology (Fig. 4). Each tooth has four roots and a crown with a taller buccal side compared to the lingual side. In occlusal view, these teeth have a relatively sharp mesiobuccal angle and a rounded distolingual angle. The buccal edge is almost straight due to the weakly undulating ectoloph. The lingual edge is weakly convex. The protoloph is thick and projects a thin wall distally that encloses the lingual and distal margins of the tooth, ultimately fusing with the distal end of the ectoloph to form a median-posterior fossa. The metaloph is weak and protrudes into the median-posterior fossa, compressing it into a crescent shape. In lateral view, the paracone shows a blunt angle, and the parastyle and metastyle ribs are weak (Fig. 3b, c).

The DP4 (Fig. 4) is deeply worn down to the roots but exhibits similar morphology to the molars, with a markedly undulating ectoloph: the parastyle and mesostyle project strongly mesiobuccally. The protoloph and metaloph may be connected distally due to deep wear. The length of the crown is approximately equal to its width.

The molars display moderate unilateral hypsodonty, resulting in a lingually curved shape. The M1 (Fig. 4) is moderately worn and has a sub-rectangular occlusal outline. The length is slightly greater than the width. The ectoloph is W-shaped with strongly projecting parastyle and mesostyle mesiobuccally. The metastyle is weak. The paracone is slightly larger than the metacone, both cusps being crescentoid in outline. The protocone is round and slightly compressed mesiodistally, with a thin protoloph (or preprotocrista) connecting to the paracone. The hypocone is smaller than the protocone, is slightly compressed buccolingually, and possesses a thin metaloph (or prehypocrista) linking to the metacone. The median transverse valley is deep, and the lingual opening is narrow where the proto-

cone and hypocone approach each other. The postfossa is enclosed by the posthypocrista running along the distal margin and fusing with the distal end of the metacone. Cingula are present along the mesial and lingual margins. A small conule is located at the opening of the median transverse valley, connected to the lingual cingulum. A small amount of cementum is present in the valleys/fossae. In lateral view, the paracone and metacone have blunt apices, and the parastyle and mesostyle ribs are prominent (Fig. 3b, c).

Morphologically, the M2 (Fig. 4) closely resembles the M1, except for its more elongate mesiodistal outline, more strongly buccolingually compressed protocone and hypocone, and thicker cementum layer. These differences appear to be due to the slighter wear. M3s are incompletely erupted, such that only parts of the ectoloph are visible.

## 4. Comparisons

While no hyracoid cranium had previously been discovered in China or East Asia, the newly found specimen clearly belongs to *Postschizotherium*, a well-documented East Asian pliohyracid from the Pliocene–Pleistocene (Teilhard de Chardin and Licent, 1936; Teilhard de Chardin, 1939; Qiu, 1981; Qiu et al., 2002; Pickford et al., 2021). This identification is based primarily on cheek tooth morphology. The specimen is relatively large, comparable to that of a female *Po. intermedium* from Tianzheng but smaller than *Po. chardini* (Qiu et al., 2002). Notably, the I3 has not undergone premolarisation, and diastemata are present between I1 and I2 and between I2 and I3. Additionally, cementum is evident, and the rostrum is widened. Consequently, the Longdan cranium is unequivocally identified as *Postschizotherium* at the genus level.

Almost all Eurasian fossil Hyracoidea belong to the Pliohyracidae, a lineage characterised by their larger dimensions and complete dental formula. Apart from *Postschizotherium*, four other genera of Pliohyracidae have been reported in late Cenozoic deposits of Eurasia: *Kvabebihyrax*, *Sogdohyrax*, *Pliohyrax* and *Hengduanshanhyrax* (Pickford et al., 2021). In China, only *Postschizotherium* and the two latter genera have been documented (Wang, 2023) (Fig. 1). However, recent discoveries have revealed the presence of a more diverse array of pliohyracids, spanning the early Late Miocene to the Middle Pleistocene (unpublished material).

The presence of *Prohyrax*, *Meroehyrax* and *Parapliohyrax* in the Lower and Middle Miocene of Africa (Fig. 1) suggests an African origin for the Pliohyracidae (Pickford and Fischer, 1987; Pickford, 2009; Rasmussen and Gutiérrez, 2010; Pickford et al., 2021), as for other lineages of Hyracoidea.

*Hengduanshanhyrax* comprises a single species, *H. tibetensis* (Zong, 1996), known from the latest Pliocene on the Tibetan Plateau (Dege County, Sichuan Province) (Fig. 1), currently represented only by an upper jaw (Chen, 2003). This genus is notably smaller than any other Eurasian species, being larger only than the primitive *Prohyrax* and *Parapliohyrax* (Fig. 5). The dental morphology of *Hengduanshanhyrax* closely resembles that of *Postschizotherium*, as initially noted. However, compared to the Longdan cranium, an additional diastema has developed between I3 and the canine (absent in *Postschizotherium*). The canine features a single root, while the P1 has three roots (in contrast to the two-rooted canine and four-rooted P1 in *Postschizotherium*). The premolars exhibit mesiodistal oblong contours (square outline in *Postschizotherium*).

*Sogdohyrax*, represented by its sole species *S. soricus* Dubrovo, 1978, was reported from the Pliocene of Tajikistan (Dubrovo, 1978) (Fig. 1). Like *H. tibetensis*, it is known only from an upper jaw. The species is large, comparable in dental dimensions to *Po. chardini* (Fig. 5). Diastemata are absent except between I1 and I2, while the I2 and I3 tend to be premolarised. The morphology is similar to *Pliohyrax* and different from *Postschizotherium*, including the Longdan cranium. Qiu et al. (2002) and Chen (2003) suggested classifying it in the latter genus. However, we retain it as a separate genus due to a distinct projection on the premaxilla followed by a deep notch (Dubrovo, 1978). This unique structure is not observed in *Pliohyrax*.

*Kvabebihyrax*, represented solely by the species *K. kachethicus*, was discovered in the Pliocene deposits of Georgia (Vekua, 1972) (Fig. 1). This genus is represented by well-preserved crania and mandibles, which provide a comprehensive understanding of the skull morphology of Pliohyracidae. The size of the smaller individual is comparable to that of the Longdan cranium (Fig. 5). Similar to *Pliohyrax*, *Kvabebihyrax* exhibits a diastema only between I1 and I2, with I2 and I3 showing premolarisation, distinguishing it from *Postschizotherium*. In dorsal view, the orbits of *K. kachethicus* project laterally but do not extend beyond the zygomatic processes, unlike the more pronounced lateral projection observed in the Longdan cranium. In lateral view, the facial region of *K. kachethicus* is higher, and the rostrum is shorter compared to the Longdan cranium. If present, the pre-orbital fossa in *K. kachethicus* is indistinct (based on observations by Pickford et al., 2021), and the nasomaxillary foramen is small and rounded, contrasting with the Longdan cranium, which features a prominent and enlarged nasomaxillary foramen within a well-developed pre-orbital fossa system. Additionally, the choanae in *K. kachethicus* are situated far caudal to the tooth row, as opposed to their closer proximity to the tooth row in *Postschizotherium*.

*Pliohyrax* is the most extensively studied genus within Pliohyracidae. The identification of *Pliohyrax orientalis* Tong and Huang, 1974, known from two isolated teeth found in a drug store of Shanxi, China, remains uncertain due to the limited taxonomic information provided by isolated teeth (Tong and Huang, 1974). Other species of *Pliohyrax* have been reported exclusively from Europe (Heissig, 1999; Pickford et al., 2021; Koufos, 2022). There

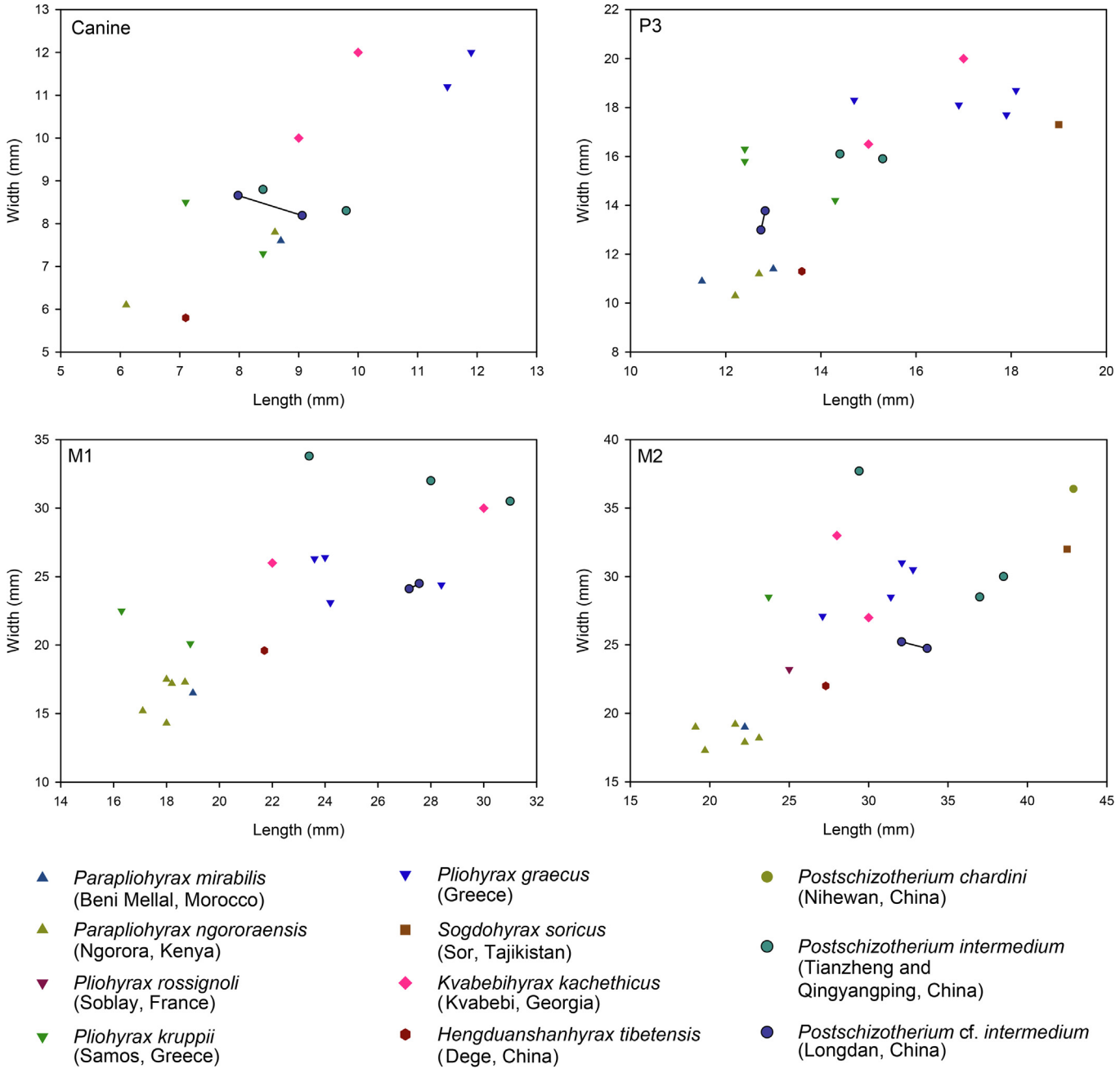



Fig. 5. Tooth measurements of pliohyracids. (a) Canine. (b) P3. (c) M1. (d) M2. The lines link the data of TYFT030 from left and right sides. Data source: *Parapliohyrax mirabilis*, after Ginsburg (1977); *Parapliohyrax ngororaensis*, after Pickford and Fischer (1987); *Pliohyrax rossignoli* and *Pliohyrax kruppii*, after Fischer and Heizmann (1992); *Pliohyrax graecus*, after Fischer and Heizmann (1992) and Pickford et al. (2021); *Sodgohyrax soricus*, after Dubrovo (1978); *Kvabebihyrax kachethicus*, after Vekua (1972); *Hengduanshanhyrax tibetensis*, after Chen (2003); *Postschizotherium chardini*, after von Koenigswald (1966); *Postschizotherium intermedium*, after Qiu et al. (2002) and the present paper.

are three species of *Pliohyrax*, *Pl. graecus*, *Pl. kruppii* Osborn, 1899, and *Pl. rossignoli* Viret, 1949 (Forsyth Major, 1899; Viret, 1949; Fischer and Heizmann, 1992). In *Pliohyrax*, there is a significant diastema between I1 and I2, while no diastema exists between I2 and I3; the I2 and I3 are elongated mesiodistally, exhibiting a sub-oval occlusal surface indicative of premolarisation. Furthermore, the rostrum in *Pliohyrax* (i.e., *Pl. graecus*, SAM 24 housed in NMB) is narrow, in contrast to the laterally expanded rostrum in *Postschizotherium*, and the two I1s diverge only slightly, unlike the highly divergent I1s in *Postschizotherium*. The nasal bone in *Pliohyrax* is relatively long with a shallow nasal notch, whereas the Longdan cranium, although relatively poorly preserved, likely had a shorter nasal bone with a deeper nasal notch, similar to *Kvabebihyrax*. Moreover, *Pliohyrax* lacks a complicated pre-orbital fossa system seen in the Longdan *Postschizotherium*. However, *Pl. graecus* is close in size to the

Longdan cranium (Fig. 5), and both have a strongly laterally projected orbit that extends beyond the zygomatic process.

*Parapliohyrax* has been reported from Africa, with species such as *Pa. mirabilis* Ginsburg, 1977 from Morocco and *Pa. ngororaensis* Pickford and Fischer, 1987 from Kenya (Ginsburg, 1977; Pickford and Fischer, 1987; Rasmussen and Gutiérrez, 2010). The skull of *Parapliohyrax* is smaller than the Longdan cranium (Fig. 5). It shares several features with the Longdan cranium, including diastemata between successive incisors, a laterally expanded rostrum, and the presence of both superior and inferior pre-orbital fossae. Notably, *Pa. mirabilis* exhibits a well-developed maxillary sinus (or palatine pocket), although due to incomplete preservation, it remains uncertain whether this sinus is as extensive as the one in the Longdan cranium. A large maxillary sinus appears to be a common feature among Pliohyracidae, also observed in some recently discovered Late Miocene specimens from China (unpublished material). However, *Parapliohyrax* differs from *Postschizotherium* in several aspects: its premolars are not reduced, it possesses a post-palatal protuberance, its permanent lower incisors have three lobes, and it features a substantial internal mandibular chamber that significantly excavates the mandibular corpus. This chamber does not appear to be equivalent to the inframedial fossa (interno-lower fossa) identified by Qiu (1981) in *Postschizotherium* cf. *chardini*, which is shallow and does not deeply excavate the mandibular corpus. As Rasmussen and Gutiérrez (2010) suggested, these structures may have evolved independently in different hyracoid lineages. Consequently, the hypothesis of a close relationship between *Postschizotherium* and *Parapliohyrax* (Qiu, 1981) requires further scrutiny. As we show above, The Longdan cranium exhibits a very high orbit with a strong laterally projection. This morphology is close to the state of both *Pl. graecus* and *K. kachethicus*. Therefore, *Postschizotherium* (as well as *Hengduanshanhyrax*, which is very close to the former) might directly evolve from *Pliohyrax* rather than from *Parapliohyrax*. Nevertheless, the idea that *Parapliohyrax* could represent an ancestral form leading to other European *Pliohyrax* lineages seems plausible.

In contrast, the African genera *Prohyrax* and *Meroehyrax* exhibit more primitive characteristics. They are relatively small, with lower-crowned teeth and poorly developed diastemata. In *Meroehyrax*, the hypocone is isolated from the ectoloph, indicating the absence of a metaloph (Rasmussen and Gutierrez, 2009). The cranium of *Prohyrax* lacks specialisation, featuring normally positioned orbits that are not laterally projected (Pickford, 1994). Its braincase is elongated, without a sagittal crest, and the nasal notch aligns with the canine. These traits starkly differentiate this African genus from the Longdan cranium.

Within the genus *Postschizotherium*, *Po. licenti* von Koenigswald, 1966 has been considered either a nomen dubium or a junior synonym of *Po. chardini* (Qiu, 1981). The latter, as the type species of *Postschizotherium*, represents the youngest and most derived form, existing during the late Early to Middle Pleistocene. Qiu et al. (2002) meticulously examined the distinctions between *Po. chardini* and *Po. intermedium*. Although significant differences were identified in the mandible, lower molars, and P4, unfortunately, these elements are absent in the Longdan cranium. Given its relatively small dental dimensions (Fig. 5) and low tooth crown, we attribute the Longdan cranium to *Po.* cf. *intermedium*.

Regarding the tooth dimensions (Fig. 5), the canine of *Po.* cf. *intermedium* from Longdan is close to *Po. intermedium* from Tianzheng, while the P3, M1 and M2 are slightly smaller than *Po. intermedium* from Tianzheng and Qiangyangping. All the tooth dimensions of *Po.* cf. *intermedium* are smaller than those of *Sogdohyrax soricus* and *Postschizotherium chardini*; and larger than those of *Parapliohyrax* spp. and *Hengduanshanhyrax tibetensis*. The M1 and M2 dimensions of *Po.* cf. *intermedium* falls in the ranges of *Kvabebihyrax kachethicus* and *Pliohyrax graecus*, and larger than *Pliohyrax kruppi*; while that of the P3 is smaller than the latter three species, revealing the reduction in dimensions of premolars of *Postschizotherium*.

## 5. Discussion

*Postschizotherium*, along with other Eurasian pliohyracids, has long fascinated researchers due to its highly specialised cranio-dental morphology. Until recently, our knowledge of *Postschizotherium* was limited to maxillae and mandibles, which revealed its unusual features, including great body size (compared with the living Procaviidae), strongly inwardly-curved hypsodont teeth, the very late eruption of P4, and the pronounced molariform tendency of its premolars and anterior cheek teeth (canine and I3) (Qiu, 1981; Qiu et al., 2002). The discovery of the Longdan cranium has further illuminated the extent of specialisation in the cranial structure of *Postschizotherium*.

One of the most striking features of the Longdan cranium is the orbit. It is cylindrical, protruding strongly laterally and slightly rostrally, with an elevation that surpasses the frontal surfaces. This characteristic has also been described in *Pliohyrax graecus* and *Kvabebihyrax kachethicus*. The high position of the orbits is often interpreted as an adaptation for a semi-aquatic lifestyle, similar to that of *Hippopotamus amphibius* (Fig. 6). A similar morphology is observed in *Choerolophodon pentelici* (Gaudry and Lartet, 1856) (Choerolophodontidae Gaziry, 1976, a proboscidean) (Pickford, 2005) and *Brachycrus sioense* (Sinclair, 1915) (Merycoidodontidae Cook, 1912, an artiodactyl) (Marriott et al., 2023). However, none of these taxa exhibit the extreme lateral projection of the orbit observed in *Postschizotherium* cf. *intermedium*. There is evidence to suggest that *Postschizotherium* may have had a retracted nasal bone, akin to the condition observed in *Kvabebihyrax kachethicus*. This implies that younger Eurasian pliohyra-

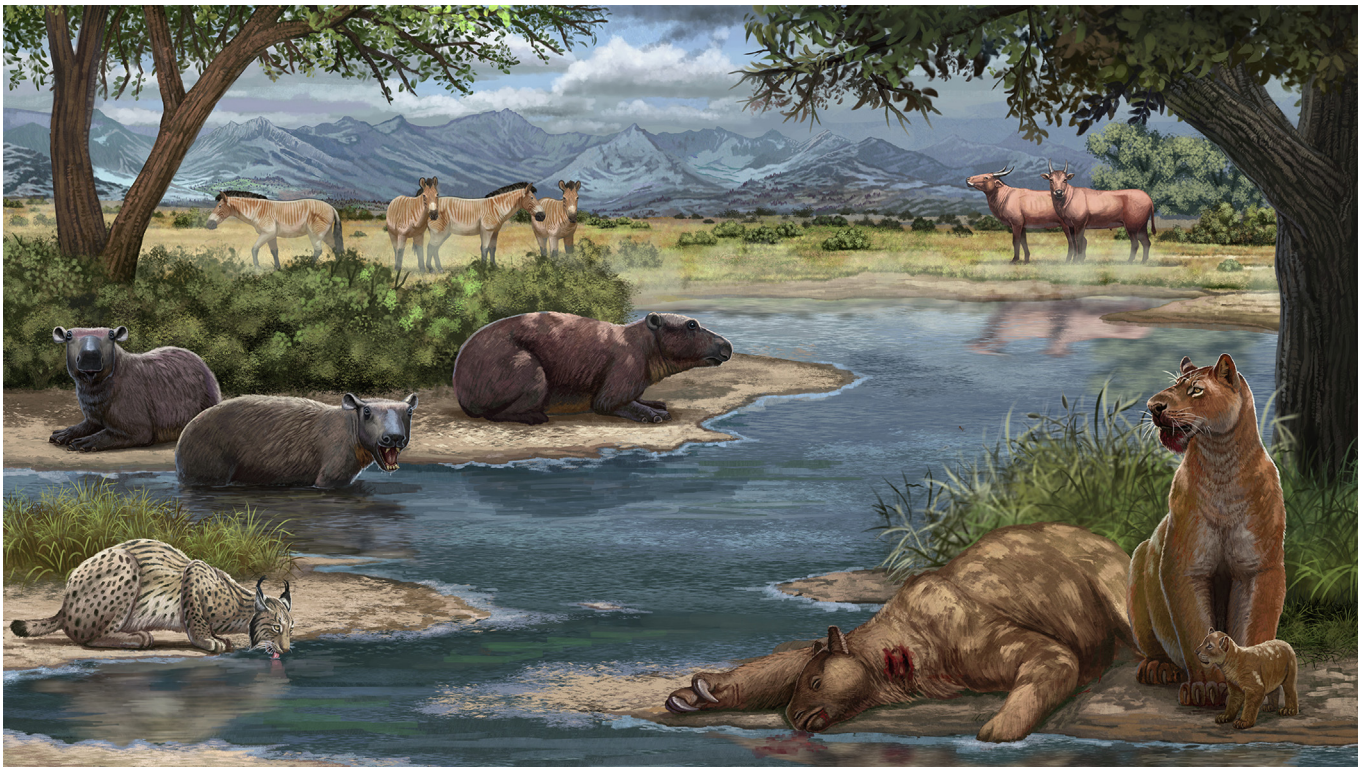


Fig. 6. Landscape and living reconstruction of *Postschizotherium* cf. *intermedium*, from Longdan, courtesy to Jian-Hao Ye.

coids, dating from the Pliocene and Pleistocene epochs, might have possessed a proboscis. Interestingly, there are remarkable morphological similarities between Eurasian pliohyracids and the North American Brachycrurinae, a group within the oreodonts (Marriott et al., 2023). Like *Postschizotherium* and *Kvabebihyrax*, *Brachycrus* exhibited a retracted nasal bone, reaching levels comparable to those found in proboscideans. It also possessed tusk-like canines and lacked diastemata. The zygomatic arches were laterally expanded, with a significant height below the orbit. The pre-orbital fossa system was large and subdivided, indicating the presence of a complex preorbital gland system. The braincase was short, and a sagittal crest was present. The mandible was heightened, with a strong union at the symphysis. *Brachycrus* may have evolved from a less specialised ancestor, such as *Eporeodon* (Marsh, 1875), in an analogous way to *Prohyrax* and *Meroehyrax* representing ancestral forms of the specialised pliohyracids. These morphological resemblances between pliohyracids and oreodonts are likely to be the result of convergent evolution, adapting to a semi-aquatic lifestyle, as commonly proposed for the two groups.

Another distinctive feature of the Longdan hyracoid is the presence of an enlarged maxillary sinus and the absence of a mandibular chamber. The existence of a mandibular chamber has been noted in some early hyracoids. Within the family Saghatheriidae, all known members exhibit this structure. However, within the families Geniohyidae, Titanohyracidae, and Pliohyracidae, this feature is only observed in certain members; others display a shallow fossa, which is considered to be an independent development from the mandibular chamber, or it may be entirely absent (Rasmussen and Gutiérrez, 2010). The presence of a maxillary sinus is less commonly recognised, previously documented only in *Parapliohyrax* (Ginsburg, 1977). However, our newly discovered cranium of *Po*. cf. *intermedium* reveals an exceptionally large maxillary sinus that significantly invades the orbital fossa. This suggests that the pronounced lateral projection of the orbit serves to accommodate the expanded maxillary sinus, necessitating a more lateral positioning of the eyeball. An enlarged maxillary sinus may also be present in other pliohyracids (unpublished material). The functional significance of the mandibular chamber and maxillary sinus remains unclear. One potential hypothesis is that these structures enhance buoyancy for the large skull when floating near riversides or in lakes.

Consequently, like other large pliohyracids, we consider that *Postschizotherium* may have been an amphibious (or hydrophilic) animal, occupying ecological niches similar to those of extant hippos (Heissig, 1999) (Fig. 6). The feeding ecology of *Postschizotherium* remains somewhat enigmatic, but it likely consumed aquatic or riparian grasses, as suggested by its pronounced unilaterally hypsodont teeth with a cover of cementum, and the highly molariform tendency of its premolars and its premolarised canine and I3. However, further research, including quantitative functional morphology and enamel stable isotope analyses,

is necessary to test this hypothesis. *Postschizotherium* also exhibits significant sexual dimorphism, with males being considerably larger than females and possessing thicker tusks, an issue previously discussed by Qiu et al. (2002).

*Postschizotherium* was first discovered in the eastern regions of China, indicating that it survived in a relatively humid palaeoenvironment. The discovery of *Po. intermedium* in the Longdan locality in Gansu Province represents the most westerly record of the genus (Fig. 1). Previous interpretations suggested that the fauna at Longdan indicated an open environment characterised by arid conditions (Qiu et al., 2004). However, recent studies, incorporating enamel stable isotope data, suggest that during the Early Pleistocene the Longdan area was more likely a mosaic of environments (Ma et al., 2023), including massifs, grasslands, woodlands and even forests (Fig. 6). This interpretation is supported by the presence of other mammalian species such as *Ursus* aff. *thibetanus* Cuvier, 1823, *Prionailurus* sp., *Hesperotherium* sp., and *Manis* sp. The occurrence of *Postschizotherium* cf. *intermedium* at Longdan also provides evidence for the presence of a relatively humid environment along the northwestern margin of the Tibetan Plateau during the earliest Pleistocene.

## 6. Conclusions

The newly discovered pliohyracid cranium from the Early Pleistocene Longdan locality represents the first recorded skull of *Postschizotherium*. This specimen, attributed to a female individual of *Postschizotherium* cf. *intermedium*, is characterised by its relatively small dimensions, moderate unilateral hypsodonty, and weakly developed I1 tusk. The cranium displays highly specialised features, such as extreme lateral projection of the orbits, a large maxillary sinus that invades the orbital fossa, and a complex pre-orbital fossa system. These distinctive traits suggest that *Postschizotherium* was probably an amphibious animal, primarily feeding on grasses and occupying ecological niches similar to those of extant hippos. The presence of *Postschizotherium* alongside other taxa at the Longdan site indicates a mosaic environment with relatively high humidity during the earliest Pleistocene epoch. This discovery provides valuable insights into the palaeoenvironmental conditions at the northwestern corner of the Tibetan Plateau during the Early Pleistocene.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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