



## Supporting Online Material for

### **Out of Tibet: Pliocene Woolly Rhino Suggests High-Plateau Origin of Ice Age Megaherbivores**

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## Supporting Online Material

**Geologic setting of Zanda Basin.** Zanda Basin is a late Miocene through Pleistocene pull-apart sag basin (Fig. S1) located just north of the high Himalayan ridgecrest in the west-central part of the orogen ( $\sim 32^\circ$  N,  $82^\circ$  E; elevation 3,700-4,500 m). It lies between the South Tibetan Detachment System (STDS) to the southwest, and the Indus Suture to the northeast and the Gurla Mandhata and Qusum (Leo Pargil) metamorphic core complexes to the southeast and northwest, respectively. The STDS is an early-mid Miocene (25) series of north-dipping, low-angle, top-to-the-north normal faults which place low-grade Paleozoic-Mesozoic metasedimentary rocks on high-grade gneisses and granites of the Greater Himalayan sequence. In the Zanda Basin region the Oligo-Miocene Great Counter Thrust, a south-dipping, top-to-the-north thrust system, modifies the Indus Suture. The age of exhumation of the Gurla Mandhata and Qusum (Leo Pargil) metamorphic core complexes has been defined by  $^{40}\text{Ar}/^{39}\text{Ar}$  analysis of micas to be  $\sim 9$  Ma (26) or 14-16 Ma (27), respectively. The axis of the basin is approximately northwest-southeast; parallel to the general arc of the Himalaya. The current outcrop extent of the basin fill is  $>9,000 \text{ km}^2$ .

The sedimentary basin fill is undisturbed and lies in angular or buttress unconformity with the underlying deformed Tethyan Sedimentary Sequence (TSS) strata. After deposition, incision by the Langqên Zangbo (Sutlej) River exposed the entire basin fill.

The basin fill consists of approximately 800 m of fluvial, lacustrine, eolian and alluvial fan deposits. The lower part of the section consists of approximately 200 m of trough cross-bedded sands and well-organized, imbricated, pebble to cobble conglomerate. Associated sedimentary structures include stacked, 3-4 meter sand-gravel filled channel and longitudinal bar.

We interpret these features as fluvial deposits laid down by large-scale rivers ancestral to the Sutlej or Indus based on provenance and paleocurrent orientation data (28). Interbedded fine-grained sand and silt horizons showing extensive soft-sediment deformation and containing abundant mammal, gastropod and plant macrofossils are interpreted as marshy bog or overbank deposits within a low-gradient fluvial setting. The middle unit (approximately 250 m) consists of an upward coarsening succession of lacustrine progradational parasequences. Individual parasequences are up to 17 m thick and range between profundal lacustrine claystones and deltaic and wave-worked sediments, including evidence of occasional desiccation. The top 350 m continues the upward coarsening progression displayed in the middle portion but becomes much coarser. The profundal lacustrine facies disappears and is replaced by deltaic or lake-margin deposits. Individual parasequences vary between deltaic or lake-margin and alluvial-fan and fan-delta conglomerates.

Since the initial establishment of the Zanda Formation as a lithological unit (29), additional formation (such as the Tuolin and Xiangze formations) or even group names (Zanda Group) were proposed (30), often based on a perceived depositional hiatus that later proved to be false (31, 32). Here we use a single unit name, Zanda Formation, for the entire basin sequence.

**Magnetostratigraphy and Biostratigraphy.** There have been no less than four independent attempts at paleomagnetic age determination of the Zanda strata during the past 11 years, although only three of these provided enough documentation to be evaluated here (28, 32, 33) (Zhu et al. (30) and Meng et al. (34) mentioned a paleomagnetic section of their own, but provided no detailed documentation). All three studies measured an 800+ m section for the total thickness of Zanda sediments, and arrived at roughly similar magnetic reversal patterns (not

surprisingly, sections with a higher density of sampling tend to detect more and shorter magnetochrons).

Qian's (33) first attempt used no independent age constraint and simply correlated his magnetic section (12 normal and 13 reversed magnetozones) to then "Chron 6" through Jaramillo Chron (6.15-1.5 Ma). Wang et al. (32) listed four fossil horizons in their more densely sampled magnetic section revealing 15 normal and 15 reversed magnetozones. Three of the horizons contain fossil mammals (*Hipparion zandaense*, *Ochotona* sp., and Dicerorhininae) and one with four species of gastropods. However, only one site yielded identifiable mammal (four cheek teeth of *Hipparion zandaense*), and the other two sites are inferred occurrences of *Ochotona* sp. (a single cheek tooth (35)) and a rhino (one metapodial (34)) collected from near the Dingdingka area, which is "40 km" north of Wang et al.'s (32) magnetic section according to Meng et al. (34, 35) (detailed locality information is not provided although this distance is probably greatly exaggerated). Furthermore, none of these fossils are well preserved or well studied enough to offer real constraints within their proposed age range of late Miocene through Pliocene.

Most recently, Saylor et al. (31) presented two more magnetic sections from the south and southeast Zanda Basin. A composite magnetic column was derived by combining each part of a section that has more magnetozones, and resulted in a total of 12 normal and 12 reversed zones. Saylor et al.'s south Zanda magnetic section was sampled from the same canyon as that by Wang et al. (32) (Zanda-Bolin section; see also Kempf et al. (36)), although individual measured segments (legs) differ from each other. It is thus reassuring that these two magnetic sections essentially replicate each other. Where Saylor et al. under-sampled at their 100-150 m level, Wang et al.'s much denser sampling revealed a relatively long reversed chron missed by Saylor

et al. (Fig. S3). For chronologic constraints, Saylor et al. (31) used past reports of vertebrate fossils (*Hipparion*, *Palaeotragus*, etc.) to constrain the Zanda strata to late Miocene through Pliocene and selected their preferred correlation by invoking a global C<sub>3</sub>/C<sub>4</sub> vegetation transition at ~7 Ma.

A partial palate of a primitive giraffe, *Palaeotragus microdon*, was recovered near the Xiangze Farm area of the northern Zanda Basin during a preliminary survey of the Quaternary geomorphology by a Chinese Academy of Sciences expedition in 1976 (29). A nearly complete skull of a new hipparionine horse, *Hipparion zandaense* Li and Li, was described from exposures near the village of Daba in the southeastern Zanda Basin (37). Additional miscellaneous materials (isolated cheek tooth of *Ochotona* (35) and a rhino (Dicerorhininae) metapodial (34)) were collected from the Dingdingka area. The above isolated reports aside, there were no systematic efforts to collect fossil vertebrates prior to our field expeditions in 2006-07 and 2009-10. The holotype woolly rhino skull was collected from south of the main road entering Zanda Basin (Fig. S2) in the middle fine-grained sequence of the Zanda Formation.

Our own mammalian faunas offer, for the first time, the most restrictive age constraints so far known. Critically, in the lower part of the sequence, we have recovered a small mammal assemblage (IVPP localities ZD0609 and 0904) that falls in the 174-186 m level of Saylor et al.'s (28, 31) south Zanda section within the top part of an alternating greenish sandstone and silt unit and just below the fine-grained lacustrine mudstone with fine laminations. The most age-diagnostic element of this small mammal assemblage is *Mimomys*, represented by three upper first molars and one lower molar. In level of crown heights, our Tibetan material is most comparable to *Mimomys* (*Aratomys*) *bilikeensis* from the early Pliocene Bilike locality of Inner Mongolia, which is the earliest representative of arvicoline rodents in China (38). Arvicoline

rodents first appear in the early Pliocene of western Siberia (39) and shortly afterward dispersed to northern Asia (38), Europe (40, 41), and North America (42-44). The appearance of these rodents thus is a highly age-diagnostic event throughout northern continents. IVPP localities ZD0609 and 0904 fall in a relatively long normal chron that we interpret to be C3n.4n, i.e., 4.997-5.235 Ma in ATNTS2004 (45) (Fig. S3).

Large carnivorans, such as *Chasmaporthetes* (IVPP locality ZD0908), *Vulpes* (IVPP locality ZD1001), *Nyctereutes* (IVPP locality ZD0624), and *Meles* (IVPP locality ZD1001), offer additional chronologic constraints, even though most of these are stratigraphically 30 to more than 200 m higher than the *Mimomys* horizon. The Asiatic first occurrences of these genera are mostly confined to the Pliocene, although occasional late Miocene records have been suggested elsewhere (46-49). Collectively they have a distinctly Pliocene characteristic.

We would like to point out that a partial maxilla fragment with cheek teeth was described from the Xiangze section as *Palaeotragus microdon* (29). We were unable to find this primitive giraffe during our own collecting. However, we did collect a large cervid (left and right partial antlers, and isolated cheek teeth) from several localities (IVPP localities ZD0624, 1040, etc.), and we suspect that these belong to the same taxon (although we have not examined the original specimen described by Zhang et al. (29)).

Overall, the fossiliferous middle Zanda sequence yields characteristic Pliocene faunas (Table S1), although the upper alluvial conglomerates and lower fluvial sandstones, from which few vertebrate fossils are found thus far, range into the Pleistocene and Miocene, respectively. Based on our paleontologic constraints, we re-interpreted previously published paleomagnetic columns from various parts of the basin, and our new age estimates (Fig. S3) of the Zanda section spans ~400 Ka to 6.1 Ma in GPTS of ATNTS2004 (45). Our alternative interpretation is

closest (but not identical) to those proposed by Qian (33) and takes into account the fast deposition in the upper conglomerates and lower fluvial sandstones.

**Additional description and comparison of the woolly rhino** (Figs. S4-S6; Tables S2-6).

*Coelodonta thibetana* has a skull length of 771 mm, close to the living white rhino *Ceratotherium simum* (mean length = 797 mm), and much longer than the living Sumatran rhino *Dicerorhinus sumatrensis* (mean length = 525 mm). The skull roof of the new species is concave and bears broadly separated parietal crests (minimum distance 46.5 mm), as in other dicerorhines, such as *Dihoplos ringstroemi* (50) and *Stephanorhinus etruscus* (51). The relative size of the nasal horn is greater than in extant and fossil rhinocerotines, and resembles those in elasmotheres (52-54) or dicerotines (55) but narrower in shape. The morphology of the lower part of the nasal septum in *Coelodonta thibetana* is not clear because the premaxilla is crushed. However, we can observe that the nasal and premaxilla are separate by a distance of 74 mm between their tips. This distance falls in the range of the basal dicerorhines (55) and extinct elasmotheres (52), and it is longer than that of *C. nihowanensis* (48). In contrast, the nasal and premaxilla of the most derived *C. antiquitatis* are in contact (56). The upper part of the septum is divided into two branches, indicating that it was fused by two thin sheets of bone. The preserved portion of the premaxilla is very narrow, indicating a reduced and edentulous premaxilla.

The nasals are very broad, as in other early *Coelodonta* (57), and their anterior ends bend downward. The nasal notch is deep, with the posterior margin above the P3/P4 boundary. The degree of nasal lengthening is similar to the state typically seen in Miocene to Pleistocene dicerotines such as *Dihoplos ringstroemi* (50, 58) or *Stephanorhinus etruscus* (51), but less than in forms with very elongated nasals such as *S. hundsheimensis* and *S. hemitoechus*, or in the

more derived species of *Coelodonta* (57). The nasals appear somewhat more lengthened and the notch correspondingly deeper than in *Coelodonta nihowanensis*. The nasal septum of *C. thibetana* is ossified along the anterior third of the nasal notch, similar to the degree of ossification in *S. hemitoechus* (59), but weak compared with more derived species of *Coelodonta* (48, 57, 60). The nasal septum has a distinct suture fused with the premaxilla, and its contact with the nasals is tight but not fused. The septum of the new woolly rhino is also relatively thin. The maximum anterior thickness is 36 mm, thinner than in *C. nihowanensis* (40 mm (48)) and *C. antiquitatis* (56 mm (61)).

The infraorbital foramen is open above the middle of P4, and the anterior border of the orbit is above the M2/M3 boundary. The lachrymal tubercle is strong, but the postorbital processes are absent on the frontal and zygomatic arch. The postglenoid process is long and strong, with a right dihedral in cross section, and it is fused with the posttympanic process to form a closed external auditory pseudomeatus.

In the atlas, the outline of the rachidian canal is mushroom-like; the fovea dentis is shallow; the alar fossa is present; the inferior alar foramen is very small; the lateral vertebral foramen is absent, which is present in *C. antiquitatis* (56). The axis is short, with a high spinous process whose cranial border is sharp; the cranial intervertebral notch is broad, but it tends to close and form an intervertebral foramen as in *C. antiquitatis* (56). The third cervical vertebra is relatively short and high, without the mammillary process, which is strongly developed as in *C. antiquitatis* (56) (Fig. S6).

The mandible is nearly complete. The lower incisors are absent, but there is a small alveolus on the left jaw, indicating the presence of a deciduous second incisor, as also seen in *C. nihowanensis* (48). In lateral view, the symphysis is elevated and forwardly positioned, which is



similar to that of *C. nihowanensis* (48). The lower border of the horizontal ramus is straight behind the level of m1. The posterior border of the mandibular symphysis is in front of the p2, more anterior than that of the Quaternary woolly rhinos (48, 56). The mandibular angle is rounded, and the ascending ramus is reclined posteriorly. *Stephanorhinus etruscus*, another known Pliocene dicerorhine with well-preserved mandible, differs from *C. thibetana* in possessing a more backward posterior symphysis reaching the p2/p3 boundary and a more vertical ascending rami (51). The backward shift of the mandibular symphysis is an evolutionary trend among species of *Coelodonta* (62). The posterior border of the symphysis in *C. nihowanensis* is situated at the p2/p3 boundary (48), whereas it is at the middle of p3 in the derived Eurasian species *C. antiquitatis* (55). The symphysis of *C. thibetana* is much more forward in comparison with those of *C. nihowanensis* and *C. antiquitatis*, representing a more primitive condition within the genus.

Dental morphology of *C. thibetana* falls well within the diagnosis of the genus (48). The P1 and p1 are absent. The crown is high, with a weak cement cover on the labial wall. The median valley is closed on the premolars. The crochet and crista are well developed, and the medi- and post-fossettes are visible at an early stage of wear, which are different from those of *Stephanorhinus*, which lacks the medi- and post-fossettes (51). The upper teeth are similar to those of *C. nihowanensis* (63), and minor differences between the two species mainly lie in the molars: the ectoloph is weakly wavy, the M1 lacks the crista, and the M2 has a less well-developed mesostyle in *C. thibetana*. The upper teeth of *C. antiquitatis* are markedly different from those of *C. thibetana* and *C. nihowanensis* in having the strongly wavy labial wall, thick cement cover, a strongly backwardly slanting protocone, and a quadrate outline in the M3 (55, 56).

The p2 has an elongate triangular outline with a paraconid, but the left p2 is absent abnormally. The differences in the p3–m3 among *C. nihowanensis*, *C. tologiensis*, *C. antiquitatis*, and *C. thibetana* are remarkable. *C. tologiensis* and *C. antiquitatis* are more derived than the other two species in having a posterior edge of the protoconid, and swollen metaconid and entoconid (56, 64). *C. nihowanensis* has strong anterior and posterior ribs on the labial wall of the trigonid (48), but *C. thibetana* possesses blunt anterior and posterior external corners on the lower teeth, and a weak anterior rib on m2-3.

**Phylogenetic Analysis.** To evaluate the phylogenetic position of *Coelodonta thibetana* within Rhinocerotinae, a phylogenetic analysis of 17 well-known rhinocerotid taxa was performed. The following taxa formed the ingroup: *Lartetotherium*, *Ceratotherium simum*, *Diceros bicornis*, *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*, *Rhinoceros unicornis*, *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus hemitoechus*, “*Dihoplus*” *kirchbergensis*, *Dihoplus megarhinus*, *Dihoplus pikermiensis*, *Dihoplus ringstroemi*, *Coelodonta nihowanensis*, *Coelodonta tologiensis*, *Coelodonta antiquitatis*, and *Coelodonta thibetana* (this study). *Ronzotherium* acted as an outgroup. The 46 characters used in this study were mainly taken from a previous analysis by Antoine (62) but several characters were modified and seven new characters were added (for a complete list of characters and the character matrix see Tables S7 and S8). Character states were scored according to published literature and personal records of museum specimens. The data set was analyzed using the branch-and-bound algorithm with ACCTRAN optimization in PAUP\* 4.0b10 (65). Characters were left unweighted and un-ordered. 'Gap' states were treated as 'missing data'. Bootstrap analysis (1000 replicates) was also performed using PAUP\* 4.0b10, and decay analysis was performed using

PAUP\* 4.0b10 and TreeRot 2.0 (66).

The branch-and-bound search found nine most parsimonious trees (tree length = 139, consistency index = 0.439, retention index = 0.569, homoplasy index = 0.561, rescaled consistency index = 0.250). The nine most parsimonious trees (MPTs), together with a strict consensus (with decay and bootstrap values shown) and 50% majority consensus of these trees, are shown in the supporting figures (Figs. S7-S9).

As can be seen in the strict consensus tree (Fig. S8), only two of the groupings found in all of the trees received over 50% bootstrap support (50% for the *C. simum* – *D. bicornis* clade and 67% for the *C. tologojensis* – *C. antiquitatis* clade), which reflects a high degree of homoplasy within the different branches. However, most clades, including the *Coelodonta-Stephanorhinus-Dihoplus* clade and the *Coelodonta* clade, received relatively good support from the decay analysis (decay value of 3). Only two clades received a decay value of 1. Both of these are for groupings within the *Stephanorhinus-Dihoplus* clade, revealing that the interrelationships between these species will change in trees with just one step longer.

For the extant rhinos (*Ceratotherium simum*, *Diceros bicornis*, *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*, *Rhinoceros unicornis*), the results of our analysis (Figs. S7-S9) are in agreement with the recent analysis by Tougard et al. (67) and Willerslev et al. (68), which were based on mitochondrial genome sequences, and with the morphological analysis by Antoine (62), which was the source of most of our characters. However, the position we recovered for *Coelodonta* in relation to the extant taxa is different from its position in Antoine (62) and Willerslev et al. (68) (no fossil taxa were included in Tougard et al.'s (67) analysis). We found that *Dicerorhinus sumatrensis* either formed a sister group with the two *Rhinoceros* species, and this clade was the sister group of the *Coelodonta-Stephanorhinus-Dihoplus* clade (Fig. S7d-f), or

the two *Rhinoceros* species formed the sister group of the *Coelodonta-Stephanorhinus-Dihoplus* clade, while *Dicerorhinus sumatrensis* was the sister taxon of this larger grouping (Fig. S7a-c, g-i). In contrast, Antoine (62) recovered *Coelodonta antiquitatis* as the sister taxon of the *Diceros-Ceratotherium* clade, whereas in Willerslev et al. (68) *Dicerorhinus sumatrensis* was the sister taxon of *Coelodonta antiquitatis*. However, in both of these analyses *Coelodonta antiquitatis* was the only extinct rhinocerotine taxon included. Thus, increasing the number of extinct rhinocerotine taxa appears to have an impact on the resulting relationships between *Coelodonta* and the extant rhinos in a morphological phylogenetic study. It is very likely that if molecular data of more numerous fossil taxa were added into the analysis of Willerslev et al. (68), the results of that study would also change, especially as the interrelationships between the extant rhino clades were not conclusively resolved. Of other (fairly) recent analyses, Groves (69), Prothero et al. (70), and Cerdeño (71) have included both *Coelodonta* and *Stephanorhinus*. In accordance with our results, they found them to be sister taxa, although in the trees of Groves (69) and Prothero et al. (70) the sister group of the *Coelodonta-Stephanorhinus* clade was *Rhinoceros* (together with *Gaindatherium* and *Punjabitherium*, which were not included in this analysis), and in the tree by Cerdeño (71) the sister group was the *Elasmotherium-Ningxiatherium* clade. We did not include any elasmotheres in our analysis because they are clearly a monophyletic group characterized by a strong suite of autapomorphies, and are evolutionary distant from *Coelodonta* and *Stephanorhinus* (62, 72).

The locomotory skeleton of *C. thibetana* is unknown, but all other woolly rhinos except the terminal *C. antiquitatis* were cursorial forms. One of the most interesting questions left open by the new discovery is whether cursoriality was the original condition of this genus. It is conceivable that the high-altitude *C. thibetana* might have been short-legged, and that the

phylogeny of *Coelodonta* will turn out to be more complicated than the simple transformation series that our present analysis suggests. A rather stocky rhinoceros metapodial from Zanda (34) might be taken as support for such a scenario although this specimen has no associated cranial or dental materials. The derived character of stronger nasal lengthening and stronger inclination of the occiput seen in *C. thibetana* compared with the younger *C. nihowanensis* might also reflect such previously unrecognized complexity.

**Additional paleoecologic considerations.** Based on their high crowned cheek teeth with cement, long nasal horn, nasal septum, backward slanting occiput, dicerorhines, except phylogenetically enigmatic *Dicerorhinus*, were reconstructed as grazers (15, 73, 74). Relatively broad nasals with an ossified septum indicate that *C. thibetana* has two large nasal cavities for increased heat exchange in frigid air. The body weight of *C. thibetana*, estimated from its skull length, is about 1800 kg (75). The body size of an endothermic mammal is important in determining its metabolic requirements. The maintenance requirements of per unit body weight decrease with increasing body weight. Among herbivores this means that absolute body size is very important in determining the fibre/protein intake ratio that an animal will be able to tolerate in its diet, as larger mammals require proportionally less protein and thus are able to tolerate a larger proportion of cellulose (76). The Zanda woolly rhino is about the same size as *C. nihowanensis* but is smaller than *C. antiquitatis*, which achieved a larger body size during the colder late Pleistocene (Tables S2-S3).

The molars, while close to the plesiomorphic primitive type seen in related genera such as *Stephanorhinus*, already show signs of the modifications that become so striking in the late Pleistocene *C. antiquitatis*, a true grazer (57). The increased molar crown height, the presence of

coronal cement, and the incipient thickening of the enamel lining of the fossettes are all indicators of a shift towards a more abrasive diet (77). The cusp tips of the upper molars are worn to a distinctly rounded shape, neither sharp as in browsing rhinoceroses nor blunt as in true grazers, also indicating a mixed diet with a significant component of grass (78). The morphology and occlusal wear of the cheek teeth thus suggests that *C. thibetana* was a mixed feeder with a tendency to graze, like *C. nihowanensis* and *C. tologojensis* (57).

The ability to sweep snow with a large, forward-leaning nasal horn may have been the most critical adaptation for surviving the harsh Tibetan winters, and as such, represents a unique evolutionary advancement for the woolly rhino lineage. Such a simple yet vital innovation, formed prior to the initiation of a permanent northern ice sheet, was a key pre-adaptation that opened the path to success for the woolly rhino in the mammoth fauna during the late Pleistocene.

**Paleodiets and paleoenvironment.** Carbon and oxygen isotopic compositions of fossil tooth enamel and bones contain valuable information about the diet and water composition, and paleotemperature (79-82). Specifically,  $\delta^{13}\text{C}$  of tooth enamel from herbivores reflects the proportion of  $\text{C}_3$  and  $\text{C}_4$  plants in their diet.  $\text{C}_3$  plants, which include all trees, cool season grasses and most shrubs, have  $\delta^{13}\text{C}$  values ranging from -20‰ to -35‰, with a mean of -27‰ (79, 83). Under water-stressed conditions and/or low atmospheric partial pressure of  $\text{CO}_2$  ( $p\text{CO}_2$ ),  $\text{C}_3$  plants are enriched in  $^{13}\text{C}$  and have  $\delta^{13}\text{C}$  values higher than the average value of -27‰. Under closed canopies,  $\text{C}_3$  plants have lower  $\delta^{13}\text{C}$  values (<-27‰) due to the influence of soil respiration (e.g., 79).  $\text{C}_4$  plants are mostly warm climate grasses and have  $\delta^{13}\text{C}$  values of -9‰ to -17‰, averaging -13‰ (79, 83). Because tooth enamel from herbivores is consistently enriched in  $^{13}\text{C}$  by ~14‰ relative to the diet due to biochemical fractionation, animals that eat  $\text{C}_3$

vegetation typically have  $\delta^{13}\text{C}$  values less than  $-9\text{‰}$ ; animals that eat  $\text{C}_4$  plants have  $\delta^{13}\text{C}$  values  $>-2\text{‰}$ ; and mixed feeders that eat both fall somewhere in between these two extremes (e.g., 79). In much of the modern Himalayan-Tibetan Plateau, which is characterized by severe water-stressed conditions and low atmospheric partial pressure of  $\text{CO}_2$  ( $p\text{CO}_2$ ), the conservative “cut-off” enamel- $\delta^{13}\text{C}$  value for a pure  $\text{C}_3$  diet should be  $-8\text{‰}$  (81). We analyzed the carbon and oxygen isotopic compositions of 110 serial and bulk enamel samples from 25 teeth or tooth fragments from a diverse group of middle Pliocene mammals (including horse, rhino, deer, and bovid) and 60 bulk and serial enamel samples from nine teeth from eight modern Tibetan wild asses (*Equus kiang*) from Zanda Basin.

The average  $\delta^{13}\text{C}$  value of enamel samples from modern wild Tibetan asses from Zanda Basin is  $-8.8\pm 1.7\text{‰}$ , indicating a  $\text{C}_3$ -based diet and consistent with the current dominance of  $\text{C}_3$  vegetation in the area. The enamel- $\delta^{13}\text{C}$  values for the time period of 3.1–4.0 Ma are  $-9.6\pm 0.8\text{‰}$  ( $n=110$ ), indicating that these ancient herbivores fed primarily on  $\text{C}_3$  vegetation and lived in an environment dominated by  $\text{C}_3$  plants (Fig. 2B). Carbon isotope analysis of fossil plant materials in the basin showed that  $\text{C}_4$  grasses were present in local ecosystems in the latest Miocene and Pliocene (31). Our enamel  $\delta^{13}\text{C}$  data, however, suggest that  $\text{C}_4$  grasses must have been a minor component of local ecosystems at  $\sim 3.1\text{--}4.0$  Ma because they were insignificant in herbivores’ diets (Fig. 2B).

The enamel-  $\delta^{18}\text{O}$  values from modern wild Tibetan asses range from  $-7.4\text{‰}$  to  $-12.8\text{‰}$ , averaging  $-8.8\pm 2.1\text{‰}$  ( $n=9$ ). Enamel samples from the mid-Pliocene herbivores yielded  $\delta^{18}\text{O}$  values ranging from  $-10.6\text{‰}$  to  $-18.9\text{‰}$ . Studies have shown that the  $\delta^{18}\text{O}$  of tooth enamel from an obligate drinker (such as horse and rhino) tracks the  $\delta^{18}\text{O}$  of local meteoric water (81, 84, 85). Using the enamel-water  $\delta^{18}\text{O}$  relationship for obligate drinkers (84), we estimated the  $\delta^{18}\text{O}$

values of modern- and paleo-water from the  $\delta^{18}\text{O}$  values of enamel from horse and rhino found in the Zanda Basin (Fig. 2C). The uncertainty in the water  $\delta^{18}\text{O}$  estimates corresponds to 1 sigma ( $1\sigma$ ) standard deviation in  $\delta^{18}\text{O}$  of enamel. The estimated modern water- $\delta^{18}\text{O}$  values are  $-11.0 \pm 2.1\text{‰}$ , which are within the measured  $\delta^{18}\text{O}$  values of modern stream waters (ranging from  $-7.3\text{‰}$  to  $-17.9\text{‰}$ ) in the Zhada Basin (31). The estimated  $\delta^{18}\text{O}$  values of paleo-water in the mid-Pliocene is  $-13.9 \pm 0.6\text{‰}$  at  $\sim 4$  Ma,  $-19.4 \pm 1.0$  at  $\sim 3.8$  Ma, and  $-18.5 \pm 0.9\text{‰}$  at  $\sim 3.5$  Ma, which are lower than the estimated modern water  $\delta^{18}\text{O}$  value based on enamel-  $\delta^{18}\text{O}$  of wild Tibetan asses (Fig. 2). This positive  $\delta^{18}\text{O}$  excursion likely indicates a shift to more arid conditions in the basin after the mid-Pliocene (Fig. 2).

**Mammals Endemic to Tibetan Plateau and Megafauna Origins.** Despite the rich Pliocene rhinoceros record of the Old World, no definitive pre-Pleistocene finds of *Coelodonta* have previously been reported; for example, none of the 173 Old World Pliocene rhinocerotid-bearing localities in the NOW database (86) include this genus (Fig. S10).

At present, the Tibetan Plateau is characterized by a high-altitude, low diversity, cold-adapted mammal fauna with over half of its species being endemic to the region due to high barriers of surrounding mountains (such as the Himalayas) and harsh environment in the high plateau (87, 88). Common extant large mammals in high Tibet include Tibetan wild yak (*Bos mutus*), Tibetan wild ass (*Equus kiang*), argali (*Ovis ammon*), bharal or blue sheep (*Pseudois nayaur*), chiru or Tibetan antelope (*Pantholops hodgsonii*), Tibetan gazelle (*Procapra picticaudata*), white-lipped deer (*Cervus albirostris*), lynx (*Lynx lynx*), snow leopard (*Panthera uncia*), etc. Of these, six have some fossil records or molecular evidence to suggest a Tibetan origin and we briefly treat them in the following paragraphs.



The Tibetan wild yak, *Bos mutus*, is the most charismatic and representative of Tibetan large mammals, and with its large body size and woolly rhino-like long, shaggy hair, may be the closest to the woolly rhino in its special adaptations to the cold open habitats. Although fossil yaks are extremely rare so far, it may have a Pleistocene distribution as far north as the Lake Baikal region in southern Russia (89, 90) and the Holocene of northern Pakistan (91). Recent molecular evidence consistently placed the Tibetan yak and European/American bison as a sister group (92-95), as did a supertree attempt (96), and most seem to agree that yak and bison arose from a common ancestor in central Asia, whereas the American bison crossed the Bering Land Bridge to invade the New World in the late Pleistocene (97, 98). Thus, the case for the cold-adapted yak to give rise to the Pleistocene bison in the northern Holarctic deserves further investigation.

The case for the argali, *Ovis ammon*, bears distinct similarities to the yak in its relationship to North American megafauna. The argali is the basal stock to give rise to the North American Dall's sheep (*Ovis dalli*) and bighorn (*Ovis canadensis*), through a transitional snow sheep (*Ovis nivicola*) of eastern Siberia (99, 100). These sheep arrived at North America as the last wave of immigrants during the Rancholabrean land mammal age (43). As in the case of above *Bison-Bos mutus* sister relationship, the preference to cold and mountainous habitats by *Ovis* seems a striking link between argali, snow sheep, and bighorn. The argali has a present distribution in the Tibetan Plateau and surrounding mountains to the north and west, and its Pleistocene distribution is much greater (101), possibly as far west as France (102), as would be expected for a cold-loving species during the Ice Age. Unfortunately, there are no Tibetan records for fossil *Ovis*, even though sheep horncores tend to be well-preserved.

A similar connection was made between the Tibetan ass, *Equus kiang*, and fossil horses in the late Pleistocene of Alaska (103, 104), although such a hypothesis has been questioned (105). Morphological similarity between *Equus kiang* and the extinct *E. sivalensis* from the Pleistocene of India and Pakistan has been noted (106), although the exact locality and age for the latter's holotype remain ambiguous (107). It seems premature to draw firm conclusions from these studies, but it is conceivable that the center of evolution of the ass group could be related to the Siwalik form (108).

The somewhat goat-like Tibetan bharal (or Blue Sheep), *Pseudois*, is presently endemic to the Tibetan Plateau, preferring mountainous terrains above the tree line between 4,000-6,000 m in elevation (109, 110). Previous records of the bharal are known in the middle to late Pleistocene of north China (111-113), reaching as far as Liaoning Province in Northeast China, more than 1,800 km northeast of the Tibetan Plateau. However, its Pleistocene record appears to be confined to mountainous areas or in caves. Such a preference to rocky terrains may be the main reason that the bharal did not expand as far north as the woolly rhino. A nearly complete left and right horncore of possibly an ancestral species of *Pseudois* was found in IVPP locality ZD0712 in Zanda Basin, 1.57 km northeast of the type locality of the new woolly rhino and stratigraphically approximately 30 m above. Distantly related to the goat rather than sheep (114, 115), the Bharal possesses a mixture of morphologic characters of both (109). The Zanda form, with its laterally divergent horncores, semi-rounded (with a slight hint of triangular) cross-sections, and relatively smooth surface, is closest to *Pseudois* among extant Tibetan bovids (109) (Fig. S11). Its horncore orientation, however, still has a significant caudal component, as contrasted to an essentially lateral orientation in modern and Pleistocene forms (112), suggesting a more primitive condition for the Pliocene Tibetan form. If this horncore does belong to

*Pseudois*, or a more primitive relative of it, then the bharal is another example of a Tibetan ancestor giving rise to Pleistocene megafauna.

The origin of the chiru (Tibetan antelope), *Pantholops hodgsonii*, offers another interesting case of a Tibetan endemic species, whose ancestry can be traced as far back as the late Miocene. In Qaidam Basin in the northern Tibetan Plateau, *Qurlignoria*, an extinct bovid with a straight, upwardly oriented horncore, has been regarded as ancestral to the chiru (116). A horncore fragment of *Qurlignoria* was found in the early Pliocene strata (IVPP locality ZD0745, ~4.2 Ma) of the Zanda Basin (Fig. S12). Intriguingly, late Miocene mammals from Qaidam Basin began to show a modest level of endemism in the Tuosu and Shengou faunas (117). Peculiar bovids, such as *Tsaidamotherium*, *Olonbulukia*, *Qurlignoria*, *Tossunnoria*, and species of dicrocerine deer (unpublished materials possibly referable to *Euprox*), are almost exclusively restricted to the Qaidam region. An extinct Pleistocene species of the chiru, *Pantholops hundesiensis*, was described from the high elevation “Hundes plain” near the present day Niti Pass of India (118). An undescribed horncore of *Qurlignoria/Pantholops* from the Plio-Pleistocene Kunlun Pass Basin (elevation 4,700-5,000 m) in north-central Tibet (119, 120) also hints at its long history in the plateau. Assuming *Qurlignoria* is closely related to *Pantholops*, as horncore morphology seems to suggest, then the case for a Tibetan origin of the chiru is strongly indicated.

The snow leopard, *Panthera (Uncia) uncia*, is another endemic Tibetan species. Although questionable Pleistocene records from Europe and Asia have been referred to the snow leopard (121-124), most of which has been refuted (125-127), a more credible reference is from a more recent discovery in an early Pleistocene locality in the “upper Siwalik” of Pabbi Hills in northern Pakistan (128, 129). We were very fortunate to have recovered cranial and dental

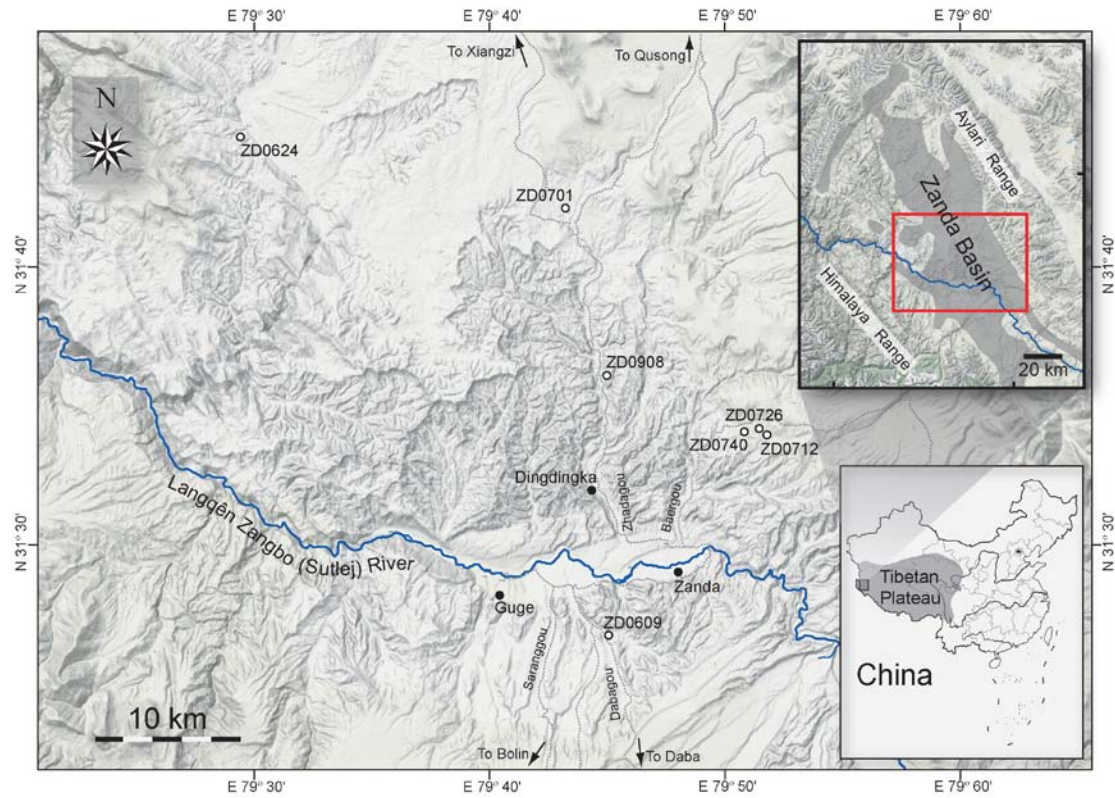
material of an ancestral snow leopard from IVPP locality ZD1001 in Zanda Basin in 2010 (Fig. S13). Its skull possesses a compressed frontonasal region and an expanded maxillary above the infraorbital foramen, features that are characteristic of the snow leopard (*I30*). ZD1001 is early Pliocene (~4.4 Ma) in age, and this new snow leopard is undoubtedly the earliest record of its kind, offering another unambiguous record of the megafauna origin in Tibet.

To sum up, of the eight endemic modern Tibetan or otherwise high altitude, cold-adapted large mammals (*Bos mutus*, *Equus kiang*, *Ovis ammon*, *Pseudois nayaur*, *Pantholops hodgsoni*, *Procapra picticaudata*, *Cervus albirostris*, *Panthera (Uncia) uncia*), fossil occurrences for three (*Pseudois nayaur*, *Pantholops hodgsonii*, *Panthera (Uncia) uncia*) can be traced to an earlier ancestry in Tibet in the late Miocene or early Pliocene. Three other large ungulates, *Bos mutus*, *Equus kiang*, and *Ovis ammon*, offer strong molecular or circumstantial fossil evidence for a Tibetan ancestral stock to give rise to forms that were able to expand to the mammoth "steppes" in northern Eurasia during the late Pleistocene, and in the case of *Bison* (sister of *Bos mutus*) and *Ovis*, were able to cross the Bering Land Bridge to settle in North America. Therefore, at least for some high latitude Holarctic megafauna components, a Tibetan origin should be seriously entertained.

Given the low diversity of modern Tibetan mammal fauna, a high percentage of them either have a long residential history in the plateau going back to at least Pliocene, suggesting long periods of habituation within the confines of the high plateau, or expanded their range during the Pleistocene to become significant players in the high latitude Holarctic megafauna. With its formidable cold climate and thin air, the Tibetan Plateau may thus have served as a habituation ground during the Pliocene, and as arctic and boreal habitats expanded during the Ice

Age, the Tibetan megafauna found itself in an advantageous position to conquer the rest of northern Eurasia and even of North America.

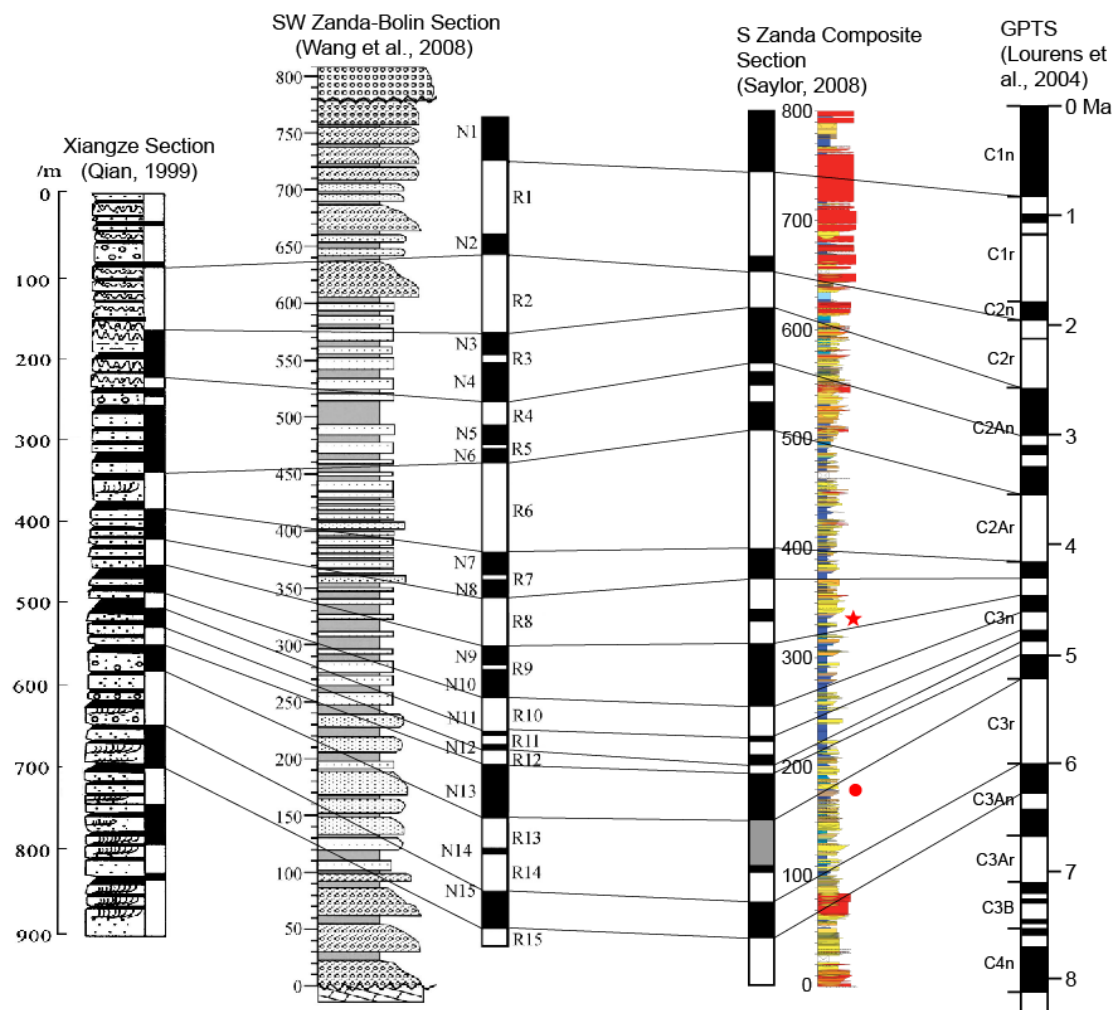
## Figures in Supporting Online Material



**Fig. S1.** Map showing important fossil localities and important geographic locations discussed in the text. Map source: Google Earth.



**Fig. S2.** Exposures of fluvio-lacustrine sediments where the holotype of *Coelodonta thibetana* sp. nov. (IVPP V15908) was found (red arrow), Zanda Basin, Ngari District, Tibet Autonomous Region, China.

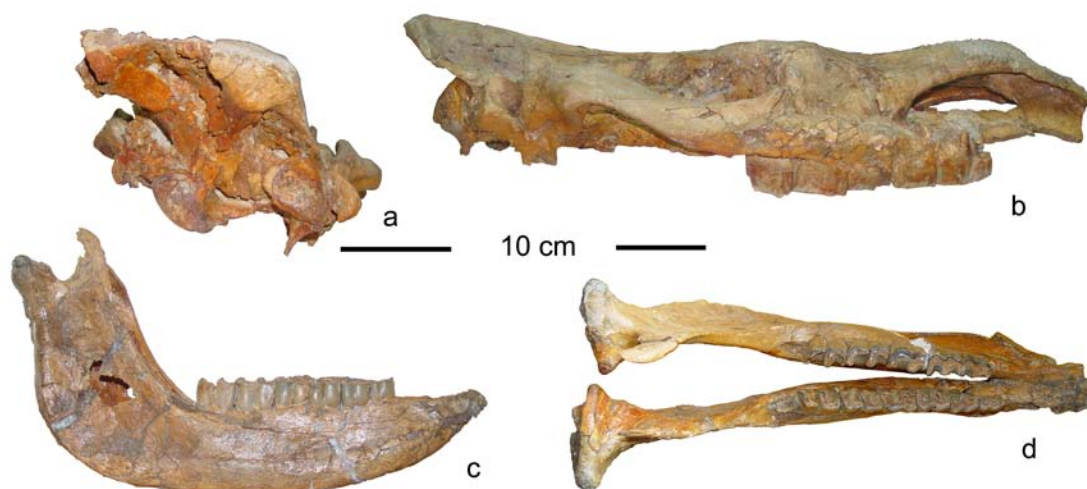


**Fig. S3.** Correlation of three published paleomagnetic sections and stratigraphic positions of key Zanda fossil mammal localities. Vertebrate fossils are placed in the nearest measured sections by Saylor (28), which are in turn correlated on the basis of intrabasin sequence stratigraphic criteria. Red star indicate woolly rhino locality (ZD0740) and red circle indicate key fossil sites (ZD0609, 0904) for biochronologic constraints. Ages for magnetic chrons in the Geomagnetic Polarity Time Scale (GPTS) are based on ATNTS2004 in Lourens et al. (45).

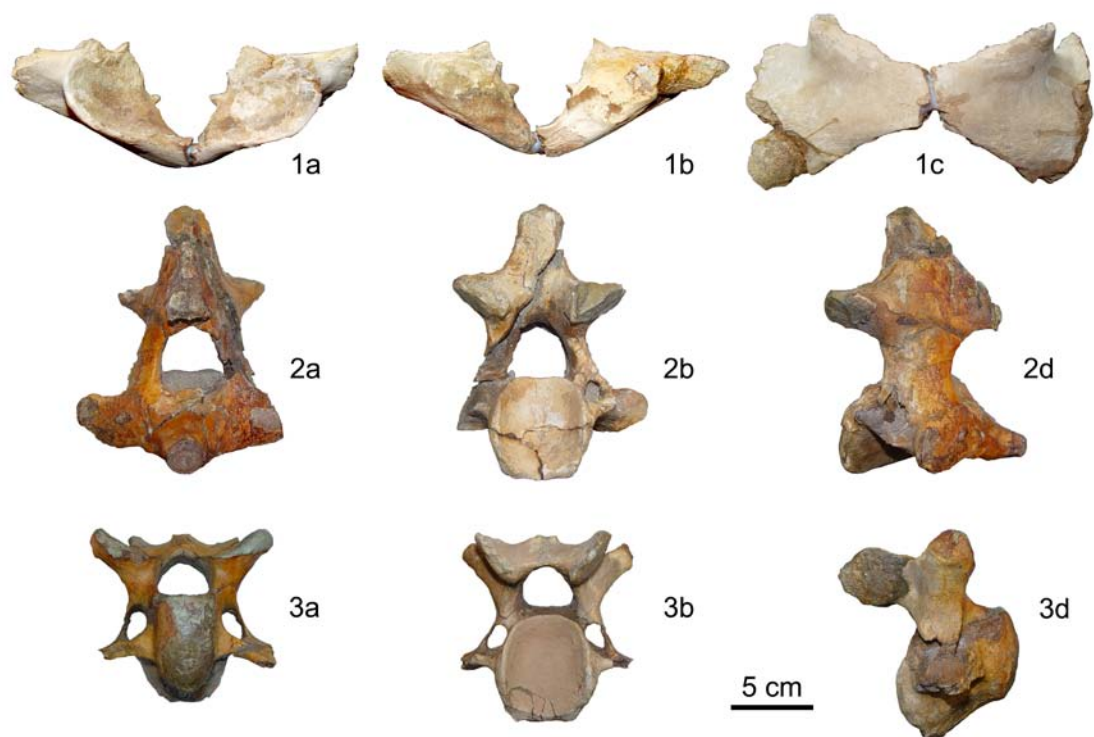




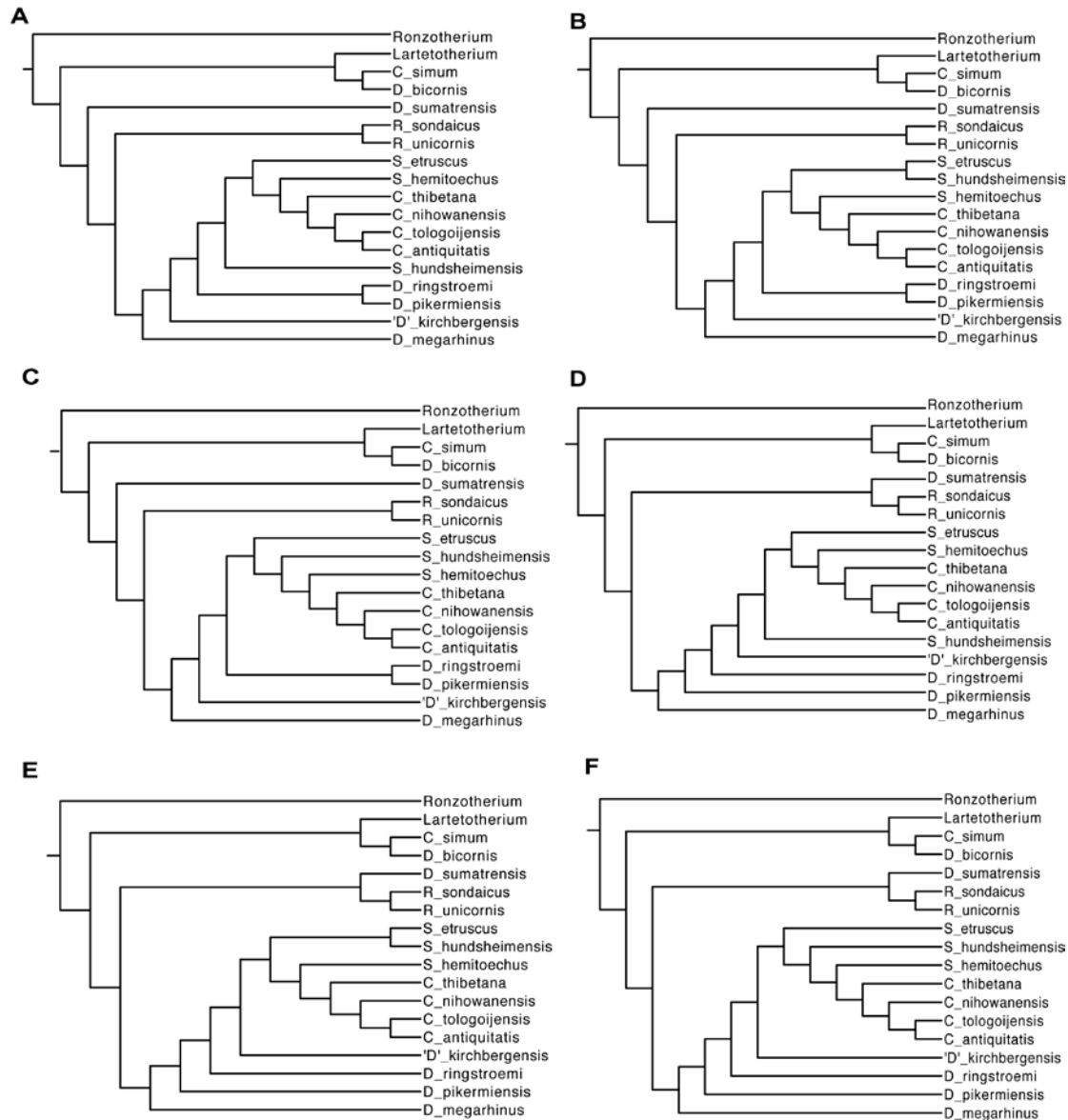
**Fig. S4.** Holotype of *Coelodonta thibetana* sp. nov. (IVPP V15908). Ventrrolateral view of the skull.



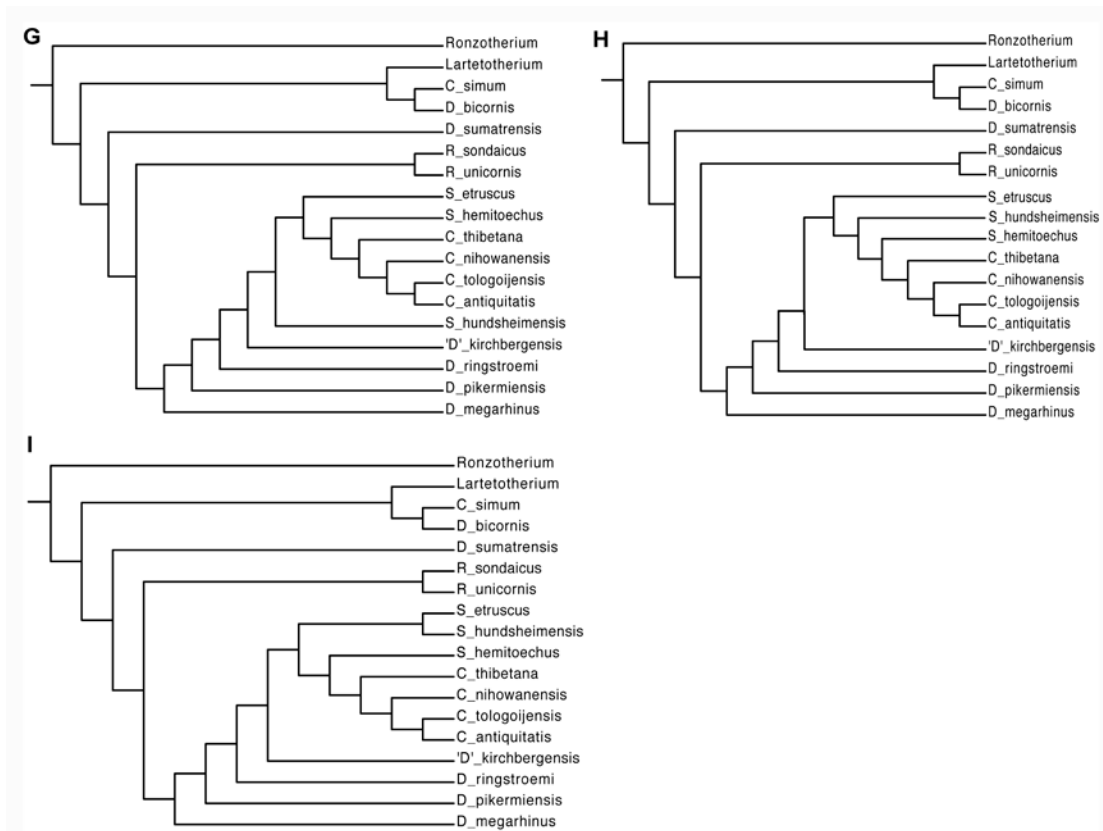
**Fig. S5.** Holotype of *Coelodonta thibetana* sp. nov. (IVPP V15908). **(a)** Occipital view of the skull; **(b)** lateral view of the skull; **(c)** lateral view of the mandible; **(d)** occlusal view of the mandible. Scale bars, 10 cm, left for a, and right for b, c and d.



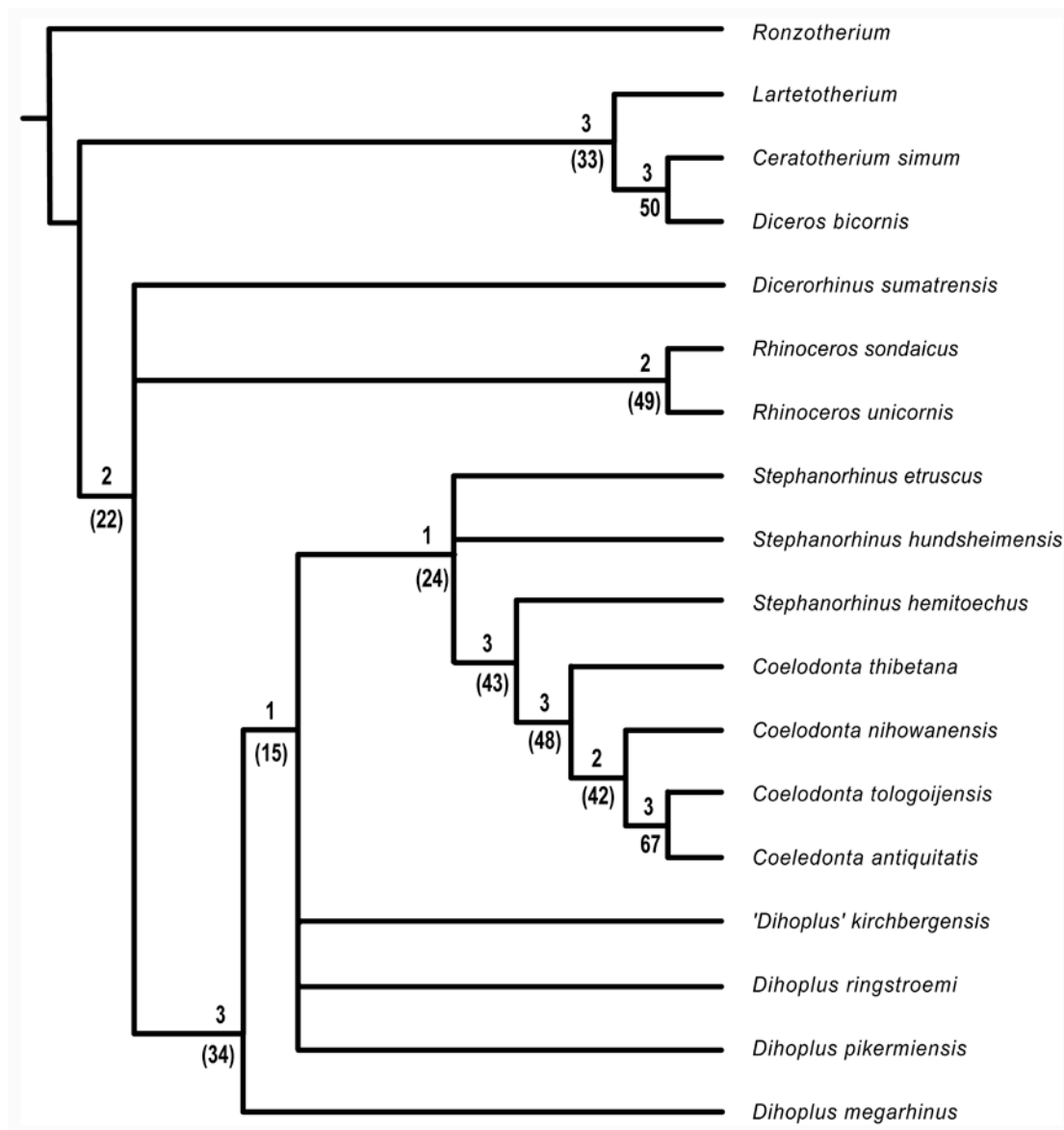
**Fig. S6.** Holotype of *Coelodonta thibetana* sp. nov. (IVPP V15908). **(1)** atlas; **(2)** axis; **(3)** third cervical vertebra. **(a)** cranial, **(b)** caudal, **(c)** ventral, and **(d)** lateral view.



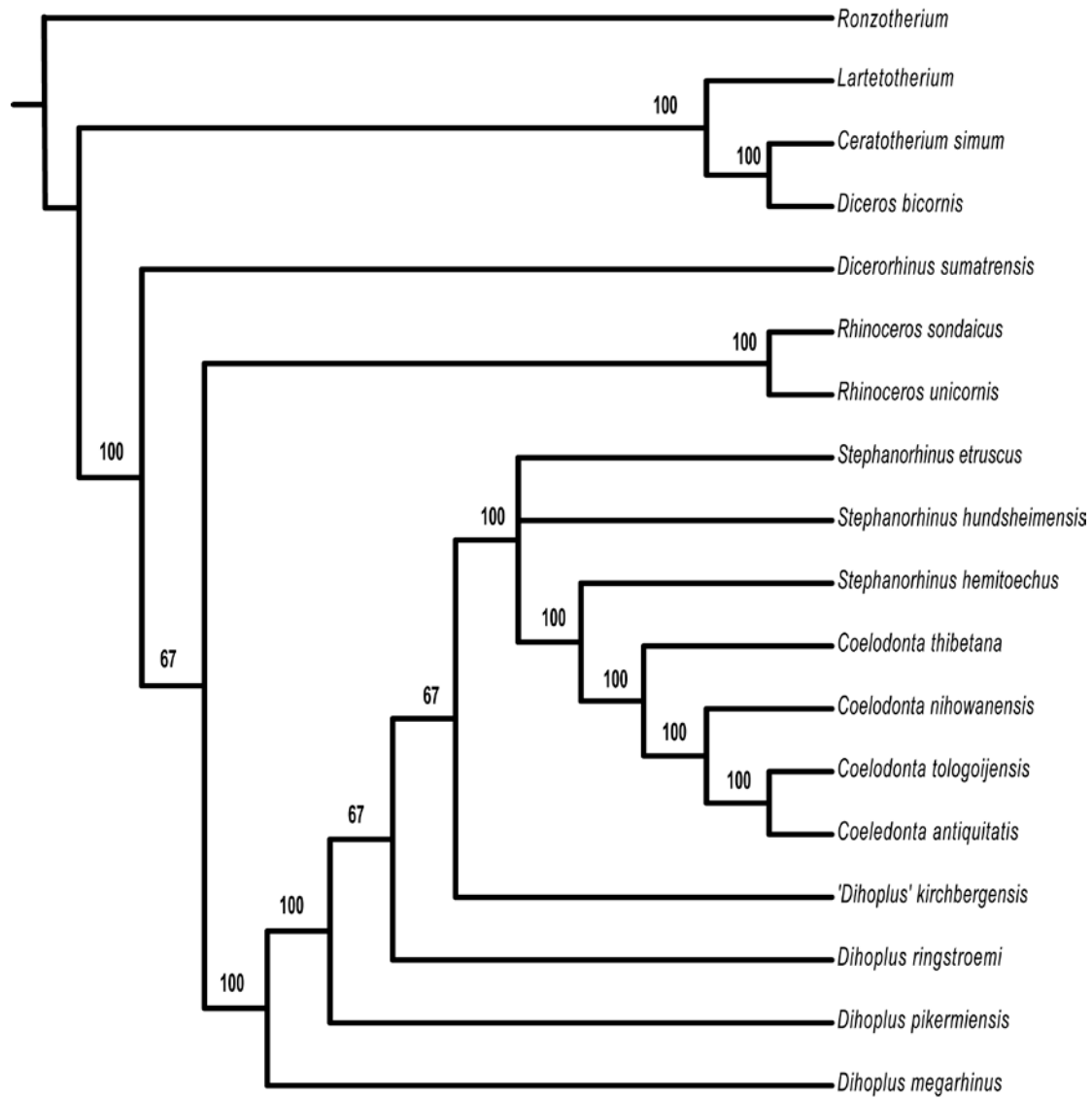
**Fig. S7.** Nine most parsimonious trees of the phylogenetic analysis of Rhinocerotini.



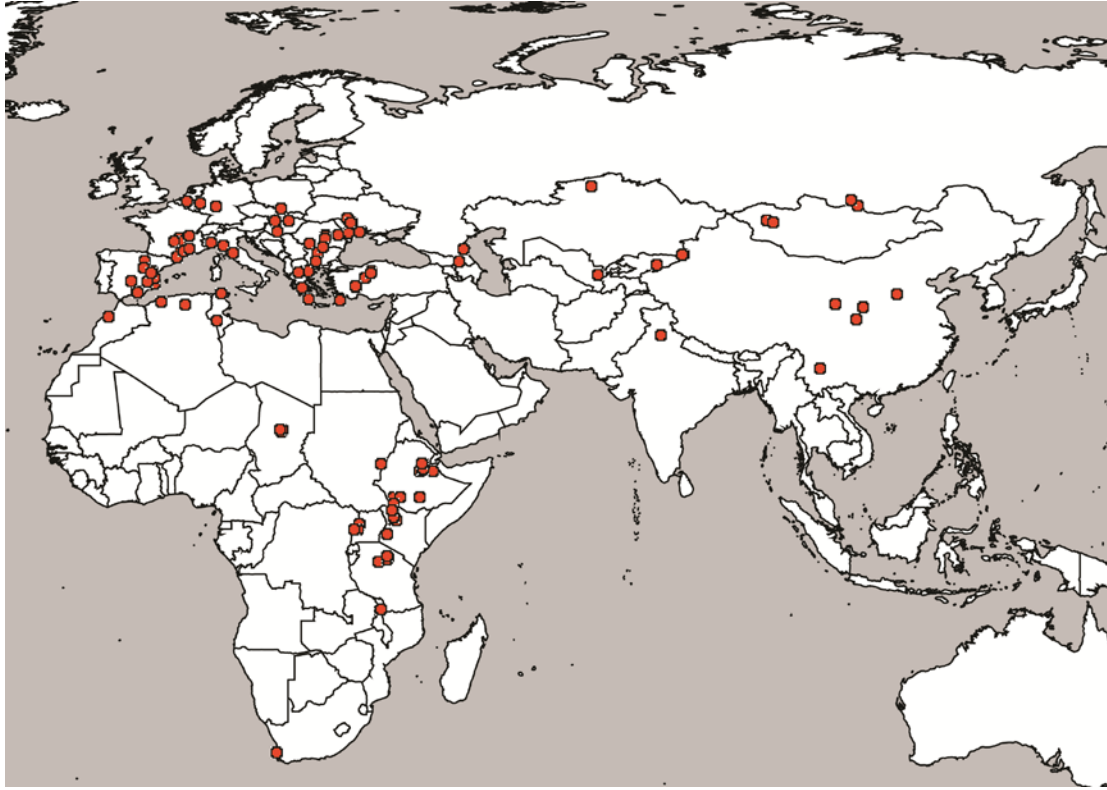
**Fig. S7.** Continued.



**Fig. S8.** Strict consensus of the 9 most parsimonious trees (Fig. S7). Decay values are above nodes and bootstrap frequencies below.

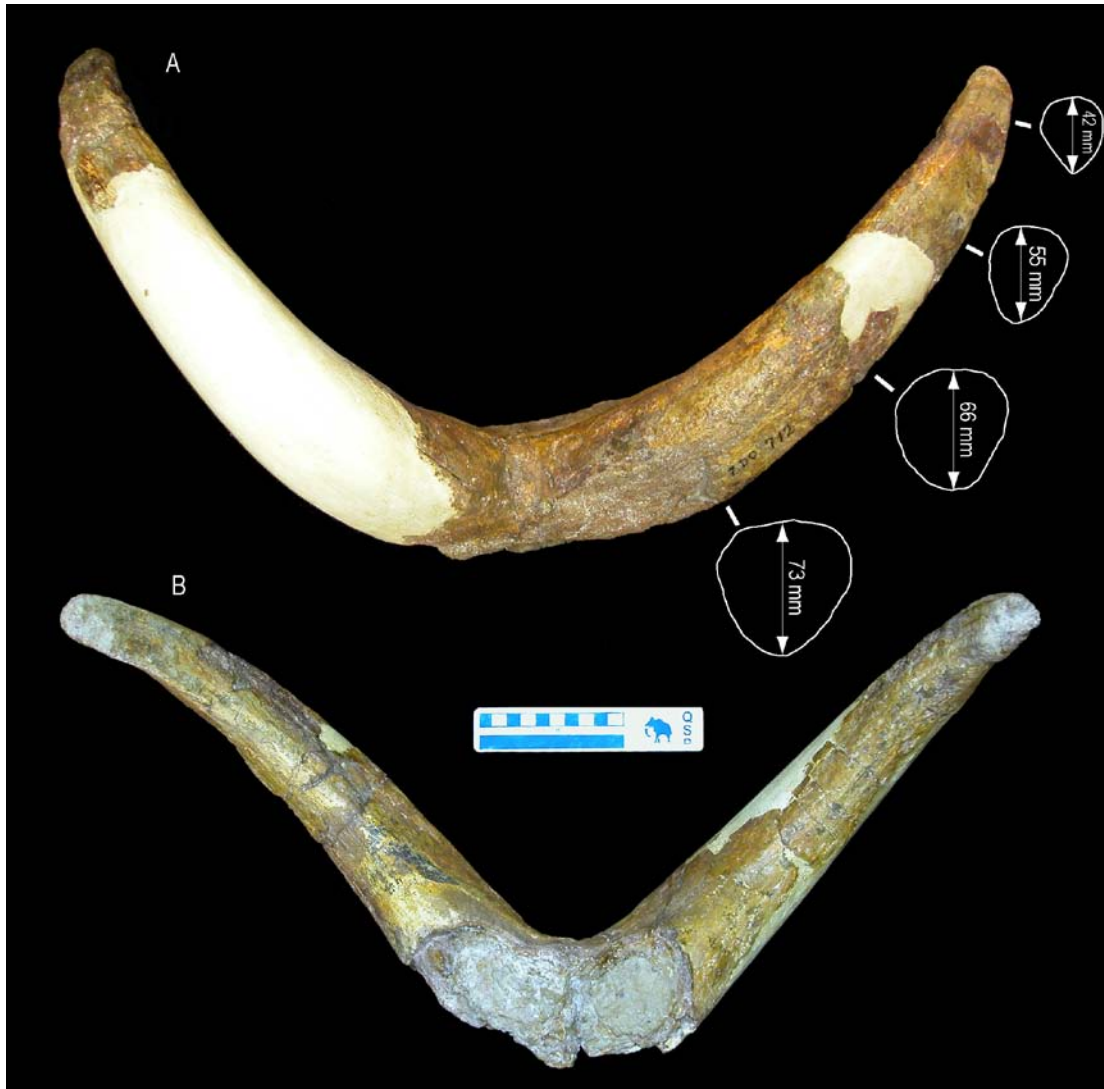


**Fig. S9.** 50% majority consensus of the 9 most parsimonious trees (Fig. S7).



**Fig. S10.** Occurrences of Rhinocerotidae in the NOW database (87) at Pliocene localities (aged between 2.59 and 5.31 Ma) of the Old World. There are a total of 229 reported occurrences in 173 localities, none of which include the genus *Coelodonta*.

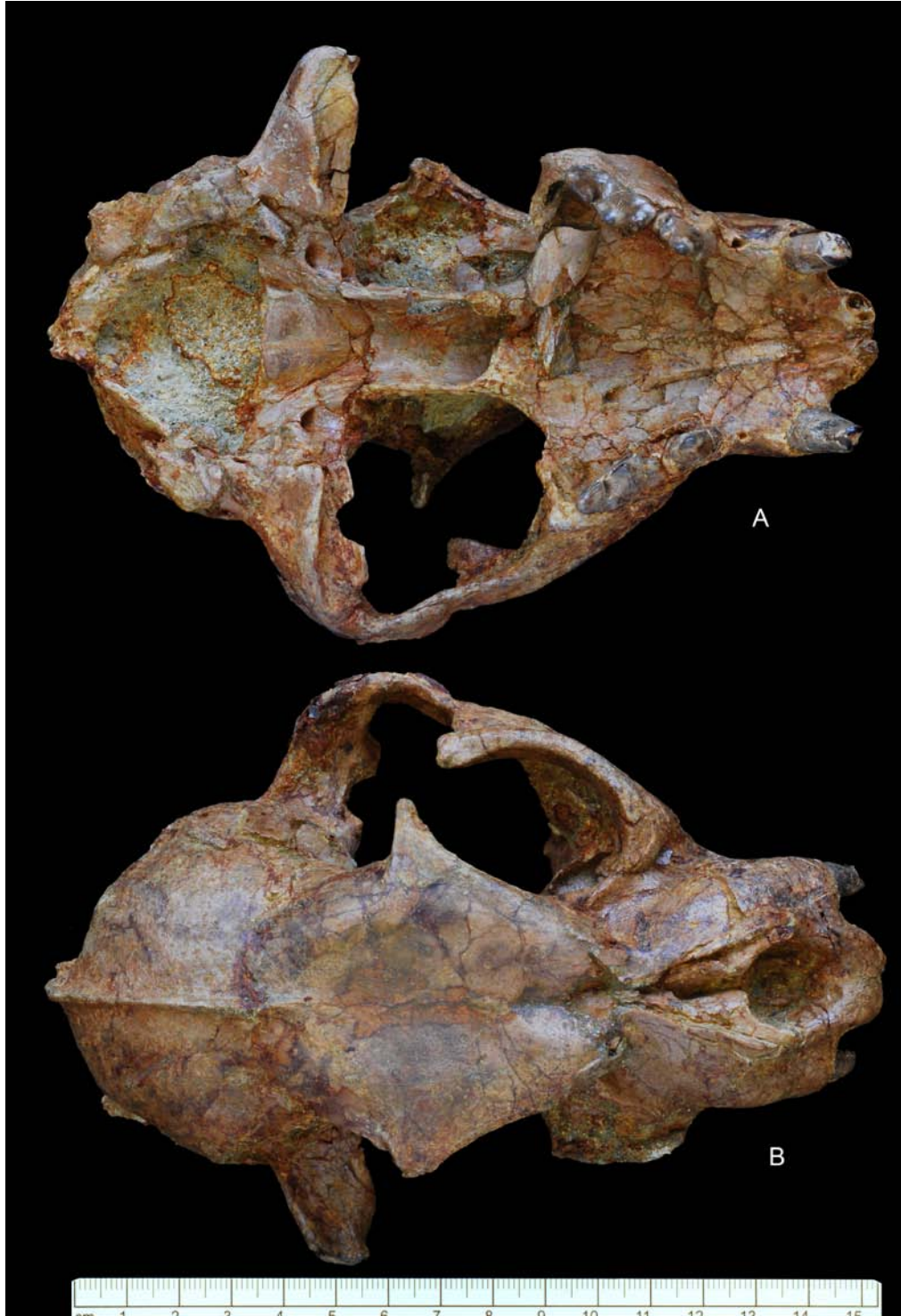




**Fig. S11.** Horncore of ?*Pseudois* sp. from ZD0712 (~3.5 Ma), Zanda Basin, southwestern Tibet. A, dorsal view and cross-section outlines of horncore; B, posterior view of horncore. Scale = 10 cm.



**Fig. S12.** *Qurlignoria* Bohlin from ZD0745 (~4.2 Ma), Zanda Basin, southwest Tibet. Relatively upright and straight (not posteriorly curved) and slightly divergent horncores with an oval cross-section are typical characters for this genus as well as the extant *Pantholops*, which has a more elongate and slender horncore. Anterior (A) and lateral (B) views of left horncore. Scale is in mm.



**Fig. S13.** A primitive snow leopard [*Panthera (Uncia)* sp.] from ZD1001 (~4.4 Ma), Zanda Basin, southwest Tibet. Somewhat smaller than extant snow leopard (*Panthera (Uncia) uncia*), the Zanda specimen displays a frontonasal compression and an expanded maxillary to the exclusion of jugal and lacrimal, features characteristic of the snow leopard. Ventral (A) and

dorsal (B) views of skull. Scale is in mm.

## Tables in Supporting Online Material

**Table S1.** Composite list of vertebrate taxa from the Zanda strata (IVPP locality numbers in parentheses).

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### Osteichthyes

#### Cyprinidae

### Mammalia

#### Insectivora

Soricidae indet. (ZD0609, 1001)

#### Carnivora

*Nyctereutes* cf. *N. tingi* (ZD0624)

*Vulpes* sp. n. (ZD1001)

*Panthera (Uncia)* sp. n. (ZD1001)

*Meles* sp. n. (ZD1001, ZD1004)

*Mustela* sp. (ZD1001)

*Chasmaporthetes* sp. (ZD0908, 1029, 0636)

#### Perissodactyla

*Hipparion zandaense* (ZD0701 and others)

*Coelodonta thibetana* new species (ZD0740)

#### Artiodactyla

*Cervavitus* sp. n. (ZD0624)

?*Pseudois* sp. n. (ZD0712)

*Antilospira/Spirocerus* sp. (ZD0701, 1001)

*Qurlignoria* sp. (ZD0604, 0745)

Bovidae gen. A (ZD1001)

Bovidae gen. B (ZD1001)

#### Proboscidea

Gomphotheriidae indet. (ZD0746, 1015, 33, 36, 46, 48)

#### Rodentia

*Aepyosciurus* sp. (ZD1001)

*Nannocricetus* sp. (ZD0609, 1001)

Cricetidae gen. et sp. nov. (ZD1001)

*Prosiphneus* cf. *P. eriksoni* (ZD1001)

*Mimomys* (*Aratomys*) *bilikeensis* (ZD0609, 0904)

*Apodemus* sp. (ZD0609, 0904)

#### Lagomorpha

*Trischizolagus* cf. *T. mirificus* (ZD0609, 0904)

*Trischizolagus* cf. *T. dimitrescuae* (ZD0726, 1001)

*Ochotona* sp. 1 (ZD0609, 0904)

*Ochotona* sp. 2 (ZD0609, 0902, 0904)

*Ochotona* sp. 3 (ZD1001)

*Ochotona* sp. 4 (ZD0726)

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**Table S2.** Cranial measurements (in mm) of *Coelodonta thibetana*, as defined by Guérin (55).

Measures	<i>C. thibetana</i>	<i>C. nihowanensis</i>	<i>C. antiquitatis</i>
	V15908	HMV0980	Mean (Guérin, 1980)
1 Distance between occipital condyle and premaxillary tip	676	620	720.8
2 Distance between nasal tip and occipital condyle	692.2	650	720.8
3 Distance between nasal tip and occipital crest	771	770	781
4 Distance between the nasal tip and notch	224	200	205.2
5 Minimal width of the braincase	109	82.5	126.4
6 Distance between occipital crest and postorbital process	349	360	335.2
7 Distance between occipital crest and supraorbital tubercle	418	390	393.8
8 Distance between occipital crest and lacrimal tubercle	443	435	412.5
9 Distance between the nasal notch and the orbit	136	139	151.4
13 Distance between occipital condyle and M3	332	317	347.3
14 Distance between the nasal tip and the orbit	369	335	373.9
15 width of occipital crest	190	145	206.9
16 width between mastoid processes	225.2	212.5	273.1
17 Minimal width between the parietal crests	46.5	32	90.5
18 Width between postorbital processes	222.5	195	218.1
19 Width between supraorbital tubercles	~244	-	248.6
20 Width between lacrimal tubercles	~320	255	286.7
21 Maximal width between the zygomatic arches	303.4	294	334
22 Width of the nasal base	178	140	165.1
23 Height of occipital face	~130	152	175.2
25 Height of skull in front of P2	~153	171	196.1
26 Height of skull in front of M1	~123	178	195.6
27 Height of skull in front of M3	~140	190	206.8
28 Width of the palate in front of P2	~94	46	64.4
29 Width of the palate in front of M1	~90	64	87.7
30 Width of the palate in front of M3	~100	77	98
31 Width of foramen magnum	62.5	45	59.9
32 Width between occipital condyles	141.4	140	157.4

**Table S3.** Mandibular measurements (in mm) of *Coelodonta thibetana* as defined by Guérin (55).

Measures	<i>C. thibetana</i>	<i>C. nihowanensis</i>	<i>C. antiquitatis</i>
	V15908	HMV0980	Mean (Guérin, 1980)
1 Length	512	508	525.6
2 Distance between symphysis and angular process	415	435	425.6
3 Height of horizontal ramus in front of p3	87.6	73.5	81.6
4 Height of horizontal ramus in front of p4	89.8	80	88.5
5 Height of horizontal ramus in front of m1	97.4	95	96.8
6 Height of horizontal ramus in front of m2	97.7	102	101
7 Height of horizontal ramus in front of m3	96.2	107	100.9
8 Height of horizontal ramus posterior to m3	104.8	112	108.4
9 Distance between horizontal rami in front of m1	-	60	61.6
10 Distance between horizontal rami in front of m3	-	68	58
11 Length of symphysis	119	86	119.6
13 Antero-posterior diameter of ascending ramus	154	164	168.4
14 Transverse diameter of condyle	101.3	99.5	99.8
15 Height at condyle	269	268	263.8
16 Height at coronoid process	311	325	331.5



**Table S4.** Measurements of cheek teeth (in mm) of *Coelodonta thibetana* (length  $\times$  width  $\times$  height).

Upper teeth	V 15908	Lower teeth	V15908
P2	33.2 $\times$ 33.4 $\times$ 27.4	p2	27.5 $\times$ 17 $\times$ 22.5
P3	37.6 $\times$ 46.6 $\times$ 26.7	p3	32.9 $\times$ 25.1 $\times$ 25.5
P4	41 $\times$ 51.8 $\times$ 30.2	p4	38.2 $\times$ 27.1 $\times$ 31.3
M1	50 $\times$ 57.4 $\times$ 31.9	m1	39.7 $\times$ 29.8 $\times$ 28
M2	54.1 $\times$ 60.5 $\times$ 43.7	m2	45.9 $\times$ 29.7 $\times$ 34
M3	60.9 $\times$ 57.2 $\times$ 52.9	m3	47.3 $\times$ 30 $\times$ 35.2

**Table S5.** Measurements of atlas of *Coelodonta thibetana* (in mm).

Measures	V15908
Total length in projection, without ventral tubercle	>121
Width between alar notches	152
Distance between inferior alar foramina	149

**Table S6.** Measurements of axis and third cervical vertebrata of *Coelodonta thibetana* (in mm).

Measures	Axis	Third cervical vertebra
Length of body	115	85
Width of the caudal articular surface	49.4	49.7
Height of the caudal articular surface	63.6	65
Total height of vertebra	171	-
Width of cranial articulation	154	117
Width of caudal articulation	103.3	81
Minimum width of body	122	64.5
Length of arch in sagittal axis	77.6	36.3
Length of arch at the base	45.5	39.2
Maximum width between transverse processes	-	122

**Table S7.** Character list. Description of characters used in the phylogenetic analysis of Rhinocerotini. Characters 1-39 are from Antoine (62), characters 40-46 are new to this study. Character numbers from Antoine (62) (in brackets) follow the character numbers used in this study, and an asterisk (\*) indicates a character has been modified from how it was used in Antoine (62).

## **Skull**

- 1 (2)** Maxillary infraorbital foramen = 0 above premolars; 1, above molars
- 2 (3)** Nasal notch = 0, above P1-3; 1, above P4-M1
- 3 (4)** Nasal septum = 0, never ossified; 1, ossified even sometimes
- 4 (5\*)** Nasal septum: ossified = 0, weakly; 1, strongly
- 5 (7)** Orbit: anterior border = 0, above P4-M2; 1, above M3
- 6 (9)** Frontal: postorbital process = 0, present; 1, absent
- 7 (10)** Maxillary: anterior base of the maxillary zygomatic process = 0, high; 1, low
- 8 (11)** Zygomatic arch = 0, low; 1, high
- 9 (15)** Skull: dorsal profile = 0, flat; 1, concave; 2, very concave
- 10 (18)** External auditory pseudo-meatus = 0, open; 1, closed
- 11 (19)** Occipital side = 0, inclined forward; 1, vertical; 2, inclined backward
- 12 (20)** Occipital nuchal tubercle = 0, little developed; 1, developed; 2, very developed
- 13 (21)** Skull: back of teeth row = 0, in the posterior half; 1, restricted to the anterior half
- 14 (24)** Nasal bones: rostral end = 0, narrow; 1, broad; 2, very broad
- 15 (31)** Frontal horn = 0, absent; 1, = present
- 16 (33)** Lateral projection of the orbit = 0, absent; 1, present
- 17 (35\*)** Frontal-parietal = 0, close frontoparietal crests; 1, distant crests

## **Mandible**

- 18 (53)** Symphysis = 0, very upraised; 1, upraised; 2, nearly horizontal
- 19 (59)** Mandibular corpus: base = 0, straight; 1, convex; 2, very convex
- 20 (60)** Ramus = 0, vertical; 1, inclined forward; 2, inclined backward

## **Teeth**

- 21 (63)** Compared length of the premolars/molars rows = 0,  $100 \times L_{P3-4} / L_{M1-3} > 50$ ; 1,  $42 < 100 \times L_{P3-4} / L_{M1-3} < 50$
- 22 (66\*)** Cheek teeth: cement = 0, absent; 1, weak or variable; 2, abundant
- 23 (68)** Cheek teeth: crown = 0, low; 1, high
- 24 (69)** Cheek teeth: crown = 0, high; 1, partial hypsodonty; 2, subhypsodonty; 3, hypsodonty
- 25 (71)** I1 = 0, present; 1, absent

- 26 (78)** i2 = 0, present; 1, absent
- 27 (91\*)** P1 in adults = 0, always present; 1, absent
- 28 (94)** P2: protocone and hypocone = 0, fused; 1, lingual bridge; 2, separate; 3, lingual wall
- 29 (97)** P2: protocone = 0, equal or stronger than the hypocone; 1, less strong than the hypocone
- 30 (113\*)** Upper molars: mediofossette = 0, absent; 1, present
- 31 (119)** M1-2: metacone fold = 0, present; 1, absent
- 32 (122)** M1-2: posterior part of the ectoloph = 0, straight; 1, concave
- 33 (134)** M3: shape = 0, quadrangular; 1, triangular
- 34 (137)** M3: protoleph = 0, transverse; 1, lingually elongated
- 35 (138)** M3: posterior groove on the ectometaloph = 0, present; 1, absent
- 36 (142)** Lower cheek teeth: trigonid = 0, angular; 1, rounded
- 37 (144\*)** Lower cheek teeth: metaconid = 0, not elongated; 1, elongated
- 38 (161)** Lower molars: hypolophid = 0, transverse; 1, oblique; 2, almost sagittal

## **Postcrania**

- 39 (279\*)** Limbs = 0, slender; 1, robust

## **Additional new characters**

- 40** Skull: nasal tip to front of orbit / front of orbit to condyles = 0, < 75; 1, 75 - 90; 2, > 90
- 41** Nasal bones = 0, flat or evenly curved; 1, angled or with raised protuberance; 2, rostrally massive
- 42** Nasal bones: anterior end = 0, horizontal; 1, bent slightly downward; 2, bent strongly downward
- 43** Nasal horn: boss = 0, rounded; 1, narrow
- 44** Nasal horn: sagittal ridge on the boss = 0, absent; 1, present
- 45** Upper molars: lingual cusp bases = 0, not bulbous (inflated, swollen); 1, bulbous
- 46** Upper molars: occlusal topography = 0, ectolophodont; 1 = plagiolophodont

**Table S8.** Data matrix used in the phylogenetic analysis of Rhinocerotini. Modified from Antoine (62), including 18 taxa (one as outgroup) and 46 characters (see Table S7 for character description). Missing data coded as '?', inapplicable characters as '-'.

Character	1					2					3					4				
Number	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Ronzotherium</i>	100-000010	0000000000	0-0-000100	1000000000	010000															
<i>Lartetotherium</i>	000-010021	1100111200	0-0-101110	1110100100	010000															
<i>D.sumatrensis</i>	0010000010	0101101100	000-001210	1010110101	000000															
<i>R.sondaicus</i>	0010000011	0101001201	000-001210	1010110100	000000															
<i>R.unicornis</i>	0010000021	0101001201	0011001211	1011111100	110000															
<i>C.simum</i>	000-110020	2202111022	0213111311	1001001200	210001															
<i>D.bicornis</i>	000-011020	1212111021	0010111210	1010110100	200000															
<i>S.etruscus</i>	0010001001	1001101101	0010111110	1110110101	110000															
<i>S.hundsheimensis</i>	0010001001	1001101100	0010111110	1110110102	110000															
<i>S.hemitoechus</i>	1110001111	2011101112	1112111110	1110110102	020000															
<i>D.ringstroemi</i>	000-001011	1001101110	0010011100	1110110102	110010															
<i>D.pikermiensis</i>	000-001011	1001101100	0010001110	0110110101	110010															
<i>D.megarhinus</i>	000-101011	1001101100	0010001210	1110110100	010010															
<i>'D'.kirchbergensis</i>	0010101011	1001101100	0011111210	1110110100	110010															
<i>C.thibetana</i>	0110111101	2011101112	0111111311	01100101?0	111001															
<i>C.nihowanensis</i>	0011000101	1011101122	0112111301	0111010100	111101															
<i>C.tologoiensis</i>	00111?1001	2012101112	11121111?1	0101000201	011101															
<i>C.antiquitatis</i>	1111111011	2012101122	1213111101	0001001211	021101															

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