

= Paraceratherium =

Paraceratherium is an extinct genus of hornless rhinoceros , and one of the largest terrestrial mammals that has ever existed . It lived from the early to late Oligocene epoch (34 ? 23 million years ago) ; its remains have been found across Eurasia between China and the Balkans . It is classified as a member of the hyracodont subfamily Indricotheriinae . " Paraceratherium " means " near the hornless beast " , in reference to Aceratherium , a genus that was once thought similar .

The exact size of Paraceratherium is unknown because of the incompleteness of the fossils . Its weight is estimated to have been 15 to 20 tonnes (33 @, @ 000 to 44 @, @ 000 lb) at most ; the shoulder height was about 4 @. @ 8 metres (16 feet) , and the length about 7 @. @ 40 metres (24 @. @ 3 feet) . The legs were long and pillar @- @ like . The long neck supported a skull that was about 1 @. @ 3 metres (4 @. @ 3 ft) long . It had large , tusk @- @ like incisors and a nasal incision that suggests it had a prehensile upper lip or proboscis . The lifestyle of Paraceratherium may have been similar to that of modern large mammals such as the elephants and extant rhinoceroses . Because of its size , it would have had few predators and a slow rate of reproduction . It was a browser , eating mainly leaves , soft plants , and shrubs . It lived in habitats ranging from arid deserts with a few scattered trees to subtropical forests . The reasons for the animal 's extinction are unknown , but various factors have been proposed .

The taxonomy of the genus and the species within has a long and complicated history . Other genera of Oligocene indricotheres , such as Baluchitherium , Indricotherium , and Dzungariotherium have been named , but no complete specimens exist , making comparison and classification difficult . Most modern scientists consider these genera to be junior synonyms of Paraceratherium , and that it contains four discernible species ; P. bugtiense (the type species) , P. transouralicum , P. prohorovi , and P. orgosensis , although the last may be a distinct genus . The most completely @- @ known species is P. transouralicum , so most reconstructions of the genus are based on it . Differences between P. bugtiense and P. transouralicum may be due to sexual dimorphism , which would make them the same species .

= = Taxonomy = =

The taxonomic history of Paraceratherium is complex due to the fragmentary nature of the known fossils and because western , Soviet , and Chinese scientists worked in isolation from each other for much of the 20th century and published research mainly in their respective languages . Scientists from different parts of the world did attempt to compare their finds to get a more complete picture of these animals , but were hindered by politics and wars . The opposing taxonomic tendencies of " lumping and splitting " have also contributed to the problem . Inaccurate geological dating previously led scientists to believe various geological formations that are now known to be contemporaneous were of different ages . Many genera were named on the basis of subtle differences in molar characteristics ? features that vary within populations of other rhinoceros taxa ? and are therefore not accepted by most scientists for distinguishing species .

Early discoveries of indricotheres were made through various colonial links to Asia . The first known indricothere fossils were collected from Balochistan (in modern @- @ day Pakistan) in 1846 by a soldier named Vickary , but these fragments were unidentifiable at the time . The first fossils now recognised as Paraceratherium were discovered by the British geologist Guy Ellcock Pilgrim in Balochistan in 1907 ? 1908 . His material consisted of an upper jaw , lower teeth , and the back of a jaw . The fossils were collected in the Chitarwata Formation of Dera Bugti , where Pilgrim had previously been exploring . In 1908 , he used the fossils as basis for a new species of the extinct rhinoceros genus Aceratherium ; A. bugtiense . Aceratherium was by then a wastebasket taxon ; it included several unrelated species of hornless rhinoceros , many of which have since been moved to other genera . Fossil incisors that Pilgrim had previously assigned to the unrelated genus Bugtitherium were later shown to belong to the new species .

In 1910 , more partial fossils were discovered in Dera Bugti during an expedition by the British palaeontologist Clive Forster @- @ Cooper . Based on these remains , Foster @- @ Cooper moved

A. bugtiense to the new genus *Paraceratherium* , meaning " near the hornless beast " , in reference to *Aceratherium* . His rationale for this reclassification was the species ' distinctly down @-@ turned lower tusks . In 1913 , Forster @-@ Cooper named a new genus and species , *Thaumastotherium* (" wonderful beast ") osborni , based on larger fossils from the same excavations , but he renamed the genus *Baluchitherium* later that year because the former name was preoccupied , as it had already been used for a hemipteran insect . The fossils of *Baluchitherium* were so fragmentary that Foster @-@ Cooper was only able to identify it as a kind of odd @-@ toed ungulate , but he mentioned the possibility of confusion with *Paraceratherium* . The American palaeontologist Henry Fairfield Osborn , which B. osborni was named after , suggested it may had been a titanotheres .

A Russian Academy of Sciences expedition later found fossils in the Aral Formation near the Aral Sea in Kazakhstan ; it was the most complete indricothere skeleton known , but it lacked the skull . In 1916 , based on these remains , Aleksei Alekseeivich Borissiak erected the genus *Indricotherium* named for a mythological monster , the " Indrik beast " . He did not assign a species name , I. asiaticum , until 1923 , but Maria Pavlova had already named it I. transouralicum in 1922 . Also in 1923 , Borissiak created the subfamily *Indricotheriinae* to include the various related forms known by then . In 1939 , Borissiak also named a new species of *Paraceratherium* from Kazakhstan , P. prohorovi .

In 1922 , American explorer Roy Chapman Andrews led a well documented expedition to China and Mongolia sponsored by the American Museum of Natural History . Various indricothere remains were found in formations of the Mongolian Gobi Desert , including the legs of a specimen standing in an upright position , indicating that it had died while trapped in quicksand , as well as a very complete skull . These remains became the basis of *Baluchitherium grangeri* , named by Osborn in 1923 .

Dzungariotherium orgosensis was described in 1973 based on fossils ? mainly teeth ? from Dzungaria in Xinjiang , northwest China . A multitude of other species and genus names ? mostly based on differences in size , snout shape , and front tooth arrangement ? have been coined for various indricothere remains . Fossils attributable to *Paraceratherium* continue to be discovered across Eurasia , but the political situation in Pakistan has become too unstable for further excavations to occur there .

= = = Species and synonyms = = =

In 1936 , American palaeontologists Walter Granger and William K. Gregory proposed that Forster @-@ Cooper 's *Baluchitherium osborni* was likely a junior synonym (an invalid name for the same taxon) of *Paraceratherium bugtiense* , because these specimens were collected at the same locality and were possibly part of the same morphologically variable species . William Diller Matthew and Forster @-@ Cooper himself had expressed similar doubts few years earlier . Although it had already been declared a junior synonym , the genus name *Baluchitherium* remained popular in various media because of the publicity surrounding Osborn 's B. grangeri .

In 1989 , palaeontologists Spencer G. Lucas and Jay C. Sobus published a revision of indricothere taxa , which is followed by most western scientists today . They concluded that *Paraceratherium* , as the oldest name , was the only valid indricothere genus from the Oligocene , and contained four valid species , P. bugtiense , P. transouralicum , P. prohorovi , and P. orgosensis . They considered most other names to be junior synonyms of those taxa , or as dubious names , based on remains too fragmentary to identify properly . By analysing alleged differences between named genera and species , Lucas and Sobus found that these most likely represented variation within populations , and that most features were indistinguishable between specimens , as had been pointed out in the 1930s . The fact that the single skull assigned to P. transouralicum or *Indricotherium* was domed , while others were flat at the top was attributed to sexual dimorphism . Therefore , it is possible that P. bugtiense fossils represent the female , while P. transouralicum represents the male of the same species .

According to Lucas and Sobus , the type species P. bugtiense from the late Oligocene of Pakistan includes junior synonyms such as B. osborni and P. zhajremensis . P. transouralicum , formerly

Indricotherium , from the late Oligocene of Kazakhstan , Mongolia , and northern China includes *B. grangeri* and *I. minus* . *P. orgosensis* , formerly *Dzungariotherium* from the middle and late Oligocene of northwest China includes *D. turfanensis* and *P. lipidus* . *P. orgosensis* may be distinct enough to warrant its original genus name , but its exact position requires evaluation . *P. prohorovi* from the late Oligocene of Kazakhstan may be too incomplete for its position to be resolved in relation to the other species ; the same applies to proposed species such as *I. intermedium* and *P. tienshanensis* , as well as genera like *Benaratherium* and *Caucasotherium* . Though the genus name *Indricotherium* is now a junior synonym of *Paraceratherium* , the subfamily name *Indricotheriinae* is still in use because genus name synonymy does not affect the names of higher level taxa that are derived from these . Members of the subfamily are therefore still commonly referred to as *indricotheres* .

In contrast to the revision by Lucas and Sobus , a 2003 paper by Chinese researchers suggested that *Indricotherium* and *Dzungariotherium* were valid genera , and that *P. prohorovi* did not belong in *Paraceratherium* . They also recognised the validity of species such as *P. lipidus* , *P. tienshanensis* , and *P. sui* . A 2004 paper by Chinese paleontologist Tao Deng and colleagues also recognised three distinct genera . Some western writers have similarly used names otherwise considered invalid since the 1989 revision , but without providing detailed analysis and justification .

== Evolution ==

The superfamily *Rhinocerotidae* , which includes modern rhinoceroses , can be traced back to the early Eocene ? about 50 million years ago ? with early precursors such as *Hyrachyus* . *Rhinocerotidae* contains three families ; the *Amynodontidae* , the *Rhinocerotidae* (" true rhinoceroses ") , and the *Hyracodontidae* . The diversity within the rhinoceros group was much larger in prehistoric times ; they ranged from dog @-@ sized to the size of *Paraceratherium* . There were long @-@ legged , cursorial forms adapted for running and squat , semi aquatic forms . Most species did not have horns . Rhinoceros fossils are identified as such mainly by characteristics of their teeth , which is the part of the animals most likely to be preserved . The upper molars of most rhinoceroses have a pi @-@ shaped (?) pattern on the crown , and each lower molar has paired L @-@ shapes . Various skull features are also used for identification of fossil rhinoceroses .

The *Indricotheriinae* subfamily , to which *Paraceratherium* belongs , was first classified as part of the *Hyracodontidae* family by Leonard B. Radinsky in 1966 . Previously , they had been regarded as a subfamily within *Rhinocerotidae* , or even a full family , *Indricotheriidae* . In a 1999 cladistic study of *tapiromorphs* , Luke Holbrook found *indricotheres* to be outside the *hyracodontid* clade , and wrote that they may not be a monophyletic (natural) grouping . Radinsky 's scheme is the prevalent hypothesis today . The *hyracodont* family contains long @-@ legged members adapted to running , such as *Hyracodon* , and were distinguished by incisor characteristics . *Indricotheres* are distinguished from other *hyracodonts* by their larger size and the derived structure of their snouts , incisors and canines . The earliest known *indricotheres* is the dog @-@ sized *Forstercooperia* from the middle and late Eocene of western North America and Asia . The cow @-@ sized *Juxia* is known from the middle Eocene ; by the late Eocene the genus *Urtinotherium* of Asia had almost reached the size of *Paraceratherium* . *Paraceratherium* itself lived in Eurasia during the Oligocene period , 23 to 34 million years ago . The genus is distinguished from other *indricotheres* by its large size , nasal incision that would have supported a muscular snout , and its down @-@ turned premaxillae . It had also lost the second and third lower incisors , lower canines , and lower first premolars .

The cladogram below follows the 1989 analysis of *Indricotheriinae* by Lucas and Sobus , and shows the closest relatives of *Paraceratherium* :

Lucas and colleagues had reached similar conclusions in a previous 1981 analysis of *Forstercooperia* , wherein they still retained *Paraceratherium* and *Indricotherium* as separate genera .

== Description ==

Paraceratherium is one of the largest known land mammals that have ever existed , but its exact size is unclear because of the lack of complete specimens . Early estimates of 30 tonnes (66 @, @ 000 lb) are now considered exaggerated ; it may have been in the range of 15 to 20 tonnes (33 @, @ 000 to 44 @, @ 000 lb) at maximum , and as low as 11 tonnes (24 @, @ 000 lb) on average . Calculations have mainly been based on fossils of *P. transouralicum* because this species is known from the most complete remains . Estimates have been based on skull , teeth , and limb bone measurements , but the known bone elements are represented by individuals of different sizes , so all skeletal reconstructions are composite extrapolations , resulting in several weight ranges . Its total body length was estimated as 8 @. @ 70 m (28 @. @ 5 ft) from front to back by Granger and Gregory in 1936 , and 7 @. @ 40 m (24 @. @ 3 ft) by Vera Gromova in 1959 , but the former estimate is now considered exaggerated . The weight of Paraceratherium was similar to that of some extinct proboscideans , with the largest complete skeleton known belonging to the steppe mammoth (*Mammuthus trogontherii*) . In spite of the roughly equivalent mass , Paraceratherium may have been taller than any proboscidean . Its shoulder height was estimated as 5 @. @ 25 m (17 @. @ 2 ft) at the shoulders by Granger and Gregory , but 4 @. @ 8 m (16 ft) by Gregory S. Paul in 1997 . The neck was estimated at 2 to 2 @. @ 5 m (6 @. @ 6 to 8 @. @ 2 ft) long by Michael P. Taylor and Mathew J. Wedel in 2013 . The teeth of *P. orgosensis* (which that species is mainly known from) are 25 percent larger than those of *P. transouralicum* , making it the largest known indricothere .

No complete set of vertebrae and ribs of Paraceratherium have yet been found and the tail is completely unknown . The atlas and axis vertebrae of the neck are wider than in most modern rhinoceroses , with space for strong ligaments and muscles that would be needed to hold up the large head . The rest of the vertebrae were also very wide , and had large zygapophyses with much room for muscles , tendons , ligaments , and nerves , to support the head , neck , and spine . The neural spines were long and formed a long " hump " along the back , where neck muscles and nuchal ligaments for holding up the skull were attached . The ribs were similar to those of modern rhinoceroses , but the ribcage would have looked smaller in proportion to the long legs and large bodies , because modern rhinoceroses are comparatively short @-@ limbed . The last vertebra of the lower back was fused to the sacrum , a feature found in advanced rhinoceroses . Like sauropod dinosaurs , Paraceratherium had pleurocoel @-@ like openings (hollow parts of the bone) in their pre @-@ sacral vertebrae , which may have helped to lighten the skeleton .

The limbs were large and robust to support the animal 's large weight , and were in some ways similar to and convergent with those of elephants and sauropod dinosaurs with their likewise graviportal (heavy and slow moving) builds . Unlike such animals , which tend to lengthen the upper limb bones while shortening , fusing and compressing the lower limb , hand , and foot bones , Paraceratherium had short upper limb bones and long hand and foot bones ? except for the disc @-@ shaped phalanges ? similar to the running rhinoceroses from which they descended . Some foot bones were almost 50 centimetres (20 in) long . The thigh bones typically measured 1 @. @ 5 m (4 @. @ 9 ft) , a size only exceeded by those of some elephants and dinosaurs . The thigh bones were pillar @-@ like and much thicker and more robust than those of other rhinoceroses , and the three trochanters on the sides were much reduced , as this robustness diminished their importance . The limbs were held in a column @-@ like posture instead of bent , as in smaller animals , which reduced the need for large limb muscles . The front limbs had three toes .

Due to the fragmentary nature of known Paraceratherium fossils , the animal has been reconstructed in several different ways since its discovery . In 1923 , W. D. Matthew supervised an artist to draw a reconstruction of the skeleton based on the even less complete *P. transouralicum* specimens known by then , using the proportions of a modern rhinoceros as a guide . The result was too squat and compact , and Osborn had a more slender version drawn later the same year . Some later life restorations have made the animal too slender , with little regard to the underlying skeleton . Gromova published a more complete skeletal reconstruction in 1959 , based on the *P. transouralicum* skeleton from the Aral Formation , but this also lacked several neck vertebrae .

There are no indications of the colour and skin texture of the animal because no skin impressions or

mummies are known . Most life restorations show the creature 's skin as thick , folded , grey , and hairless , based on modern rhinoceroses . Because hair retains body heat , modern large mammals such as elephants and rhinoceroses are largely hairless . American palaeontologist Donald Prothero has proposed that , contrary to most depictions , Paraceratherium had large , elephant @-@ like ears that it used for thermoregulation . The ears of elephants enlarge the body 's surface area and are filled with blood vessels , making the dissipation of excess heat easier . According to Prothero , this would have been true for Paraceratherium ; he points to robust bones around the ear openings . The palaeontologists Pierre @-@ Olivier Antoine and Darren Naish have expressed scepticism towards this idea .

= = = Skull = = =

The largest skulls of Paraceratherium are around 1 @.@ 3 metres (4 @.@ 3 ft) long , 33 to 38 centimetres (13 to 15 in) at the back of the skull , and 61 centimetres (24 in) wide across by the zygomatic arches . Paraceratherium had a long forehead , which was smooth and lacked the roughened area that serves as attachment point for the horns of other rhinoceroses . The bones above the nasal region are long and the nasal incision goes far into the skull . This indicates that Paraceratherium had a prehensile upper lip similar to that of the black rhinoceros and the Indian rhinoceros , or a short proboscis or trunk as in tapirs . The back of the skull was low and narrow , without the large lambdoid crests at the top and along the sagittal crest , which are otherwise found in horned and tusked animals that need strong muscles to push and fight . It also had a deep pit for the attachment of nuchal ligaments , which hold up the skull automatically . The occipital condyle was very wide and Paraceratherium appears to have had large , strong neck muscles , which allowed it to sweep its head strongly downwards while foraging from branches . One skull of P. transouralicum has a domed forehead , whereas others have flat foreheads , possibly because of sexual dimorphism . A brain endocast of P. transouralicum shows it was only 8 percent of the skull length , while the brain of the Indian rhinoceros is 17 @.@ 7 percent of its skull length .

The species of Paraceratherium are mainly discernible through skull characteristics . P. bugtiense and P. orgosensis share features such as relatively slender maxillae and premaxillae , shallow skull roofs , mastoid @-@ paroccipital processes that are relatively thin and placed back on the skull , a lambdoid crest which extends less back , and an occipital condyle with a horizontal orientation . P. transouralicum has robust maxillae and premaxillae , upturned zygomata , domed frontal bones , thick mastoid @-@ paroccipital processes , a lambdoid crest that extends back , and occipital condyles with a vertical orientation . P. orgosensis is distinguished from the other species by the larger size of its teeth , and distinct crochets of its molars .

Unlike most primitive rhinoceroses , the front teeth of Paraceratherium were reduced to a single pair of incisors in either jaw , which were large and conical , and have been described as tusks . The upper incisors pointed downwards ; the lower ones were shorter and pointed forwards . Among known rhinoceroses , this arrangement is unique to Paraceratherium and the related Urtinotherium . The incisors may have been larger in males . The canine teeth otherwise found behind the incisors were lost . The incisors were separated from the row of cheek teeth by a large diastema (gap) . This feature is found in mammals where the incisors and cheek teeth have different specialisations . The upper molars , except for the third upper molar that was V @-@ shaped , had a pi @-@ shaped (?) pattern and a reduced metastyle . The premolars only partially formed the pi pattern . Each molar was the size of a human fist ; among mammals they were only exceeded in size by proboscideans , though they were small relative to the size of the skull . The lower cheek teeth were L @-@ shaped , which is typical of rhinoceroses .

= = Palaeobiology = =

Zoologist Robert M. Alexander has suggested that overheating may have been a serious problem in Paraceratherium due to its size . According to Prothero , the best living analogues for Paraceratherium may be large mammals such as elephants , rhinoceroses and hippopotamuses .

To aid in thermoregulation , these animals cool down during the day by resting in the shade or by wallowing in water and mud . They also forage and move mainly at night . Because of its large size , Paraceratherium would not have been able to run and move quickly , but they would have been able to cross large distances , which would be necessary in an environment with a scarcity of food . They may therefore have had large home ranges and have been migratory . Prothero suggests that animals as big as indricotheres would need very large home ranges or territories of at least 1 @,@ 000 square kilometres (250 @,@ 000 acres) and that , because of a scarcity of resources , there would have been little room in Asia for many populations or a multitude of nearly identical species and genera . This principle is called competitive exclusion ; it is used to explain how the black rhinoceros (a browser) and white rhinoceros (a grazer) exploit different niches in the same areas of Africa .

Most predators in their habitat were relatively small ? about the size of a wolf ? and were not a threat to Paraceratherium . Adult individuals would be too large for most predators to attack but the young would have been vulnerable . Bite marks on bones from the Bugti beds indicate that even adults may have been preyed on by 10 @-@ to @-@ 11 @-@ metre (33 to 36 ft) -long crocodiles , *Crocodylus bugtiensis* . As in elephants , the gestation period of Paraceratherium may have been lengthy and individuals may have had long lifespans . Paraceratherium may have lived in small herds , perhaps consisting of females and their calves , which they protected from predators . It has been proposed that 20 tonnes (44 @,@ 000 lb) may be the maximum weight possible for land mammals , and Paraceratherium was close to this limit . The reasons mammals cannot reach the much larger size of sauropod dinosaurs are unknown . The reason may be ecological instead of biomechanical , and perhaps related to reproduction strategies . Movement , sound , and other behaviours seen in CGI documentaries such as " Walking With Beasts " are entirely conjectural .

= = = Diet = = =

The simple , low @-@ crowned teeth indicate that Paraceratherium was a browser with a diet consisting of relatively soft leaves and shrubs . Later rhinoceroses were grazers , with high @-@ crowned teeth because their diets contained grit that quickly wore down their teeth . Studies of mesowear on Paraceratherium teeth confirm the creatures had a soft diet of leaves ; microwear studies have yet to be conducted . Isotope analysis shows that Paraceratherium fed chiefly on C3 plants , which are mainly leaves . Like its perissodactyl relatives the horses , tapirs , and other rhinoceroses , Paraceratherium would have been a hindgut fermenter ; it would extract relatively little nutrition from its food and would have to eat large volumes to survive . Like other large herbivores , Paraceratherium would have had a large digestive tract .

Granger and Gregory argued that the large incisors were used for defence or for loosening shrubs by moving the neck downwards , thereby acting as picks and levers . Tapirs use their proboscis to wrap around branches while stripping off bark with the front teeth ; this ability would have been helpful to Paraceratherium . Some Russian authors suggested that the tusks were probably used for breaking twigs , stripping bark and bending high branches and that , because species from the early Oligocene had larger tusks than later ones , they probably had a more bark than leaf based diet . Since the species involved are now known to have been contemporaneous , and that the differences in tusks are perhaps sexually dimorphic , the latter idea is not accepted today . Herds of Paraceratherium may have migrated while continuously foraging from tall trees , which smaller mammals could not reach . Osborn suggested that its mode of foraging would have been similar to that of the high @-@ browsing giraffe and okapi , rather than to modern rhinoceroses , whose heads are carried close to the ground .

= = Distribution and habitat = =

Remains assignable to Paraceratherium have been found in early to late Oligocene (34 ? 23 million years ago) formations across Eurasia , in modern @-@ day China , Mongolia , India , Pakistan , Kazakhstan , Georgia , Turkey , Romania , Bulgaria , and the Balkans . Their distribution may be

correlated with the palaeogeographic development of the Alpine @-@ Himalayan mountain belt . The range of Paraceratherium finds implies that they inhabited a continuous landmass with a similar environment across it , but this is contradicted by palaeogeographic maps that show this area had various marine barriers , so the genus was successful in being widely distributed despite this . The fauna which coexisted with Paraceratherium included other rhinoceroses , artiodactyls , rodents , beardedogs , weasels , hyaenodonts , nimravids and cats .

The habitat of Paraceratherium appears to have varied across its range , based on the types of geological formations it has been found in . The Hsanda Gol Formation of Mongolia represents an arid desert basin , and the environment is thought to have had few tall trees and limited brush cover , as the fauna consisted mainly of animals that fed from tree tops or close to the ground . A study of fossil pollen showed that much of China was woody shrubland , with plants such as saltbush , mormon tea (Ephedra) , and nitre bush (Nitraria) , all adapted to arid environments . Trees were rare , and concentrated near groundwater . The parts of China where Paraceratherium lived had dry lakes and abundant sand dunes , and the most common plant fossils are leaves of the desert @-@ adapted Palibinia . Trees in Mongolia and China included birch , elm , oaks , and other deciduous trees , while Siberia and Kazakhstan also had walnut trees . Dera Bugti in Pakistan had dry , temperate to subtropical forest .

= = Extinction = =

The reasons Paraceratherium became extinct after surviving for about 11 million years are unknown , but it is unlikely that there was a single cause . Theorised reasons include climate change , low reproduction rate , and invasion by gomphothere proboscideans from Africa in the late Oligocene . Gomphotheres may have been able to considerably change the habitats they entered , in the same way that African elephants do today , by destroying trees and turning woodland into grassland . Once their food source became scarce and their numbers dwindled , Paraceratherium populations would have become more vulnerable to other threats . Large predators like Hyaenaelurus and Amphicyon also entered Asia from Africa during the early Miocene ; these may have predated Paraceratherium calves . Other herbivores also invaded Asia during this time .