

THE KINGDON FIELD GUIDE TO AFRICAN MAMMALS

By
Jonathan Kingdon



pp. i-xviii, 1-465

ACADEMIC PRESS
Harcourt Brace & Company, Publishers
SAN DIEGO LONDON BOSTON
NEW YORK SYDNEY TOKYO TORONTO

1997

RHINOCEROSES RHINOCEROTIDAE

Browse (Black) rhinoceros
Grass (White) rhinoceros

Diceros bicornis
Ceratotherium simum

When animals have become as scarce as rhinoceroses have today it is difficult to describe them as successful. Yet living African rhinos were, until very recently, the widespread, abundant, advanced and successful representatives of a family that had seen a very wide range of types in the past (i.e. 30 fossil genera).

Recognition: Rhinos are the second largest land animals only surpassed by elephants in bulk and weight. They have relatively short, powerfully muscled legs, a short neck and a massive head, armed with a nasal horn or horns. Contrary to popular belief rhinos are not ponderous and slow but are capable of running or galloping fast. Their long, heavy bodies are densely bound masses of reinforced bone and muscle enclosed in very thick skin. Most of the rhino's great weight is taken on the broad central toe but two smaller hooved toes on each foot spread the load and enhance stability. Other characteristics include backward-facing genitalia which fire powerful horizontal squirts of urine. ♂♂ lack a scrotum and have undescended testes.

Genealogy: The earliest rhinos were small, agile animals, something between a tapir and a horse in appearance. Large, horned forms came later (about 30 million years ago) and originated in Asia. Among the several lines that entered Africa was a close relative of the living Sumatran rhino (*Dicerorhinus*). This genus survived from at least 20 million years ago to less than 1 million years ago. Of the two surviving African species, the browse rhino has the longer fossil history. The grass rhino appears to have split from *Diceros* ancestors some 8 million years ago and has shown continuous adaptation towards grazing ever since.

Geography: Browse and grass rhinos are exclusive to Africa. Various species of the more primitive Sumatran type were also common in Africa and Europe and fossil deposits show that rhinos were conspicuous and common inhabitants of most Old World ecosystems until relatively recent times.

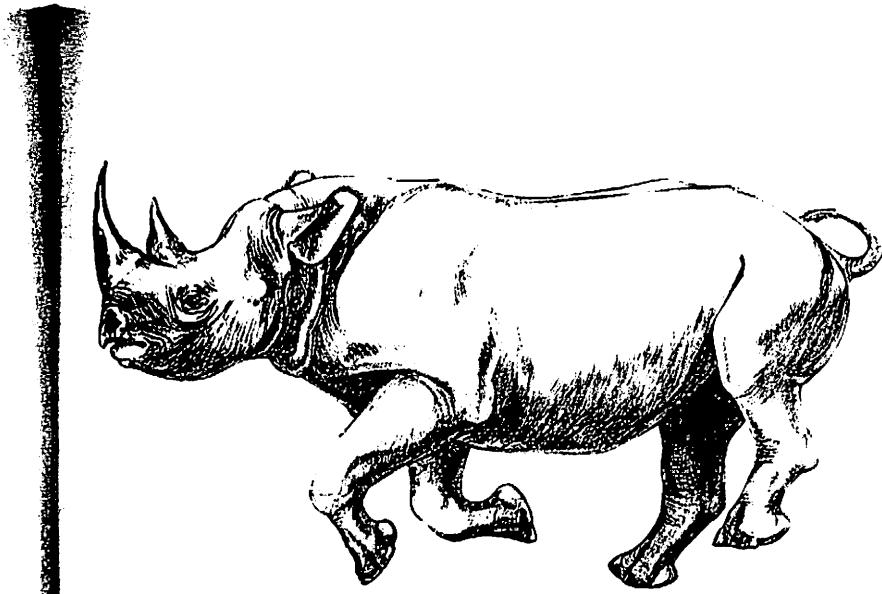
Ecology: The main rhino speciality is an ability to feed on coarse plant material. Rhinos are more selective than elephants but less so than most antelopes. Temperature control, digestion and scent communication all depend upon water and rhinos are unable to survive extreme droughts. Nonetheless, rhinos formerly suffered very low levels of natural mortality, a trait that goes with long life (up to 50 years) and a slow breeding rate.

Natural history: Rhinos display territorial behaviour yet can tolerate high densities and may even live in small herds. The tolerance of dominant individuals, particularly ♂♂, appears to vary by species, by region and in response to changes in density. Home ranges are marked with dung and urine.

Adaptations: Rhinoceros horns are solid keratin (like toenails or cows' horns). They are not set over a core but on a well-butressed pediment that transfers all the stresses and strains of stabs, swipes and tosses to skull and forequarters (a rhino has been known to toss an adult horse into the air). Occasionally the rudiments of a third or fourth horn may grow on the muzzle and forehead of rhinos and there was a tendency towards clusters of horns on the heads of various extinct species.

The teeth can withstand a long life of chewing on tough vegetation and are deeply embedded in bony mandibles. Their food is gathered in by very muscular lips. An envelope of thick, wrinkled skin partially disguises their magnificent heads. Rhino heads are almost architectural models of form and function. Enclosing the vital sense organs and articulated by huge jaw and neck muscles, the skull is reinforced against its own weight. Often dubbed 'prehistoric', rhinos are no more bizarre or 'primitive' than a pig or a cockerel and should be endowed with a future, not just a past.

Status: The extreme vulnerability of rhinos under genuinely wild conditions (due to the great price paid for their horns) has reduced almost all species to something close to domestication. Until cultural and environmental attitudes have changed, rhino survival will continue to depend upon captive or closely managed populations.

Browse (Black) rhinoceros *Diceros bicornis*

Other names: Fr. Rhinocéros noir. Ger. Spitzmaulnashorn. Swah. Faru.
Measurements: HB 290–375cm. T 60–70cm. SH 137–180cm. W 700–1,400kg.

Recognition: A very large mammal, its thickest skin forming inflexible plates over the shoulders, haunches, sides, forehead and cheeks. Skin around the muzzle, eyes, ears, undersides and legs is thinner and more flexible. The grey skin colour is most evident during the rains. Mud-wallowing and rolling in dust or ash discolours most hides during the dry season. Behind the shoulder, the dorsal silhouette swings down and back to raised haunches. The head has a short forehead and a very muscular, mobile mouth ending in a sharply pointed upper lip.

The three toes leave characteristic tracks. Other signs of the rhino's presence include rubbed trees, rocks and termitaries, well-scattered dung middens and habitually sprayed urine-posts.

Subspecies: Browse rhinos are highly variable and 23 subspecies have been named. Six regional populations correspond very approximately with named subspecies. *D. b. bicornis* (Cape): the largest, now extinct. *D. b. minor* (south and south-east, to Tanzania). *D. b. michaeli* (upland E Africa). *D. b. chobiensis* (SW Africa). *D. b. brucii* (NE Africa): the smallest, now extinct. *D. b. longipes* (W and central Africa).

Distribution: At one time a large part of sub-Saharan Africa in all but the wettest and driest areas (maximum dry-season range within 25km of water). Contemporary populations are on the brink of extinction and only hold out in a wide scatter of minuscule pockets (see map).

Habitat: Browse rhinos favour edges of thickets and savannahs with areas of short woody regrowth and numerous shrubs and herbs. They are naturally scarce or absent in closed-canopy forests and woodlands and the more extensive areas of grassland. Where woody and leafy forage could support them, rhinos were formerly found at very high densities (i.e. up to 23 animals, 17 wholly sedentary, in 2.6km²). Where they were very common, smooth rhino pathways, dung piles, urine spray sites and rubbing posts were much in evidence.

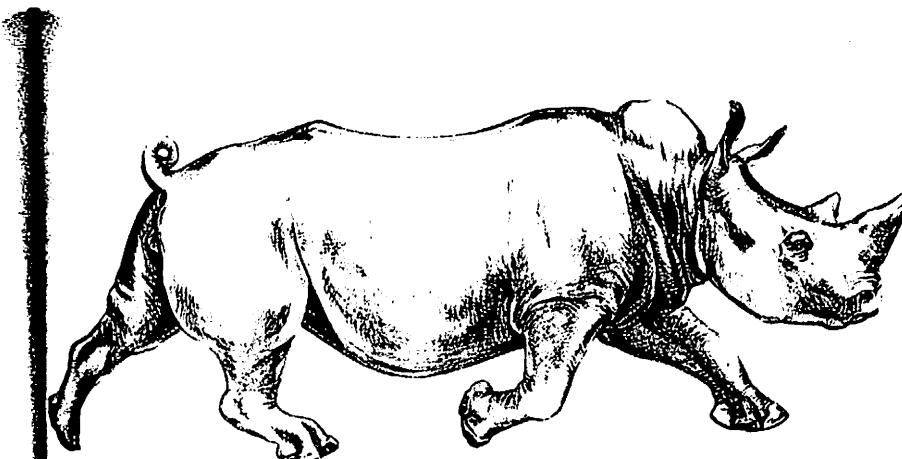
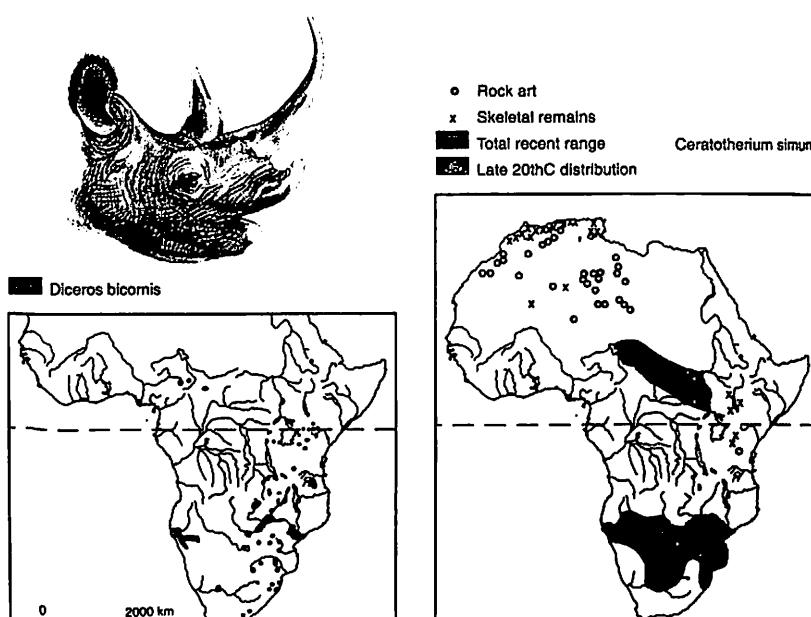
Food: Low-level browse (leaves, twigs and branches), typically in *Acacia*, thicket, hard-pan and riverine plant communities. Some 200 species from 50 families recorded. Browse rhinos have special seasonal preferences for legumes and certain other plants are always avoided. Salt is a major attraction and their taste for salt is exploited by many tourist lodges. Animals can go for up to 5 days without water if their food is moist; otherwise they are always found within daily walking distance of water. Horns are occasionally used to loosen soil around roots or to break branches above the lips' reach.

Behaviour: A ♀ with her young is the basic social unit. Adult ♀♀ may form temporary associations and animals that share a part or all of their range have an easy-going familiarity with one another instead of the aggression that is elicited by total strangers. Home ranges can cover over 130km², but some are as small as 2.6km². Overtly territorial behaviour is also very variable. ♂♂ in high-density areas are well acquainted with, and generally tolerant of, their neighbours (except in the presence of an oestrous ♀). ♂♂ in low-density areas meet less frequently and are more likely to be aggressive. Decline can be accelerated in an already thinned population because a few very aggressive ♂♂ not only miss encounters with ♀♀ in heat but their intolerance of other ♂♂ further lessens the frequency of matings. Displays between ♂♂ resemble those of stallions: there is much strutting, broadside with lowered head, flattened ears and rolling eyes. Various snorts during encounters seem to have different shades of meaning. Rhinos utter series of snorts interspersed with pauses and very loud grunts and screams which punctuate serious fighting.

One young is born after a gestation of 15–16 months. It is soon mobile and begins browsing vegetation before it is 1 month old. It sucks milk for up to 1 year and only begins to drink water after 4 or 5 months. A mother generally drives off her previous offspring before a new birth and the interval between births ranges from 2 to 5 years. Both sexes are capable of reproduction at 4 or 5 years old but ♂♂ can seldom compete with established ♂♂ before the age of 10 years. In spite of a life spanning more than 40 years, this is one of the slowest recruitment rates of any large mammal.

Adaptations: Although all-out frontal charges occur in high-intensity fighting, browse rhinos tend to use their horns more like clubs or staves than rapiers. Mild jousting may be accompanied by shoulder-to-shoulder pushing and leaning. Weight and horn size are easily tested this way but scent and behaviour generally reveal the dominant individual. Avoidance or submission follow.

Status: Human pride, superstition and greed have combined to ensure astronomical prices for horns in the form of dagger handles, cups, supposed medicines and aphrodisiacs. In the late 1960s some 70,000 browse rhinos were estimated to survive in Africa. This was a fraction of the numbers existing at the turn of the century. By 1990 the total number of browse rhinos living within 38 officially protected conservation areas (ranging in size from 55,000 to 62km²) was about 3,300. This accounted for most of the rhinos that survived in Africa in 1990. If these areas were secured and managed for the animals benefit, their potential stock could be as high as 80,000. Listed as Appendix 1 (CITES), Endangered (IUCN).



Grass (White) rhinoceros *Ceratotherium simum*

Other names: Fr. Rhinocéros blanc. Ger. Witrenoster. Swah. Kiaru ya majani.

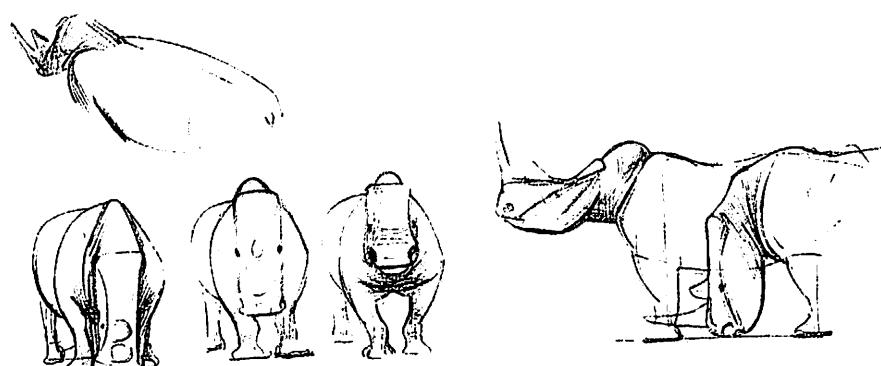
Measurements: HB 360–420cm. T 80–100cm. SH 170–185cm. W 1,400–2,000kg (♀), 2,000–3,600kg (♂).

Recognition: Although formerly called 'white', this very large rhino is of similar skin colour to the browse rhino. The highest point behind the shoulder is midback (due to tall dorsal and lumbar vertebrae) rather than the haunches. The head is long (especially the forehead). The mouth is very wide, flat fronted and set low over the chin. The flexible neck forms a prominent hump when the head is raised. Spoor are more elongate than those of the browse rhino, with greater separation of toes and a prominent cleft at the back.

Subspecies: Southern grass rhino, *C. s. simum* (southern savannahs); northern grass rhino, *C. s. cottoni* (northern savannahs).

Distribution: Fossils, bones and rock art suggest that this species was formerly abundant all over the better-watered grasslands of Africa (including much of the present Sahara). In historic times it ranged to the shores of L. Chad but reached its nadir at the turn of this century with minuscule populations in two widely separated localities: Zululand and the Zaire-Sudan-Uganda borderlands.

Habitat: A preference for short-grass areas and seasonal movements to avoid waterlogged long grass confirm that this species evolved within a larger ungulate community that maintained short swards. In areas of high density the rhinos themselves maintain grazing lawns. Where territories are maintained by resident bulls their border-patrolling and scent-marking leave foot-scuffs, dung middens, urine sprays, rubbing posts and horned vegetation along boundaries. Linear pathways may form between grazing and waterpoints.

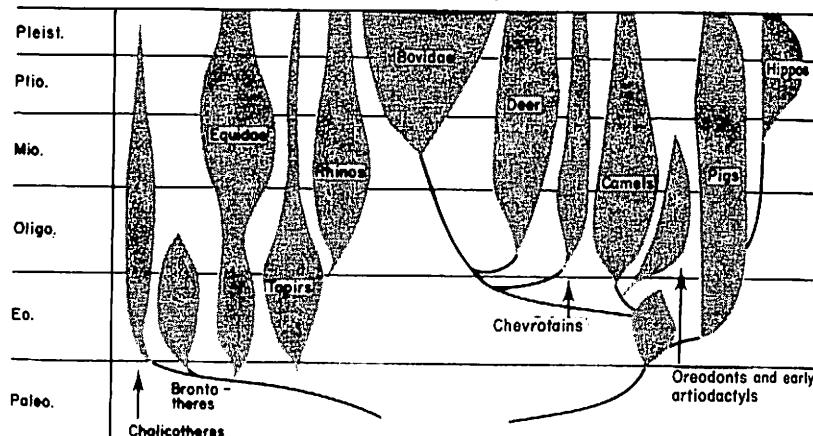


Food: Short grasses, typically *Cynodon*, *Digitaria*, *Heteropogon* and *Chloris* species in well-trampled, well-drained, wet-season concentration areas, are preferred. After dry-season fires, grass rhinos may move into regrowth dominated by *Themeda*, *Hyparrhenia* and *Setaria*. Biting flies and direct sun may influence seasonal movements by restricting the rhinos to ridges or shaded areas for a time. Frequent alternation between grazing and resting changes to long midday rests at the height of the dry season.

Behaviour: ♀♀ and their immediate offspring occupy large (4–12km²) overlapping home ranges where they frequently graze alongside one or more ♀ neighbours. ♂♂ defend territories but their size and their owners' tolerance is related to population density. In crowded Zululand parks ♂ territories can be as small as 0.75–2.6km². Grass rhinos are extremely vocal, with a wide repertoire of utterances. Infantile squeaks and pantings in adults become loud chirps, gasps and puffings (contact) or snarls and squeals of distress. Dominant ♂♂ grunt and bellow challenges at other ♂♂ or court ♀♀ with a low, pulsing cry. One well-developed but hornless young is born after a 16-month gestation. It first grazes at about 2 months and is driven away by its mother at about 2–3 years of age. ♀♀ do not usually breed until they are about 5 years old, dropping their first calf at 6½–7 years of age.

Adaptations: This species evolved from a common ancestor that was very similar to the living browe rhino; modifications in the proportions of the mouth, skull and neck enabled it to become a more efficient, short-grass grazer. Thus the neck has become short but has to crank up a heavier, longer head. This is achieved by the tall vertebral spines, web of tendons and bunched muscles that give the animal its neck 'hump'. Broad, flat-edged lips enable short grass to be cropped efficiently. Long grass is grazed more clumsily.

Status: After millennia of decline the southern form of the grass rhino was brought back from the brink of extinction through the efforts of one man, B. Vaughan-Kirby. From 10–20 animals in the earliest years of this century, the present population now approaches 5,000. The northern form was formerly more widespread and abundant but is now reduced to a few dozen animals in one or a very few localities. It is listed as Critically Endangered (IUCN). The southern form is at lower risk but is dependent on rigorous protection and maintenance of its CITES Appendix 1 status, which prohibits trade in its horns.



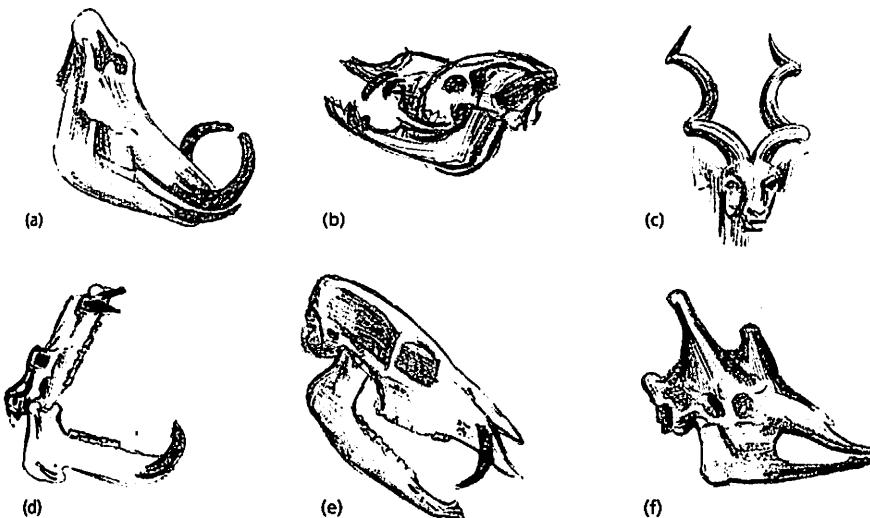
Possible scheme for radiation of artiodactyls.

EVEN-TOED UNGULATES ARTIODACTYLA

The artiodactyls embrace all the horned antelopes and cattle, deer, giraffes, camels, chevrotains, pigs and hippopotamuses. They are one of the most important and successful of mammal lineages. The earliest types were not very different from carnivores, had prominent canine teeth and an omnivorous diet. They are distinguished by their even toes with the axis passing between the third and 4th digits which bear the body's weight in all members of the family.

The most significant feature of this group is the progressive improvement of their digestion through a system of storing, rechewing and sifting of the food and a symbiosis with bacteria and protozoans living within the chambers of the stomach. These break down cellulose and release nutrients.

The skulls of living artiodactyls have been adapted to specific modes of combat requiring elaboration of canines, incisors, horns or antlers. Artiodactyls also show very diverse social and ecological adaptations.



Artiodactyl skulls. (a) Warthog. (b) Camel. (c) Kudu antelope. (d) Hippo. (e) Chevrotain. (f) Giraffe.

The principal threat to African artiodactyls is their continuing replacement by a few exotic domesticates. An ever-expanding livestock industry is eroding and exterminating natural communities of animals and plants on a huge scale. The latter are among Africa's most valuable assets because of their greater diversity, complexity, productivity and sustainability. The livestock industry operates within a kind of conceptual Dark Age in which promoters, consumers and practitioners pursue exploitation of domestic animals in ignorance of the ecological matrix from which their meat mountains and milk quotas derive. Their activities expand at inordinate cost to the long-term health of African environments and natural resources.

THE KINGDON FIELD GUIDE TO AFRICAN MAMMALS

Jonathan Kingdon

BALFOUR LIBRARY
9624
CAMBRIDGE



HELM
1997

XVIII, 476

Copyright © 1997 Jonathan Kingdon

First published by Academic Press, 1997

Reprinted with corrections, 2001

Reprinted by Christopher Helm, 2003

Published by Christopher Helm, an imprint of A&C Black Publishers Ltd.,
37 Soho Square, London W1D 3QZ

ISBN 0-7136-6513-0

A CIP catalogue record for this book is available from the British Library.

All rights reserved. No part of this publication may be reproduced or used in
any form or by any means – photographic, electronic or mechanical,
including photocopying, recording, taping or information storage and
retrieval systems – without permission of the publishers.

A & C Black uses paper produced with elemental chlorine-free pulp,
harvested from managed sustainable forests.

www.acblack.com

Typeset by Selwood Systems, Midsomer Norton
Printed in Great Britain by Butler and Tanner, Frome, Somerset

10 9 8 7 6 5 4 3

RHINOCEROSES RHINOCEROTIDAE

Browse (Black) rhinoceros
Grass (White) rhinoceros

Diceros bicornis
Ceratotherium simum

When animals have become as scarce as rhinoceroses have today it is difficult to describe them as successful. Yet living African rhinos were, until very recently, the widespread, abundant, advanced and successful representatives of a family that had seen a very wide range of types in the past (i.e. 30 fossil genera).

Recognition: Rhinos are the second largest land animals only surpassed by elephants in bulk and weight. They have relatively short, powerfully muscled legs, a short neck and a massive head, armed with a nasal horn or horns. Contrary to popular belief rhinos are not ponderous and slow but are capable of running or galloping fast. Their long, heavy bodies are densely bound masses of reinforced bone and muscle enclosed in very thick skin. Most of the rhino's great weight is taken on the broad central toe but two smaller hooved toes on each foot spread the load and enhance stability. Other characteristics include backward-facing genitalia which fire powerful horizontal squirts of urine. ♂♂ lack a scrotum and have undescended testes.

Genealogy: The earliest rhinos were small, agile animals, something between a tapir and a horse in appearance. Large, horned forms came later (about 30 million years ago) and originated in Asia. Among the several lines that entered Africa was a close relative of the living Sumatran rhino (*Dicerorhinus*). This genus survived from at least 20 million years ago to less than 1 million years ago. Of the two surviving African species, the browse rhino has the longer fossil history. The grass rhino appears to have split from *Diceros* ancestors some 8 million years ago and has shown continuous adaptation towards grazing ever since.

Geography: Browse and grass rhinos are exclusive to Africa. Various species of the more primitive Sumatran type were also common in Africa and Europe and fossil deposits show that rhinos were conspicuous and common inhabitants of most Old World ecosystems until relatively recent times.

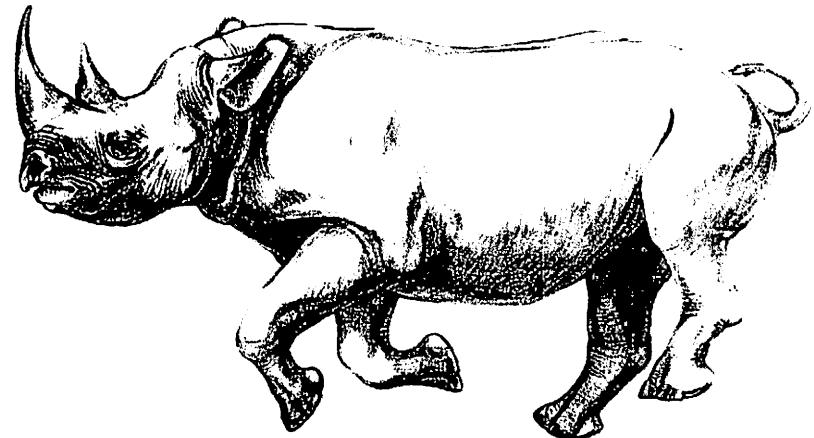
Ecology: The main rhino speciality is an ability to feed on coarse plant material. Rhinos are more selective than elephants but less so than most antelopes. Temperature control, digestion and scent communication all depend upon water and rhinos are unable to survive extreme droughts. Nonetheless, rhinos formerly suffered very low levels of natural mortality, a trait that goes with long life (up to 50 years) and a slow breeding rate.

Natural history: Rhinos display territorial behaviour yet can tolerate high densities and may even live in small herds. The tolerance of dominant individuals, particularly ♂♂, appears to vary by species, by region and in response to changes in density. Home ranges are marked with dung and urine.

Adaptations: Rhinoceros horns are solid keratin (like toenails or cows' horns). They are not set over a core but on a well-butressed pediment that transfers all the stresses and strains of stabs, swipes and tosses to skull and forequarters (a rhino has been known to toss an adult horse into the air). Occasionally the rudiments of a third or fourth horn may grow on the muzzle and forehead of rhinos and there was a tendency towards clusters of horns on the heads of various extinct species.

The teeth can withstand a long life of chewing on tough vegetation and are deeply embedded in bony mandibles. Their food is gathered in by very muscular lips. An envelope of thick, wrinkled skin partially disguises their magnificent heads. Rhino heads are almost architectural models of form and function. Enclosing the vital sense organs and articulated by huge jaw and neck muscles, the skull is reinforced against its own weight. Often dubbed 'prehistoric', rhinos are no more bizarre or 'primitive' than a pig or a cockerel and should be endowed with a future, not just a past.

Status: The extreme vulnerability of rhinos under genuinely wild conditions (due to the great price paid for their horns) has reduced almost all species to something close to domestication. Until cultural and environmental attitudes have changed, rhino survival will continue to depend upon captive or closely managed populations.

Browse (Black) rhinoceros *Diceros bicornis*

Other names: Fr. Rhinocéros noir. Ger. Spitzmaulnashorn. Swah. Faru.

Measurements: HB 290–375cm. T 60–70cm. SH 137–180cm. W 700–1,400kg.

Recognition: A very large mammal, its thickest skin forming inflexible plates over the shoulders, haunches, sides, forehead and cheeks. Skin around the muzzle, eyes, ears, undersides and legs is thinner and more flexible. The grey skin colour is most evident during the rains. Mud-wallowing and rolling in dust or ash discolours most hides during the dry season. Behind the shoulder, the dorsal silhouette swings down and back to raised haunches. The head has a short forehead and a very muscular, mobile mouth ending in a sharply pointed upper lip.

The three toes leave characteristic tracks. Other signs of the rhino's presence include rubbed trees, rocks and termitaries, well-scattered dung middens and habitually sprayed urine-posts.

Subspecies: Browse rhinos are highly variable and 23 subspecies have been named. Six regional populations correspond very approximately with named subspecies. *D. b. bicornis* (Cape): the largest, now extinct. *D. b. minor* (south and south-east, to Tanzania). *D. b. michaeli* (upland E Africa). *D. b. chobensis* (SW Africa). *D. b. brucii* (NE Africa): the smallest, now extinct. *D. b. longipes* (W and central Africa).

Distribution: At one time a large part of sub-Saharan Africa in all but the wettest and driest areas (maximum dry-season range within 25km of water). Contemporary populations are on the brink of extinction and only hold out in a wide scatter of minuscule pockets (see map).

Habitat: Browse rhinos favour edges of thickets and savannahs with areas of short woody regrowth and numerous shrubs and herbs. They are naturally scarce or absent in closed-canopy forests and woodlands and the more extensive areas of grassland. Where woody and leafy forage could support them, rhinos were formerly found at very high densities (i.e. up to 23 animals, 17 wholly sedentary, in 2.6km²). Where they were very common, smooth rhino pathways, dung piles, urine spray sites and rubbing posts were much in evidence.

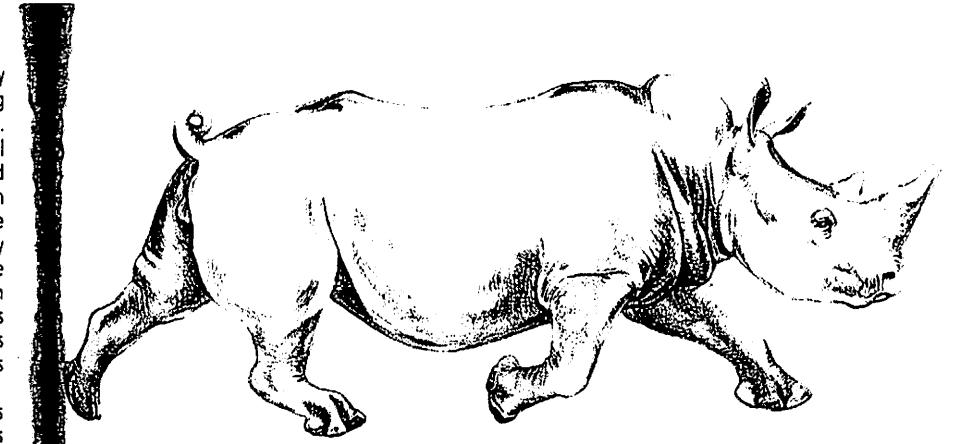
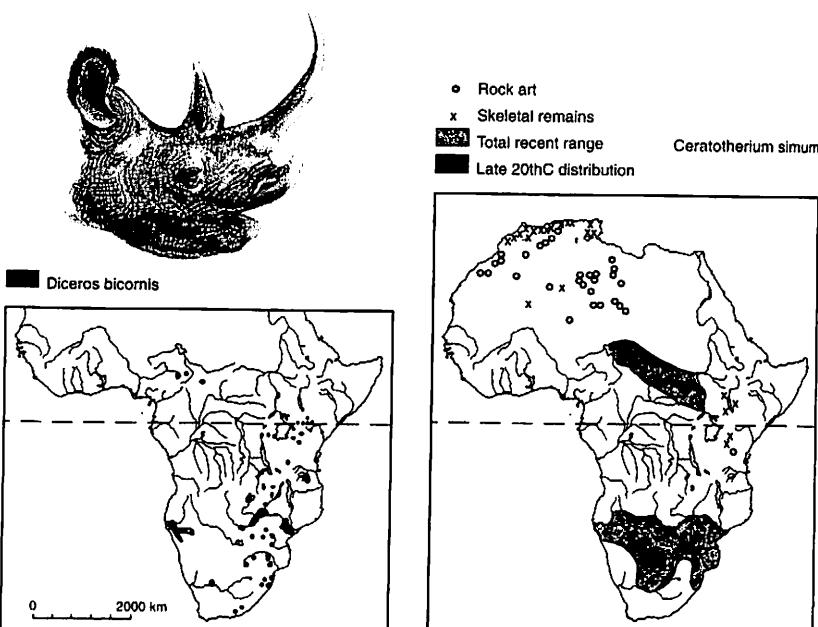
Food: Low-level browse (leaves, twigs and branches), typically in *Acacia*, thicket, hard-pan and riverine plant communities. Some 200 species from 50 families recorded. Browse rhinos have special seasonal preferences for legumes and certain other plants are always avoided. Salt is a major attraction and their taste for salt is exploited by many tourist lodges. Animals can go for up to 5 days without water if their food is moist; otherwise they are always found within daily walking distance of water. Horns are occasionally used to loosen soil around roots or to break branches above the lips' reach.

Behaviour: A ♀ with her young is the basic social unit. Adult ♀♀ may form temporary associations and animals that share a part or all of their range have an easy-going familiarity with one another instead of the aggression that is elicited by total strangers. Home ranges can cover over 130km², but some are as small as 2.6km². Overtly territorial behaviour is also very variable. ♂♂ in high-density areas are well acquainted with, and generally tolerant of, their neighbours (except in the presence of an oestrous ♀). ♂♂ in low-density areas meet less frequently and are more likely to be aggressive. Decline can be accelerated in an already thinned population because a few very aggressive ♂♂ not only miss encounters with ♀♀ in heat but their intolerance of other ♂♂ further lessens the frequency of matings. Displays between ♂♂ resemble those of stallions: there is much strutting, broadside with lowered head, flattened ears and rolling eyes. Various snorts during encounters seem to have different shades of meaning. Rhinos utter series of snorts interspersed with pauses and very loud grunts and screams which punctuate serious fighting.

One young is born after a gestation of 15–16 months. It is soon mobile and begins browsing vegetation before it is 1 month old. It sucks milk for up to 1 year and only begins to drink water after 4 or 5 months. A mother generally drives off her previous offspring before a new birth and the interval between births ranges from 2 to 5 years. Both sexes are capable of reproduction at 4 or 5 years old but ♂♂ can seldom compete with established ♂♂ before the age of 10 years. In spite of a life spanning more than 40 years, this is one of the slowest recruitment rates of any large mammal.

Adaptations: Although all-out frontal charges occur in high-intensity fighting, browse rhinos tend to use their horns more like clubs or staves than rapiers. Mild jousting may be accompanied by shoulder-to-shoulder pushing and leaning. Weight and horn size are easily tested this way but scent and behaviour generally reveal the dominant individual. Avoidance or submission follow.

Status: Human pride, superstition and greed have combined to ensure astronomical prices for horns in the form of dagger handles, cups, supposed medicines and aphrodisiacs. In the late 1960s some 70,000 browse rhinos were estimated to survive in Africa. This was a fraction of the numbers existing at the turn of the century. By 1990 the total number of browse rhinos living within 38 officially protected conservation areas (ranging in size from 55,000 to 62km²) was about 3,300. This accounted for most of the rhinos that survived in Africa in 1990. If these areas were secured and managed for the animals benefit, their potential stock could be as high as 80,000. Listed as Appendix 1 (CITES), Endangered (IUCN).



Grass (White) rhinoceros *Ceratotherium simum*

Other names: Fr. Rhinocéros blanc. Ger. Witrenoster. Swah. Kiaru ya majani.

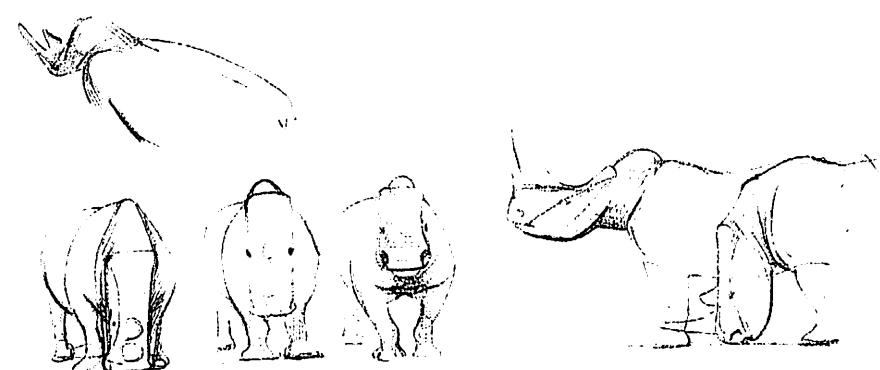
Measurements: HB 360–420cm. T 80–100cm. SH 170–185cm. W 1,400–2,000kg (♀), 2,000–3,600kg (♂).

Recognition: Although formerly called 'white', this very large rhino is of similar skin colour to the browse rhino. The highest point behind the shoulder is midback (due to tall dorsal and lumbar vertebrae) rather than the haunches. The head is long (especially the forehead). The mouth is very wide, flat fronted and set low over the chin. The flexible neck forms a prominent hump when the head is raised. Spoor are more elongate than those of the browse rhino, with greater separation of toes and a prominent cleft at the back.

Subspecies: Southern grass rhino, *C. s. simum* (southern savannahs); northern grass rhino, *C. s. cottoni* (northern savannahs).

Distribution: Fossils, bones and rock art suggest that this species was formerly abundant all over the better-watered grasslands of Africa (including much of the present Sahara). In historic times it ranged to the shores of L. Chad but reached its nadir at the turn of this century with minuscule populations in two widely separated localities: Zululand and the Zaire-Sudan-Uganda borderlands.

Habitat: A preference for short-grass areas and seasonal movements to avoid waterlogged long grass confirm that this species evolved within a larger ungulate community that maintained short swards. In areas of high density the rhinos themselves maintain grazing lawns. Where territories are maintained by resident bulls their border-patrolling and scent-marking leave foot-scuffs, dung middens, urine sprays, rubbing posts and horned vegetation along boundaries. Linear pathways may form between grazing and waterpoints.

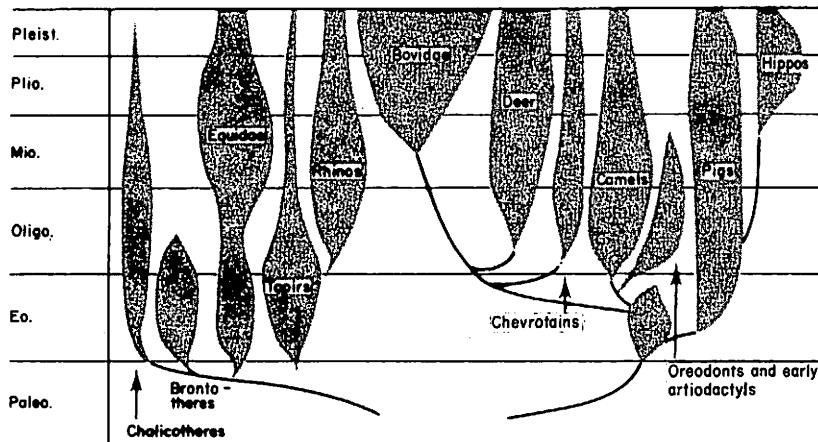


Food: Short grasses, typically *Cynodon*, *Digitaria*, *Heteropogon* and *Chloris* species in well-trampled, well-drained, wet-season concentration areas, are preferred. After dry-season fires, grass rhinos may move into regrowth dominated by *Themeda*, *Hyparrhenia* and *Setaria*. Biting flies and direct sun may influence seasonal movements by restricting the rhinos to ridges or shaded areas for a time. Frequent alternation between grazing and resting changes to long midday rests at the height of the dry season.

Behaviour: ♀♀ and their immediate offspring occupy large (4–12km²) overlapping home ranges where they frequently graze alongside one or more ♀ neighbours. ♂♂ defend territories but their size and their owners' tolerance is related to population density. In crowded Zululand parks ♂ territories can be as small as 0.75–2.6km². Grass rhinos are extremely vocal, with a wide repertoire of utterances. Infantile squeaks and pantings in adults become loud chirps, gasps and puffs (contact) or snarls and squeals of distress. Dominant ♂♂ grunt and bellow challenges at other ♂♂ or court ♀♀ with a low, pulsing cry. One well-developed but hornless young is born after a 16-month gestation. It first grazes at about 2 months and is driven away by its mother at about 2–3 years of age. ♀♀ do not usually breed until they are about 5 years old, dropping their first calf at 6½–7 years of age.

Adaptations: This species evolved from a common ancestor that was very similar to the living browse rhino; modifications in the proportions of the mouth, skull and neck enabled it to become a more efficient, short-grass grazer. Thus the neck has become short but has to crank up a heavier, longer head. This is achieved by the tall vertebral spines, web of tendons and bunched muscles that give the animal its neck 'hump'. Broad, flat-edged lips enable short grass to be cropped efficiently. Long grass is grazed more clumsily.

Status: After millennia of decline the southern form of the grass rhino was brought back from the brink of extinction through the efforts of one man, B. Vaughan-Kirby. From 10–20 animals in the earliest years of this century, the present population now approaches 5,000. The northern form was formerly more widespread and abundant but is now reduced to a few dozen animals in one or a very few localities. It is listed as Critically Endangered (IUCN). The southern form is at lower risk but is dependent on rigorous protection and maintenance of its CITES Appendix 1 status, which prohibits trade in its horns.



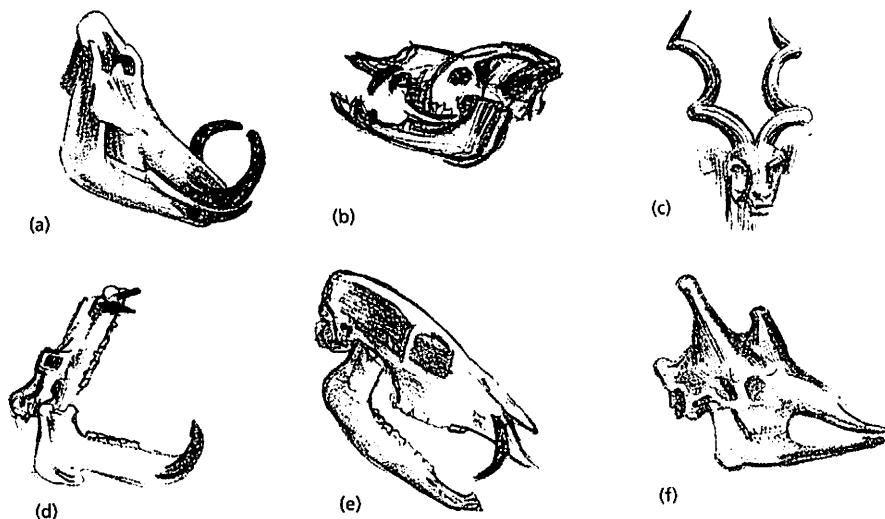
Possible scheme for radiation of artiodactyls.

EVEN-TOED UNGULATES ARTIODACTYLA

The artiodactyls embrace all the horned antelopes and cattle, deer, giraffes, camels, chevrotains, pigs and hippopotamuses. They are one of the most important and successful of mammal lineages. The earliest types were not very different from carnivores, had prominent canine teeth and an omnivorous diet. They are distinguished by their even toes with the axis passing between the third and 4th digits which bear the body's weight in all members of the family.

The most significant feature of this group is the progressive improvement of their digestion through a system of storing, rechewing and sifting of the food and a symbiosis with bacteria and protozoans living within the chambers of the stomach. These break down cellulose and release nutrients.

The skulls of living artiodactyls have been adapted to specific modes of combat requiring elaboration of canines, incisors, horns or antlers. Artiodactyls also show very diverse social and ecological adaptations.



Artiodactyl skulls. (a) Warthog. (b) Camel. (c) Kudu antelope. (d) Hippo. (e) Chevrotain. (f) Giraffe.

The principal threat to African artiodactyls is their continuing replacement by a few exotic domesticates. An ever-expanding livestock industry is eroding and exterminating natural communities of animals and plants on a huge scale. The latter are among Africa's most valuable assets because of their greater diversity, complexity, productivity and sustainability. The livestock industry operates within a kind of conceptual Dark Age in which promoters, consumers and practitioners pursue exploitation of domestic animals in ignorance of the ecological matrix from which their meat mountains and milk quotas derive. Their activities expand at inordinate cost to the long-term health of African environments and natural resources.