



Body mass of the giant rhinos (Paraceratheriinae, Mammalia) and its tendency in evolution

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ABSTRACT

As the largest land mammal that ever lived on the earth, giant rhinos have received much attention from researchers around the world. Here, we use linear models based on limb bone length and circumference measurements of many living animals to estimate the body mass of giant rhinos, with the help of a new composite skeleton of the giant rhino (*Dzungariotherium* sp.) from the Qingshuiying Formation, Lingwu, northern China. Our estimate suggests that *Dzungariotherium* sp. from Lingwu is one of the largest giant rhinos known, with a body mass of 20,558 kg. Under the limitation of materials, we estimated the body mass of giant rhinos in as many species as possible by different methods. The body masses of other giant rhinos are also estimated with adjustments based on the new composite skeleton. The data obtained on *Dzungariotherium* have been considered together with other data on giant rhinos to observe the evolutionary tendency of the group at a large geological scale. It shows that giant rhinos experienced a rapid body size increase since the Late Eocene and divided into three stages, coinciding with the global temperature falling and the spread of the open environment.

ARTICLE HISTORY

Received 15 January 2022
Accepted 22 June 2022

KEYWORDS

Giant rhino; body mass; linear model; Oligocene; Lingwu; China

Introduction

Giant rhinos (common name for Paraceratheriinae) belong to a unique lineage of Rhinocerotidae, and lived in Eurasia in ~40–22 Ma, mainly in China, Pakistan, Kazakhstan, Mongolia, and other regions of Asia, but they were also found sporadically in Eastern Europe (Borissiak 1923; Gromova 1959; Qiu and Wang 2007; Prothero 2013).

There are seven generally recognised genera (*Juxia*, *Urtinotherium*, *Paraceratherium*, *Dzungariotherium*, *Benaratherium*, *Aralotherium*, and *Turpanotherium*) in the subfamily Paraceratheriinae, and *Dzungariotherium* is generally considered to be the largest land mammal ever (Qiu and Wang 2007). Paraceratheriinae belongs to the family Paraceratheriidae, which is one of the four branches (Amynodontidae, Hyracodontidae, Rhinocerotidae, and Paraceratheriidae) of Rhinocerotidae that evolved in the Early Eocene (Deng et al. 2021). Another subfamily of Paraceratheriidae is Forstercooperiinae (including *Pappaceras* and *Forstercooperia*) (Qiu and Wang 2007; Deng et al. 2021), although a recent study suggested that Forstercooperiinae should be separated from Paraceratheriidae, and represents a more primitive family (Bai et al. 2020). Paraceratheriinae appeared in the Middle Eocene in Inner Mongolia, flourishing in the Oligocene, and went extinct at the beginning of the Miocene (Qiu and Wang 2007; Li et al. 2017), and see the phylogeny figure of Deng et al. (2021). Its body size increased rapidly during its evolution and then shrank again near its final extinction (Qiu and Wang 2007). Many researchers have tried estimating the body mass of giant rhinos (Alexander 1989; Gingerich 1990; Fortelius and Kappelman 1993; Paul 1997; Qiu and Wang 2007; Deng 2009; Prothero 2013; Larramendi 2015), and these studies are summarised in Table 1.

Alexander (1989) extrapolated the body length of *Indricotherium transouralicum* (= *Paraceratherium asiaticum*) and African buffalo *Syncerus caffer*, to which he believed *P. asiaticum* reconstructed shape was similar, and estimated that the body mass of *P. asiaticum* could reach 34 tonnes.

Gingerich (1990) used each measurement of limb bones, longest metacarpal, and metatarsal to predict the body mass of *Baluchitherium grangeri* (= *Paraceratherium grangeri*) through regression analysis, and finally, he divided the results into two categories and averaged them, considering the smaller one weighs about 9 tonnes, and the larger type weighs 14–15 tonnes.

Fortelius and Kappelman (1993) used several different methods. Based on the head-and-body length data, they used two different restored body length data of the *Indricotherium transouralicum* (= *Paraceratherium asiaticum*) skeleton, and the estimate given by the linear model was 13–27 tonnes. Based on the different linear models of the measurements of the skull, the body mass of *P. asiaticum* is estimated to be 7–16 tonnes, with an average value of 9.6 tonnes. The use of different linear models on teeth measurements to estimate the average body mass of *Baluchitherium bugtiense* (= *Paraceratherium bugtiense*) gives an estimate of 6.5 tonnes, the average body mass of *P. asiaticum* is 8 tonnes, and the average body mass of *Paraceratherium prohorovi* (= *Aralotherium prohorovi*) is 10.7 tonnes. According to the different linear models of proximal limb bones, *P. asiaticum* weighs 5–17 tonnes, and *P. bugtiense* weighs 9–15 tonnes.

Paul (1997) used the method of reconstructing the volume model and estimated that *Paraceratherium transouralicum* (= *Paraceratherium asiaticum*) weighs about 16.4 tonnes, and believed that this result may be slightly underestimated.

Table 1. Summary of studies on body mass of giant rhinos.

Authors	Method	Materials	Species	Body mass
Alexander (1989)	Extrapolated of African buffalo <i>Syncerus caffer</i>	Body length	<i>P. asiaticum</i>	34 t
Gingerich (1990)	Linear models	Limb bones, longest metacarpal, and metatarsal	<i>P. grangeri</i>	smaller about 9 t; larger type 14–15 t
Fortelius and Kappelman (1993)	Linear models	Head-and-body length	<i>P. asiaticum</i>	13–27 t
		skull	<i>P. asiaticum</i>	7–16 t, average 9.6 t
		Teeth	<i>P. bugtiense</i>	6.5 t
		Teeth	<i>P. asiaticum</i>	8 t
		Teeth	<i>A. prohorovi</i>	10.7 t
		Proximal limb bones	<i>P. asiaticum</i>	5–17 t
		Proximal limb bones	<i>P. bugtiense</i>	9–15 t
Paul (1997)	Reconstructing the volume model	Skeleton	<i>P. asiaticum</i>	16.4 t
Qiu and Wang (2007)	Linear models	Head-and-body length	<i>J. sharamurenensis</i>	0.75–0.89 t
		Head-and-body length	<i>P. lepidum</i>	15 t
Deng (2009)	Linear models	Teeth	<i>D. orgosense</i>	24 t
Tsubamoto (2014)	Linear models	Astragalus	<i>P. bugtiense</i>	12.7 t
Larramendi (2015)	Reconstructing the volume model	Skeleton	<i>P. asiaticum</i>	17.1 t

Qiu and Wang (2007) used the linear model of body length and body mass and used the parameters of the existing ungulates and the whole ungulates as a reference. They inferred that the body mass of *Juxia sharamurenensis* is about 749–888 kg, and the body mass of *Paraceratherium lepidum* is around 15 tonnes.

Deng (2009) estimated that the body mass of *Dzungariotherium orgosense* was about 24 tonnes by using the parameters and equation (artiodactyls+ perissodactyls) of Legendre (1986) on the lower first molar.

Prothero (2013) believed that large-sized paraceratheres could reach 15–20 tonnes, considering the limitations of metabolism and digestion.

Tsubamoto (2014) used linear models of astragalus measurements to estimate the body mass of *Baluchitherium grangeri* (= *Paraceratherium grangeri*), and the mean was 12.7 tonnes.

Larramendi (2015) used Paul's model and used different specific gravity to infer that the body mass of *Paraceratherium transouralicum* (= *Paraceratherium asiaticum*) was 17.1 tonnes.

Some of these studies did not use strict statistical models, and many measurements had not been published by the time of these researches. The estimation using body length is greatly influenced by the body plan of animals, and it is difficult to ensure the reliability of the results no matter using only rhinoceroses, or general ungulate species as a reference in the absence of similar species reference. The estimation using the tooth area is affected by the feeding and digestion pattern of species. However, the size of giant rhinos is greatly larger than any other group of rhinos, so there must be something unique in its feeding, and the method using tooth area as the predicted variable, may not be accurate. Note that the large size also suggests that we cannot be sure that linear models fit correctly for such extremely big animals. Even if it seems that postcranial dimensions and body mass fit linearly across many clades, the models suffer from a lack of robustness when reaching extreme parameters (Campione and Evans 2012).

The body mass of the giant rhinos is closely related to their evolution, as well as to the age and environment in which they lived. In the past, only *Juxia sharamurenensis*, *Paraceratherium lepidum*, and *P. asiaticum* are known to have relatively complete skeletons, which limits our understanding of the body plan of giant rhinos. In this study, we propose to estimate body mass of more giant rhinos under a uniform standard and explore their size evolution. To do so, we notably rely on the data of a new composite skeleton of

Dzungariotherium sp. (as shown in Figure 1, the taxonomical determination and anatomical details will be published in other articles) housed in the Biye Palaeontological Museum in Fugu County, Shanxi Province. The limb bones (humerus, femur, radius, and tibia) length and circumference of living mammals were used as a reference to estimate the body mass of *Dzungariotherium* sp. from Lingwu and other giant rhinos, since limb bones, as supporting bones, have the most direct correlation with body mass (Qiu and Wang 2007). Given the scarcity and incompleteness of giant rhino fossil materials, little data are available for all four long bones of the giant rhinos. To discuss the evolution of body mass of this lineage, we also estimate the body mass of each giant rhino by establishing a separate model for each limb bone, as most species has only one or two long bone known. The limb bone allometric trend of giant rhinos is different from those in other Rhinocerotidae, and all long bones follow a different evolutionary trend, such as humeral shape strongly derived and following the common allometric trend of all rhinos, while the radius remains extremely plesiomorphic and relatively much more slender than in other derived rhinos (Mallet 2020; Mallet et al. 2021, 2022). Making separate models for each limb bone can also help reduce the impact of this difference. To unify the standard, here we used the skeleton of *Dzungariotherium* sp. and *Juxia sharamurenensis* to scale the limb models results for those with only part of the limb bones. We then compared our results with that of the previous studies, and try to explore the size evolution of giant rhinos accordingly.

Geological background of *Dzungariotherium* sp. skeleton

The giant rhino skeleton was found from Qingshuiying Village, Lingwu, Ningxia Hui Autonomous Region in northern China (the topography of the locality is shown in Figure 2). It is preliminarily identified as *Dzungariotherium* sp. as it has a strong reduction of the premaxilla and upper incisors, and the paroccipito-posttympanic process is thickened transversely, with its lateral border far external to condyle. The fossils from this region were first reported by Young and Chow (1956), and they named the fossil bearing formation as the Qingshuiying Formation. They found here *Paraceratheriinae* gen. et sp. indet. (= *Baluchitherium grangeri*), *Cyclomylyus lohensis*, *Entelodon mongoliensis* (= *Archaeotherium ordosius*) and *Schizotherium* sp. (Young and Chow 1956). Later, the age was determined as the Early Oligocene (Wang 1997).

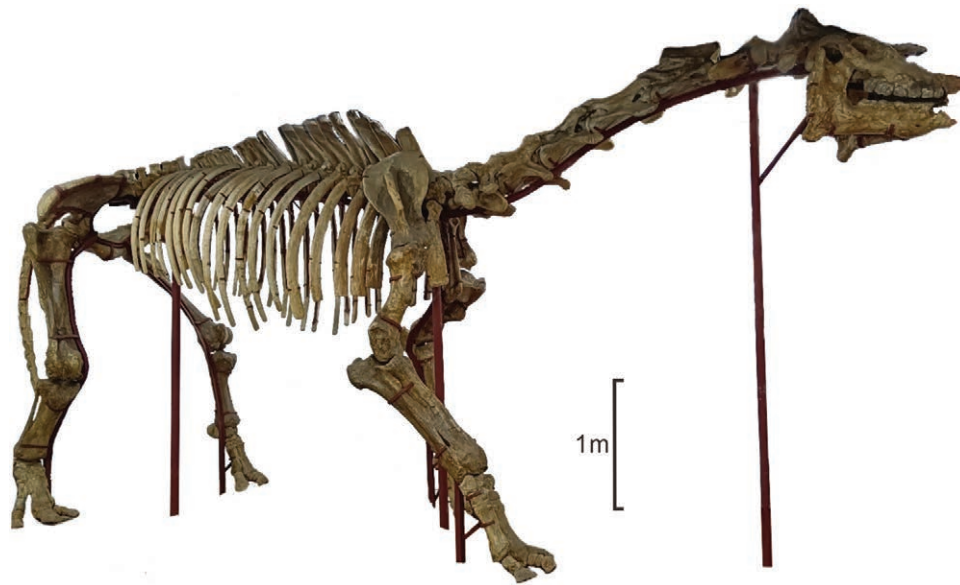


Figure 1. Mounted composed skeleton of *Dzungariotherium* sp. from Lingwu.

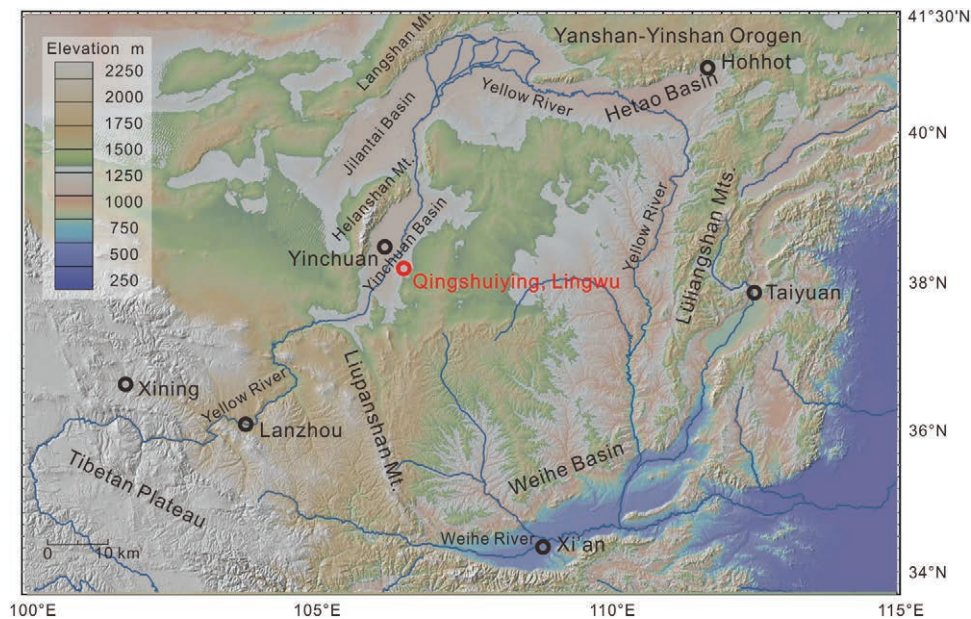


Figure 2. Fossil locality of Lingwu County, Ningxia Hui Autonomous Region, China. Background map from geomapapp.

Since April 2014, a large number of Oligocene mammalian fossils have been found in the sandstone of the Qingshuiying Formation, Lingwu County. The discovered materials are typical paraceratheria fauna elements, including numerous complete skulls and postcranial bones of the giant rhino (including the composite skeleton used in this study), as well as hyracodonts, chalicotheres, entelodonts, and hyaenodonts (these materials have not yet been published). As the new specimen of *Dzungariotherium* sp. seems to be derived in Paraceratheriinae, and according to the chronological inference of an unpublished *Schizotherium* sp. nov. from the same locality, the age of *Dzungariotherium* sp. is temporarily set as the late Early Oligocene in this study, pending on deeper study of the fauna and locality.

Material and methods

Data training the linear model

To construct the linear model allowing to estimate the body mass, we collected the length and circumference data of the four major long bones, i.e., humerus, femur, radius, and tibia as the training data. Limb bone data (McMahon 1975; Guérin 1982; Christiansen 1999a) and body mass data (Christiansen 1999b, 2002; Meiri et al. 2021) of 453 individuals from 155 living mammal species were collected from the literature. Since not all individuals of living species have the corresponding body mass data, we used the average value of limb bone and body mass as the raw data. Limb bone measurements and body mass data for these living species are shown in Table A1.

In addition, we did not separate different genders as most of the training data of the living species we used are gender-neutral average values published by other researchers. In the past, there has been controversy over whether some observed differences between different individuals of giant rhinos with similar morphology are sexually dimorphic or only interspecific (Lucas and Sobus 1989; Spassov 1989; Dashzeveg 1991; McKenna and Bell 1997; Qiu et al. 2004), no definite evidence supports a significant difference between male and female body size in giant rhino species. Therefore, we do not have evidence to determine the gender of the giant rhino limb bone materials used in this study.

Fossil materials used in body mass estimation

The limb bone data of *Dzungariotherium* sp. specimen housed in the Biye Palaeontological Museum (Fugu, Shaanxi Province) were measured by authors, and the limb bones data of other giant rhinos (here we use the data of *Juxia sharamurenensis*, *Urtinotherium intermedium*, *Paraceratherium grangeri*, *P. asiaticum*, *P. bugtiense*, *P. lepidum*, and *Aralotherium prohorovi*) were taken from Borissiak (1923), Forster-Cooper (1923), Granger and Gregory (1936), Wood (1938), Gromova (1959), and Qiu and Wang (2007). Some of the unavailable measurements were measured and calculated on published figures.

The limb bones of *Dzungariotherium* sp. were measured with a tapeline, accurate to 1 mm. Other fossil materials used are shown in Table A2.

Principal component analysis (PCA)

In search of species whose body plan is more like giant rhinos, we tried using limb bone measurements of *Juxia sharamurenensis*, *Dzungariotherium* sp. (since only they have complete skeletons available), and 155 living mammals to explore the limb bone characteristics of giant rhinos. The body plan of the large-sized paraceratheres is very different from those of living rhinos and other ungulates. The neck and limbs (relative to their trunks) of giant rhinos are much longer than those of other rhinos, so horses have been used as a reference to estimate the body mass by previous authors (Qiu and Wang 2007). The method of calculating with limb bone data is based on a similar body mass-bearing model, so it will be better to select existing species with a similar proportion to the large-sized paraceratheres. We performed a principal component analysis to study the limb bone proportion of giant rhinos, and selected proper living species to train the linear model based on their position in PCA space as Figueirido et al. (2011) did. The ratios of other measurements to the length of the humerus were used as raw data. To test whether these data are suitable for PCA, we performed Bartlett's test of sphericity and Kaiser–Meyer–Olkin Measure of Sampling Adequacy. These tests (Revelle and Revelle 2015; Wickham et al. 2015) and PCA were performed in R (R Development Core Team 2016). Parts of the figure plots were also made in the software package ggplot2 (R Development Core Team

2016; Wickham 2016) in this software. R code regarding PCAs is provided in Appendix. On the other hand, some authors suggested that the estimation of the linear regression model could not be limited by the body plan of the animal. For example, Campione and Evans (2012) proposed that, although the limb scaling have significant differences, the relationship between proximal (stylopodial) limb bone circumference and body mass is highly conserved in extant terrestrial mammals and reptiles. We also performed calculations using data without PCA screening, and the specific content is shown in the appendix.

Linear models

Multivariate linear regression models were trained using the species selected above to estimate the body mass of the giant rhinos. The length and circumference measurements of the four limbs (humerus, femur, radius, and tibia) were logged and regressed with the logged body mass. Akaike information criterion is used in model selection of stepwise regression of the four limb bones. Since the four limb bone materials of most species of giant rhinos were not all present, we have established a linear model for the length and circumference of each limb bone and body mass separately. The formulas and parameters of these five models are shown in Table 2. The results presented in the Results section are the mean of the calculated results of the combined stepwise regression model and the four individual limb bone models. Campione and Evans (2012) suggested that the circumference of the humerus and femur could provide estimates with higher applicability. We also performed estimation based on circumference measurements, and the results obtained are not much different (Given material limitations, there are only four results available and statistical analysis is not possible) from those of other models established. We did not use the quadratic model here since there is still controversial whether this method is better than the linear model (Campione 2017). Considering the theoretical additional weighting problem of averaging it with other models, we included its results in Table A5 and did not use it in Results section. All calculations were performed in R (R Development Core Team 2016) and are included in the appendix.

The available bone materials and data of giant rhino limbs are quite limited. Some of them used here have only one individual, so the estimation results cannot represent the mean body size of a species. The viewpoints in the Discussion are also limited by this question. If there are multiple specimens, the mean value is used for calculation.

Since some species of giant rhinos have no long bone materials, the linear model of Legendre (1986), which uses the area of the lower first molar (m1) to estimate the body mass, was used as a supplement for comparison.

$$\ln X = a \ln Y + \ln b$$

where X is the body mass (in g) and Y is the crown area (length × width, in mm)

Table 2. Regression functions and associated statistics for the measurements of limb bones. BM, body mass, in kg; HL, humerus length; HC, humerus circumference; RL, radius length; RC, radius circumference; FL, femur length; FC, femur circumference; TL, tibia length; TC, tibia circumference; n, sample size; e, Residual standard error; MR², Multiple R-squared; AR², Adjusted R-squared; F, F-statistic; p, p-value.

Element	Functions	n	e	MR ²	AR ²	F	p
Humeral	$\text{Log}_{10}(\text{BM}) = -2.60305 - 0.03877 \text{Log}_{10}(\text{HL}) + 2.50124 \text{Log}_{10}(\text{HC})$	90	0.1372	0.9628	0.962	1127	< 2.2e-16
Radial	$\text{Log}_{10}(\text{BM}) = -2.1396 - 0.2333 \text{Log}_{10}(\text{RL}) + 2.6096 \text{Log}_{10}(\text{RC})$	90	0.2037	0.9182	0.9163	488	< 2.2e-16
Femoral	$\text{Log}_{10}(\text{BM}) = -3.3560 + 0.3721 \text{Log}_{10}(\text{FL}) + 2.3609 \text{Log}_{10}(\text{FC})$	90	0.1473	0.9572	0.9562	972	< 2.2e-16
Tibial	$\text{Log}_{10}(\text{BM}) = -2.7983 - 0.1367 \text{Log}_{10}(\text{TL}) + 2.7871 \text{Log}_{10}(\text{TC})$	90	0.1413	0.9606	0.9597	1060	< 2.2e-16
step	$\text{Log}_{10}(\text{BM}) = -2.5377 + 1.2738 \text{Log}_{10}(\text{TL}) + 1.5469 \text{Log}_{10}(\text{HC}) - 0.3039 \text{Log}_{10}(\text{RL})$	90	0.127	0.9685	0.9674	882.2	< 2.2e-16

The length and width data of m1 used comes from Qiu and Wang (2007), Li et al. (2017), and Deng et al. (2021). If a species uses more than one m1, the average value is used. See Table A3 for the m1 materials. Despite a massive skull with huge dental rows, giant rhinos appear to have relatively smaller heads than more derived rhinos when compared to their general size. So the parameters of artiodactyls+ perissodactyls ($a = 1.564$, $b = 3.267$) was used in this study. In species with available limb bones we prefer the results of the limb bone equations over teeth equation.

Scale

For promoting the accuracy of the results and to facilitate a unified body mass comparison within Paraceratheriinae, the body mass of paraceratheres estimated with only isolated limb bones was scaled based on the standards of *Juxia sharamurenensis* and *Dzungariotherium* sp. More specifically, the ratio of the result obtained by the following formula and the result of *Dzungariotherium* sp. obtained by the formula (*Urtinotherium* uses that of *J. sharamurenensis* whose body plan is closer) is multiplied by the geometric mean of all formula results of *Dzungariotherium* sp.

$$W_r = W_{r \text{ single}} \frac{W_{D \text{ mean}}}{W_{D \text{ single}}}$$

Where W_r is the body mass after scaling (in kg); $W_{r \text{ single}}$ is the body mass of a paraceratheres calculated using a certain limb bone; $W_{D \text{ single}}$ is the body mass of a *Dzungariotherium* sp. calculated using the same limb bone with $W_{r \text{ single}}$; $W_{D \text{ mean}}$ is the mean of the body mass of *Dzungariotherium* sp. calculated using each individual bone (except radius) and stepwise regression for four limb bones.

Mapping the body mass to a phylogenetic tree

To better study the evolutionary tendency of giant rhino body mass, we used some of the body mass data of extinct rhinos (mainly Rhinocerotidae, the sister group of Paraceratheriidae) from literature (Cole 1997; Deng 2009; Etienne et al. 2020), and fit them with the phylogenetic tree (using R package phytools (Revell 2012)) to show the body mass evolution trend of the superfamily Rhinocerotioidea. See Table A4 for specific data sources. The phylogenetic tree used here is composed of multiple related studies (Pandolfi 2015; Wang et al. 2016; Tissier et al. 2020; Deng et al. 2021).

Results

Result of PCA

The p-value of the sphericity test is significantly smaller than 0.05, and the overall MSA of KMO is 0.79, indicating that the data we used are suitable for PCA. The importance of components and loadings of PCA are shown in Table A6 and A7.

The first two principal components of PCA jointly explained 87.02% of the total variance. The first component (explaining 62.03% variance) is positively correlated with all the original ratios, and the correlation with the perimeter data is greater than that of the length. The first component is positively correlated with all variables, and the effect of the circumference is greater. Since these variables are obtained by dividing each measurement by the length of the humerus, PC1 also represents the relative length of the humerus to other limb bones. The second principal component (explaining 24.99% variance) is negatively correlated with all circumferences and positively correlated with length. It partially represents the robustness of these limbs.

Figure 3 shows the result of PCA (the first two principal components). The visualisation of the eigenvectors for each parameter along the two first axes is shown in Figure A1. A visualisation of the eigenvectors for each parameter along the two first axes is in the appendix. *Juxia sharamurenensis* is close to horses in morphospace, PC1 scores are also close to hippos and living rhinos. *Dzungariotherium* sp. has high scores on the first two principal components, especially the score of the first principal component surpassed all other species. But its PC2 value is not maximal, slightly lower than some species of hippos and rhinos. Its ratio of the length of the humerus to the length of the femur (HL/FL in Table A1 represents it) is indeed the smallest among these species. It can be seen that the elongation of the femur is more obvious than that of the humerus in the gigantism of the paraceratheres. The relatively short humerus seems to be a common feature of most living Perissodactyla. The score of the family Tapiridae is lower, but it is still greater than 0.

The score of the second principal component of *Juxia sharamurenensis* is negative, slightly lower than that of horses, while the score of *Dzungariotherium* sp. is much higher than that of *J. sharamurenensis*, and reaches that of the living rhinos. This shows that the bones of large-sized paraceratheres are significantly more robust than those of *Juxia*. The scores of the two elephants on the second principal component are smaller than those of the large-sized paraceratheres.

The scores of the two principal components of *Juxia* are most similar to those of Equidae. Some studies used horses as a reference for recovery and even body mass estimation of *Juxia* (Qiu and Wang, 2007) is therefore reasonable. However, the body plan of *Dzungariotherium* sp. (and most other derived paraceratheres) is different from that of *Juxia*, and quite different from any modern species investigated. In the regression, we excluded 65 species with PC1 scores less than -1 and used the remaining 90 species to perform regression analysis, whose body plans are relatively closer to giant rhinos.

Using the limb bone data of the remaining 90 living species as the training data, several equations shown in Table 2 are obtained. According to the R square values, the equation of the stepwise regression is best fitted by integrating the data of the humerus, femur, tibia, and radius. This is in line with the general expectation that multiple regression is more reliable. According to R^2 , all equations, except those using the radius, appear reliable.

Among the regression using single bone measurements, the equation given by the humeral data is the best fit for the extant species, followed by that of the tibia and femur. The fitness of the equation predicted by the radius size is the lowest ($R \text{ square} = 0.9163$, others are above 0.95), and the prediction results of the body mass of *Dzungariotherium* sp. and five living rhinos are also the smallest among all the formulas. This is mainly as the ratio and load-bearing capacity of the radius varies greatly among the species. Mallet et al. (2021) said that shape of the radius of giant rhinos remains extremely close to some much smaller species, such as *Hyrachyus*. In fact, the radius/femur length ratio is also different in various species of paraceratheres (may be affected by fossil preservation and species identification). Therefore, except for *Urtinotherium intermedium*, which only has radius material, the results obtained from the prediction of radius data are not used in further analyses.

Estimation of body mass of the giant rhinos

Using the humerus, femur, tibia, and comprehensive linear models (only *Urtinotherium intermedium* used radius) in Table 2, we estimated the body mass of *Dzungariotherium* sp. from Lingwu and

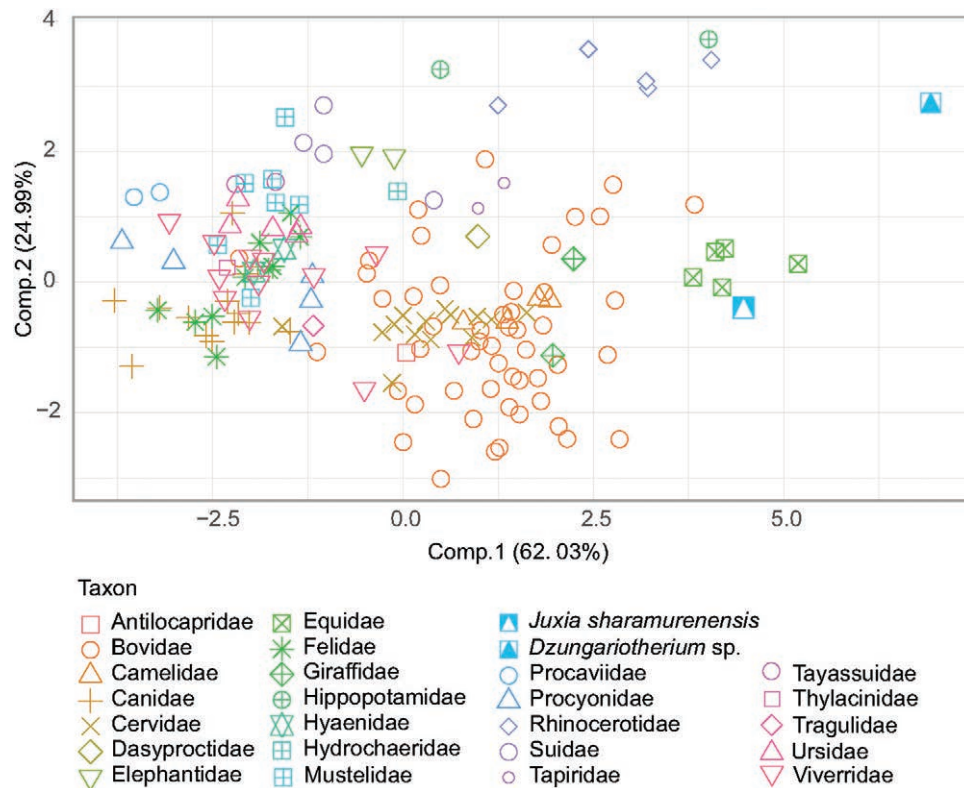


Figure 3. PCA plot of limb bones of giant rhinos and other mammalian groups.

many other giant rhinos. The final result is the average of the results obtained with these equations after scaling. The model based on m1 crown area is supplemented, and the results are summarised in Table 4 with differences between these two methods.

Our estimation of the body mass of *Juxia sharamurenensis* is 1,482 kg. It is distinctly larger the previous estimation around 749–888 kg (Qiu and Wang 2007), but smaller than the living white rhinoceros *Ceratotherium simum* and Indian rhinoceros *Rhinoceros unicornis*. Although the length of limb bones of *Juxia* is distinctly longer than that of extant rhinos, and the distal limb bones are especially elongated (more than 60% of the average of five living rhino species), the circumference data are smaller than those of the white rhino and Indian rhinoceros. Therefore, it is clear that the limbs of *Juxia* are proportionally much slenderer than those of the living rhinoceroses. This indicates that it is taller but thinner than that of any living rhinos, so a body mass not greater than the large living rhino species is not surprising.

Our estimation of the body mass of *Dzungariotherium* sp. from Lingwu is 20,558 kg, which is close to the view of about 15–20 t of the largest giant rhinos that most previous studies believed. In terms of head length (126–143 cm) and limb bone length, it is one of the largest known paraceratheres. Among the results estimated by five models for *Dzungariotherium* sp., except the radius equation, which is 14.8 t, the results of the other equations are relatively close, which are concentrated in 19.4–21.7 t. This confirms that the form of the radius does not follow the same allometric trend than other bones. It has been mentioned above that the accuracy of the radius model is not as good as other models, and the outliers in *Dzungariotherium* sp. are also one of the reasons why we do not use the results of the radius model. In the Methods section, we mentioned that we also used the training data not screened by PCA for calculation, and the results obtained (in Table A5) are generally

larger (p-value of two-sample paired tests is 0.02, mean difference is 1258.5 kg) than the results used PCA. The body mass of *Dzungariotherium* sp. calculated in this way is about 25 t.

There are no limb bone data of *Urtinotherium parvum* and *Turpanotherium elegans*. Their body mass estimations are based on scaling with other giant rhinos with similar morphology, which are only for reference. The data of *Urtinotherium parvum* is obtained by scaling the length of MtIII based on *Juxia sharamurenensis*. *Paraceratherium linxiaense* has a complete skull, but no limb bones. According to the ratio of the skull to *Dzungariotherium*, a body mass is estimated for reference. *Turpanotherium elegans* is obtained based on *Aralotherium prohorovi* according to the ratio of mandible and teeth (see details below).

Urtinotherium evolved from *Juxia* (Deng et al., 2021) and represents the initial of the gigantism of paraceratheres. However, the fossil materials of *Urtinotherium* are rare, and only *Urtinotherium intermedium* has a complete radius, *U. parvum* does not have any long bones or m1. The robustness (circumference divided by length) of this *U. intermedium* radius is almost the same as that of *Juxia sharamurenensis*. Therefore, it is speculated that the proportion of the smaller and more primitive *Urtinotherium parvum* is also close to that of *J. sharamurenensis*. *U. parvum* is the smallest and most primitive giant rhinos discovered so far except for *Juxia*. To discuss it together with other giant rhinos, we used the ratio of *U. parvum* to the MtIII of *J. sharamurenensis* to infer the size of the long bones. The results obtained are for reference only. In this way, the body mass of *U. parvum* is estimated as 2,692 kg. The body mass of *U. intermedium*, based on the right radius, and comprehensively scaled according to the *J. sharamurenensis*, is 4,940 kg.

Paraceratherium grangeri is represented by abundant material, but the stratigraphy and identification are unclear. Granger and Gregory (1936) classified all large-sized paraceratheres fossils from Mongolia and Inner Mongolia in China into *Baluchitherium grangeri*

(= *P. grangeri*) and divided them into four levels according to their sizes. In this study, the humerus and radius materials classified as level II are selected for body mass estimation, as their size is more compatible with the size of the skull as the type specimen. The estimation result is 13,905 kg (The estimation result using the femoral and tibial material classified into level IV is only 8,928 kg). *Paraceratherium asiaticum*, also known as *Indricotherium transouralicum* in the past, is famous for a complete skeleton exhibited in the Moscow Palaeontological Museum. However, the measurement data are not available, only the circumference data of humerus, femurs, and radius are used here. The geometric mean of the three results is 12,007 kg, which is slightly smaller than that of *P. grangeri*.

Paraceratherium bugtiense only has the humerus and femur data, and the result estimation after scaling and averaging is 9,112 kg, which is smaller than both *P. grangeri* and *P. asiaticum*. The length of the humerus of the giant rhino is about 0.83 of that of *P. grangeri*, and the circumference ratio is 0.90.

The material of *Paraceratherium lepidum* comes from different individuals. According to published data (Qiu and Wang 2007), the humerus and radius can be used for estimation. The combined result is 14,630 kg. Since the result of the radius is not used, in fact, this result is only from one humerus of *P. lepidum*. *P. lepidum* also has a complete right tibia and fibula material, but it was not used due to lacking circumference data. The humerus and radius of *P. lepidum* are the proportionally shortest (compared with the femur) and most robust among the paraceratheres species investigated, and the circumference is 1.19 times that of *P. bugtiense* which is close in length. Since the perimeter coefficient in the regression formula of humerus and body mass is much larger than the length, the calculation result of *P. lepidum* is the largest in *Paraceratherium*, even if the length of the humerus of *P. grangeri* and *P. asiaticum* is significantly larger than that of *P. lepidum*. The size of the skull and teeth of *P. lepidum* is also the largest in the genus *Paraceratherium* (the cranium size of *P. linxiaense* is relatively close to it). According to Deng et al. (2021), *P. lepidum* is one of the most advanced species in *Paraceratherium*. It can be seen that the body plan in the giant rhinos tends to become more robust during evolution.

Aralotherium prohorovi only has humerus and radius data. The estimation result is 6,614 kg using the humerus. The material of *A. prohorovi* comes from multiple individuals. Since Gromova (1959) did not give all the data for each individual in her article, only the average value can be used for calculation. But judging from the length of the three radius specimens she gave (665 cm, 731 cm, 985 cm), the sizes of these materials vary greatly. *A. prohorovi* is indeed a relatively small type of the giant rhino, but it is still larger than *Urtinotherium intermedium* based on the dental size.

Turpanotherium does not have complete long bones available for body mass estimation. Since the skeletal morphology of its type species *Turpanotherium elegans* is similar to *Aralotherium prohorovi* and *Benaratherium callistrati* (Qiu and Wang, 2007), it is scaled according to the ratio of the bone data of *A. prohorovi* and estimation a result of 4,448 kg for reference.

Discussion

Limb bone ratio

The results of the principal component analysis reflected the proportion of the limb bones of paraceratheres. From *Juxia* to *Dzungariotherium*, the limb bones of paraceratheres became gradually stronger, and the limb bones of the Lingwu *Dzungariotherium* were stronger than almost all the existing species used in the study. Measured by the circumference/length of the limb bones (in Table A1), the humerus and tibia of the giant rhinos are the most robust, but the radius and femur are less robust than those of hippos and living rhinos, respectively. However, most of the other species in the giant rhinos are more slender than the living rhinos. Some proportions in the limb bones of the giant rhinos are shown in Table 3. It can be seen that the robustness of the bones is not completely related to the absolute body mass. The proximal limb bones become elongated far faster than the distal limb bones do, especially in the hind limbs. These two characteristics reflect the adaptation to the great body mass of giant rhinos during their evolution. Strong limb bones can provide stronger support. The femur of giant rhinos is longer than tibia, and the extent is more significant in larger species of giant rhinos. The ratio of femur/tibia length of the *Dzungariotherium* sp. is as high as 1.8, which is more than that of living elephants (1.6–1.7) and far exceeds that of other living ungulates. It suggests that the proximal range of motion of the derived paracerather legs is smaller.

There is a certain difference in the results of body mass estimation using limb bones and m1 area, and the latter is smaller in most species. This possibly shows that the teeth of derived paraceratheres are relatively small, so the estimation of tooth area shows that the results are generally small. But the two-sample paired tests showed that the difference was not significant, with a p-value of 0.29 and a mean difference of 694.9 kg. Several paraceratheres have large body masses estimated using m1, but most of these species have insufficient limb bone data. *Urtinotherium intermedium* has only one radius, and the long bone data of *Aralotherium prohorovi* is the average value of some materials with large differences in size, while *Turpanotherium elegans* does not have long bones (scaled according to *A. prohorovi*). So the differences between the two methods shown by these species are not necessarily reliable.

Comparison with previous estimations

Our linear model using skeleton data has several advantages over previous research. PCA shows the uniqueness of the body plan of paraceratheres. Therefore, the direct scaling method of Alexander (1989) is probably not accurate. Later, researchers repeatedly mentioned the inconsistency of fossil materials used in the past and the unreasonable restoration methods (Fortelius and Kappelman 1993; Paul 1997).

Table 3. Proportions of paracerather limb bones. Among them, *Juxia sharamurenensis* is the measured value (in mm), and the rest are the ratios to *J. sharamurenensis*. See Table 2 for abbreviations. mass, the results of body mass estimation from limb bone regression functions (in kg).

	HL	RL	FL	TL	HC/HL	RC/RL	FC/FL	TC/TL	mass
<i>Juxia sharamurenensis</i>	456	625	610	585	0.46	0.28	0.35	0.35	1482
<i>Urtinotherium intermedium</i>		1.67				0.28			4940
<i>Aralotherium prohorovi</i>	1.37	1.27		1.02	0.66	0.50			6614
<i>Paraceratherium grangeri</i>	2.24	1.92			0.52	0.38			13,905
<i>Paraceratherium asiaticum</i>	2.04	1.71	2.02	1.47	0.52	0.37	0.39		12,007
<i>Paraceratherium bugtiense</i>	1.86		1.97	1.35	0.56		0.33		9112
<i>Paraceratherium lepidum</i>	1.85	1.38		1.23	0.67	0.47			14,630
<i>Dzungariotherium</i> sp. from Lingwu	2.15	1.74	2.36	1.40	0.65	0.45	0.38	0.61	20,558

Table 4. Comparison of body mass inferred by two methods based on limb bone length and m1 area (in kg).

	limb bones	m1	difference
<i>Juxia sharamurenensis</i>	1482	1127	-24%
<i>Urtinotherium parvum</i>	2692		
<i>Urtinotherium intermedium</i>	4940	6102	+24%
<i>Aralotherium prohorovi</i>	6614	9348	+41%
<i>Aralotherium sui</i>		13,355	
<i>Paraceratherium grangeri</i>	13,905	12,338	-11%
<i>Paraceratherium huangheense</i>		14,494	
<i>Paraceratherium asiaticum</i>	12,007	9305	-23%
<i>Paraceratherium bugtiense</i>	9112	5787	-36%
<i>Paraceratherium linxiaense</i>	10,917	8675	-21%
<i>Paraceratherium lepidum</i>	14,630	13,770	-6%
<i>Turpanotherium elegans</i>	4448	5864	+32%
<i>Dzungariotherium turfanense</i>		11,573	
<i>Dzungariotherium tienshanense</i>		19,575	
<i>Dzungariotherium orgosense</i>		18,299	
<i>Dzungariotherium</i> sp. from Lingwu	20,558	19,348	-6%

Gingerich (1990) selected the limb bone materials from the AMNH 26166 specimen classified as Class II *Baluchhitherium grangeri* (= *Paraceratherium grangeri*) by Granger and Gregory (1936). Since each measurement (such as humerus length, metacarpal diameter, etc.) is used separately, the body mass results obtained vary from 2.8 tonnes to 24.8 tonnes, with an average of about 9 tonnes. In this study, the estimation of *P. grangeri* also uses AMNH 26166 humerus and radius, and the result is 13.9 tonnes. The training samples used by Gingerich came from 36 species in seven orders, of which there were no existing species in Perissodactyla. Most of the body plans of these species are far different from those of paraceratheres. The estimation results are also very different. Using the same humerus specimen, the body mass estimated by the humerus length is 2,819 kg, and the body mass estimated by the humerus diameter is 15,314 kg, which reflects the principle of allometry. The estimate based on humerus diameter is close to our result of 13,905 kg.

Gingerich (1990) also used a grade I third metacarpal material AMNH 26175 to scale AMNH 26166, and estimated that the average body mass of the grade I *P. grangeri* was 14–15 tonnes. However, the AMNH 26175 material only has a third metacarpal missing the distal end. From the figure given by Granger and Gregory (1936), it is indeed slightly larger than the AMNH 26166 third metacarpal, but it is difficult to give an accurate estimation. The size of the type specimen AMNH 18650 of *P. grangeri* is also grade II, so the body mass of grade I *P. grangeri* is not estimated in this study.

Fortelius and Kappelman (1993) estimated the body length restoration of multiple *Indricotherium transouralicum* (= *Paraceratherium asiaticum*) skeletons, and estimated grade II according to the scaled-down body length of grade I *P. grangeri* given by Granger and Gregory (1936), III, IV corresponding to the body length and estimation. Among them, the results of grade II according to the parameters of all ungulates and non-selenodonts (equations from Damuth, 1990) are 15.1 tonnes and 13.6 tonnes, respectively, which are in agreement with the 13.9 tonnes estimated according to the grade II limb bones in this study. According to the body lengths (740 cm and 870 cm) recovered by Gromova (1959) and Granger and Gregory, the body mass of *P. asiaticum* are 14.7 tonnes and 24.3 tonnes, respectively. This may indicate that the recovery of the former is more reasonable.

Fortelius and Kappelman (1993) chose bicondylar length, zygomatic width, and their product as the basis for body mass estimation with skull, and used parameters from four taxa (all ungulates, non-selenodont, hyraco-rhino, and rhinoceroses) to estimate separately. The average body mass of *Paraceratherium grangeri*

is 9.6 tonnes. The skull of paraceratheres is relatively small compared to its body, so this result may also be underestimated. Using the same group of parameters as the basis of molar length, the estimation is similar to the results with the area of m1 in this study, all except *Paraceratherium prohorovi* (= *Aralotherium prohorovi*) are smaller than the estimation of the results with the limb bones. Based on limb bones, the average body mass of *Paraceratherium asiaticum* is 11 tonnes, and that of *P. bugtiense* is 12.4 tonnes. *A. prohorovi* is 6.7 tonnes. These results are relatively close to our estimation. In their study, there was also a big difference between the results of the limb bones of *A. prohorovi* and teeth, and the difference between the limb bones speculation results was very large (3.8–17.4 tonnes). This confirms that Gromova (1959) has certain problems with the limb bone materials classified as *Paraceratherium prohorovi*. They are likely to belong to more than one species.

The body mass of *Paraceratherium lepidum* estimated by Qiu and Wang (2007) is similar to our estimation, but their body mass estimation of *Juxia sharamurenensis* is only about half of our result. Qiu and Wang used parameters from different sources in the calculations and finally used the head-body length and body mass regression model with the two sets of parameters of ungulates and odd-hooves to obtain the results. But at the same time, they also used the data of humerus length and femur length, respectively, and estimation with Equidae parameters, and the results obtained were 1.527 tonnes and 1.437 tonnes, respectively. These two results were not adopted by them as they were far away from the other results, but in fact, they are close to the estimation by the limb bone data in this study. The results of our principal component analysis also show that the body plan of *J. sharamurenensis* is indeed close to that of Equidae. Therefore, the body mass of *Juxia* estimated by Qiu and Wang (2007) is probably underestimated.

The method and parameters used in estimation using the area of the lower first molar in this study are the same as those used by Deng (2009), but as the average body mass of the two *Dzungariotherium orgosense* materials are used, an average body mass of 18.3 tonnes is obtained.

Tsubamoto (2014) used the cross-sectional area of the tibial trochlea and width of the tibial trochlea on astragalus to build the regression models, the (geometric) mean of *Paraceratherium bugtiense* body mass results was 12.7 tonnes, with the 95% prediction interval ranging from 10.9 to 13.7 tonnes. It was a bit bigger than the 9,112 kg we calculated.

Paul (1997) and Larramendi (2015) used a volume model reconstruction method. The accuracy of this method is highly dependent on the accurate restoration of bones and muscles. Paul did not give a specific reconstructed model, so we cannot evaluate its accuracy. Larramendi followed the volume of 17.3 m³ derived from Paul's model, and they inferred that *Paraceratherium transouralicum* (= *Paraceratherium asiaticum*) weighs about 17 tonnes, which is five tonnes larger than the results obtained in this study.

Except for the study of *Juxia sharamurenensis* (Qiu and Wang, 2007) and multiple *Indricotherium transouralicum* (= *Paraceratherium asiaticum*) skeletons (Alexander 1989; Fortelius and Kappelman 1993; Paul 1997; Larramendi 2015), none of the previous studies has appendicular skeleton data. Researches using skeleton material were often only based on the measurements of body length and the individual bone measurements were often used separately to estimate (Gingerich 1990; Fortelius and Kappelman 1993). Therefore, this study can better utilise and integrate the information of the skeleton measurements using multivariate linear model training from a large selected dataset.

Body mass evolution of the giant rhinos

The body mass estimations computed for giant rhinos in the present study, associated with other body mass estimations retrieved in literature, allow us to visualise the evolution of weight in Rhinocerotidae throughout their evolution. Figure 4 shows the body mass mapped with the phylogenetic tree of Rhinocerotidae. The red end represents the small body mass, the blue end represents the large body mass. The rapid change of colour in branch suggests faster body size growth in this lineage.

The evolution of body mass is shown in the Figure 5 and Figure A2. It can be seen that the body size evolution of paraceratheres can be divided into three stages according to the general tendency of body mass growth based on current evidence.

Apparition

The first stage is the ancestral stage of paraceratheres, the evolution from *Pappaceras* to *Juxia*. After the Early Eocene Climatic Optimum, the global temperature continued to drop, and the living environment of paraceratheres in the early stage, such as the Erlian Basin (42°–44°N, 110°–114°E), was affected by this and became relatively open and/or dry environments (Gong et al. 2019). The increase of body mass in Paraceratheriidae during this period did not exceed the maximum body growth rate of Rhinocerotidae (referring to the slope in Figure 5 qualitatively). But with this growth rate, *Juxia sharamurenensis*, which lived in the late Middle Eocene to the early Late Eocene (42–38 Ma), became one of the largest terrestrial mammals at that time. The first giant rhino was found in Inner Mongolia, Henan, and Shanxi provinces of China. The former was an open area with a subtropical climate and others

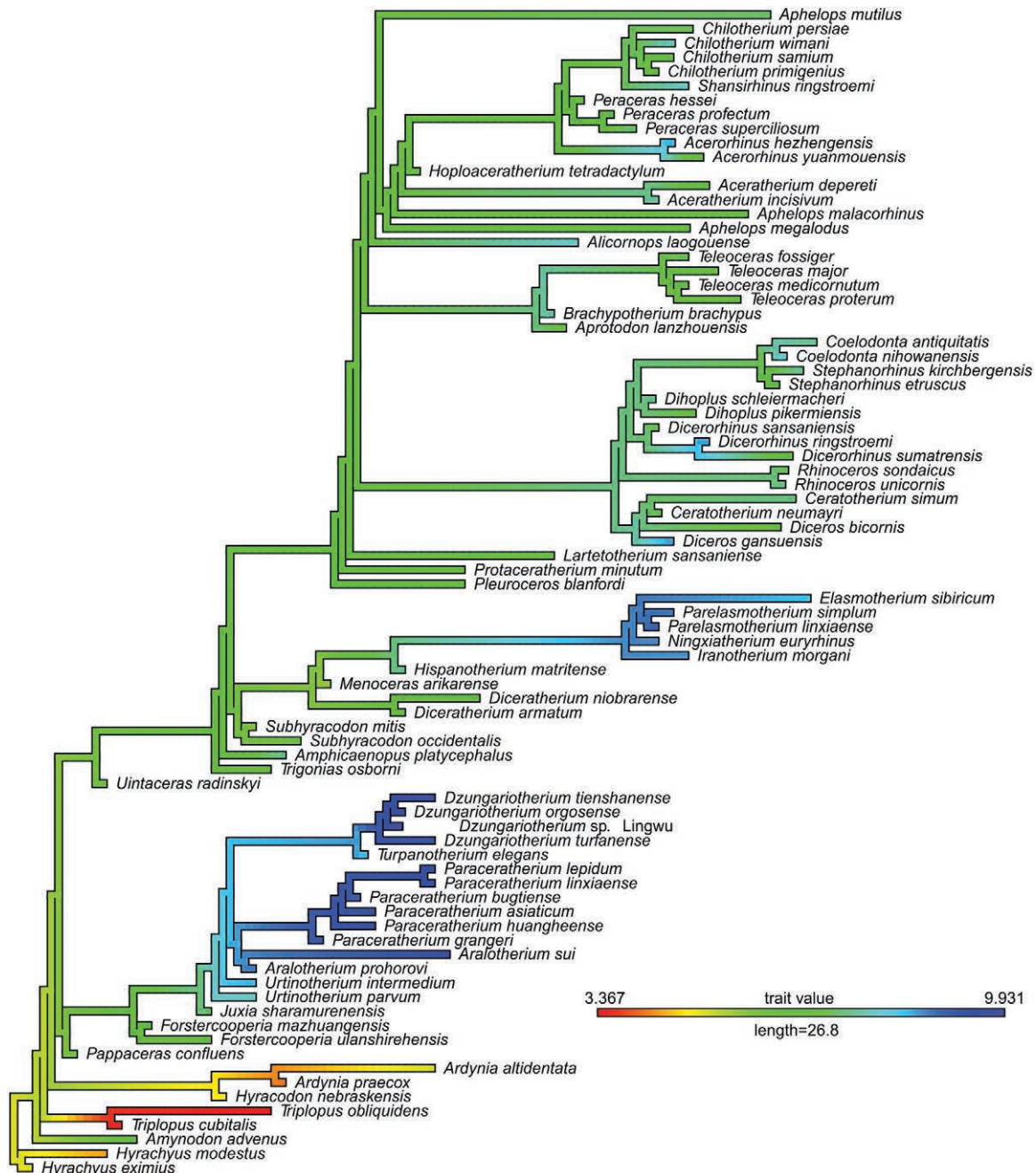


Figure 4. Body mass evolution of Rhinocerotidae. Body mass values have been ln-transformed.

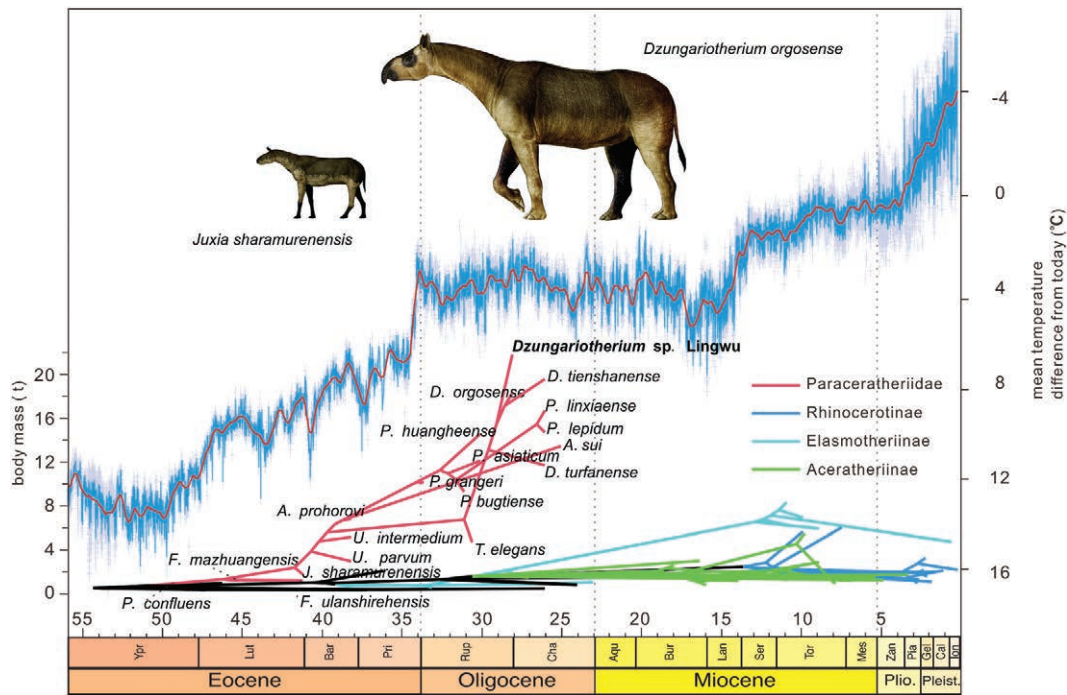


Figure 5. Correspondence of body mass evolution and global temperature change curve (curve from (Westerhold et al. 2020)). The details of non-Paraceratheriidae are provided in appendix. Art work by Yu Chen.

were low mountainous areas with dry and hot climates (Qiu and Wang 2007). The Sharamurunion, period that *Juxia* was found from, has a suitable climate and a wide variety of flora and fauna. Rhinocerotidae in the Erlan Basin replaced Tapiroidea and became the dominant group in the perissodactyls, especially represented by Amynodontidae, which has a higher diversity at that time of six species (Bai et al. 2018). The large mesonychid *Andrewsarchus* and oxyaenid *Sarkastodon* become extinct, and the larger size of *Juxia* can help it effectively defend against attacks by small carnivores. The PCA results show that *J. sharamurensis* has a similar ratio of long bones to that of horses, and the morphology of its limbs also suggests that it may still be good at running fast (Qiu and Wang 2007). The limbs of *Juxia* are still adapted to running, probably making it easier to escape from predators than the larger brontotheriid *Rhinotitan* did (Wang et al. 2019).

Rapid increase

The second stage is the evolution from *Juxia* to *Urtinotherium* in the late Late Eocene. This is the fastest period of body mass increase in the evolutionary history of paraceratheres, far exceeding the growth rate seen of any lineage of Rhinocerotidae. *Urtinotherium intermedium*, weighed about 5 tonnes, is among the largest animals living in the same environment, such as brontotheriid *Embolotherium andrewsi* (Bai et al., 2018). The large size can probably help it resist the attack of predators, and benefits feeding on leaves at a high position, also helping to reduce the loss of heat to resist the continuous cold environment of the Late Eocene (Tardif et al. 2021). At the same time, the distribution of *Urtinotherium* also spread south from northern China to Yunnan. According to Qiu and Wang (2007), there was an arid zone in central and western China in the Palaeogene that was located at a latitude of 30°–50°, and the distribution of paraceratheres also falls in this zone. At this time, the climate in these regions was similar to the current savanna (Qiu and Wang 2007), and the huge size of paraceratheres may allow it to migrate long distances in such an environment.

Diversification

The third stage is the differentiation of derived paraceratheres in the Oligocene, and most of the paraceratheres found so far are the products of this stage. After another drastic cooling at the turn of the Eocene and Oligocene, *Urtinotherium* became extinct, replaced by larger paraceratheres such as *Paraceratherium* and *Dzungariotherium*. At this stage, the body mass of paraceratheres generally grows at a speed between that of the first two stages, but within the genus *Dzungariotherium*, the speed is even faster than that of the first stage. The extent of climate change in the Oligocene has decreased and has always remained in a relatively dry and cold state (Tardif et al. 2021). The giant rhino fossils in Lingwu were produced in a set of light grey-green sandy mudstone, which contains a gypsum layer with a thickness of more than 5 cm. Some bones are also filled with gypsum, which also reflects the relatively dry environment at that time. According to palaeoecological reconstruction, the average annual temperature of Central Asia in the Oligocene can reach 10–20°C. The ecological types are temperate broad-leaved forests, shrubs, and savanna mainly (Tardif et al. 2021). The paraceratheres that have expanded their distribution range have gradually differentiated in their niches, and several paraceratheres species have coexisted (Qiu et al. 2004; Qiu and Wang 2007). The distribution range of paraceratheres has expanded again, crossing the Qinghai-Tibet region that has not yet uplifted to a sufficient height, reaching Kazakhstan and other parts of Central Asia, and reaching the edge of Eastern Europe (Deng et al. 2020). The giant rhinos probably can not adapt to the forest environment due to their huge size, and they did not reach Western Europe, which was warmer and wetter than East Asia (Qiu and Wang 2007).

After Paraceratheriidae went extinct from the Late Oligocene to the Early Miocene, branches of Rhinocerotidae, Elasmotheriinae and Rhinocerotinae began to evolve in the direction of increasing size. Elasmotheriinae feed on the gradual flourishing grass and has evolved high-crown teeth with complex folds, moving in a specialisation direction completely different from that of the

giant rhinos. Perhaps due to the lack of a long neck to feed on leaves of tall trees, the body mass growth rate and upper limit of Elasmotheriinae are far below the level of paraceratheres.

Conclusion

This study constitutes an attempt to estimate the sizes of all giant rhinos by using a dedicated method and comparing them to the previous estimates. The body masses of many giant rhino species have been estimated for the first time. The extreme body mass of Paraceratheriidae, here confirmed and renewed, placing them as among the largest land mammals that ever existed (*Dzungariotherium* sp. with 20.6 tonnes). Giant rhinos show a faster and unusually high evolutionary rate of body mass increase than that of any other rhinos. The three stages of their body mass evolutionary history, apparition, rapid increase, and diversification are recognised. Giant rhinos have experienced a rapid body size increase since the Late Eocene, coinciding with the global temperature falling and the spread of the open environment.

Acknowledgments

We thank the organizers of Second Tibetan Plateau Scientific Expedition for financial and logistic support during the field work. We thank B.-Y. Liu and G.-Y. Wang for their help in studying the specimen under their care, S.-Q. Wang and W.-F. Dong for discussion. We thank Y. Chen for providing the restored images of *Juxia sharamurensis* and *Dzungariotherium orgosense*, which were used in Figure 5. We thank C. Mallet, N. Handa, and an anonymous reviewer's suggestions, which greatly improve the quality of this work. This research was supported by the Chinese Academy of Sciences (XDB26000000, XDA20070203), and the Chinese Natural Science Foundation Program (42102001).

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Chinese Academy of Sciences [XDB26000000, XDA20070203]; Second Comprehensive Scientific Expedition on the Tibetan Plateau [2019QZKK0705]; Chinese Natural Science Foundation Program [42102001].

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