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The first Asian skeleton of *Diaceratherium* from the early Miocene Shanwang Basin (Shandong, China), and implications for its migration route

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ABSTRACT

Owing to the scarcity of records, the Asian evolution and migration of *Diaceratherium,* a large extinct genus of rhinoceros of the Teleoceratini, remain unclear. The skeleton described herein, from the early Miocene Shanwang Basin in China, is identified as *Diaceratherium shanwangense*, a species originally defined based on upper cheek teeth. This skeleton features a large body, short horn-bearing nasal bones, moderately retracted nasal notch at the P3 level, and the metapodials that are less massive than those in other previously identified species of *Diaceratherium*. Mammalian fossils reported from the Oligocene–Miocene transition of the Old World, such as *Dorcatherium* and *Amphicyon*, have indicated a migration route between Europe and Eastern Asia via Southern and South-eastern Asia, namely along the southern margins of the Tibetan Plateau. However, the fossil remains of *Diaceratherium* reported in this study were discovered in eastern China, which represents the second accurate record of the genus in Asia (together with its presence in Kazakhstan). Consequently, given the temporal range and geological distribution of *Diaceratherium*, we propose that the expansion of this genus to the eastern part of the continent occurred via a route following the northern margins of the Tibetan Plateau, which if verified, represents an alternative expansion route differing from the established routes of other mammals.

1. Introduction

1.1. Geological setting

The Shanwang Basin in eastern China is filled with sediments of diatomaceous lacustrine shales, fluvial sandstones, and volcanic and volcaniclastic rocks, which contain numerous exceptionally well-preserved fossils (Young, 1936, 1937; Pei et al., 1963; Deng et al., 2003). The sedimentary sequence has been named the Shanwang Series, in which the Shanwang Formation is placed between the underlying Niushan Formation and the overlying Yaoshan Formation (Young, 1936; Sun, 1961; Pei et al., 1963; Yan et al., 1983; Li et al., 1984; Sun et al., 2002; Deng et al., 2003). To date, most of the fossils found in this area have been recovered from the lacustrine diatomite shale within the Shanwang Formation, which was deposited during the early Miocene, approximately 18 million years ago (Deng et al., 2003; He et al., 2011; Qiu and Qiu, 2013). The reconstructed flora of the early Miocene Shanwang Basin indicates that currently the mean annual temperature was within the range 10.9–14.5 °C and the mean annual precipitation was between 1107.3 and 1880.0 mm (Sun et al., 2002; Yang et al., 2007). The vertebrate fossils indicate that during the early Miocene, the Shanwang Basin had a closed forest environment and a predominantly tropical or subtropical climate (Yan et al., 1983; Qiu and Qiu, 2013).

The fossil record of the early Miocene Shanwang Basin includes the remains of at least 25 mammalian taxa, along with those of six birds, three reptiles, eight amphibians, and six teleosteans (Deng et al., 2003; Qiu and Qiu, 2013), which collectively comprise the Xiejiahe Fauna (formerly referred to as the Shanwang Fauna) (Qiu and Qiu, 2013). The

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fossil fauna of the Shanwangian Stage/Age includes taxa from the early Miocene Shanwang Basin that are characterized by the co-occurrence of relict genera of the Oligocene and newly emerged genera of the Neogene, and is comparable to the Orleanian (MN 3–MN 5) European Land Mammal Age (Li et al., 1984; Deng et al., 2003). Other assemblages referred to as Shanwangian include the Sihong Fauna from eastern China and the Xishuigou Local Fauna, Gashunyinadege Fauna, Upper Aoerban Fauna, Urtu Local Fauna, and Duitinggou Local Fauna from north-western China (Tong et al., 1995; Qiu et al., 2013).

1.2. Records of Diaceratherium

Diaceratherium is an extinct genus of rhinoceros, the species of which are the second largest Teleoceratini from the late Oligocene–early Miocene (Cerdeño, 1993; Heissig, 1999, 2017; Becker et al., 2009). In recent years, the taxonomy of this genus has undergone review, with Jame et al. (2019) confirming seven valid species: *D. tomerdingense* Dietrich, 1931, *D. lemanense* (Pomel, 1853), *D. aurelianense* (Nouel, 1866), *D. asphaltense* (Depéret and Douxami, 1902), *D. aginense* (Répelin, 1917), and *D. lamilloquense* Michel, 1983 (in Brunet et al. 1987), all of which are from Western Europe, and *D. askazansorense* Kordikova, 2001, from Asia. Following a revision of the European taxa, Jame et al. (2019) rejected the previous proposal of the synonymies of *D. tomerdingense* with *D. aginense* (Antoine and Becker, 2013; Becker et al., 2018) and *D. tomerdingense* and *D. asphaltense* with *D. lemanense* (Boada-Saña et al., 2007), as well as the relocation of *D. aurelianense* in the genus *Prosantorhinus* (Heissig, 1974, 2017), and also commented on the doubtful generic attribution of *D. massiliae* Ménouret et Guérin, 2009, following Antoine and Becker (2013).

In addition to *D. askazansorense*, other references to *Diaceratherium* in Asia relate to the assessments of Borissiak (1927), who determined *D. aurelianense* var. *gailiti* from the Turgai area of Kazakhstan (not mentioned by Kordikova, 2001); Marivaux et al. (2004), who assigned an isolated P2 specimen (presently lost) from central Thailand to *D.* cf. *lamilloquense*; and Sizov and Klementiev (2015), who mentioned *Diaceratherium* sp. cf. *D. aginense* from the Tagay site in Siberia. However, these assignments await further confirmation. The rhinocerotids remains discovered in earliest Miocene Bugti Hills, Pakistan, include *Mesaceratherium*, *Plesiaceratherium*, *Protaceratherium*, *Brachypotherium*, *Prosantorhinus*, and *Bugtirhinus*, but *Diaceratherium* is absent which have previously been assigned as *Brachypotherium* sp. by Antoine et al. (2013) could potentially belong to *Diaceratherium* (Métais et al., 2009; Antoine et al., 2010) (P. O. Antoine, personal communication to X. Lu, 2021). However, given the necessity of a full revision, this record is not further considered in the present paper. Thus, even though most species appear to have been endemic to Western Europe, the record of *Diaceratherium* in Asia implies vicariant events or intermittent eastward pathways during the late Oligocene and early Miocene (Antoine and Becker, 2013; see also Jame et al., 2019). In contrast, rhinoceroses within the tribe Teleoceratini arrived in North America during the early Hemingfordian period (early Miocene), represented by the single genus *Teleoceras* (Prothero, 2005; Short et al., 2019).

With respect to the Shanwang Basin, Wang (1965) described the species "*Plesiaceratherium*" *shanwangensis* from the Xiejiahe locality, whereas at a later date, Xie (1982) attributed a new specimen from the same locality to this taxon. More recently, Lu et al. (2016) have re-assigned both *P. shanwangensis* and *Aceratherium* sp. (Wang, 1965; Hu, 1957; Xie, 1982) from the Shanwang Basin as *Plesiaceratherium gracile*. On the basis of the present detailed study of a skeleton from the early Miocene Shanwang Basin, we have been able to confirm the presence of the Teleoceratini in Eastern Asia. It has also provided us with an opportunity to undertake a taxonomic re-evaluation of the species *P. shanwangensis*, which different authors have previously classified into either the genera *Brachypotherium* or *Diaceratherium* (Yan et al., 1983; Deng et al., 2003; Qiu and Qiu, 2013; Qiu et al., 2013). However, although these authors had been aware of this skeleton, it is described for the first time herein.

2. Material and methods

In this paper, we focus on a well-preserved skeleton (STM 44–98) found in the Jijiazhuang locality of the Shanwang Basin, and is currently stored at the Tianyu Museum of Natural History, Pingyi (China), (Fig. 1). Although discovered in 2003, the skeleton has never been described in detail, which can be ascribed to the fact that details of the specimen are only partially exposed. Accordingly, certain characteristics, including the cheek teeth and numerous limb bones, could not be fully investigated, with only the foot bones being partially measurable (rapidly and without permission to remove the fossil from its showcase). These restrictive circumstances have also hindered photography of the specimen with high quality and from different views. We compared this specimen with the holotype (IVPP V 3026) of the previously described *P. shanwangensis* from the Xiejiahe locality, within the same basin, as well as with the remains of other species of *Diaceratherium* (from bibliographic sources). Hereafter, following the International Commission on Zoological Nomenclature (1999), we adopt *shanwangense* as the specific epithet to be used in conjunction to the re-assigned generic name *Diaceratherium*.

The systematic position of teleoceratines has been discussed by many authors. In recent papers, Antoine et al. (2010), Antoine and Becker (2013) included it within the Tribe Rhinocerotini, whereas, Heissig (1999, 2017) have insisted the traditional classification suggestion. In

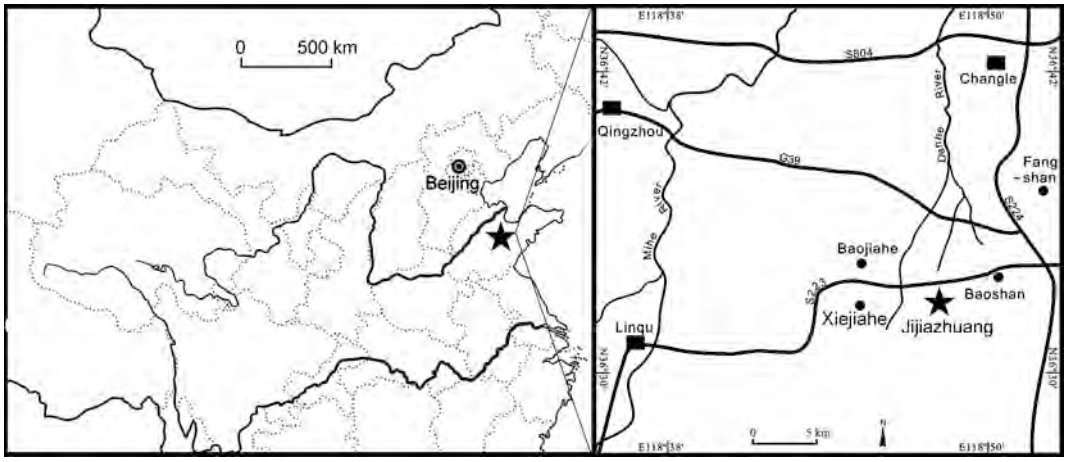

Fig. 1. Geographical location of Jijiazhuang locality in Shanwang Basin, Shandong Province, China. [planned for page width].

this paper, we follow Heissig's (2017) suggestion about teleoceratines, and include *Diaceratherium* in this group.

Morphological descriptions follow the standard terminology applied to perissodactyls, particularly for rhinocerotids (e.g. Guérin, 1980; Cerdeño, 1993; Qiu and Wang, 2007, among others), and measurements are based on the widely used protocol developed by Guérin (1980).

Institutional Abbreviations: **IVPP V**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; **STM**, Tianyu Museum of Natural History, Pingyi, Shandong, China.

Anatomical Abbreviations: **M/m**, upper/lower molar; **P/p**, upper/lower premolar.

3. Systematic palaeontology

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1921
Subfamily ACERATHERIINAE Dollo, 1885
Tribe Teleoceratini Hay, 1902

DIACERATHERIUM Dietrich, 1931

Type Species: *Diaceratherium tomerdingense* Dietrich, 1931

Included Species: *Diaceratherium lemanense*, *D. aurelianense*, *D. asphaltense*, *D. aginense*, *D. lamilloquense*, *D. shanwangense*, and *D. askazansorense*. See the aforementioned comments regarding the different taxonomic proposals for these species.

Diagnosis: Medium-sized rhinoceros, with a small terminal nasal horn. Strong premaxillae have a pair of large I1. Infraorbital foramen and posterior border of nasal notch are above P3. Occipital part raised. Symphysis moderately widened. Mandible with a horizontal ventral edge. Four robust functional metacarpi. All upper incisors and canines reduced, but with large I1 (up to 60 mm) and tusk i2. Upper premolars fully molarized or with lingual bridge. Upper cheek teeth without crista, but both crochet and antecrochet present. Moderately constricted protocone and hypocone of upper molars. Labial cingulum fully present or slightly reduced.

Horizon and Locality: Late Oligocene to early Miocene (MP 29–MN 4); Spain, France, Germany, and Switzerland (Europe); Kazakhstan, Thailand, and China (Asia).

DIACERATHERIUM SHANWANGENSE (Wang, 1965)

(Figs. 2–3; Figs. S1–S7; Tables 1–3)
1965, *Plesiaceratherium shanwangensis* Wang, original description
1983, *Brachypotherium shanwangensis* Wang, Yan et al., p. 215
2003, *Brachypotherium shanwangensis* Wang, Deng et al., p. 317
2003, *Diaceratherium* sp., Deng et al., p. 317
2013, *Diaceratherium* sp., Qiu and Qiu, p. 144
2015, *Diaceratherium* sp., Deng, p. 96
2016, *Plesiaceratherium shanwangensis* Wang as a synonym of *Plesiaceratherium gracile* Young, Lu et al., p. 2

Holotype: IVPP V 3026, left maxilla, with P2–M3.

Type Horizon and Locality: Shanwang Formation, early Miocene Shanwangian Stage/Age of China, corresponding to the MN 4 (middle of Orleanian) of Europe; Xiejiahe locality in the Shanwang Basin, Shandong Province, China (Fig. 1).

Referred Materials: STM 44–98, adult skeleton, with well-preserved cranial and postcranial bones, from the Jijiazhuang locality of the Shanwang Basin, Shandong Province, China.

Amended Diagnosis: Medium-sized species with shorter nasal bones than *D. aginense*, saddle-shaped skull roof, moderately retracted nasal notch above P3, as in *D. asphaltense*, orbit above M1, short posterior edge of the external auditory pseudomeatus, tall and broad zygomatic arch, large incisors, and robust but longer metapodials than those of *D. aginense*. A small terminal nasal horn present. Facet for the pyramidal carpus present on distal extremity of radius. The upper cheek teeth subhypsodont; the parastyle, paracone rib, antecrochet, and crochet are developed; both the protocone and hypocone are constricted; the lingual cingulum is developed, but the labial cingulum is absent. Proximal width of magnum close to but smaller than height. The second and third astragalus facets in calcaneus are not continuous. Facet for fibula is present on calcaneus.

3.1. Description

Skull: The dorsal profile of the skull is slightly undulated on the two anterior thirds, rising posteriorly. The nasal bone is stout, with a developed lateral droop. The middle part is slightly concave, and the anterior part is slightly raised, with a small bump at the tip, which is narrow yet blunt. There is a small horn boss situated on the anterior fourth of the nasals (Fig. 2). The nasal notch has a U-shaped profile and extends backwardly to the level of the anterior part of P3. The infraorbital foramen is below the posterior rim of the nasal notch and opens forwardly, with a rounded entrance. The premaxilla extends beyond the level of the nasal tip and holds a large upper incisor (I1); its posterior part tapers gradually and terminates below the posterior edge of the nasal notch. The lacrimal tubercle is a long narrow crest. The anterior rim of the orbit lies above the middle of M1. The upper rim of the orbit terminates at a very short postorbital process of the frontal bone. The zygomatic arch rises posteriorly, similar to the posterior third of the skull and lies high above the cheek teeth approximately 30 mm from the alveolar edge. The posterior region is untapered, with the upper edge protruding to form a process above the external auditory pseudomeatus. The temporal condyle is prominent and has a concave forward profile.

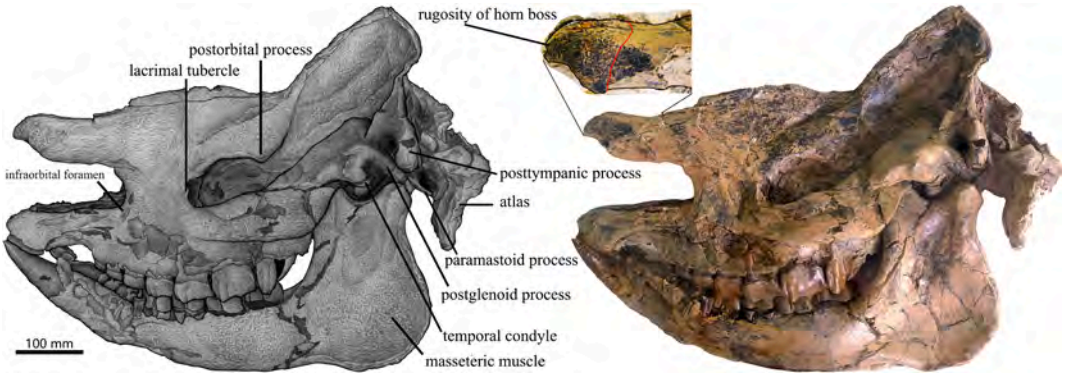

Fig. 2. Skull of *Diaceratherium shanwangense* STM 44–98, left view. The region of horn boss is marked by red dash line, and the dark line delimits boundary between nasal bone and diatomaceous shales. [planned for page width] (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

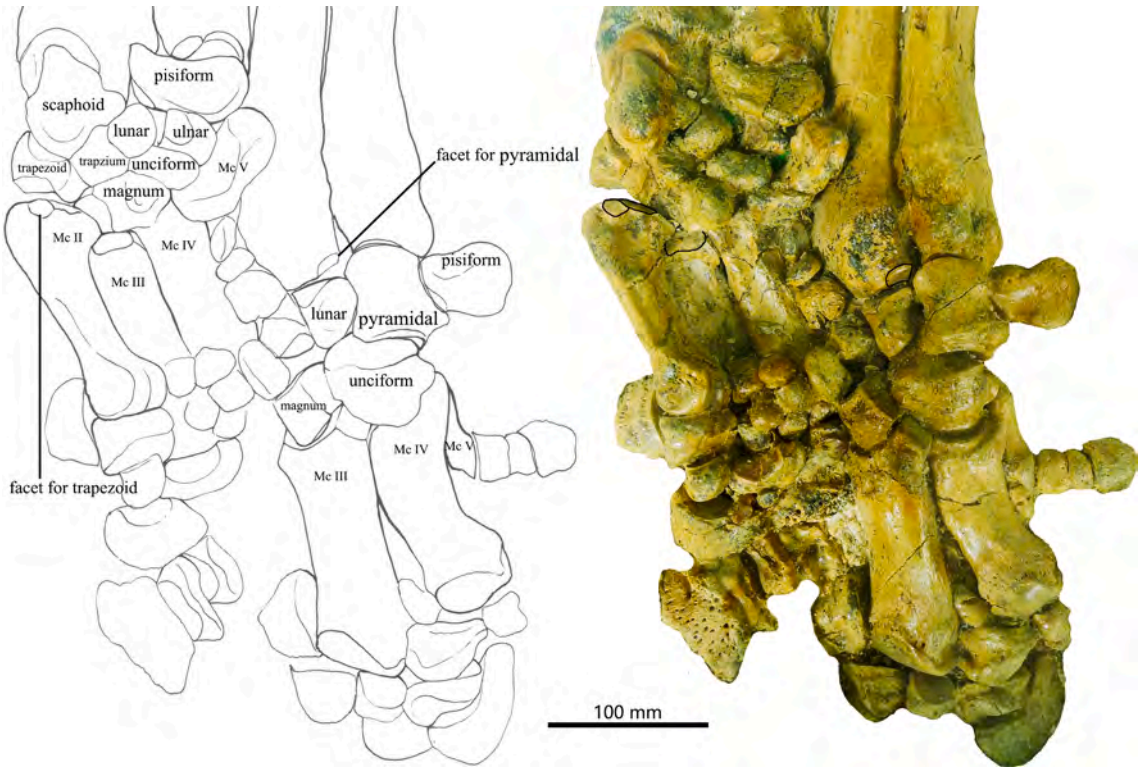

Fig. 3. Carpus, metacarpus, phalanges, and distal part of radius and ulna of *Diaceratherium shanwangense* STM 44–98. Original and schematic drawing. [planned for page width].

The external auditory pseudomeatus has a wide, round, and steep entrance and is ventrally closed by contact between the post-tympanic and postglenoid processes. The posterior edge of the entrance is short and restricted to the lower half of the temporal crest. The paramastoid process is bent backwardly, whereas the occipital face is inclined in a forward direction, and the parietal crests in the sagittal crest are not fused. The temporal crest on the roof of the skull is not incised posteriorly.

Mandible: The ventral edge of the horizontal ramus is smoothly convex, slightly upwardly curved at the symphysis, and with a marked concavity prior to the posterior mandibular angle. This angle is blunt and expands backwards. The posterior edge of the ascending ramus is inclined forwards, and the lateral depression of the masseteric muscle is deep and located in the upper half of the ascending ramus.

Teeth: Upper incisor I1 is large, the long axis of which extends backwardly and slightly outwardly. Lower incisor i2 tapers rapidly from the root to the crown tip, with the occlusal surface being directed upwardly in the upper third, but curved slightly outwardly down to the root. The upper cheek teeth consist of DP1–M3 and the lower cheek teeth p2–m3. Features on the cheek teeth are observable only on the labial walls, as other areas are unexposed. There is no labial cingulum; the upper cheek teeth exhibit a prominent parastyle and paracone rib; and the metacone rib and mesostyle are absent (Fig. 2).

Postcranial Bones: The postcranial bones are well preserved, but only partially accessible for morphological description and comparison.

The atlas has a short and wide spinous process with a long anterior end (Supp. 1: Fig. S1). The other cervical vertebrae are poorly preserved. The spinous process is high, shortening progressively on the first nine thoracic vertebrae, and is short and slightly variable on the posterior eight. The articular facets of the rib head in the fifth and sixth thoracic vertebrae are shallow and oval. The rib tubercle facets of the posterior two thoracic vertebrae are notably smaller than those of the thoracic vertebrae anterior to the last two (Supp. 1: Fig. S1). Five lumbar vertebrae are present, the first of which has a vertebral body and spinous process similar to that of the posterior thoracic vertebrae. The preserved fourth and fifth lumbar vertebrae exhibit a long transverse process, with that in the fifth lumbar vertebra being longer. In the fifth lumbar vertebra, the posterior edge of the transverse process is medially concave, lateral to which is an oblique articular facet for the crest of the ilium (Supp. 1: Fig. S2). The sacrum is composed of five sacral vertebrae, which display isolated short spinous processes and fused transverse processes; a sacral foramen is present between the vertebrae (Supp. 1: Fig. S2). The lateral edges of the transverse processes of the final sacral vertebra and the first coccygeal vertebra are connected, although not fused. The spinous and transverse process of the coccygeal vertebrae are considerably shorter than those on the sacrum, and progressively decrease in size posteriorly; the fifth coccygeal vertebra is fully reduced, as a short cylindrical bone with four weak sagittally extended crests.

In the forelimb, the humerus shows the deltoid tuberosity located on the upper half of the bone, continuing on the humeral crest, tuber scapula is large, and the distal extremity has a large lateral epicondyle showing prominent outward expansion, indicating a strong muscle extensor of the forearm (Supp. 1: Fig. S3). The radius has an articular facet for the pyramidal carpus in the distal extremity (Supp. 1: Fig. S4). The medial articular facet for the radius is fusiform in the distal extremity of the ulna, with two narrow ends. The ulna has a concave posterior edge, the narrower point of which is around the central part of the shaft. The olecranon is short and stout, forming an open angle with the diaphysis.

None of the carpal bones have exposed articular facets, although some general features are observable: the semilunate has a round distal end at the anterior face; the proximal width of the magnum is close to but smaller than its lateral height; in the unciform, the articular facets for the pyramidal and the semilunate form a blunt angle (Fig. 3).

The metacarpals are short and stout (Fig. 3). Mc V is present and functional, and Mc II has a medial articular facet for the trapezoid. In Mc III, the lateral articular facet for Mc IV is continuous with that for the magnum. The shaft of Mc IV is outwardly curved at its middle part. The

Table 1
Measures (in mm) of the skull STM 44–98 of *Diaceratherium shanwangense* from the early Miocene Shanwang Basin, China, compared with other species of *Diaceratherium*: *D. ag*, *D. aginense* (Laugnac, France; Répelin, 1917); *D. as*, *D. asphaltense* (Pyrimont-Challonges, Becker et al., 2009); *D. au*, *D. aurelianense* (Turgai, Kazakhstan, Borissiak, 1927; and Neuville-aux-Bois, France, Cerdeño, 1993); *D. le*, *D. lemanense* (from Gannat, Becker et al., 2009).

	STM 44–98	*D. le*	*D. as*	*D. ag*	*D. au*
Distance between occipital condyle and premaxilla	>526	554	–	–	–
Distance between occipital condyle and nasal tip	>515	539	625	–	–
Distance between nasal tip and occipital crest	>459	509	–	540	428
Distance between nasal tip and bottom of nasal notch	128	167.5	193	–	160
Minimal width of braincase	–	–	–	–	–
Distance between occipital crest and postorbital process	>166	–	305	–	266
Distance between occipital crest and supraorbital process	>214	–	325	340	–
Distance between occipital crest and lacrimal tubercle	>252	324	360	–	–
Distance between nasal notch and orbit	78	52.5	85	100	85
Distance between occipital condyle and M3	>196	193	260	–	–
Distance between nasal tip and orbit	202	220.5	278	–	–
Width of occipital crest	–	–	–	–	
Width of paramastoid processes	–	–	175	–	269
Minimal width between parietal crests	–	–	17	–	–
Width between postorbital processes	–	150	140	–	171
Width between supraorbital processes	–	166	135	–	–
Width between lacrimal tubercles	–	–	140	–	–
Maximal width zygomatic arches	–	217	~290	340	350
Width of nasal base	–	59	80	–	130
Height of occipital surface	–	–	–	–	–
Cranial height in front of P2	~79	191	100	–	–
Cranial height in front of M1	~220	195	95	–	–
Cranial height in front of M3	~206	157	–	–	–
Width of palate in front of P2	–	–	52.5	–	–
Width of palate in front of M1	–	–	69	–	–
Width of palate in front of M3	–	–	72	–	–
Width of foramen magnum	–	–	48	53	53
Total Length of skull (with incisors)	499	–	–	500	–
Height of horizontal ramus before p4	52	–	–	~60	–
Height of horizontal ramus before m1	55	–	–	–	–
Height of horizontal ramus before m2	66	–	–	–	–
Height of horizontal ramus before m3	74	–	–	–	–
Height of horizontal ramus behind m3	83	–	–	–	–
Height of coronoid process	280	–	–	–	–
Antero-posterior diameter of ascending ramus	164	–	–	–	–

left Mc III is 158 mm in length.

Within the pelvic girdle (Supp. 1: Fig. S2), the anterior border (or crest) of the wing of the ilium is regularly convex, with its medial part bearing a shallow concavity for articulation with the transverse process of the final lumbar vertebra. The wing of the ilium is well expanded, with nearly symmetrical medial and lateral surfaces; the latter is somewhat narrower. The tuber sacrale of both wings are in contact with each other.

The proximal epiphysis of the femur (Supp. 1: Fig. S5) is incomplete, and the third trochanter is short and situated in the upper half of the shaft. The distal epiphysis is wide and robust; the trochlea has a shallow but wide middle groove, and the lateral crest limits a concave lateral surface. The fossa in the lateral condyle of the extensor and popliteus muscles is distinct.

The patella, which is displaced from its original anatomical position (Supp. 1: Fig. S5), is large with a rounded distal end.

In the tibia, which is not fused with the fibula (Supp. 1: Fig. S6), the intercondylar crest is acute, and the ligament sulcus is deep and wide. In the distal extremity, the medial malleolus is long and round. The fibula articulates with the tibia below the proximal surface of the latter, and it is laterally curved to fit with the tibia; laterodistally, it has a deep groove for attachment of the lateral extensor tendon (not shown in figure).

In the tarsus, the astragalus has a steep articular facet for the fibula. The first calcaneus facet has a short distal extension, whereas the second facet is flat. In the dorsal view, the dorsoplantar edge of the astragalus is contorted. The calcaneus has separated second and third astragalus facets, and there is a small fibular facet (Supp. 1: Fig. S7-S8). The tuber calcis is strong, with a rounded tip. The sustentaculum forms an approximate right angle with the body of the calcaneus, and is continuous, without forming a tubercle. The cuboid mainly exposes the lateral face, showing the posterior tuberosity distally extended over the distal articular facet; a substantiable portion of the proximal facet for the calcaneus is observable and projects laterally (Supp. 1: Fig. S8). Other tarsals are covered by other bones, and are thus inaccessible. On the lateral side, the left Mt IV bears a strong tuberosity for attachment of the tendon below the proximal articular facet. The exposed ventral side of the distal part of several metatarsal bones shows an obvious middle keel in the trochlea, some of which preserve the sesamoids in an anatomical position (Fig. S7-S8).

3.2. Comparisons

Among the main features of the well-preserved skeleton STM 44–98 is a small-horned nose. Although this characteristic is present in a number of Eurasian rhinocerotids, several of these taxa can readily be ruled out as candidates for specimen STM 44–98, based on either this or other features: Elasmotheriinae include gracile rhinoceroses with cemented and hypsodont cheek teeth; Diceratheriinae invariably bear a pair of horn bosses on the nasal bone; and Rhinocerotinae (including rhinocerotini and dicerorhini) are characterized by a shallow nasal notch, behind which lies an infraorbital foramen (Heissig, 1989; Prothero et al., 1986; Antoine, 2002). In contrast, both the horned nasal and other characteristics of STM 44–98, such as the enlarged incisors, reduced nasal notch, relatively large body, and relatively less massive metapodials, are consistent with those of the Teleoceratini, particularly *Diaceratherium* (Pomel, 1853; Nouel, 1866; Depéret and Douxami, 1902; Roman, 1912; Répelin, 1917; Dietrich, 1931; Brunet et al., 1987; Cerdeño, 1993; Becker et al., 2009), and is also consistent with the preliminary assignments of authors, which, nevertheless, were made without sufficient justification (Deng et al., 2003; Qiu and Qiu, 2013). This skeleton is different from *Brachypotherium*, especially in having a nasal horn and less advanced metapodials; it is also different from *Prosantorhinus*, because in the latter the nasal horn is subterminal, the metapodial is massive, and the body size is smaller (Heissig, 1989, 1999, 2017; Cerdeño, 1993; Antoine and Becker, 2013). We therefore further confirmed the taxonomical identity of STM 44–98 as *Diaceratherium*.

Although Wang (1965) originally differentiated "*Plesiaceratherium*" *shanwangensis* from *Brachypotherium*, this species was subsequently recognized as a teleoceratine and included in *Brachypotherium* or *Diaceratherium* (e.g. Yan et al., 1983). Moreover, Yan and Heissig (1986) excluded it from the genus *Plesiaceratherium* in a list of synonymies, although offered no further comments by way of justification. In turn, Lu et al. (2016) synonymised '*P.*' *shanwangensis* with *P. gracile*, a species likewise recorded in the Jijiazhuang locality (i.e. skull and mandible STM 44–68, Lu et al., 2016: Fig. 2), based on certain cheek teeth similarities. However, these authors failed to fully consider the cheek teeth

Table 2
Tooth measurements (length/width/height, in mm) of STM 44–98 of *Diaceratherium shanwangense* from the early Miocene Shanwang Basin, China, compared with other species of *Diaceratherium*: *D. sh*, *D. shanwangense* (Shanwang Basin, Wang, 1965); *D. ag*, *D. aginense* (Laugnac, France, Répelin, 1917); *D. as*, *D. asphaltense* (NMB-SAU 1662, Saulcet, France, Becker et al., 2009:tab. 7); *D. au*, *D. aurelianense* (Neuville-aux-Bois, France, Nouel, 1866); *D. la*, *D. lamilloquense*, (La Milloque, France, after Becker et al., 2009:tab. 7), *D. le*, *D. lemanense* (Cindré, France, after Becker et al., 2009: tab. 7); *D. to*, *D. tomerdingense* (Tomerdingen, Germany, Dietrich, 1931).

	STM 44–98	*D. sh*	*D. la*	*D. le*	*D. as*	*D. ag*	*D. au*	*D. to*
DP1	~15/-/-	21/23/-	–	21/20/-	25/24/18	25/20/21	–	25/-/-
P2	~21/-/-	33/46/-	28/37/-	26/31/-	33/39/24	31/43/27	25/35/-	31/31/33
P3	~28/-/-	42/52/-	32/41/-	32/40/-	36/48/27	36/50/36	30/46/-	34/42/35
P4	36/-/-	43/61/-	34/47/-	34/-/-	37/50/27	35/53/-	38/55/-	35/47/42
M1	48/-/-	–	46/49/-	42/52/-	48/52/24	47/61/37	42/58/-	~~4746/42~~ 47/46/42
M2	53/-/-	–	49/54/-	46/53/-	52/55/31	54/60/44	50/60/-	52/51/42
M3	–	63/58/-	43/53/-	57/46/50	44/51/31	–	52/55/-	–
I1	50/-/12	–	–	–	48/19/20	–	62/27/-	–
i2	93/-/-	–	–	–	–	–	–	–

Table 3
Measures (in mm) of metacarpus STM 44–98 of *Diaceratherium shanwangense* from the early Miocene Shanwang Basin, China, compared with other species of *Diaceratherium*: *D. ag*, *D. aginense* (Répelin, 1917); *D. au**, *D. aurelianense* from Neuville (Cerdeño, 1993); *D. au***, *D. aurelianense* var. *gailiti* (Borissiak, 1927); *D. le*, *D. lemanense*, and '*D.*' *ma*, '*D.*' *massiliae* (Ménouret and Guérin, 2009). Anatomical abbreviations: art., articulation; dia, diaphysis; dis., distal; L, length; max., maximal; prox., proximal; TD, transversal diameter.

	L	TD prox.	TD dia.	TD dis.max.	TD dis.art.
McIII					
STM44-98	158	–	–	–	–
D. le	177	83	58	73	64
'*D.*' *ma*	174	62	52	61	44
*D. au**	124	53.4	43.2	55.5	47.6
*D. au***	115	–	–	42	–
D. ag	126	46	42	52	39
Mc IV					
STM44-98	114	49	37	51	38
D. to	100	–	30	–	–
D. le	113	–	26	–	–
'*D.*' *ma*	139	47	38	48	41
*D. au**	106	42	29.5	43.8	36.5
*D. au***	90	–	–	32	–
D. ag	105	36	27	35	30

of *Diaceratherium*, the upper premolars of which lack a crista, crochet, and lingual bridge (Pomel, 1853; Nouel, 1866; Depéret and Douxami, 1902; Roman, 1912; Répelin, 1917; Dietrich, 1931; Cerdeño, 1993; Becker et al., 2009, 2018; Jame et al., 2019), whereas these structures are invariably present on the upper premolars of *Plesiaceratherium*; the only exception being *P. fahlbuschi* and *P. balkanicum*, which lacks a lingual bridge (Young, 1937; Heissig, 1972; Yan et al., 1983; Yan and Heissig, 1986; Lu et al., 2016; Becker and Tissier, 2019). In addition, the dentition of *P. gracile* (in general and particularly STM 44–68 described by Lu et al., 2016) is characterized by proportionally narrower upper premolars than those observed in '*P.*' *shanwangensis*. Accordingly, we reject the synonymy proposed by Lu et al. (2016) and consider that the species '*P.*' *shanwangensis* should be placed within the genus *Diaceratherium*, as previously proposed (Yan et al., 1983; Deng et al., 2003; Qiu and Qiu, 2013; Qiu et al., 2013). In the same paper, Lu et al. (2016) described the putative remains of *P. gracile* discovered in the Shanwang Basin, some which had previously been identified by Xie (1982) as '*P*'. *shanwangensis* and *Aceratherium* sp.; the synonymies that are herein confirmed.

Inevitably, our initial comparison of STM 44–98 with other species of *Diaceratherium* is with *D. shanwangense*, given that this species has also been described from the Shanwang Basin. However, this comparison is hampered by the fact this species is generally identified based on an upper dental series and some isolated teeth, whereas the cheek teeth of STM 44–98 are mostly covered, and thus inaccessible. Nevertheless, a row of cheek teeth and labial walls visible in the STM 44–98 specimen do permit a comparison of certain features. The parastyle and the paracone rib of these cheek teeth are well developed, whereas the metacone rib and mesostyle are absent, as is the labial cingulum in both upper and lower cheek teeth. These characteristics are comparable to those of the holotype of *D. shanwangense*, on the basis of which, we assume that the skeleton is a specimen of the taxon described by Wang (1965). For size, it is slightly sagittally shorter than the holotype, but close to other species of the genus. In contrast, features of the skull morphology and the general size and proportions substantially reduce the likelihood that STM 44–98 is a specimen of the smaller and slenderer *P. gracile* (e.g. Yan and Heissig, 1986) discovered in the same locality. Furthermore, the postcranial bones of STM 44–98 differ from *P. gracile*: its magnum has a proximal width approximating to its height, but in latter it has a much higher outline; Mc III is much shorter than *P. gracile*, which has slender Mc IV than STM 44–98, with the ratio (length/proximal width) 5.5 and 2.3, respectively.

The establishment of the Asian species *Diaceratherium askazansorense* is based on material previously described, but not identified in species level, by de Bonis et al. (1997) as *Diaceratherium* sp., the remains of which include two mandibular fragments, an astragalus, and a calcaneum. Kordikova (2001) identified the specimens as *D. askazansorense*. The lower cheek teeth have features in common with those of *Diaceratherium*, and also with *Brachypotherium* and *Plesiaceratherium*, including a developed paralophid, a notably oblique protolophid, and reduced labial and lingual cingulae. Among the observable characteristics, a reduced cingulum is also observed in STM 44–98, although the ventral profile of its horizontal ramus (albeit incomplete) appears to be less convex than that of STM 44–98 (Kordikova, 2001: Fig. 5-1a/3a), and has a less marked posteroventral inflexion. In addition, the posterior end of the symphysis of *D. askazansorense* (at the p2 level) is more anteriorly located than in other species of *Diaceratherium* (Roman, 1911; Répelin, 1917; Cerdeño, 1993). According to de Bonis et al. (1997: p. 232), the calcaneum has a strong tubercle and the width of astragalus is greater than its height (up to 115% of the height), which is like the proportions seen in *D. lemanense* and *D. aginense*, although of smaller dimension than that in *D. aurelianense* (Répelin, 1917; Cerdeño, 1993; Jame et al., 2019). The astragalus of *D. askazansorense* also differs from that of STM 44–98 in that it has a wider and shallower trochlea with a medial ridge that is clearly lower than the lateral ridge, as well as a wider distal facet of the cuboid, which in the anterior view occupies approximately one-third of the distal width of the astragalus. This wider articular facet for the cuboid in *D. askazansorense* indicates that the astragalus has a stronger articulation with the cuboid than that observed in other species of *Diaceratherium* (Répelin, 1917; Cerdeño, 1993; Jame et al., 2019).

The remains from the Turgay region (Kazakhstan) originally described by Borissiak (1927) as "*Brachypotherium*" *aurelianense* var. *gailiti* clearly differ from STM 44–98, in that they have a V-shaped nasal notch, a more robust metapodials (after measurements of Mc IV; see Table 3), and a posterior part of the skull that is less elevated.

Compared with that of the Western European species of *Diaceratherium*, the skull of specimen STM 44–98 is closer to that of

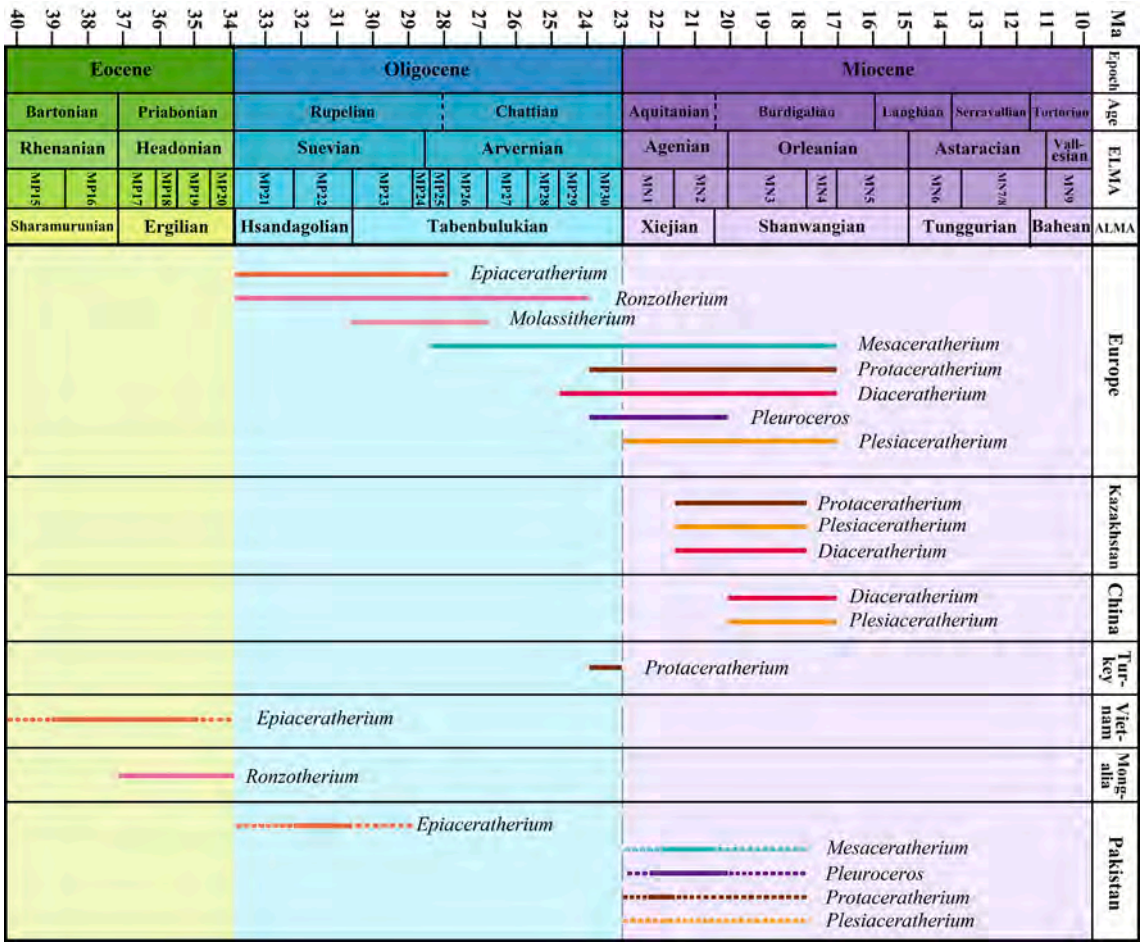

Fig. 4. Temporal ranges of rhinocerotid genera during the Late Oligocene-Early Miocene transition in the different areas around Old World. ELMA is for European Land Mammal Ages, and ALMA is for Asia Land Mammal Ages. Biochronologic ranges revised from Borissiak (1927), Young (1937), Brunet (1979), de Bonis et al. (1997), Heissig (1969, 1999), Kordikova (2001), Deng et al. (2003), Antoine et al. (2003, 2008, 2013), Becker et al. (2013), Böhme et al. (2013), Scherler et al. (2013), Pandolfi et al. (2017), Prieto et al. (2017), Blanchon et al. (2018), Jame et al. (2019), Tissier et al. (2020). [planned for page width].

D. aurelianense from the early Miocene (Nouel, 1866; Ginsburg et al., 1981; Cerdeño, 1993; Becker et al., 2009), notably with respect to the higher elevation of the posterior part of the skull in this species. The angle between the plane from the occipital border to M3 and the horizontal plane is $> 60°$, whereas it is approximately 50° in *D. asphaltense* (Roman, 1912), which is known to has occurred from the earliest Miocene (MN 1). The nasal notch in STM 44–98 is at a level (anterior half of P3) similar to that seen in *D. aurelianense*, *D. lemanense*, and *D. asphaltense*, although is shallower than that in *D. aginense*, the nasal notch of which reaches P4 (Répelin, 1917). However, Jame et al. (2019: Fig. 8D) have described one specimen of this latter species in which the notch is at the P3 level. *D. aginense* (Répelin, 1917) also differs from other species in the anterior border of the orbit at the M2 level, a slenderer zygomatic arch, proportionately longer nasal bone and with respect to the posterior rim of the external auditory pseudomeatus, which is extended to a greater extent to the upper part of the occipital side. Furthermore, the zygomatic arch in STM 44–98 is stronger than that in *D. aurelianense*, the region below the orbit is higher than that in *D. lemanense*, and the anterior border of the orbit (above M1 in STM 44–98) is more anteriorly placed than in *D. asphaltense*, that is, above M2 (Heissig, 1999; Becker et al., 2009). Moreover, *D. asphaltense* also differs from other species in the following aspects: the lateral edge of the nasals is anteriorly reduced, the entrance of the external auditory pseudomeatus is anteroposteriorly flattened, and a process is present at the posterior border of the orbit on the zygomatic arch.

With respect to dentition, I1 of STM 44–98 is moderately enlarged (50 mm), being closer to that of *D. asphaltense* (47 mm) and *D. aginense* (56 mm) than to I1 in *D. aurelianense* (62 mm), which is characterized by the largest I1 among the described species of *Diaceratherium* (Nouel, 1866; Répelin, 1917; Becker et al., 2009). However, the fact that the occlusal pattern of the cheek teeth in STM 44–98 is not directly observable considerably limits the scope for comparisons (Table 2). Nevertheless, STM 44–98 still shows the following characteristics that are similar to other species within this genus: a developed parastyle and paracone rib, the absence of a metacone rib, and a long metastyle. Moreover, the cement is absent on the labial walls of both upper and lower cheek teeth.

The limb bones of STM 44–98 appear to be similar to those of *D. aurelianense* in terms of the deltoid tuberosity in the upper half of the humerus, the closed posterior edge and strong olecranon of the ulna, and the developed lateral epicondyle. However, these species differ with respect to the third trochanter of the femur, which is more distally extended in *D. aurelianense* (Nouel, 1866; Borissiak, 1927; Cerdeño, 1993).

A comparison of the limb bones of STM 44–98 with those of *D. lemanense* described by Jame et al. (2019) revealed several features in common: the third trochanter of the femur is located at the upper half of the diaphysis, there is a strong posterior process on the distal articulation of the tibia, and there is no connection between the second and third articular facets of the astragalus and the calcaneus. However, the two differ in that *D. lemanense* is characterized by a blunt lateral ridge on the distal trochlea of the femur, compared with the acute edge seen in the

Fig. 5. Distribution and possible migration route of *Diaceratherium* throughout Eurasia from Late Oligocene to Early Miocene. European localities are summarized in a few dots; all Asian localities are marked. 1, *D. lamilloquense* from La Milloque, France; 2–4, *D. lemanense* from Gannat (France), Wischberg (Switzerland), and Oppenheim (Germany); 5–6, *D. asphaltense* from Saulcet and Pyrimont-Challonges (France); 7, *D. tomerdingense* from Tomerdingen (Germany); 8–10, *D. aginense* from Laugnac (France), Vaud (Switzerland), Hessler (Germany); 11–14, *D. aurelianense* from Molí Calopa and Rubielos de Mora (Spain), Marsolan and Neuville-aux-Bois (France); 15, *D. aurelianense* var. *gailiti* from Turgai (Kazakhstan); 16, *D. askazansorense* from Askazansor (Kazakhstan); 17, *D. shanwangense* from Xiejiahe (China). References for locality: 1, Michel (1983); 2, Roman (1911); 3, Schaub and Hürzeler (1948); 4, Tobien (1980); 5, Hugueney (1997); 6, Depéret and Douxami (1902); 7, Dietrich (1931); 8, de Bonis (1973), Heissig (1999); 9, Engesser et al. (1993); 10, Tobien (1980), Heissig (1999); 11–12, Cerdeño (1992); 13, Antoine et al. (2000); 14, Nouel (1866); 15, Borissiak, (1927); 16, Bonis (1973), Kordikova (2001); 17, present paper. Different colors refer to different species. Paleomap from website https://deeptimemaps.com/. [planned for page width].

STM 44–98 specimen, and there is no obvious ligament sulcus in the proximal epiphysis of the tibia, which is prominent in STM 44–98 (Fig. S6).

D. aginense is clearly similar to STM 44–98 with regards to the outline of the ulna, the position and development of the third trochanter and trochlea of the femur, the proximal articulation between the tibia and fibula, the long round medial malleolus of the tibia, and massive metapodials (Répelin, 1917). However, the two also differ in a number of characters; for example, in *D. aginense*, the deltoid tuberosity is located more distally; the articular facet between the radius and the pyramidal carpus, which is absent in STM 44–98, is visible; and the narrowest point of Mc III is located approximately in the middle of the shaft (Répelin, 1917), whereas in STM 44–98, both the lateral and medial sides of Mc III are irregular, and the narrowest point lies at a higher level.

The type species of the genus *D. tomerdingense*, Mc III of which has a length/width ratio of approximately 3.3 (Dietrich, 1931), has a shorter Mc IV than either STM 44–98 or *D. lemanense*, whereas *D. lemanense* and *D. massiliae* have a longer Mc III than STM 44–98 (Table 3), and the length/width ratio of Mc III in *D. lemanense* is 2.4 (measured according to Ménouret and Guérin, 2009). Moreover, Mc III in *D. aginense* is relatively shorter than that in STM 44–98 (Table 3).

In summary, on the basis of the short nasal and skull lengths, shallow nasal notch (at the P3 level), relatively large upper incisors, and relatively long but robust metapodials, *D. shanwangense* appears to be characterized by a morphology that less specialized than *D. aurelianense*.

4. Discussion

4.1. Mammalian fossils of the Xiejiahe Fauna

The faunal exchanges between Europe and Asia, which commenced at some stage during the Eocene–Oligocene transition, appear to have been correlated with global cooling events and were characterized by the Grande Coupure and Mongolian Remodelling (Stehlin, 1909; Prothero and Berggren, 1992; Meng and McKenna, 1998; Ye et al., 2002; Hooker et al., 2004; Hren et al., 2013; Wasiljeff et al., 2020). Since then, the faunal migration around Eurasia is continuous. By the Earlier Miocene, among the 25 mammalian taxa listed in the Xiejiahe Fauna, certain genera are common to the fauna of both Europe and North America, such as small mammals in the genera *Lanthanotherium*, *Eutamias*, and *Myotis* (Li et al., 1983; Qiu and Lin, 1986), and members of the carnivorous genera *Amphicyon*, *Phoberocyon*, *Pseudaelurus*, and *Ysengrinia* (Young, 1937; Li et al., 1983; Qiu and Gu, 1986; Qiu et al., 1986). Although rodents in the genus *Ansomys*, which were relatively widely distributed across Eurasia during the Neogene period, initially appear in the earliest Miocene Xiejian fauna, the earliest and most primitive species have been recorded from the Oligocene strata of North America (Hopkins, 2004). Among the large mammals of the Shanwang Basin that have been identified, several are noted for their widespread geological distribution, among which are species in the equid genus *Anchitherium*, which initially appeared in North America during the early Miocene (MacFadden, 1998) and subsequently spread to Europe and Asia during the Orleanian and Shanwangian periods, respectively (e.g. Abusch-Siewert, 1983; Li et al., 1983; MacFadden, 1998; Bernor and Armour-Chelu, 1999; Alberdi et al., 2004; Qiu and Qiu, 2013 Abusch-Siewert, 1983). Among the Rhinocerotidae, the remains of *Plesiaceratherium* appear in the earlier Miocene of France, with *Plesiaceratherium aquitanicum*, followed by *P. lumiarense*, *P. platyodon*, and *P. gracile*, which appear in the MN 4 biostratigraphic zone in Spain, France, and China, respectively, whereas *P. fahlbuschi* has been recorded from the MN 5 zone in Germany (Mermier, 1895; Heissig, 1972, 1999; Antunes and Ginsburg, 1983). The tragulid genus *Dorcatherium* was widely distributed in Africa and Eurasia, initially being recorded during the earliest period of the Miocene in Pakistan (Antoine et al., 2013). These fossils are older than those from the Shanwang Basin, which are from the late early Miocene (Qiu and Qiu, 2013). Furthermore, *Hyotherium* in the family Suidae was recently recorded in the earliest Miocene strata of Hang Mon, Vietnam (Covert et al., 2001; Prieto et al., 2017). Among the fossils retrieved from sediments dated to the late early Miocene of the Shanwang Basin, *Hyotherium* is represented by *H. shanwangense* and *H. penisulus*, although these fossils are younger than those discovered in Vietnam (Deng et al., 2003; Qiu and Qiu, 2013). In the family Amphicyonidae, *Amphicyon* has been recorded in Western Europe, and also has a widespread distribution in Asia, with the earliest records corresponding to the early to late early

Miocene of the Bugti Hills site in Pakistan, particularly the occurrence of *A. shabazi* (Antoine et al., 2013). Moreover, an isolated i3 specimen from the early Miocene sediments of Hang Mon, Vietnam, has tentatively been assigned as *Amphicyon* cf. *giganteus* (Prieto et al., 2017), and previous studies indicate that specimens of *Amphicyon* are relatively abundant in the Shanwang Basin (Young, 1937; Qiu and Qiu, 2013).

The occurrence of these genera in different geographical regions indicates a faunal exchange among North America, Asia, and Europe from the Paleogene to Neogene periods (Qiu, 1987; Lopatin, 1997; Hopkins, 2004; Storch and Qiu, 2004; Kelly and Korth, 2005; Korth, 2007; Wang et al., 2009). Furthermore, these geographical and temporal distributions, at least in the case of large mammals, indicate that these faunas may have migrated from Western Europe to Eastern Asia through central Asia, that is, along a migration route that follows the northern margins of the Tibetan Plateau.

4.2. Rhinocerotids during the Oligocene–Miocene transition

Among the rhinocerotids that arrived in Europe during the early Oligocene, *Epiaceratherium* Abel, 1910, which is known from the earliest Oligocene (MP21) of Monteviale, Italy, and several Oligocene localities in France, Switzerland, Germany, and the Czech Republic (Uhlig, 1999; Pandolfi et al., 2017; Tissier et al., 2020), is considered the most primitive, with brachyodont cheek teeth and a small body size (Fig. 4). Two other rhinocerotid genera appearing in Europe during this period are *Ronzotherium* Aymard, 1854 (MP21–MP30) and *Molassitherium* Becker et Antoine, 2013 (MP23–MP27) (Roman,1912; Heissig, 1969; Brunet, 1979; Uhlig, 1999; Becker et al., 2013; Scherler et al., 2013; Pandolfi, 2015). In Asia, remains of *Ronzotherium* and *Epiaceratherium* are reported from the late Eocene of Erdilin, Mongolia, and the late Middle to Late Eocene of Na Duong, Vietnam, respectively, which are chronologically older than their European counterparts (Dashzeveg, 1991; Böhme et al., 2013).

In Eurasia, however, the earliest unequivocally identified remains of *Diaceratherium* are from the Late Oligocene of La Milloque in France (Michel, 1983; Brunet, 1987). During the early Miocene, this genus appears to have been distributed in numerous regions in Western Europe (Pomel, 1853; Nouel, 1866; Depéret and Douxami, 1902; Roman, 1911; Répelin, 1917; Dietrich, 1931; Tobien, 1980; Michel, 1983; Cerdeño, 1992; Engesser et al., 1993; Heissig, 1999; Fortelius, 2003; Becker et al., 2009; Jame et al., 2019), whereas in Asia, in addition to the described skeleton from the Shanwang Basin, *Diaceratherium* has been reported from the early Miocene of the Turgai and Betpakdala regions in Kazakhstan (de Bonis, 1997; Kordikova, 2001; Antoine et al., 2013), as well as some uncertain records in the earliest Miocene strata in Pakistan, Thailand, and eastern Siberia.

Among three other rhinocerotid genera occurring in Europe between the late Oligocene and early Miocene, *Pleuroceros* is a small to medium-sized genus, with the earliest record in the late Oligocene (MP30) of Billy, France (Hugueney, 1997; Antoine and Becker, 2013), surviving into the early Miocene (MN 2) of Pappenheim, Germany (Schlosser, 1902; Heissig, 1999; Antoine and Becker, 2013). The earliest remains of *Protaceratherium* come from the late Oligocene of Frankfurt, Germany, and these rhinocerotids appear to have been widely distributed among the early Miocene localities of Western Europe (Roman, 1914; Cerdeño, 1992; Heissig, 1999; Antoine et al., 2013; Scherler et al., 2013). Representatives of the third of these genera, *Mesaceratherium*, appeared during the Late Oligocene and survived into the early Miocene (MN 4) of Gaimersheim, Germany and Thézels, France (Heissig, 1999; Antoine and Becker, 2013; Scherler et al., 2013; Blanchon et al., 2018; Tissier et al., 2020). These three genera have also been recorded in Asia. For example, *Dicerorhinus tagicus* var. *betpakdalensis* Borissiak, 1938 from the early Miocene of the Betpakdala Steppe, Kazakhstan, was re-assigned by de Bonis et al. (1997) as *Protaceratherium betpakdalense* (see also Kordikova, 2001). *Protaceratherium* is also known from the Late Oligocene of Anatolia in Turkey and the earliest Miocene of Pakistan and northern Vietnam (Antoine et al., 2008; Prieto et al., 2017) (Fig. 4). *Mesaceratherium* and *Pleuroceros* have been recorded from the early Miocene (MN1) of Bugti Hills in Pakistan, being represented by *M. welcommi* and *P. blanfordi*, respectively (Lydekker, 1884; Antoine et al., 2010), the latter of which is also known to have occurred during the early-phase Miocene (23–21 Ma) of Hang Mon, Vietnam (Prieto et al., 2017). Notably, however, representatives of these two genera have yet to be found in central or Eastern Asia.

Based on our current knowledge, it would appear that *Diaceratherium*, along with *Mesaceratherium*, *Pleuroceros*, and *Protaceratherium*, originated in Europe, with earliest records dating from the Late Oligocene (MP25 for *Mesaceratherium*, MP30 for the latter two genera) (Heissig, 1969; Tissier et al., 2020). In Kazakhstan, *Diaceratherium* and *Plesiaceratherium* have been found in the early Miocene strata of the Betpakdala steppe region (MN 2–MN 3) (Bonis, 1973; Kordikova, 2001), the former has also been found in the Turgai region of Kazakhstan (Borissiak, 1927). Given the known localities of *Diaceratherium* in Asia, we suggest that the arrival of these rhinocerotids in the easternmost regions of Asia (e.g. Shanwang Basin, China) may have followed a migration route along the northern margins of the Tibetan Plateau rather than via the southern margins (Fig. 5), which contrasts with the route proposed for other mammals such as those in the genera *Dorcatherium*, *Hyotherium* and *Amphicyon* (see the Introduction section), which are assumed to have migrated via a southern route.

5. Conclusion

The new fossil described herein is like previously described specimens of *Diaceratherium*, and represents the first complete skeleton of this genus discovered in Asia. The features of the newly retrieved fossil are also consistent with the previously invalidated rhinoceros '*Plesiaceratherium*' *shanwangensis* excavated from the same locality: its nasal and skull lengths are relatively shorter, the nasal notch is moderately retracted at the P3 level, and the metapodials are longer and more robust. We have consequently revalidated the species '*Plesiaceratherium*' *shanwangensis* and re-assigned the new skeleton as *Diaceratherium shanwangense*. Contrary to the current consensus, which maintains that during the Oligocene–Miocene transition, mammals migrating between Western Europe and Eastern Asia preferentially followed a route via the southern margins of the Tibetan Plateau, the temporal ranges and geographical extent of *Diaceratherium* indicate that the eastward expansion of this genus during the Oligocene–Miocene transition probably occurred along the northern margins of the Tibetan Plateau.

CRediT authorship contribution statement

Xiaokang Lu: Conceptualization, Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Esperanza Cerdeño:** Writing – review & editing. **Xiaoting Zheng:** Investigation, Resources. **Shiqi Wang:** Validation, Field investigation. **Tao Deng:** Conceptualization, Funding acquisition, Supervision, Project administration, Investigation, Writing – review & editing.

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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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaesx.2021.100074.

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