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A cranium of "*Gazella*" *nihensis* from Pliocene of Qinghai-Tibetan Plateau and the differentiation of early Antilopina

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Abstract

Fossils of Antilopina were often referred to and classified under the genus name "*Gazella*", except for some Miocene spiral horned antelopes; however, their true taxonomic attribution is difficult to determine due to the significant morphological variation observed in large fossil samples. Species of two extant genera within Antilopina that are widely distributed in China are *Gazella subgutturosa* and *Procapra* spp. Assigning abundant fossil specimens identified as "*Gazella*" from China to these two extant groups is particularly challenging. Molecular phylogenetic studies have revealed that *Gazella* and *Procapra* belong to two distinct clades within Antilopina. Therefore, the study of fossil "*Gazella*" is crucial for understanding the differentiation and evolutionary history of Antilopina, which includes a diverse array of genera that lived in Eurasia and Africa. In this article, we describe a newly discovered cranium of "*Gazella*" *nihensis* from the Pliocene Epoch on the Qinghai-Tibetan Plateau. The new cranium exhibits several distinctive features: the braincase is considerably elongated, with the occipital condyles protruding caudally beyond the paroccipital process; the cranial-facial axis is weakly curved, and the horn cores are strongly inclined caudally. The morphology is distinct from most other members of Antilopina. We testified the view that "*Gazella*" *nihensis* is possibly related with the living *Procapra* because of these specialized features. Interestingly, in "*Gazella*" *nihensis*, the elongated braincase that is less bent from the facial axis resembles that of the living *Litocranius walleri*; and the strongly caudally inclined horn core that of the living *Ammodorcas clarkei* and *Antidorcas marsupialis*. These similarities may be the result of parallel evolution, but further research is needed to explore this interesting resemblance.

Keywords: Antilopinae; *Gazella*; *Procapra*; Pliocene; Tibetan Plateau

1. Introduction

Fossil "*Gazella*" are prevalent from the Miocene to recent in Eurasia and Africa (Gentry and Heizmann, 1999; Gentry, 2010; Gentry et al., 2014). Living *Gazella*-like taxa have been reclassified into different genera such as *Nanger*, *Eudorcas*, *Antidorcas*, and *Ammodorcas*, largely due to the advancements in molecular phylogenetics (Hassanin et al., 2012; Bärmann et al., 2013b). For fossil species under *Gazella*, determining their true phylogenetic positions remains challenging. This difficulty stems from two key challenges: 1) both conserved and convergent morphological characters obscure attempts to reconstruct phylogenetic relationships among fossil lineages, and 2) significant intraspecific variation complicates the bound-

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aries between species. As Teilhard de Chardin and Trassaert (1938) noted: "Who among the paleontologists would dare to proclaim his faith in the value and practical use of the various species of *Gazella* reported in the scientific literature for Pontian only (Pikermi, Samos, and Maragha)?". Given this uncertainty, we use quotation marks when referring to fossil *Gazella*-like taxa until more comprehensive studies can resolve their true phylogenetic relationships.

The genus "*Gazella*" in Eurasia, particularly in northern China, presents a complex and intricate taxonomic history. Schlosser (1903) was the first to report abundant "*Gazella*" specimens from the *Hipparion* fauna of northern China, including species such as "*Gazella*" *palaeosinensis* Schlosser, 1903, "*G.*" *altidens* Schlosser, 1903, "*G.*" *dorcadoides* Schlosser, 1903, and "*G.*" *gaudryi* (Schlosser, 1903) (originally *Protetraceros gaudryi*). These species were primarily identified based on dental material without precise locality information. Teilhard de Chardin and Piveteau (1930) and Teilhard de Chardin and Young (1931) further expanded the known species by establishing *Gazella sinensis* Teilhard de Chardin and Piveteau, 1930, *G. blacki* Teilhard de Chardin and Young, 1931, and *G. paotehensis* Teilhard de Chardin and Young, 1931, respectively from the Pleistocene, Pliocene, and late Miocene. Bohlin (1935) conducted a comprehensive study of *Gazella* from the *Hipparion* fauna of northern China, adhering to the taxonomic system established by Schlosser (1903). He reassigned *Gazella palaeosinensis* to ?*Tragoreas* (later recognized as *Dorcadoryx*, though this remains questionable) and questioned the validity of *Gazella paotehensis*. Teilhard de Chardin and Trassaert (1938) reported a wealth of *Gazella* material from the uppermost upper Miocene to the lower Pleistocene, categorizing them into three sub-groups: the *G. gaudryi* sub-group, the *G. blacki* sub-group, and the *G. sinensis* sub-group. These groups are thought to represent evolutionary stages corresponding to the late Miocene, Pliocene, and early Pleistocene, respectively. Bohlin (1938) described two new species from the Pliocene and lower Pleistocene of northern China: *G. kueitensis* Bohlin, 1938 from the Kuide Basin (Fig. 1) in Qinghai Province and *G. paragutturosa* Bohlin, 1938 from the lower Pleistocene. The latter was considered to belong to the living *Procapra* group. Kurtén (1952) confirmed the validity of *Gazella paotehensis* based on variation analysis. Over time, *Gazella* has frequently been reported in Late Cenozoic mammalian assemblages in northern China due to its abundance.

Chen (1997) provided a comprehensive revision of *Gazella* from the Yushe Basin (Fig. 1), which had previously been studied by Teilhard de Chardin and Trassaert (1938). In addition to confirming the already established species *Gazella gaudryi*, *G. blacki*, and *G. sinensis*, Chen (1997) described three new species: *G. gaozhuangensis* Chen, 1997, *G. yushensis* Chen, 1997, and *G. nihensis* Chen, 1997. She proposed two evolutionary lineages: one comprising *G. gaozhuangensis*, *G. blacki*, and *G. sinensis*; and the other with *G. yushensis*, *G. nihensis*, and *G. paragutturosa*, both derived from the late Miocene *G. gaudryi*. More recently, Zhang and Yang (2016) described a complete skeleton of *G.* cf. *lydekkeri* Pilgrim, 1937 from the Lantian region (Fig. 1), representing the Bahean age

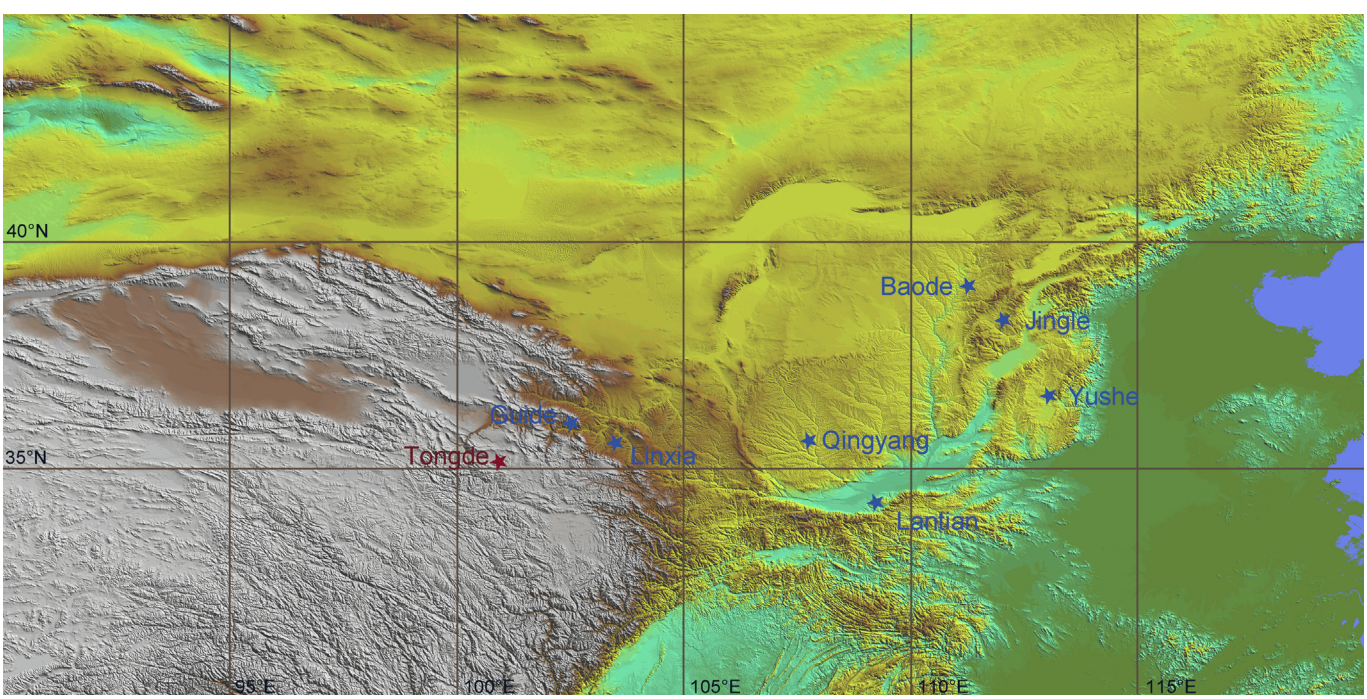


Fig. 1. Map showing Chinese "*Gazella*" fossil localities regarding to this article. The red star represents the study locality, and blue stars represent other localities yielding "*Gazella*".

(early late Miocene, see Deng et al., 2019). Li (2015, 2018) and Li et al. (2018) conducted extensive studies of "*Gazella*" specimens from the upper Miocene of the Linxia Basin and Qingyang region (Fig. 1). They further validated "*G.*" *paotehensis* and designated a new type specimen for this species. These studies collectively contribute to a more nuanced understanding of the evolutionary history and taxonomy of "*Gazella*" in northern China. Bai et al. (2023) described *Gazella sinensis*, *G. blacki* and *Procapra* cf. *przewalskii* (Büchner, 1891) from the lower Pleistocene of Tianzhen (Nihewan Basin). Except for clarifying *G.* cf. *subgutturosa* (Güldenstädt, 1780) (sensu Teilhard de Chardin and Piveteau, 1930) being conspecific with *G. sinensis*, they thought that at least partial materials of *G. paragutturosa* should be transferred to *Procapra* as *P. gutturosa* (Pallas, 1777).

Recently, a new "*Gazella*" cranium was discovered in Tongde County, Qinghai Province, on the Qinghai-Tibetan Plateau (Fig. 1). The age of this specimen is estimated to be Pliocene based on the occurrence of *Anancus*, an indicator for this age. Its characteristics make the fossil worthy of careful and detailed study, as they may provide valuable insights into the evolutionary history and diversification of these antelopes.

Anatomical abbreviations: aa, anterior semicircular canal ampulla; asc, anterior semicircular canal; Bo, Basioccipital; Bs, Basisphenoid; ca, cochlear aqueduct; cc, common crus; c co, condyloid canal; c f, facial crest; c n, nuchal crest; coc, cochlea; c su, supraorbital canal; c t, temporal crest; eab, external auditory tube; ec, endocast; E pp, perpendicular plate of the ethmoidal; es, endolymphatic sac; e s p, presylvian sulcus; et, Eustachian tube; F, frontal; f c, fenestra cochleae; f co, condyloid fossa; f h, hypoglossal foramen; f it, infratemporal fossa; f j, jugular foramen; f l, lacrimal foramen; f m, foramen magnum; f ma, mastoid foramen; f mx, maxillary foramen; f o, foramen ovale; f op, optic foramen; f or, foramen orbito-rotundum; f po, pre-orbita fossa; f pc, post cornual fossa; f s, stylomastoid foramen; f so, supra-orbital foramen; f v, fenestra vestibuli; la, lateral semicircular canal ampulla; Lo, lacrimal orifice; lsc, lateral semicircular canal; lv, lamina vaginalis; M, maxillary; M3, the third molar; ma, mastoid; O, occipital; Oc, occipital condyle; Op, external occipital protuberance; P, parietal; pa, posterior semicircular canal ampulla; pgl, post-glenoid ledge; p m, muscular process; p p, paroccipital process; p pt, pterygoid process; psc, posterior semicircular canal; S, squamosal; sac, saccule; s F-P, suture between frontal and parietal; sl, secondary lamina; s m F, medial suture between frontal bones; s P-O, suture between parietal and occipital; t ab, anterior tuberosity of occipital; tb, tympanic bulla; tc, temporal canal; t co, temporal condyle; tl, temporal line; t pb, posterior tuberosity of occipital; tv, tympanohyal vagina; ut, utricule; V, vomer; va, vestibular aqueduct; v f a, alar foramen; v f at, common opening for alar foramen and transverse foramen; v f i, interveterbral foramen; v f t, transverse foramen; v p t, transverse process of vertebra; v p a, posterior articulation of vertebra; v sp, vertebral spine.

Institutional abbreviations: AMNH, American Museum of Nature History, New York, USA; GSIQ, Geological Survey Institute of Qinghai, Xining, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; THP, Tianjin Natural History Museum, Tianjin, China.

2. Geological setting

The fossil-bearing strata were exposed in a deep gully cut by the Baqu River, a tributary of the Yellow River. The locality belongs to the Zeku Composite Foreland Basin of the Kunlun-Qilian-Qinling orogenic system (Geological Survey Institute of Qinghai, 2017). The fossil was found from a set of yellow mudstones, exhibiting strongly cemented blocky layered carbonated blocks or thick layers. This set of strata has yielded gastropods such as *Cathaica fassiola*, *Valvata baikalensis*, *Succinea crythrophana*, and *Gyraulus* cf. *sibicus*. In addition, *Anancus* sp. has been collected from the same layer at the eastern side of the Baqu River in the Tongde Basin margin. The age was estimated to be the Pliocene because of the occurrence of *Anancus*, an indicator of Pliocene.

3. Material and methods

The described cranium is housed in the GSIQ, the comparative materials in the IVPP and THP, and the extant specimens are from AMNH.

The terminology of ruminant teeth follows Bärmann and Rössner (2011). The terminology of cranial anatomy follows Sisson (1953). Three-D surface scanning was done using an Artec Spider handheld scanner, providing high-resolution images that highlight intricate morphological details and measurements were taken directly on the 3D model with a precision of 0.01 mm.

An industrial micro-computed tomography scanner, GE v|tome|x m300&180 (GE Measurement & Control, Wuntsdorf, Germany) was performed to obtain high-resolution computed tomographic images of the bony labyrinths of "*G.*" *nihensis*. The 3D models (Supplementary data S1) were reconstructed using VGStudio Max 3.0 software.

A cladistic analysis was performed to examine the phylogenetic relations of Antilopinae. We constructed a morphological data matrix including 62 taxa, with 56 extant species of Antilopinae. Apart from "*G.*" *nihensis*, four fossil species of Miocene "*Gazella*" ("*G.*" *gaudryi*, "*G.*" *paotehensis*, "*G.*" *lydekkeri*, and *Linxiatragus dengi* Wang et al., 2023) were included in the data set, and *Turcocerus grangeri* Pilgrim, 1934, a fossil hypsodontine, was selected as the outgroup. The morphological characters were based on Bärmann (2012) and Wang et al. (2023) and only slightly revised (Supplementary data S2); the scorings of the taxa were after Bärmann (2012) and Li (2018), and scored by us based on extant specimens in AMNH and BMH collections (Supplementary data S2). The most parsimonious reconstruction was performed by the program TNT 1.1 (Goloboff et al., 2008) using New Technology search (Supplementary data S3), and strict consensus tree was reported.

4. Systematic paleontology

Family Bovidae Gray, 1821
Subfamily Antilopinae Gray, 1821
Tribe Antilopini Gray, 1821
Sub-tribe Antilopina Gray, 1821

"*Gazella*" *nihensis* Chen, 1997
(Figs. 2, 3; Tables 1, 2)

Type specimen: THP 10408, a nearly complete cranium.
Type locality and age: Locality 48, Yinjiao of the Yushe Basin.
Referred specimen: GSIQ QHHS6 (Figs. 2, 3), a cranium, most of the facial part and palate are broken, with the right M3 preserved. The left horn core is broken in the middle. The mandible is crashed lacking lower teeth. The atlas and axis are preserved.
Locality of the new specimen: Guashize (35°14'24.00"N, 100°35'51.73"E), Tongde County, Hainan Tibetan Autonomous Prefecture, Qinhai Province (Fig. 1).
Description: The size of the Tongde specimen is comparable to that of the living *G. subgutturosa*, but slightly smaller than the living *Procapra gutturosa*.

Cranium (Fig. 2a–h): most of the facial portion of the cranium is missing, with only the right M3 (third molar) remaining. The cranium exhibits slight dorsoventral compression.

The horncores of the Tongde specimen are robust, with pedicles of moderate length. In lateral view, the horncore exhibits a weak caudal curvature but is strongly inclined caudally, more so than in most *Gazella*-like taxa (with the exception of THP 10408, the type specimen of "*G.*" *nihensis*). In rostral view, the two horncores are positioned moderately close to each other and diverge moderately. The morphology is like the condition of *Procapra*, different from *G. subgutturosa* of which the two horn cores are more converge at the pedicle–horncore boundary. The horncore is moderately transversely compressed at its base, with a moderate obliquity of the cross-sections. The oval cross-section gradually becomes circular as it extends. The lateral surface flattens little (Fig. 2b, black circles). The surface of the horncore is marked by numerous fine grooves running along its length. Additionally, three to four deep grooves are present on the dorsal side of the horncore, originating from the proximal part; the largest groove runs along the ventral side of the horncore. The supra-orbital foramen (f so) is slit-like and deeply situated within a triangular supra-orbital fossa located at the rostromedian root of the pedicle. A small, circular post-cornual fossa (f pc) is deeply excavated into the caudolateral root of the pedicle.

The middle suture of the frontal bones (s m F) is highly indented and swells in the center, forming a longitudinal crest. This crest is perpendicular to the frontal-parietal sutures (s F-P). The frontal bone slightly sinks in both rostro- and caudo-medial regions; however, the cranial roof remains nearly flat, almost without dorsal bulging. The frontal sinus is poorly developed, as observed on the left side due to damage, and does not extend into the horncore. The perpendicular plate of the ethmoidal bone (E pp) and the frontal pole of the cerebral endocast are visible. The latter shows a clear presylvian sulcus (e s p) and adjacent gyrus.

The orbit is laterally projected, with a more pronounced projection in the caudal region. However, it has been dorso-ventrally compressed during the taphonomy. Within the orbit, the maxillary foramen (f mx, the caudal opening of the maxillary channel) is located deeply in a fossa of the rostro-ventral border, and a small lacrimal foramen (f l) is very close, and dorsal to the maxillary foramen. There is a round ventral exit of the supra-orbital canal (c su), and the optic foramen (f op) is large and located at the very ventral position of the orbital fossa. The sutures surrounding the lacrimal can be well recognized. A large, irregular orifice (Lo) is situated just rostral to the lacrimal process, a feature also observed in some specimens of *Procapra gutturosa*. Although only the caudal part of the right side is preserved, the pre-orbital fossa appears deep. The facial crest (c f) is moderately developed, and the facial part is very low, like that in *Litocranius walleri* (Brooke, 1878).

The braincase is notably elongated. In dorsal view, the braincase exhibits lateral swelling due to dorsoventral compression. The frontal-parietal and parietal-occipital sutures (s P-O) are parallel and perpendicular to the sagittal plane. A weak triangular tuberosity with a caudal apex is present in the center of the parietal bone. The temporal lines (tl) converge weakly, maintaining a wide distance between them. The dorsal length of the occipital bone is long, and the nuchal crest (c n) forms a relatively acute angle, approximately 110°. In caudal view, the occipital tuberosity (Op) is large and shaped like an equilateral triangle with a ventral apex. It gives rise to a thin middle nuchal crest that extends ventrally to the foramen magnum. Two tuberosities are present at the dorsal border of the foramen magnum (f m). The foramen magnum itself is wide, bordered by triangular occipital condyles (Oc) on each side. On the dorsal border at the middle of the right lateral side, there is a large fossa that houses the mastoid foramen (f ma, that of the left side is broken).

In lateral view, the braincase axis is only weakly bent relative to the facial axis. The temporal crest (tc) runs obliquely across the braincase, indicating a low temporal fossa. The occipital surface can be well-observed from this angle. The paroccipital process (p p) is long and slender, projecting strongly ventrally with a slight curve. The occipital condyle (Oc) is positioned more caudally than the paroccipital

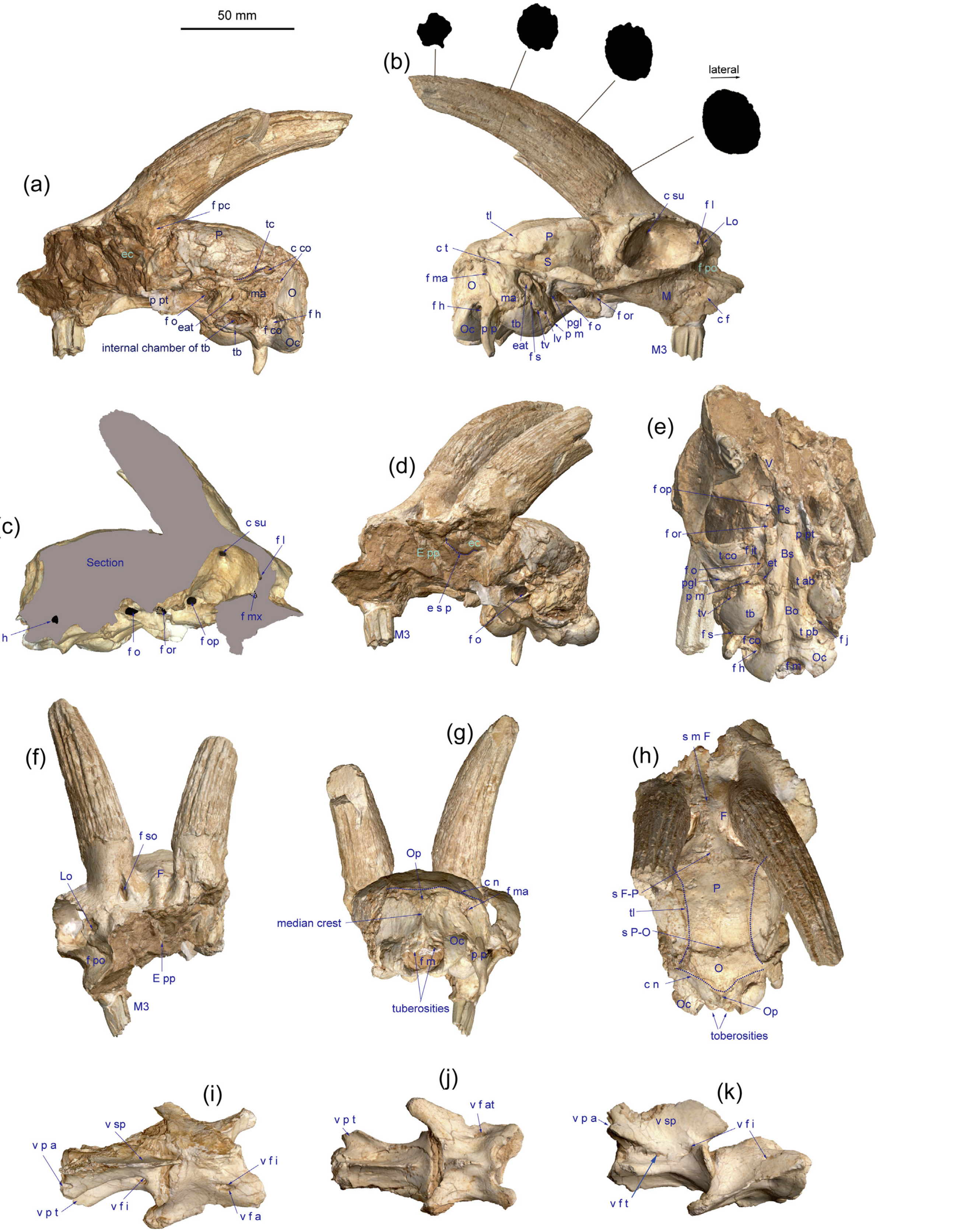


Fig. 2. "*Gazella*" *nihensis* (GSIQ QHHS6) from Tongde. (a–h) Cranium, in left lateral (a), right lateral (b), right sagittal section (c), rostrolateral (d), ventral (e), rostral (f), caudal (g), and dorsal (h) views, in which (b) shows the cross-sections of horn core, (c) shows a series of foramens surrounding the braincase and in the orbital fossa, and (d) shows the rontal pole of the cerebral endocast and the vertical plate of ethmoidal. (i–k) Atlas and axis, in dorsal (i), ventral (j), and lateral (k) views. For abbreviations, see the anatomical abbreviations in 1. Introduction.

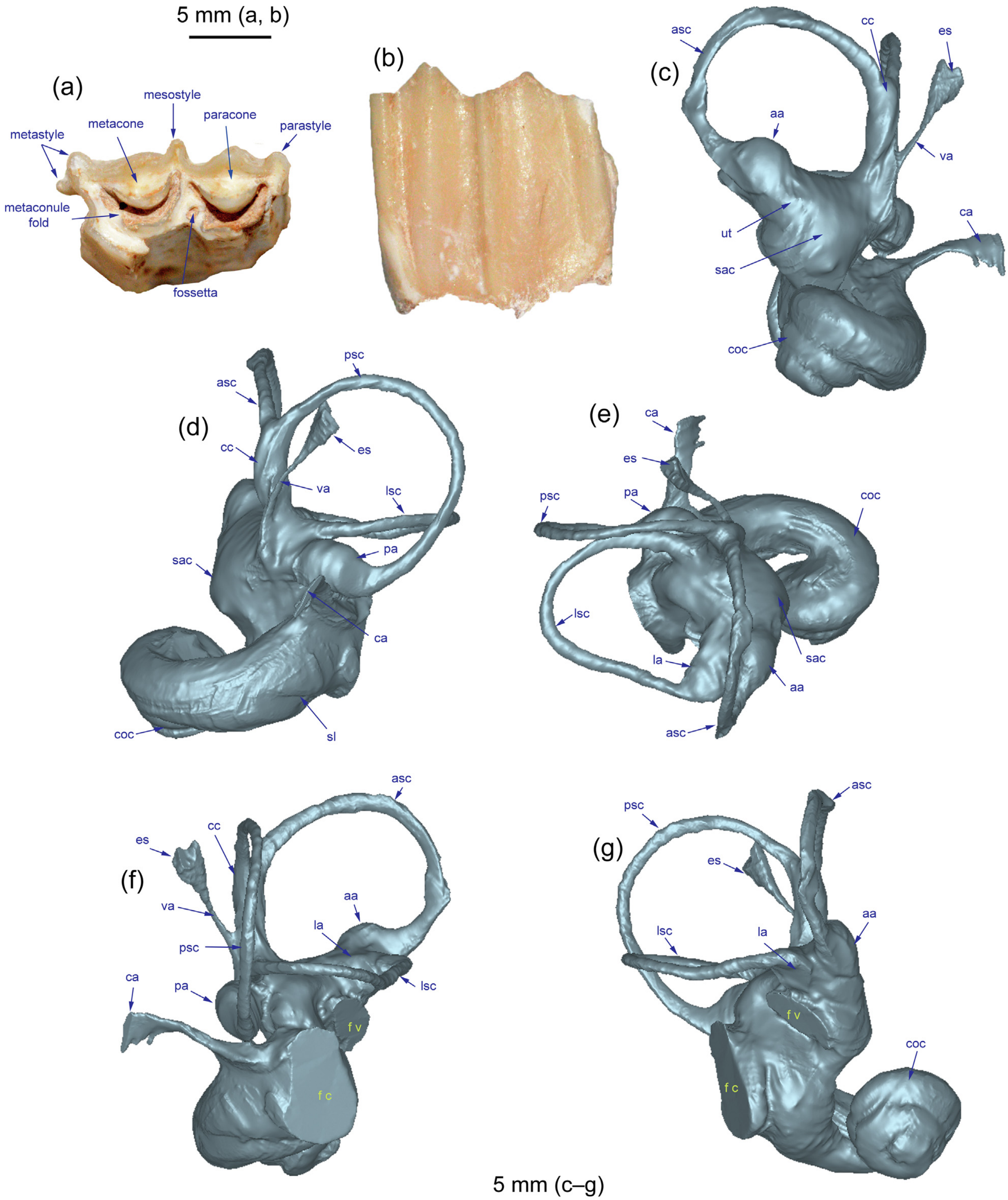


Fig. 3. "*Gazella*" *nihensis* (GSIQ QHHS6) from Tongde. (a, b) Right m3, in occlusal (a) and buccal (b) views. (c–g) Endocast of right bony labyrinth, in medial (c), occipital (d), dorsal (e), lateral (f), and rostral (g) views.

process. The mastoid-tympanic region is large and diamond-shaped. The tympanic bulla (tb) resembles that of *Procapra gutturosa*, not as strongly ventrally bulged as in *G. subgutturosa*. The lateral side of the left tympanic bulla is broken, revealing a large olive-shaped chamber within the tympanic bulla. Also from the broken left lateral side, dorsal to the mastoid-tympanic region, a narrow temporal channel (tc) runs obliquely along the caudo-ventral margin of the braincase, opening into a large condyloid canal (c co) at its caudal extremity. The tympanohyal

Table 1
Horn core measurements (in mm). DAP, ant-posterior diameter; DT, transversal diameter.

Locus	Remaining anterior length	DAP × DT at base	100 × DAP/DT at base	DAP × DT at 30 mm	DAP × DT at 60 mm	DAP × DT at 90 mm
Left	61.59	28.77 × 24.11	119.32	23.28 × 20.28		
Right	114.25	30.05 × 22.66	132.61	23.76 × 20.89	20.55 × 17.98	14.03 × 14.00

Table 2
Cranial and upper cheek teeth measurements (in mm), after Bärmann et al. (2013b). × 2 means measurements on one side to the sagittal plan.

Left/median	Right	Explanation
25.41	27.31	Bulla length
	19.5	Bulla width
13.94		Distance between horn pedicles
	113.17	Distance, orbit to condyle (measured parallel to tooth row)
30.61		Distance between supra-orbital foramina
20.51 × 2		Horn base distance (distance of the anteriormost parts of the pedicles)
22.35	22.70	Horn pedicle diameter 1 (medio-lateral)
27.69	27.92	Horn pedicle diameter 2 (antero-posterior)
17.82		Inter-bullae distance
99.3		Length of frontal + parietal
30.26		Length of basioccipital (at sagittal plane)
65.21		Length of frontal
39.46		Length of parietal
40.03		Orbit diameter (parallel to tooth row)
40.69		Occipital height, braincase complete
27.59		Occipital height, occiput only (dorsal of foramen magnum)
47.78 × 2		Width across orbits (maximum width of frontals)
58.02		Width of braincase
20.24		Width of basioccipital anterior
21.71		Width of basioccipital posterior
40.93		Width of condyle
31.64 × 2		Width across paramastoid processes
41.54 × 2		Zygomatic width (behind orbits)

vagina (tv) is located at the rostral part of the bulla. The lamina vaginalis (lv) does not completely enclose the vagina, leaving a caudal slit where the stylomastoid foramen (f s) lies deep within. The tympanic bulla is strongly expanded caudally, covered by rough mastoid bone. The external auditory tube (eat) is circular and lacks a meatal fissure. It is closely adjacent to the mastoid caudally and the temporal crest of the squamosal dorsally, but is very distant from the post-glenoid ledge (pgl).

In ventral view, the occipital condyles are sub-triangular with a broad inter-condyloid notch. The condyloid fossa (f co) is relatively wide and houses two small hypoglossal foramina (f h). The basioccipital bone between the anterior and the posterior tuberosities (t ab and t pb) shows a sub-rectangular shape, and the basisphenoid bone tapers rostrally. The posterior basilar tuberosities display two stout transverse crests that give rise to strong rostrally extended crests, terminating in a rough anterior basilar tuberosity. A shallow groove runs along the midline between the two lateral crests, while the middle crest is poorly developed. The tympanic bulla (tb) appears obliquely rectangular in ventral view. It is smaller than that of *G. subgutturosa* and similar in size to *Procapra gutturosa*. However, the tympanohyal vagina (tv) only slightly excavates the bulla. The muscular process is clearly visible, sheltering a small opening of the Eustachian tube (et).

The post-glenoid ledge (pgl) is robust, and the post-glenoid foramen is completely sheltered by the inflated tympanic bulla. The temporal condyle (t co) exhibits weak ventral convexity. Medial to the temporal condyle and lateral to the sharp pterygoid crest (p pt), a deep infratemporal fossa (f it) contains a large oval foramen (f o). Rostral to the alisphenoid bone, a deep pit hosts the large foramen orbito-rotundum (f or). The presphenoid is cylindrical, and the thin vomer is laterally deformed.

Tooth (Fig. 3a, b): Only the left M3 is present, but the lingual wall is broken. In occlusal view, the paracone swells in both lingual and buccal directions, while the metacone only swells in the lingual direction. The para-, meso-, and metastyles are all projected buccally, with the latter, slightly thinner than the former two, also extending distally in the middle of the tooth crown. A small enamel fossetta is present at the center, and a metaconule fold is present at the distal wall of the posterior fossa. In buccal view, the crown is relatively high with parallel ribs of the para-, meso-, and metastyles. The paracone rib is prominent, whereas the metacone rib is weak. Measurements: 14.98 × 7.09 × 14.01 mm (length × remaining width × height).

Bony labyrinth (Fig. 3c–g): The cochlea (coc) twists 2.5 turns. The first turn detaches slightly from other turns. The cochlear fenestra (f c) is very large, having an elliptical contour, and facing laterally and slightly rostrally. The cochlear aqueduct (ca) is laterally compressed and nearly perpendicular to the first turn of the cochlea. The secondary lamina (sl) is observed on the first turn of the cochlea. The vestibule is swelled. The utricule (ut) and saccule (sac) are not clearly shown, especially the former, only weakly bulging. The vestibular fenestra (f v) is just below the lateral semicircular canal ampulla (la). It is smaller than the cochlear fenestra, but is still large, showing an oblique elliptical contour.

For the semicircular canals, the common crus (cc) is thick and long. The anterior semicircular canal (asc) and the posterior semicircular canal (psc) are in a same height. The lateral semicircular canal (lsc) is not straight, showing a ventral bend in the middle, and in dorsal view, it is slightly rostro-caudally compressed rather than circular. The lateral insertion of the lateral canal is higher above the posterior semicircular canal ampulla (pa), at between the root of the cc and pa, this morphology is typical in Bovidae. The vestibular aqueduct (va) is slim and short, it extends laterally obliquely off the cc. The endolymphatic sac (es) is small and conical.

Cervical vertebrae (Fig. 2i–k): The atlas and axis are articulated and they are not elongated. The wings of the atlas are moderately projected laterally, extending mainly in the caudal direction. The anterior articulations are deeply incurved. The intervertebral and alar foramina (v f i and v f a) are elongated and close to each other. Dorsally, the thin dorsal arch possesses a high dorsal tuberosity that is posteriorly positioned. Ventrally, a shallow lateral atlantal fossa holds the common opening of the alar and transverse foramen (v f at). The ventral tubercle is located in the middle of the ventral arch. The spinal process (v sp) of the axis is very large, but its dorsal edge is broken. The intervertebral foramen (v f i) is large and perforates the cranial part of the centrum. The posterior articulations (v p a) and the transverse process (v p t) are less laterally expanded. A small transverse foramen (v f t) is present in the middle of the centrum. The ventral spine is sharp and strongly extends ventrally.

5. Comparisons and discussion

The Tongde specimen undoubtedly belongs to the *Gazella*-like taxa, which are typically included in the monophyletic Antilopini. In the previous studies of *Gazella*-like fossils from China, a regular issue is to clarify the two lineages represented by *Procapra* and *Gazella*, which survive until today (*G. subgutturosa*, *Procapra gutturosa*, *P. picticaudata* Hodgson, 1846, and *P. przewalskii*). However, the phylogeny of the crown Antilopini has been a considerable debate. Hassanin et al. (2012) and Bärmann et al. (2013a) suggested that within Antilopini, Procaprina and Raphicerina, as well as Antilopina and Ourebina, respectively form sister groups, and these pairs further constitute sister groups. On the other hand, Bärmann (2014) and Chen et al. (2019) suggested that Raphicerina is the most basal group, and in the remaining groups, Procaprina is the sister group of Antilopina and Ourebina (Fig. 4). All studies reveal that *Procapra* and "*Gazella*" are phylogenetically distant groups within Antilopini, diverging approximately 10 Ma. Therefore, species of fossil "*Gazella*" may represent the stem group of the Antilopini, involving more complicated issues concerning the originations of all lineages within Antilopini. Determining the true phylogenetic positions of these *Gazella*-like taxa remains a difficult task. At present, we continue to use the name "*Gazella*" but with quotation marks to indicate the uncertainty.

In China, numerous species of fossil "*Gazella*" have been established. These species are generally subdivided into three groups based on their evolutionary stages and geological ages: the Miocene "*G.*" *gaudryi* group, the Pliocene "*G.*" *blacki* group, and the early Pleistocene "*G.*" *sinensis* group Teilhard de Chardin and Trassaert (1938). The "*G.*" *gaudryi* group includes several species such as "*G.*" *gaudryi*, "*G.*" *paotehensis*, "*G.*" *dorcadoides*, "*G.*" *altidens*, "*G.*" *gaozhuangensis*, and possibly "*G.*" cf. *lydekkeri*. The validity of some species has been widely debated, for example, "*G.*" *paotehensis* (Bohlin, 1935, 1938, 1939; Teilhard de Chardin and Trassaert, 1938; Li et al., 2018). Additionally, some names, like "*G.*" *altidens* and "*G.*" *gaozhuangensis*, have rarely been used since their establishment. Among all species except for "*G.*" *gaozhuangensis*, the sizes are small, and the braincase is short with a strong curvature from the facial part. The teeth are usually relatively low-crowned. These features are distinctly different from those of the Tongde specimen.

The "*G.*" *sinensis* group of the lower Pleistocene is poorly defined and characterized by large size and strong, vertically erected horncores on the braincase (Teilhard de Chardin and Piveteau, 1930). The braincase itself is short and strongly curved from the facial part. These features are distinctly different from those of the Tongde specimen. In addition to the "*G.*" *sinensis* group, other taxa coexisted in the lower Pleistocene of China, such as "*G.*" *paragutturosa* (Bohlin, 1938) (see below, the next 6th paragraph).

The "*G.*" *blacki* group includes: "*G.*" *blacki*, "*G.*" *yushensis*, "*G.*" *nihensis* (Teilhard de Chardin and Trassaert, 1938; Chen, 1997), and possibly "*G.*" *kueitensis*. "*Gazella*" *kueitensis* was discovered in the Guide Basin, very close to the present locality. The deposits of the Guide Basin belong to the Heerjia Formation of the Pliocene and coexist with *Anancus cuneatus* Teilhard de Chardin and Trassaert, 1937, a typical Pliocene proboscidean. "*G.*" *kueitensis* shares some similarities with the Tongde specimen, including a relatively long braincase and a similar basicranial region. This includes an oblique rectangular tympanic bulla with a weak tympanohyal vagina, and anterior and posterior basilar tuberosities connected by a

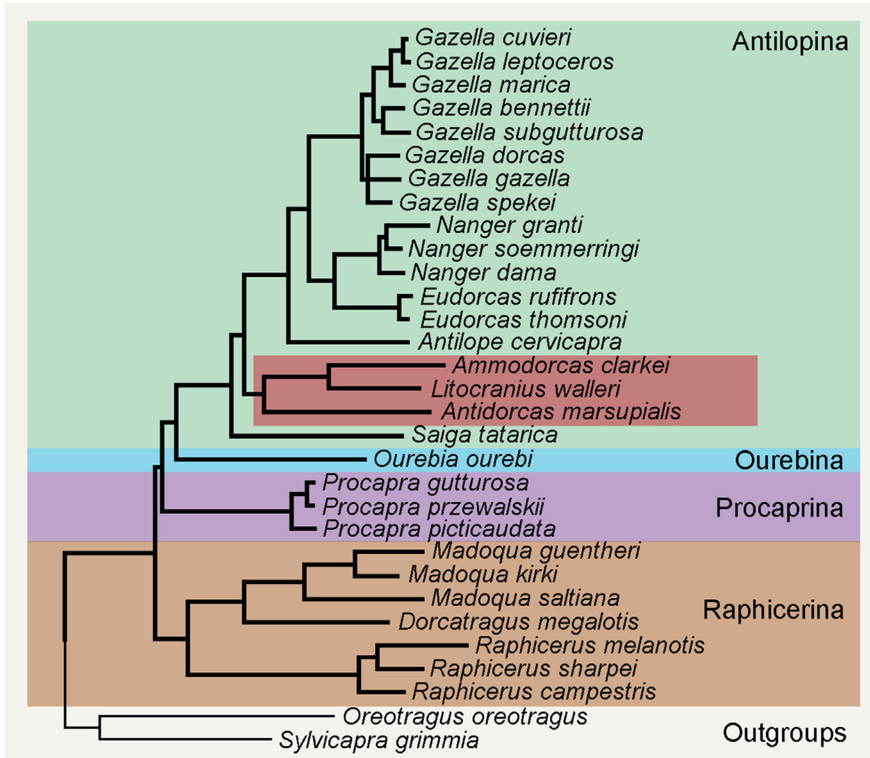


Fig. 4. Phylogenetic relationships among living Antilopini, redrawn after Bärmann (2014). The red frame represents the clade comprising *Litocranius*–*Ammodorcas*–*Antidorcas*.

strong crest on each side, rendering a shallow median groove. However, there are also differences between "*G.*" *kueitensis* and the Tongde specimen. The most striking one is that the cranial axis of "*G.*" *kueitensis* is more strongly bent from the facial axis than that of the Tongde specimen. Furthermore, while the braincase of "*G.*" *kueitensis* is long, it is still shorter than that of the Tongde specimen. Additionally, the horncore of "*G.*" *kueitensis* is more erect and not as strongly inclined caudally as that of the Tongde specimen. If these differences are considered intraspecific variations, the Tongde specimen appears to be attributable to "*G.*" *kueitensis*.

However, when considering taxa from the Yushe Basin, things become more complicated. Teilhard de Chardin and Young (1931) established "*G.*" *blacki* based on horncores and mandibles from the Pliocene of the Jingle region. The cheek teeth are hypsodont, and the p4 is relatively primitive with the anterior and posterior valleys being lingually open. The horn cores are relatively small; however, this might be due to the juvenile ontogenetic stage. Therefore, isolated horn cores cannot provide sufficient taxonomic information. Teilhard de Chardin and Trassaert (1938) further included a large number of "*Gazella*" material (mostly from Pliocene) from the Yushe Basin into their "*G.*" *blacki* sub-group (referred to as the "*G.*" *blacki* group in this article). Bohlin (1939) believed that new material provided more complete diagnostic characters of "*G.*" *blacki* than the type material from Jingle region, leading him to synonymize "*G.*" *kueitensis* with "*G.*" *blacki*. However, the "*G.*" *blacki* group from the Yushe region exhibits highly morphological variety. Indeed, "*G.*" *kueitensis* resembles some specimens within this group, such as THP 22886 (the type specimen of "*G.*" *yushensis*, Fig. 5), but differs from others.

Chen (1997) re-studied "*Gazella*" specimens from the Yushe region and subdivided the "*G.*" *blacki* group into three species: "*G.*" *blacki*, "*G.*" *yushensis*, and "*G.*" *nihensis* (Fig. 5). For the latter two species she newly established, she only assigned the type specimens, i.e., THP 22886 for "*G.*" *yushensis* and THP 10408 for "*G.*" *nihensis* (Fig. 5); however, she did not assign each specimen of the large sample (nearly 30 specimens) to the three species. We have mentioned that the type specimen of "*G.*" *yushensis* closely resembles "*G.*" *kueitensis*, and differs from the Tongde specimens in having a more bent brain case, as well as slightly shorter braincase and more erect horncores. Therefore, "*G.*" *yushensis* Chen, 1997 appears to be a junior synonym of "*G.*" *kueitensis* Bohlin, 1939.

Another species, "*G.*" *nihensis* (THP 10408), is very close to the Tongde specimen (Fig. 5). In both specimens, the braincase axis is almost not bent from the facial axis, resulting in a nearly straight dorsal line of the cranial roof. In all *Gazella*-like genera, including "*G.*" *paragutturosa* (see below, the next 2nd paragraph), the cranial roof is more or less bent. The braincase of "*G.*" *nihensis* is elongated and longer than that of "*G.*" *kueitensis* and "*G.*" *yushensis*.

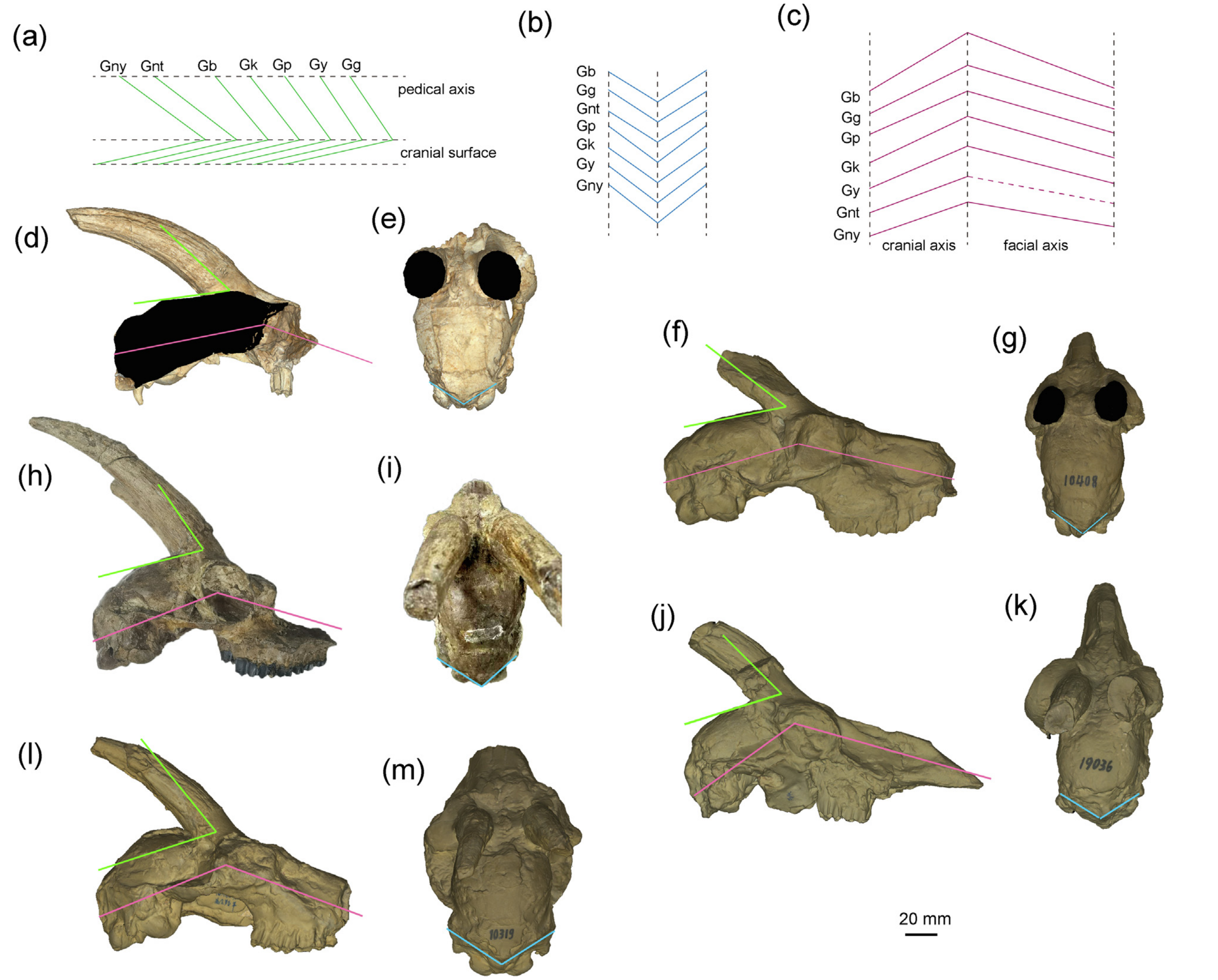


Fig. 5. Comparisons of some fossil "*Gazella*" in China. (a–c) Line drawings showing the morphological comparisons of horncore pedical inclination (green lines and below) (a), nuchal crest angle (cyan lines and below) (b), and cranial-facial curvature (pink lines and below) (c). (d–m) Photos of fossil "*Gazella*" for morphological comparison, including "*G.*" *nihensis*, GSIQ QHHS6 from Tongde, in median sagittal (d) and dorsal (e) views, and a cast of the type cranium, THP 10408 in right lateral (f) and dorsal (g) views; "*G. yushensis*", THP 22886, the type specimen, in right lateral (h) and dorsal (i) views; "*G.*" *blacki*, a cast of THP 19036, in right lateral (l) and dorsal (m) views; "*G.*" *gaozhuangensis*, a cast of THP 10319, in right lateral (j) and dorsal (k) views. Abbreviations: Gb, "*G.*" *blacki*; Gg, "*G.*" *gaozhuangensis*; Gk, "*G.*" *kueitensis*; Gnt, "*G.*" *nihensis* from Tongde (the study specimen); Gny, "*G.*" *nihensis* from Yushe (the type specimen); Gp, "*G.*" *paragutturosa*; Gy, "*G. yushensis*", THP 22886 (the type specimen). Data of "*G.*" *kueitensis* and "*G.*" *paragutturosa* were obtained from Bohlin (1938).

The morphology of the basi-cranium, including the tympanic bulla, is also similar between the two species. The tooth crown is high, and the horn cores are caudally inclined strongly at a similar angle from the cranial roof. However, in "*G.*" *nihensis*, the horn cores are somewhat slender compared to those of the Tongde specimen, and the facial part is higher than that of the Tongde specimen. Given that the thickness of the horn core likely represents intraspecific variation, the Tongde specimen can be regarded as the same species as "*G.*" *nihensis*. Although we cannot confidently determine whether "*G.*" *nihensis* is a valid species or merely a morphological variation of "*G.*" *kueitensis* or even "*G.*" *blacki*, we currently assign the Tongde specimen to "*G.*" *nihensis*.

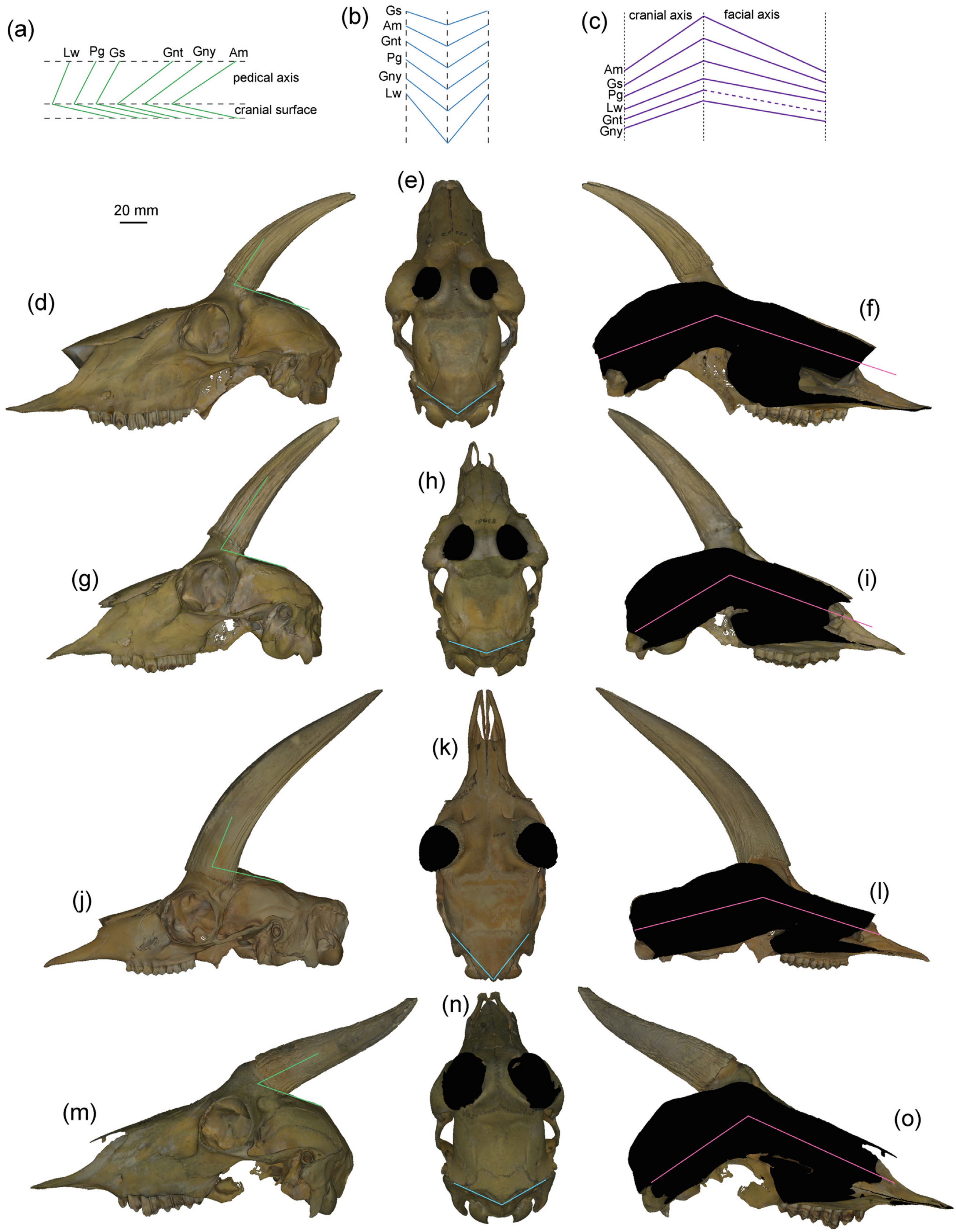
Chen (1997) did not specify which specimens were attributed to "*G.*" *blacki*. However, there does appear to be a third morphological form, apart from "*G.*" *nihensis* and "*G.*" *kueitensis* (= "*G.*" *yushensis*), within the "*G.*" *blacki* group described by Teilhard de Chardin and Trassaert (1938). For example, THP 19036, a male cranium (Fig. 5), has a braincase that is even shorter than "*G.*" *kueitensis* with a stronger curvature from the facial axis. The horn cores are almost perpendicular to the braincase roof, distinct from that of "*G.*" *nihensis*. Chen (1997) believed that "*G.*" *blacki* was directly derived from "*G.*" *gaozhuangensis*, which was referred to as "*G.*" *gaudryi*, form B, in Teilhard de Chardin and Trassaert (1938) (Fig. 5).

Bohlin (1938) established "*G.*" *paragutturosa* based on several lower Pleistocene localities. He thought that "*G.*" *paragutturosa* belongs to the *Procapra* group. Chen (1997) further recognized an evolutionary line: "*G. nihensis*" — "*G. yushensis*" (*kueitensis*) — "*G.*" *paragutturosa*. "*G.*" *paragutturosa* is slightly larger than "*G.*" *nihensis* from Tongde and Yushe. The braincase is relatively long, with the occipital surface strongly facing laterally, and the condyles being caudally to the paroccipital process. However, the sample of "*G.*" *paragutturosa* also shows variations. For example, the cranial from Loc. 64 (Huailai of Hebei Province) slightly differs from that from Loc. C (Mianchi of Henan Province) in the shorter braincase that is slightly more bent, and the latter one resembles "*G.*" *nihensis* more than the former. The difference between the Loc. C and Loc. 64 cranial just resembles the difference between "*G.*" *kueitensis* and "*G.*" *nihensis*, which is also the reason we did not confidently verify the validity of "*G.*" *nihensis*. Nevertheless, we agree with the previous thought that "*G.*" *nihensis* is morphologically closer to *Procapra* spp. than to *G. subgutturosa*. *P. gutturosa* possesses smaller bullae and relatively longer braincase than *G. subgutturosa*. However, whether "*G.*" *nihensis* belongs to the *Procapra* lineage does not leap to conclusion, because the strongly elongated cranium that is little bent from the facial axis, and the strongly caudally inclined horn core in "*G.*" *nihensis* are very specialized features that is absent in *Procapra* spp.

Until now, we have not discussed other *Gazella*-like taxa outside of China. Other Eurasian "*Gazella*" species include at least Miocene "*G.*" *deperdita* (Gervais, 1847), "*G.*" *capricornis* (Wagner, 1848), "*G.*" *pilgrimi* Bohlin, 1935, "*G.*" *mytilinii* Pilgrim, 1926, "*G.*" *ancyrensis* Tekkaya, 1973, "*G.*" *lydekkeri* (Pilgrim, 1937; Solounias, 1981; Kostopoulos, 2005; Bibi and Güleç, 2008; Kostopoulos and Bernor, 2011), and the Pliocene and Pleistocene "*G.*" *borbonica* Depéret, 1884, "*G.*" *bouvrainae* (Kostopoulos, 1996), and "*G.*" *aegaea* Athanassiou, 2002 (Depéret, 1887; Kostopoulos and Athanassiou, 1997; Athanassiou, 2002). In previous studies, the Miocene species are often confusing because of intraspecific variation and interspecific overlapping (Pilgrim, 1937; Solounias, 1981; Kostopoulos, 2005; Bibi and Güleç, 2008; Kostopoulos and Bernor, 2011). However, resent studies indicate that these species can be well separated based on careful morphometrical investigations (Kostopoulos, 2016; Orak et al., 2021). Particularly, "*G.*" *lydekkeri*, which was ever thought to be synonymized with "*G.*" *pilgrimi* (Solounias, 1981), now is considered to be a pivot species that is positioned at the base of the whole Antilophini (Bärmann, 2014).The Miocene taxa are small (except for "*G.*" *mytilinii*) with relatively low tooth crowns, and the Pliocene and Pleistocene "*Gazella*" species have relatively larger sizes with higher tooth crowns, and some are even larger than "*G.*" *sinensis* (Athanassiou, 2002). However, all these species possess shorter braincases, and more or less bent cranial-facial axes. They clearly differ from "*G.*" *nihensis*.

Fossil records of "*Gazella*" from Africa begin in the late middle Miocene. The genus is not diverse until the Pliocene. "*Gazella*" sp. from Fort Ternan is possibly the earliest known representative of the genus (Gentry, 1970, 2010). Other species are mostly found in the Pliocene and Pleistocene sites, including extant species such as "*G.*" *thomsonii* (Günther, 1884) (*Eudorcas thomsonii*), "*G.*" *rufifrons* (Gray, 1846) (*E. rufifrons*), "*G.*" *granti* (Brook, 1872) (*Nanger granti*), *G. dorcas* (Linnaeus, 1758), and "*G.*" *cuvieri* Ogilby, 1841 (Gentry, 2010). Most of these taxa, including living species, differ from "*G.*" *nihensis* from Tongde and Yushe in having shorter braincases and more or less bent cranial-facial axes, as well as more erected horn cores, similar to most fossil taxa. However, it should be noted that some of the extant Antilopina also have some features like "*G.*" *nihensis*. First, the living *Litocranius walleri*, the gerenuk or long-necked gazelle, possesses a greatly elongated braincase, even longer than that of "*G.*" *nihensis* (Fig. 6). Specifically, the squamosal part of the occipital (dorsal surface of the occipital) is greatly caudally projected, showing a sharp occipital angle smaller than 90°. The curvature between the cranial-facial axes is small and the facial part is low, both features being close to that of "*G.*" *nihensis*. However, in *Litocranius walleri*, the tympanic bulla is laterally compressed, and the horn cores are more erect and laterally divergent. These features are distinct from "*G.*" *nihensis*. The caudally projected occipital in *L. walleri* may be related to the elongation of the neck. However, on one hand, other long-necked gazelles, such as *Ammodorcas clarkei* (Thomas, 1891) and *Nanger dama* (Pallas, 1766), have an occipital part in a normal condition. On the other hand, "*G.*" *nihensis* has a normal axis that did not elongate. Therefore, the elongation of the braincase in "*G.*" *nihensis* and *L. walleri* appears to be a parallel evolution, but with unknown functional selection pressure. Second, another two taxa, the living *Antidorcas marsupialis* (Zimmermann, 1780), the springbok, and *Am. clarkei* possess a pair of horncores that are strongly caudally inclined. This feature is close to that of "*G.*" *nihensis*, although in *An. marsupialis* and *Am. clarkei* the horncores are slightly anteriorly bent, distinct from that of other antilopines. Nevertheless, in *An. marsupialis* and *Am. clarkei* (Fig. 6), the cranium is more bent from the facial axis than that of "*G.*" *nihensis*. Interestedly, *L. walleri*, *Am. clarkei* and *An. marsupialis*, are phylogenetically closely related — *Litocranius* and *Ammodorcas* constitute a monophyletic group, which is the sister group of *Antidorcas* (Fig. 4). The cranial morphology between *Litocranius* and *Ammodorcas*/*Antidorcas* is great. However, they are linked by "*G.*" *nihensis*, which possesses the specialist characters of both groups. However, in spite of widely separated in time and space (Pliocene of the Qinghai-Tibetan Plateau and Africa), "*G.*" *nihensis* and the *Litocranius*–*Ammodorcas*–*Antidorcas* clade should be further investigated.

Our maximum parsimony analysis employing New Technology search generated two equally most parsimonious trees, with the strict consensus topology (Fig. 7)


(a)
Lw Pg Gs Gnt Gny Am
pedical axis
cranial surface
(b)
Gs
Am
Gnt
Pg
Gny
Lw
(c)
cranial axis
facial axis
Am
Gs
Pg
Lw
Gnt
Gny
20 mm
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)

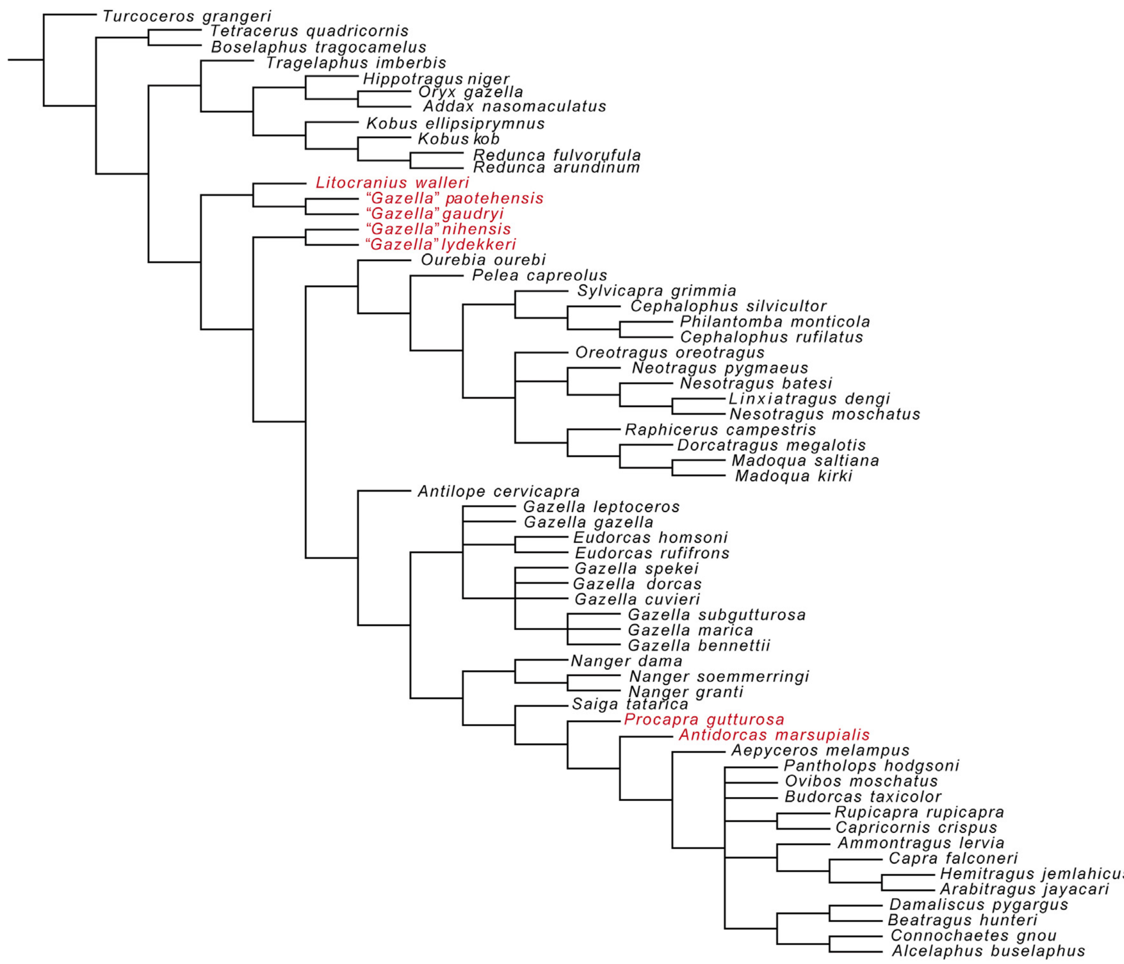


Fig. 7. The strict consensus tree from two most-parsimonious trees using TNT 1.1 (see Supplementary data S3) with tree length of 731, CI (consistency index) of 0.198, RI (retention index) of 0.623. The taxa discussed in the present article are marked in red.

revealing three critical relationships: *L. walleri* forms a basal antilophine clade with "*G.*" *gaudryi* and "*G.*" *paotehensis*, followed by the secondary divergence of "*G.*" *nihensis* and "*G.*" *lydekkeri* as sister to crown Antilophini, while *Antidorcas marsupialis* clusters phylogenetically with *P. gutturosa*, demonstrating distinct separation from both *L. walleri* and "*G.*" *nihensis*. Despite inherent limitations in morphological bovid systematics due to pervasive craniodental homoplasy, our reconstruction positions *L. walleri* in close proximity to those fossil "*Gazella*" taxa. Notably, the phenotypic convergence between "*G.*" *nihensis* and extant African antelopes — potentially reflecting either retained plesiomorphy or adaptive parallelism — highlights evolutionary dynamics among open-habitat specialists, underscoring the complex interplay of morphological evolution and ecological adaptation in antilophine phylogeny.

6. Conclusions

In this article, we described a new "*Gazella*" cranium from Tongde, on the Qinghai-Tibetan Plateau. The new cranium shows a considerably elongated braincase and a weakly curved cranial-facial axis with strongly caudally inclined horn cores. The new specimen slightly differs from "*G.*" *kueitensis* from the adjacent region of the same age and resembles "*G.*" *nihensis* from the Pliocene of the Yushe

Fig. 6. Comparisons of selected living Antilopini and "*G.*" *nihensis*. (a–c) Line drawings showing the morphological comparisons of horncore pedical inclination (green lines and below) (a), nuchal crest angle (cyan lines and below) (b), and cranial-facial curvature (pink lines and below) (c). (d–o) Photos of living Antilopini for morphological comparison, including *P. gutturosa*, AM 57252 in left lateral (d), dorsal (e), and median sagittal (f) views; *G. subgutturosa*, AM 83691 in left lateral (g), dorsal (h), and median sagittal (i) views; *Litocranius walleri*, AM 98139 in left lateral (j), dorsal (k), and median sagittal (l) views; *Antidorcas marsupialis* AM 233054 in left lateral (m), dorsal (n), and median sagittal (o) views. Abbreviations: Am, *An. marsupialis*; Gnt, "*G.*" *nihensis* from Tongde (the study specimen); Gny, "*G.*" *nihensis* from Yushe (the type specimen); Gs, *G. subgutturosa*; Lw, *L. walleri*; Pg, *P. gutturosa*.

region. Although we are not certain whether "*G.*" *nihensis* is a synonym of "*G.*" *kueitensis*, the considerably elongated braincase in the former is a distinct feature that differs from most known fossil and extant *Gazella*-like species. At present, we suspect the previous opinion that "*G.*" *nihensis* is closely related to living *Procapra*, since although existing some resemblances, some specialized features, such as strongly elongation cranium that is little bent from the facial axis, and the strongly caudally inclined horn core in "*G.*" *nihensis* are absent in *Procapra* spp. However, these features are present in some African Antilopina, such as *L. walleri*, *Am. clarkei* and *An. marsupialis*, this problem should be further explored. The new specimen exhibits several important features that are potentially significant for understanding the evolution of *Gazella*-like taxa not only in China but also globally. Further research on this specimen could help clarify taxonomic relationships and contribute to our broader understanding of the "*Gazella*" evolution.

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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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palwor.2025.200960.

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