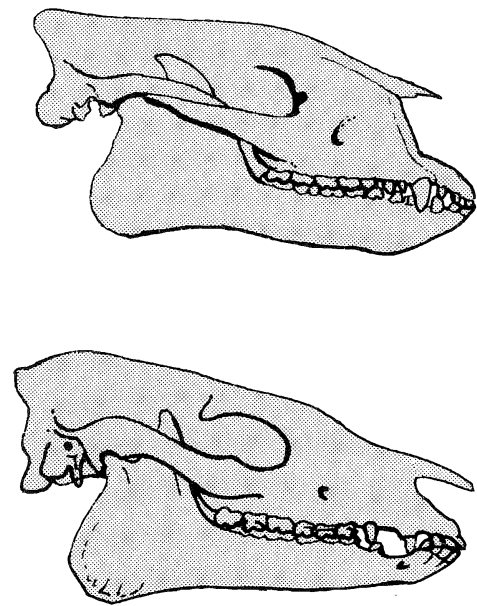


Perissodactyls

Perissodactyla
Equidae
Rhinocerotidae

Perissodactyls must have emerged from a primitive ungulate group, probably during the later Palaeocene, a period that is poorly represented in the fossil record. Their most likely ancestors are condylarths, some of which were probably omnivorous but had the general mien of carnivores or insectivores, with a full dentition, differentiated canines and a relatively long skull.

Although it is too large and too late to be considered directly ancestral, *Phenacodus* (see Volume I, p. 376) is intermediate in the structure of its heavily nailed feet and in some features of its skull and dentition between a generalized early mammal and the primitive Eocene *Hyracotherium*.

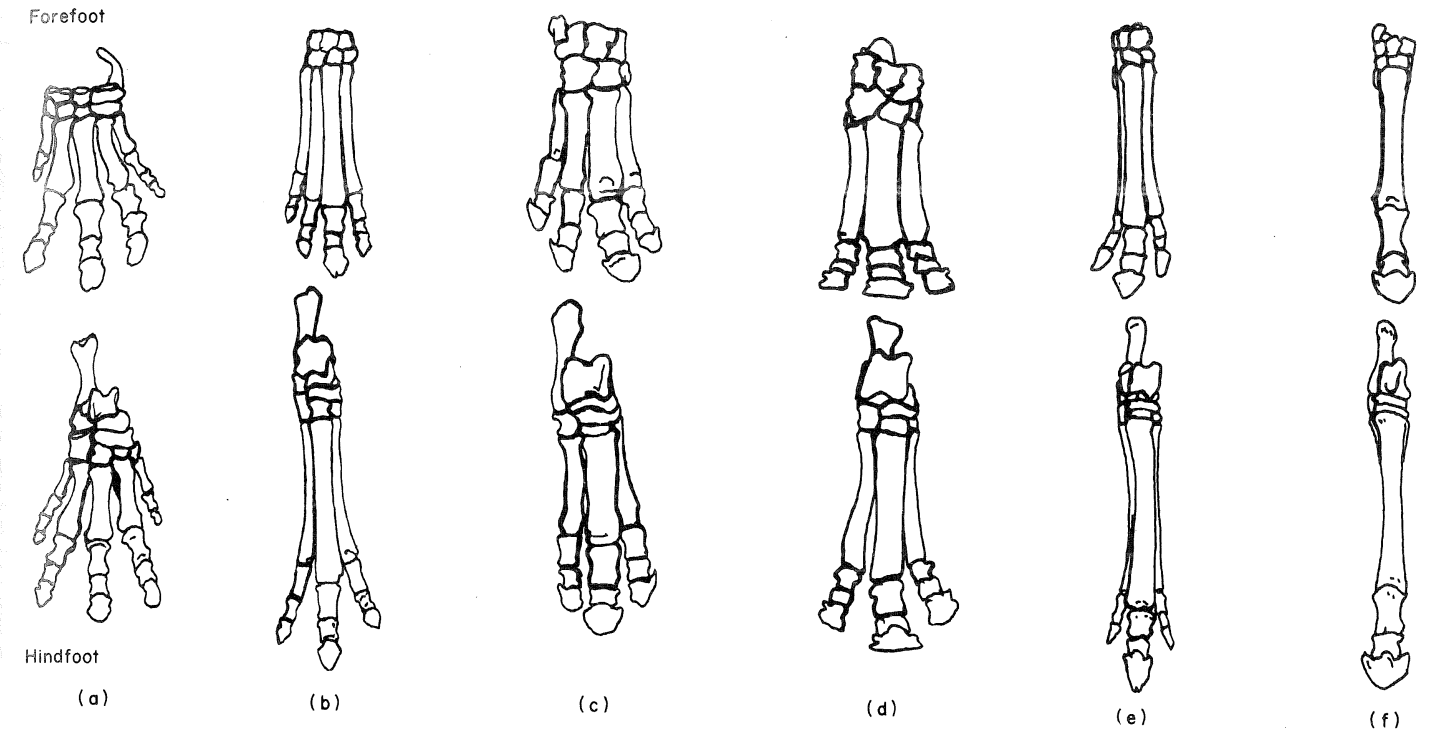


Skulls of Eocene condylarth, *Phenacodus primaevus* and *Hyracotherium* compared.

Hyracotherium is the earliest perissodactyl and may be close to the common ancestor of horses, rhinoceroses and tapirs although its slender proportions already anticipate those of the equids. Its niche may have been close to that of the living tragulids.

Later, perissodactyls tended to be large and to carry their weight on three toes and in modern equines on only one toe, hence the clumsy anglicization "Odd-toed hoofed mammals".

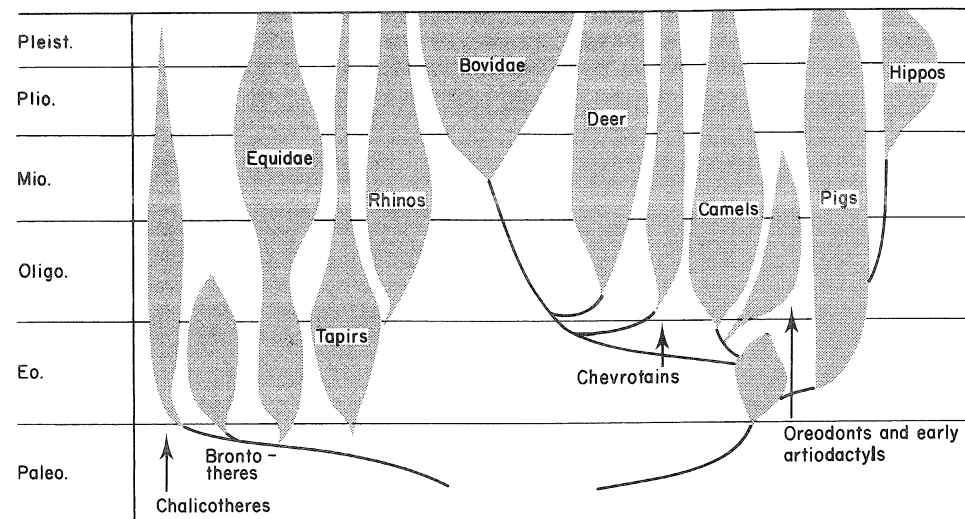
Perissodactyls diversified in the Eocene and were among the most abundant of herbivore types in America and Eurasia up to the Miocene.



Above: Perissodactyl lower limbs: forefoot above, hindfoot below. (a) *Phenacodus* (Condylarth); (b) *Hyracotherium* (primitive perissodactyl); (c) *Tapirus* (Tapir); (d) *Diceratherium* (Miocene rhinoceros); (e) *Miohippus* (Miocene horse); (f) *Equus*

Left: forefoot, black rhino.



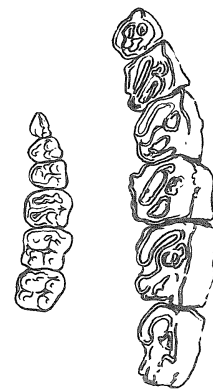


Superior digestive assimilation by advanced artiodactyls probably led to competition and the progressive elimination of perissodactyls from all the ordinary herbivore niches but the survivors appear to have become specialists in coarse feeding, or in the case of the grass rhino, *Ceratotherium*, an advantage may have been gained through gigantism. Browsing rhinos can feed on woody vegetation too tough for the bovids' leaf-plucking mouth and the horses have the advantage that their teeth can manage the wiriest grasses, while *Equus* may have acquired some competitively superior adaptations in their social life (see p. 128).

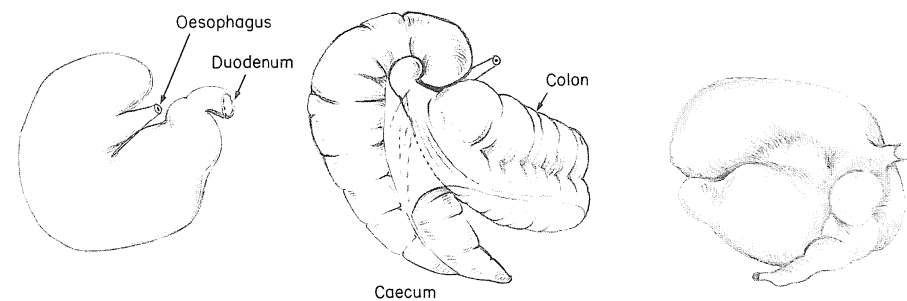
In Africa, perissodactyls have always occupied special niches and arrived too late ever to have been a dominant group (see Volume I, pp. 55—58).

The relatively late adaptation in Africa of *Ceratotherium* to a grass diet is interesting, suggesting that large size may confer a high level of immunity from predation and reduce the impact of competition in rich well-watered habitats.

It has been calculated that the ruminant type of digestion is advantageous up to a body weight of 1.800 kg (Van Soest in Janis, 1976). Janis (1976) regarded large size in rhinos as a strategy to avoid ruminant competition and



Left: *Hyracotherium* Right: *Ceratotherium*.



Stomach and caecum of *Equus*

Complex chambered stomach of an advanced ungulate

suggested that the rhinos might be regarded as representing a real adaptive response of the Tapiroidea to changing evolutionary pressures at the end of the Eocene.

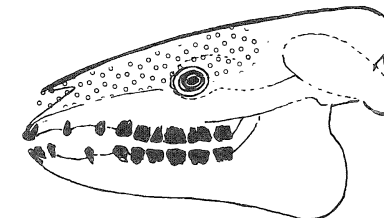
Turning to the origins of perissodactyls as herbivores, Janis (1976) thought they adopted a diet containing cellulose during the Palaeocene while they were still relatively small. She pointed out that all small-sized herbivores that eat a lot of coarse vegetable matter, lagomorphs, hyraxes and some rodents have developed caecal fermentation and she considered that the body size of ancestral perissodactyls was the critical factor in determining the type of digestion.

If quantities of herbage are always available the perissodactyl system is actually superior to rumination at digesting a high fibre content. There are no advantages in rumination for a very small animal and Van Soest (in Janis, 1976) regards 5 kg as the minimal body weight at which rumination would be viable. It is known that ruminants developed very much later than perissodactyls (see table) and it is likely that artiodactyls adopted a truly herbivorous diet when they were already relatively large.

Only two of the three living families have ever been represented in Africa and it is possible that the tapirs never entered Africa because their niche was pre-occupied by early proboscids.

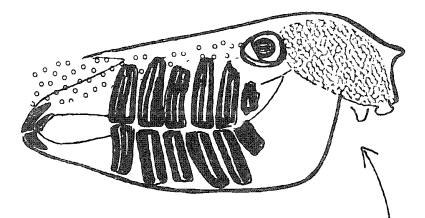
FEATURES INFLUENCING FORM IN PERISSODACTYLS

Archaic perissodactyl features



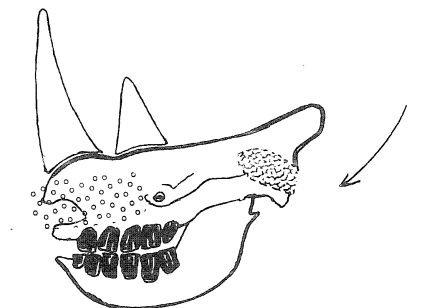
Vegetarian diet; rel. high crowned molars, deep jaws. Increasing size trend. Well developed olfaction in extended cylindrical skull.

Equid features



Medium-large size. Elongation of neck, legs and skull. Vision well developed; high head carriage. Diastema, molars with very high crowns with deep rooting. Incisors cut and pull grass. *Defence*: speed. *Weapons*: teeth and hooves.

Rhinocerotid features



Great size and weight. Heavy head, low carriage. Short plantigrade limbs. Vision poor; olfaction good. Incisors and diastema lost, lips gather food. *Defence*: size and horns. *Weapons*: nasal horns.

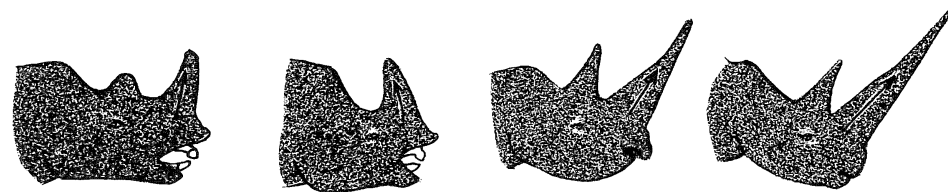
Ceratomorphs

Ceratomorpha Rhinocerotidae

Genera

Diceros
Ceratotherium

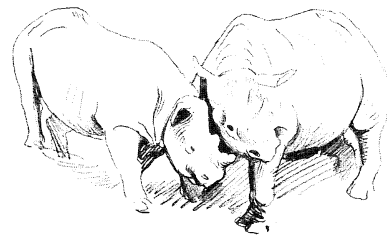
When animals have become as scarce as the rhinoceroses are today it is difficult to describe them as successful without tedious qualification. Yet there is good reason to regard the living African rhinos as advanced and successful representatives of a family that has seen a very wide range of species and types in the past.



Dicerorhinus *Rhinoceros* *Diceros* *Ceratotherium*

Their name describes that unique peculiarity, the nasal horns: a characteristic that is probably as highly developed in the living species as it has ever been in any of their ancestral forms. It is interesting to note that there is a gradient in the size of horns in different rhino species. *Ceratotherium*, living a semi-social life in the most exposed habitats, has the longest horns while the Oriental rhinos, living a more solitary existence in dense jungle, have the shortest. It is possible that long horns get more in the way in a dense habitat but their employment in intra- and extraspecific defence is probably more developed in the former species. Furthermore there are phylogenetic implications; the short-horned oriental *Dicerorhinus* is a genus known from the Oligocene, whereas *Ceratotherium* only evolved in the Pliocene and is undoubtedly much more advanced.

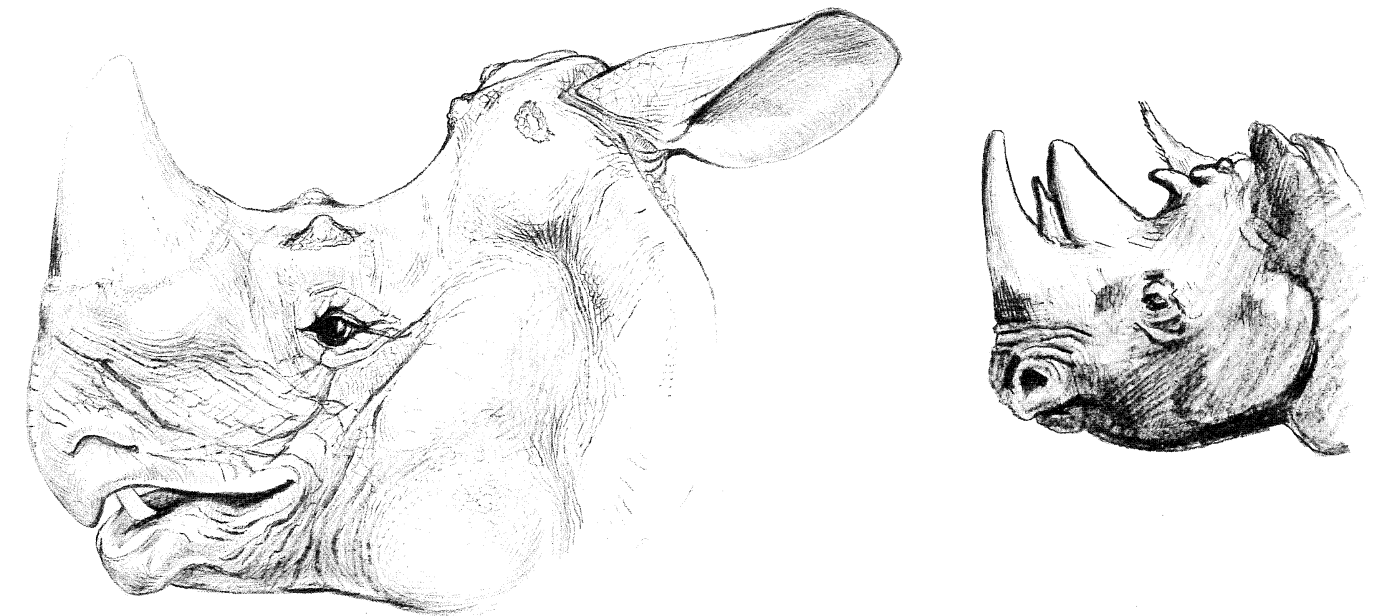
In the long-horned African rhinoceroses, horns tend to be used more as clubs than rapiers, particularly in the early stages of a fight. These sideways swipes, which occasionally cause horns to split, probably have a phylogenetic origin in defensive movements that deflected direct thrusts of the horns but have become ritualized into an effective and relatively harmless way of testing strength and may even be accompanied by shoulder pushing without horn stabbing (p. 115). A major conflict is of relatively rare occurrence because a dominant rhino is recognized by his scent and behaviour and elicits



From a photograph by F. Hartmann (1970).

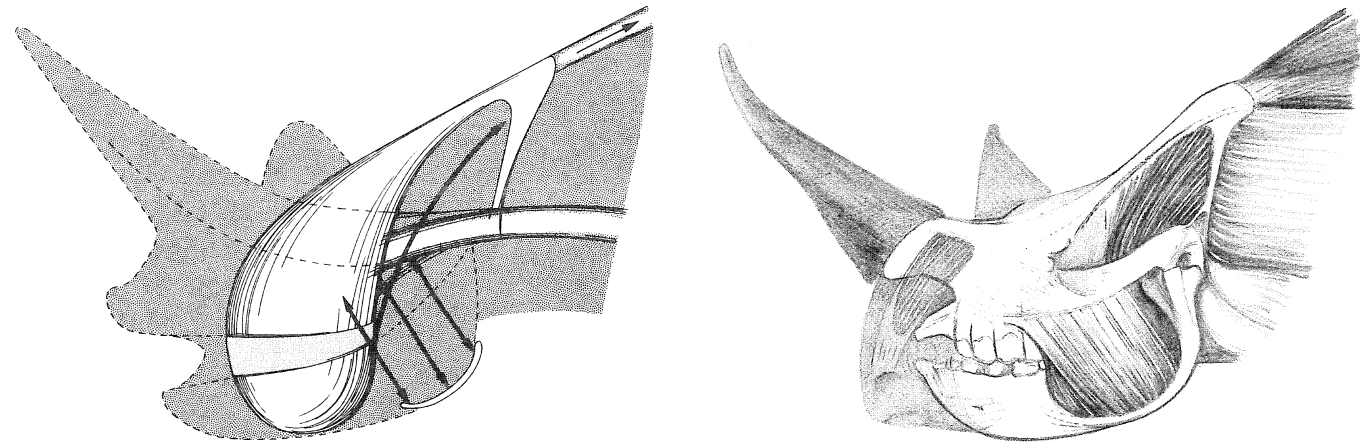
submission or avoidance in all other rhinos living in his territory. The richer the resources and the more open the environment the more frequent are contacts likely to be. It is therefore possible that ritualization has proceeded further in the African species than in the short-horned, forest-dwelling rhinos of Asia. It would be interesting to compare the details of horn fights or clashes in the more primitive *Dicerorhinus* and *Rhinoceros* with those of the African genera. The imminent extinction of *Dicerorhinus* makes the possibility of such comparisons sadly remote. Females are well able to defend themselves but they seldom fight. A mother protecting her offspring during a capture campaign has been seen to toss a 450 kg horse high into the air easily, which illustrates the strength of rhinos and emphasizes how dangerous all-out fighting with horns can be.

Very occasionally a rhino is born without horns. Conversely, the rudiments of a third or fourth horn may sometimes appear either behind the others or on other parts of the body. The famous engraving of an Indian rhino by Dürer shows just such a supplementary horn on its nape; however this picture was a copy from a Portuguese artist's work and the spike might have been an artistic elaboration. Areas of reinforced and rugose bone on fossils suggest that there was a general tendency towards clusters of knobs or horns on the head of various extinct rhinos.



The earliest and most primitive ancestral families, Hyrachidae and Hyracodontidae had no trace of horns and small "running rhinoceroses" were evidently fast and agile and would have resembled something between a tapir and a horse in appearance.

Left: Great Indian rhinoceros, showing sites of small accessory horns above the eyes and on the forehead. Right: Black rhinoceros from a photograph by K. Sheldrick (1975).



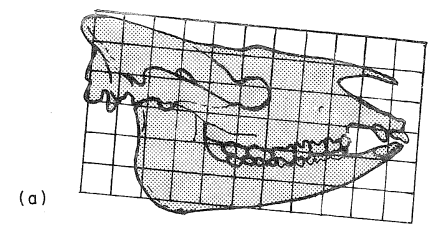
Ceratotherium: principal mass of skull in relation to mastication, horns, vertebral column and suspension.

All the perissodactyls have retained their dependence on the sense of smell for information and intraspecific communication, but the rhinos live in a world in which scents are the prime regulators of their social existence. Both their rhinencephalon and olfactory chamber are exceptionally large (Friant, 1955). The latter is accommodated beneath the cantilevered nasal bones which have had to be well buttressed to take the stress of the keratinous horn (see drawing). The massive teeth have even stronger bony bases and reinforcement of the forehead and occipital area allows an adequate support for the weight of such a heavy head as well as providing a bony shield for the brain. Enclosing large cranial, olfactory and buccal cavities, articulated by huge jaw and neck muscles, reinforced against its own weight and the extension of its horns, a rhino skull is a splendidly architectural model of form and function.

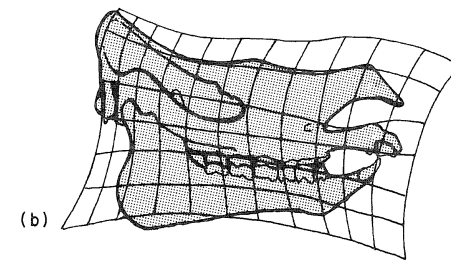
Ancestral rhinos, such as *Trigonias* and *Caenopus* had a diastema, incisors, even canine teeth and the nearly extinct *Dicerorhinus* of South-East Asia has retained short tusks in the front of its mouth. The African rhinos, instead, have lost their incisors and there are now only bony vestiges in front of the cheek teeth which have made a phylogenetic migration forward to the front of the mouth and head while the lips alone do all the cropping or plucking of food. A habit that may derive from the time when they had incisors is the snarl; Oriental rhinos actually bite but the African species employ the snarling gesture when they are on the defensive and being threatened by a superior.

Dicerorhinus has been found in the Upper Oligocene in Asia and in Europe and Africa in the Miocene and members of this genus were once very widespread. The woolly rhinos of the ice ages, *Coelodonta*, were closely related to this genus.

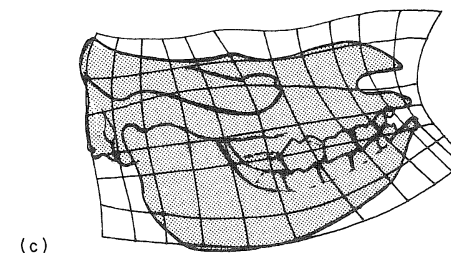
At least one rhinoceros species, *Paradiceros mukiri*, appears at Fort Ternan and this species may have been ancestral to both living species as well as to the extinct *Diceros pachygnathus* which occurred in Europe. Previous to this the hornless *Aceratherium* and *Brachypotherium* (belonging to separate and dead-end branches) appear in the East African Miocene.



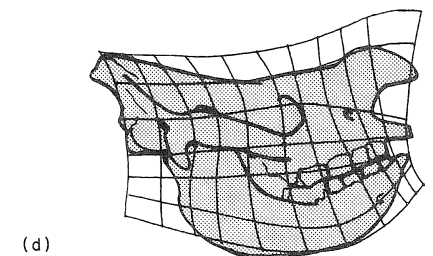
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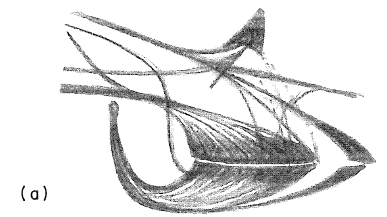
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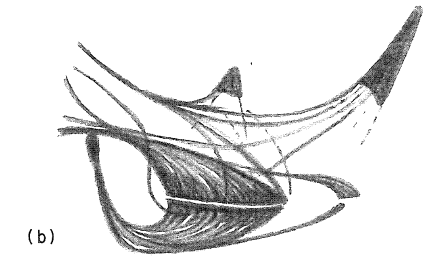
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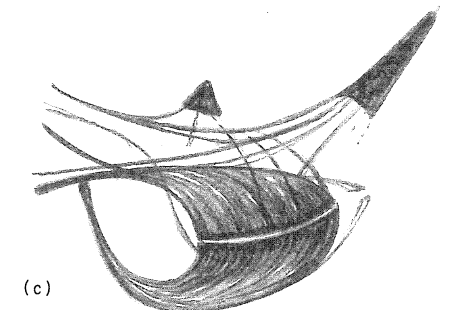
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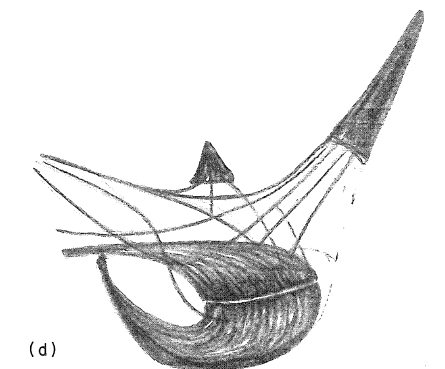
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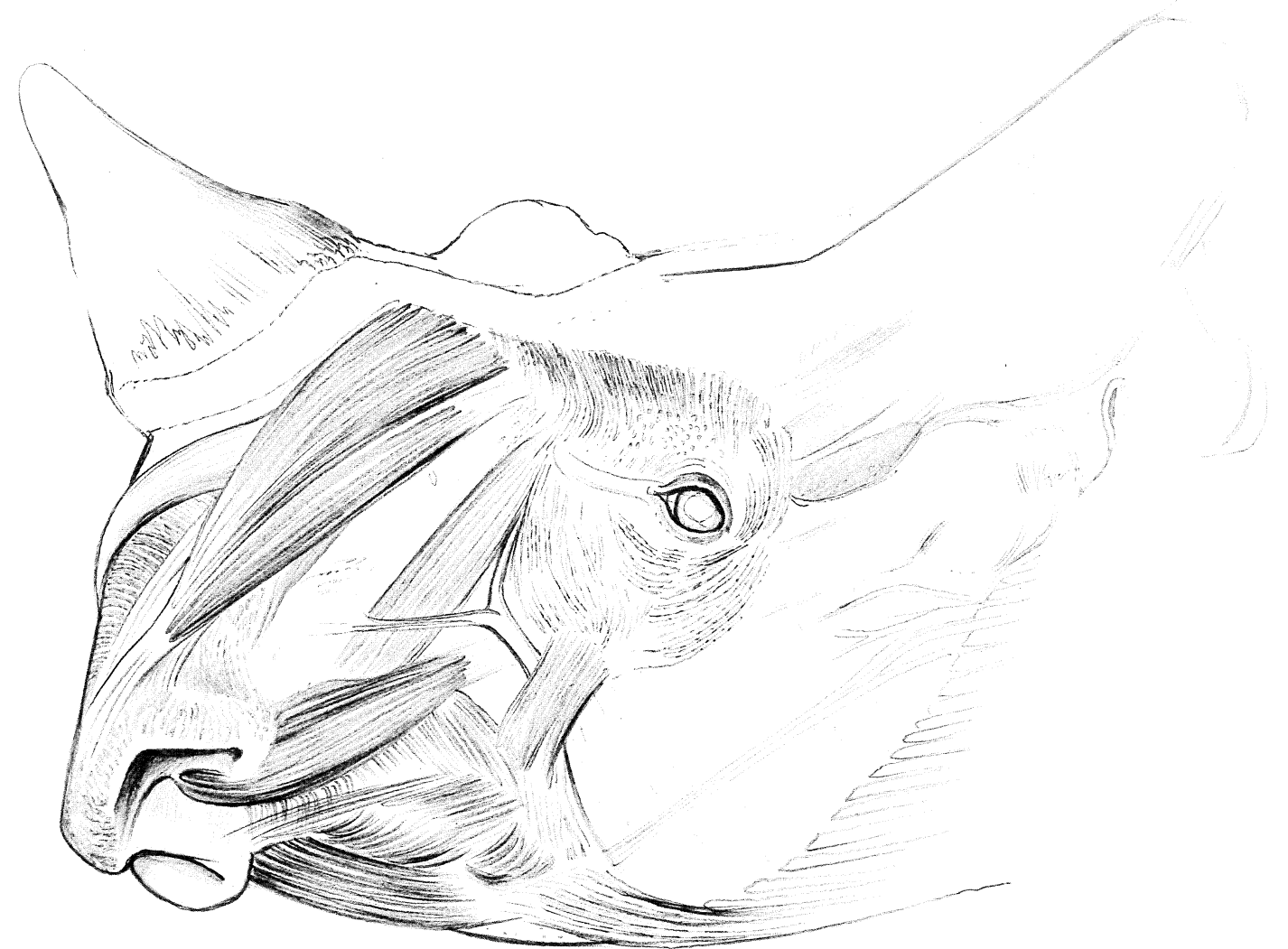
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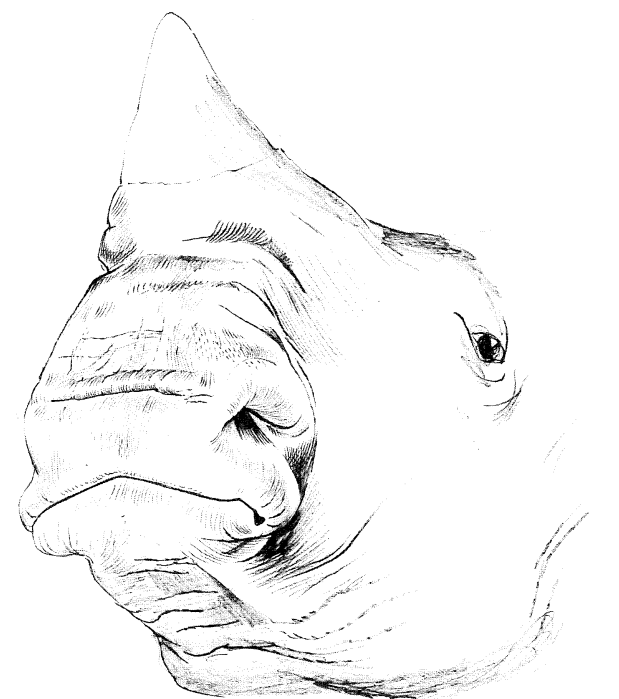
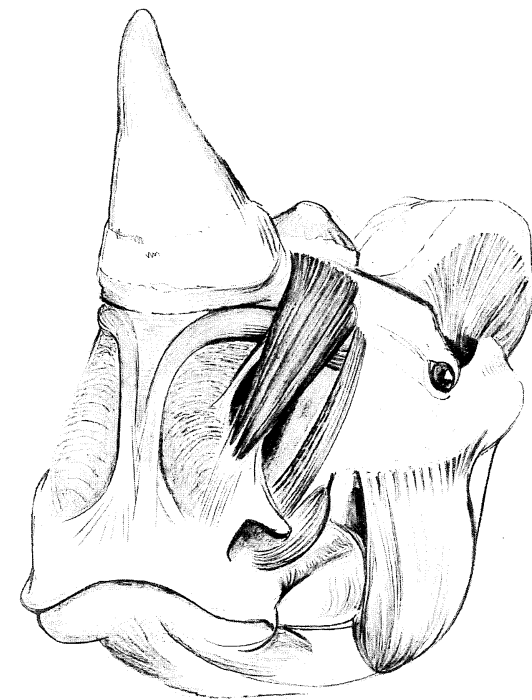
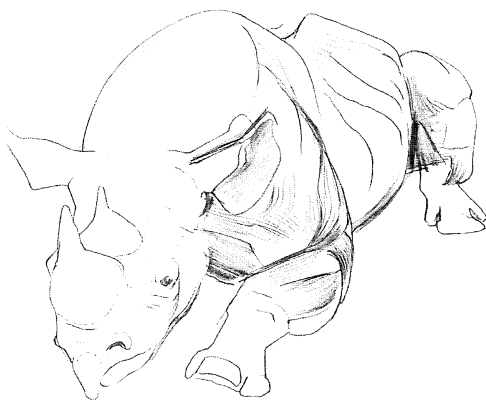
By the early Pleistocene both modern genera are present, *Diceros* in its present form while *Ceratotherium praecox* from Chemeron (4 million years old) still shows decided resemblances to *Diceros* but is probably directly ancestral to *C. simum* (Hooijer and Patterson, 1972). A Pliocene rhino from Samos, *Diceros pachygnathus*, has some characteristics of both genera and it has been suggested that they should be lumped in a single genus. Examining blood proteins, Osterhoff and Keep (1970) noted a great genetic variability in *Ceratotherium* while *Diceros* showed no variability whatever. Inferring from work on domestic animal breeding, they link this variability with an active stage of development, in which case the black rhino should be the more stabilized species. *Diceros* possesses 84 chromosomes while *Ceratotherium* has 82.

Buttressing of the skull in rhinoceroses in relation to teeth and horns.
(a) *Caenopus* (Oligocene);
(b) *Dicerorhinus* (Oligocene-Present);
(c) *Paradiceros mukiri* (Pliocene);
(d) *Ceratotherium* (Pleistocene-Present).



Above and below: *Diceros*;
Opposite: *Ceratotherium*.

By invading the open grassland, *Ceratotherium* has departed furthest from the ancestral rhino niche of browsing coarse vegetation in thick undergrowth. The implications of this change are readily manifested in a comparison between *Ceratotherium* and *Diceros*. The most commonly described difference between the two species is in the structure of the mouth. The upper lip of *Diceros* is a pointed prehensile organ capable of wrapping round twigs, leaves, fruit and grass and thorns and drawing them into the mouth where they can be chewed or snapped off by the premolars. *Ceratotherium*, on the other hand, has flat-fronted lips, a very broad mouth which is especially adapted to crop short or medium-length grass and more hypsodont teeth. The acquisition of grazing habits has had far-reaching effects on form. Like horses, the ancient, gracile rhinos had relatively long necks so that dropping the mouth down to ground level was no problem, but as the true rhinos developed towards their present proportions they followed the common trend of increasing size, as body and head became heavier, limbs and neck got shorter. Contrary to popular belief, rhinos are not slow ponderous beasts because the greater leverage and flexibility of a light long-limbed animal has been replaced by the greater thrust and power of their well muscled bodies

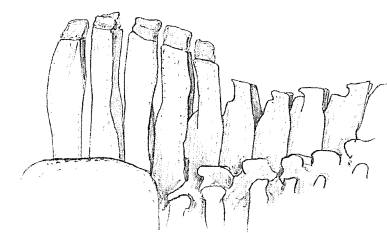




(Smith and Savage, 1955). A more compact form allows tighter control of balance when galloping so that the neck must be short and the trunk relatively rigid. Paradoxically the browsing *Diceros* has a longer neck than the grazing *Ceratotherium* which has instead lengthened the head to reach the ground. Most particularly the occipital crest of *Ceratotherium* is exceptionally high, this may be influenced by the height of the glenoid condyle but the greater depth behind the poll improves leverage from the neck musculature while the backward sweep of the occipital crest slightly shortens its extent. Nonetheless, when the head is in the grazing position, the angle between the back of the head and the thoracic spines is wide and shallow; at least three times as wide as when the head is raised in the galloping or alert position. To overcome the shallowness of the angle, the last cervical spine is exceptionally long and mobile and acts as a fan spoke extending the arc of the hypertrophied *ligamentum nuchae*. The blade-like thoracic vertebrae are also exceptionally tall and have a unique adaptation to improve their flexibility without loss of strength; each spine has a posterior slot along its length into which the forward edge of the next spine can insert. As this arrangement only occurs in the white rhino it is evidently adapted to the extraordinary amount of contraction involved in raising a long heavy head. The demand for both strength and flexibility in the area of greatest bending moments would be particularly great during the gallop, at which time the head may be carried quite high (see drawing).

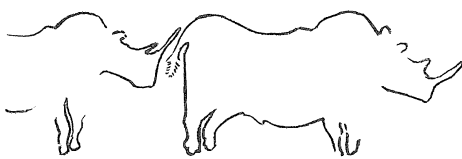
While on the brink of extinction today, rhinoceroses were evidently very widespread in the past. Numerous fossil rhinos have been found scattered across Africa and Eurasia. The woolly rhinoceros was carved and painted by stone-age artists right across the Palaearctic zone and preserved remains have been excavated from the permafrost of Siberia and the bogs of Europe. Schaurte (1960) reviewed the cave paintings and other early representations of rhinos. Likewise images of African rhinos are found wherever there are wall-paintings by cave-dwelling hunters and grass rhinos appear in rock paintings in North-central Tanzania, in the rock engravings from numerous localities in the Sahara and in the Kalahari, all areas where they long ago ceased to exist.

The ecological speciality of the rhinos was probably their capacity for



Thoracic vertebrae of *Ceratotherium*.

Grass rhinos depicted in Kisesse rock shelter near Kondoa, Tanzania.



feeding on coarser plant material than most of the artiodactyls, yet with greater selectivity and less damage to the vegetation than elephants. Originally rhinos may have lived wherever there was a perennial supply of such food and water.

African rhinos depend on water for temperature control and they are capable of sweating to the point where their bodies are streaming with moisture. These scent-oriented animals have also a secondary use for water in their dependence on frequent sprays of urine for communication. Although it is only the sexually active minority that employ this device, the system would be less effective for a physiology designed to be economical of water.

Wallows are another necessity for rhinos and the wallowing habit probably assists temperature control, although it may have other incidental benefits.

Drought has been known to kill large numbers of rhino of both species. There was a massive mortality of *Diceros* in Tsavo in the drought of 1961. As conditions worsened in this area, rhinos from a wide catchment area concentrated around the only permanent water. Some months before the drought reached its peak there were reports of widespread and severe fighting among the rhinos. This phenomenon was possibly the product of the ecological disturbance shattering the established land-tenure network and is discussed later.

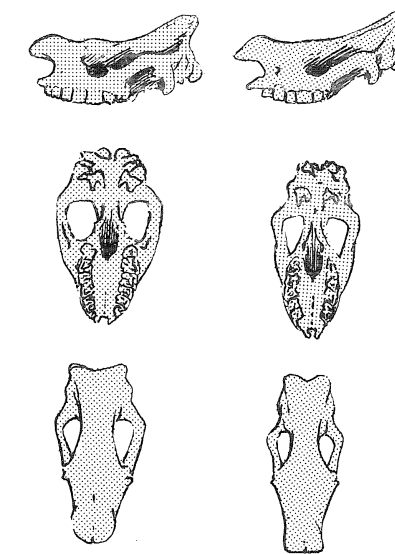
Thousands of elephants concentrated along the river and inflicted colossal damage on the surrounding bush. The forage for rhinos was thus reduced still further or actually destroyed. At the height of the drought rhinos were mainly dying of starvation but disease and stress were also playing a part. Elephants therefore appear to compete for browse with *Diceros* during periods of stress for both species. Whether grazing ungulates compete directly with *Ceratotherium* under similar conditions is not known, for relevant observations of the 1932 drought in Zululand are not available but Foster (1961) reported a decline in numbers at this time. However, there is a strong implication that both rhino species are susceptible to severe droughts and to the competition for reduced resources that attend them.

Large requirements of food and drink militate against rhinos during periods of extreme stress and their slow breeding inhibits a rapid recovery afterwards, so non-competitiveness with other herbivorous animals is most apparent over such periods and one can guess at similar factors leading to the decline of extinct rhino species.

The two modern genera are probably more adaptable and competitive than their collaterals and ancestors. Furthermore their recent decline is mainly due to man, but they also provide contemporary models for our understanding of the process of extinction.

Unaffected by rinderpest, they also appear to have a high level of resistance to anthrax, which is said to be endemic in African rhinos (Heppes, 1958). A low level of natural mortality has been noted in most rhino populations and this trait may be linked with their slow breeding rate.

Contemporary predators very rarely tackle an adult rhino and their imperviousness to predation is probably of long-standing. (Sabre-tooths might have been a major hazard in the Pleistocene but numbers of other pachydermatous mammals would also have been proportionally greater.)



Diceros *Ceratotherium*

Both species adapt their activity to the seasons, in that they rest for much longer in the middle of the day during the dry season. Otherwise their activity tends to alternate between feeding and resting throughout the day and night. Well-marked paths going to water or connecting feeding areas and wallows show that their habits are regular. These paths often pass through thick vegetation when it would be just as easy to skirt round it and the rhinos seem actively to seek the scratching sensation of twigs and thorns; they also like to rub on stumps and stones. In addition to the rewards of scratching an itch these habits may serve rhinos to help advertise their presence for the flakes of mud deposited or dropped off in this way possibly carry enough scent to be detectable to another rhino. If this is so, it is only one of several ways in which rhinos communicate with one another by scent. Apart from oestrous females only territorial male rhinos squirt urine and Owen-Smith (1974) showed that the frequency of squirting was highest in boundary areas between two *Ceratotherium* territories. He also considered this to be the main sign of territorial behaviour as a vanquished bull ceases squirting the moment he loses a contest. Urine probably identifies a rhino and his/her condition for other rhinos. Dung middens also serve as scent posts throughout the animals' home range, but Owen-Smith saw territorial bull *Ceratotherium* visiting particularly large middens on the borders of their territories where deep hollowing testified to the vigour with which the feet were scraped through them. He also saw non-territorial males use the same middens but with less ritual, as they may fail to wipe their feet in the dung or do it with less vigour and so probably make less smelly trails.

Scent trails provide the means by which both rhino species can meet or avoid conspecifics and encounters have been seen to be actively sought out by rhinos sniffing along trails. Non-territorial rhinos or territory holders off their own ground probably avoid other males, but there is evidence that resident males hasten to challenge invaders and that the distinctive urine ceremony is connected with territorial assertion. A male usually sprays urine over a landmark, a tussock, bush, stone or occasionally over a dung midden site, after which he lowers the head and thrashes his horn from side to side as if in the preliminaries to a challenge. This may be accompanied by backward shuffling or foot-scuffing and quick forward steps as if to challenge a non-existent rival. At times, the weaving of the head and horn turns into a savage onslaught on the bush or tussock. This horning behaviour has impressed many observers and has been widely interpreted as redirected aggression against an enemy. Owen-Smith's study established that *Ceratotherium* males have a well defined territorial system and although *Diceros* has been less intensively studied, there seems little doubt that the broad outlines of their social system are very similar. Only mature males are solitary and tend to restrict their movements even more than other classes. Both the density of rhinos and the food resources of the region are likely to influence the size of male territories.

Both these factors vary enormously. As many as 23 *Diceros*, of all sexes and ages, have been known to live in the 3 sq km of Lerai, Ngorongoro, 17 of them permanently. Even in the midst of inhospitable and extensive lava flows, *Diceros* can exist at surprisingly high densities and Root (personal communication) has seen 18 animals living in an area of about 15 sq km. Both species of rhino tend to crowd a suitable habitat rather than disperse out rapidly in



search of new ground. Five *Ceratotherium* per sq km of the Umfulozi Park has led to deterioration of the habitat and it is unlikely that densities of this order could be matched elsewhere; in the Kyle National Park, Condy (1973) found two *Ceratotherium* per 3 sq km and territories of 5—11 sq km. In Kidepo National Park, the overall density of black rhinos in 1970 was estimated at one per 10 sq km. The existence of male territories is obscured from casual observation by the tolerance of territory owners to other male rhinos (including former owners), so long as they show subordination in the dominant male's presence. Because the subordinate animal often displays noisy behaviour that gives every sign of being threatening, this has also tended to hide the true nature of confrontations between males, as has the behaviour of a territory owner the moment he steps outside the strict limits of his land. At such times, as on a trip to water, his movements become more tentative and should he meet any other rhinos, whether bull, cow or adolescent, while off his territory, he tends to avoid them. Owen-Smith (1974) has described some of the varied responses of other classes to a territorial male *Ceratotherium* on his own ground.

"A subsidiary bull responds to an approach by a territorial bull by standing his ground, uttering loud rasping bellows with forward thrust head and flattened ears. He may even take a few quick paces towards the territorial bull. Despite their seemingly intimidatory nature, these gestures are to be interpreted as defensive threats. This snarl-threat is employed by cows and adolescents against an approach by a bull, and, among subadults, usually by the smaller animal. The territorial bull may approach simply to stare horn to horn, or may clash horns briefly. Such a horn clash is fended off by the subsidiary bull to the accompaniment of trumpeting shrieks. Engagements between a territorial bull and a subsidiary bull which is resident within his territory are usually very brief, and the territorial bull soon walks off, leaving the other bull standing. More often, however, the territorial bull simply wanders on past as if oblivious of the other bull's presence, despite nervous snorts and grunts from the latter. The two bulls may not infrequently be observed grazing or resting together peacefully only 20—30 m apart."

When there is a true contest for a territory the vanquished animal is seldom pursued far, nor is he normally attacked any further once he has fallen. There are scattered reports of extensive fighting among rhinos, which have usually been interpreted as competition by bulls in rut, but closer observation suggests that these outbreaks, which occur in both species, are mainly contests for territories by wandering males and are most likely to occur when the equilibrium of land tenure has been upset by ecological or other disturbances.

Unless they are in oestrus, females do not have their movements impeded by other rhinos and the extent of their range is determined by the resources of the area. These resources are shared by other females, subadults and non-territorial males. Females or subadults of both species wander over an average range of 10—12 sq km, with a wide range of variation. These classes, which are completely non-territorial and tolerant of other rhinos, are most frequently in twos. Most females accompany their latest young one and this association is the closest and most consistent bond in rhino society and is only broken just before the birth of a new calf. The rejected three- or four-year-old then forms a new bond, preferably with another youngster of the same



sex, or it may link up with an unattached female. Very occasionally the mother may tolerate its return some time after the birth of the new calf and, if the new baby is lost, the old association may be resumed. It has been suggested by Owen-Smith (1975) that the main social difference between *Diceros* and *Ceratotherium* is that the subadults of the latter are more gregarious.

When drinking sites become scarcer during the dry season, rhinos may walk greater distances away from their normal home range and especially attractive food or wallow sites may also draw numbers together into temporary congregations. The behaviour of such commuting rhinos is seldom indicative of their social status, as all classes tend to be equally diffident off their own ground.

Sexual behaviour would seem to be initiated entirely by the scent clues produced by the oestrous females. Courtship is cumbersome and exceptionally lengthy. The male on whose territory a female stands blocks her departure and, by attending her constantly appears to forge a temporary bond for the period of her oestrus, and very occasionally for a longer period. As she is invariably accompanied by her last young one or by some older female, the bull's advances involve a triangle. In the early stages of courtship, the cow and her satellite both repel his approaches and the bull may actually attack the cow's companion; she in turn may defend the victim and quite serious fighting can break out. The risk of conflict is evidently offset by the male being extraordinarily cautious but also persistent in his courtship. His capability for damaging the young or the female is probably countered to some extent by the fact that females are just as well armed and sometimes nearly as heavy as the males. The fact that subadult companionships may be between members of the opposite sexes as well as between bachelors, shows that the only period in which rhinos assume obvious sexual roles are when a female comes into oestrus. Both the oestrous female and the dominant male advertise their sex and their condition by means of economic but frequent sprays of urine, and any other form of sexual differentiation is superfluous. I have observed a female with a small calf at heel make frequent sprays while threatening another female at a waterhole so the squirting may have a more general link with assertive behaviour.

Owen-Smith (1975) pointed out that the rhinos' peculiar form of territoriality provides a most efficient and economic way of regulating competition for reproductive rights. He noted that at population levels that are close to the carrying capacity of the habitat, territoriality is favoured by a limited potential for surplus food, by relatively sedentary and solitary habits, by the physical risks of fighting, by year-round breeding and by the vulnerability of very prolonged courtship to interference.

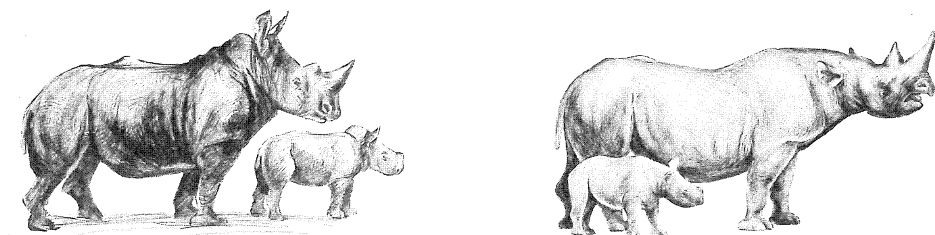
Copulation is only effected after the male has thoroughly accustomed the female to his approach and broken down her defensive reactions. Unusual calls, circling and posturing, as well as prodding on her belly and chin resting on her rump, appear to appease her and enlist her co-operation. There are several observed instances of young female *Diceros* behaving towards the male in a manner resembling a playful calf, with active curiosity alternating rapidly with flight impulses.

Although breeding is continuous, there is evidence that mating peaks occur in both species and these have some correlation with the end of the dry

season and early rains, so that a connexion between fresh green growth and the stimulation of oestrogens in the female is possible.

Gestation lasts 15 to 16 months and the young are on their feet in less than half an hour. After a period of some weeks' seclusion within a small sheltered locality, the mother wanders more widely with her young one, who keeps extremely close to her. Females of *Ceratotherium* tend to follow their young, whereas *Diceros* generally lead theirs. The dependence of the young on the mother is total and orphans usually starve unless they are weaned or can form an attachment to another female.

Favourite zoo animals, rhinos are generally not difficult to keep and breed and have a life expectancy of 35 to 50 years.





**Black
rhinoceros,
Browse
rhinoceros
(*Diceros
bicornis*)**

Family Rhinocerotidae
Order Perissodactyla
Local names
 Faru (Kiswahili), Kifau (Kisambara),
 Infwoko (Kingiha), Mbusya, Mbila
 (Kikamba), Bia (Siha, Chagga), Huria,
 Munyi (Kikuyu), Mburia (Kipare),
 Mpuria (Kimeru), Mpenbee (Kinyaturu),
 Mpembele (Kinyiramba), Mpela (Kitaita),
 Kizima, Pera (Kirabai), Isabhi (Kijita),
 Mela (Kihehe), Omuga, Amuka (Lwo),
 Enkula (Luganda), Muni (Kisamburu),
 Emunyi (Masai), Enkura (Lunyoro), Ejiji
 (Madi), Amosing (Ateso), Kipsirikto
 (Kalenjin), Kurrbatit (Sebei),
 Kipsirichet (Kipsigis), Kibawit (Elkoni),
 Warses (Kiliangulu), Weyil (Somali).

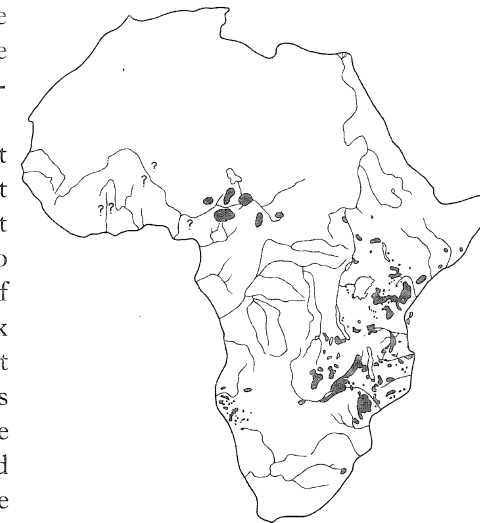
Measurements
head and body
 3.4 (3—3.75) m
height
 1.66 (1.4—1.8) m
tail
 70 cm
weight
 996—1,362 kg

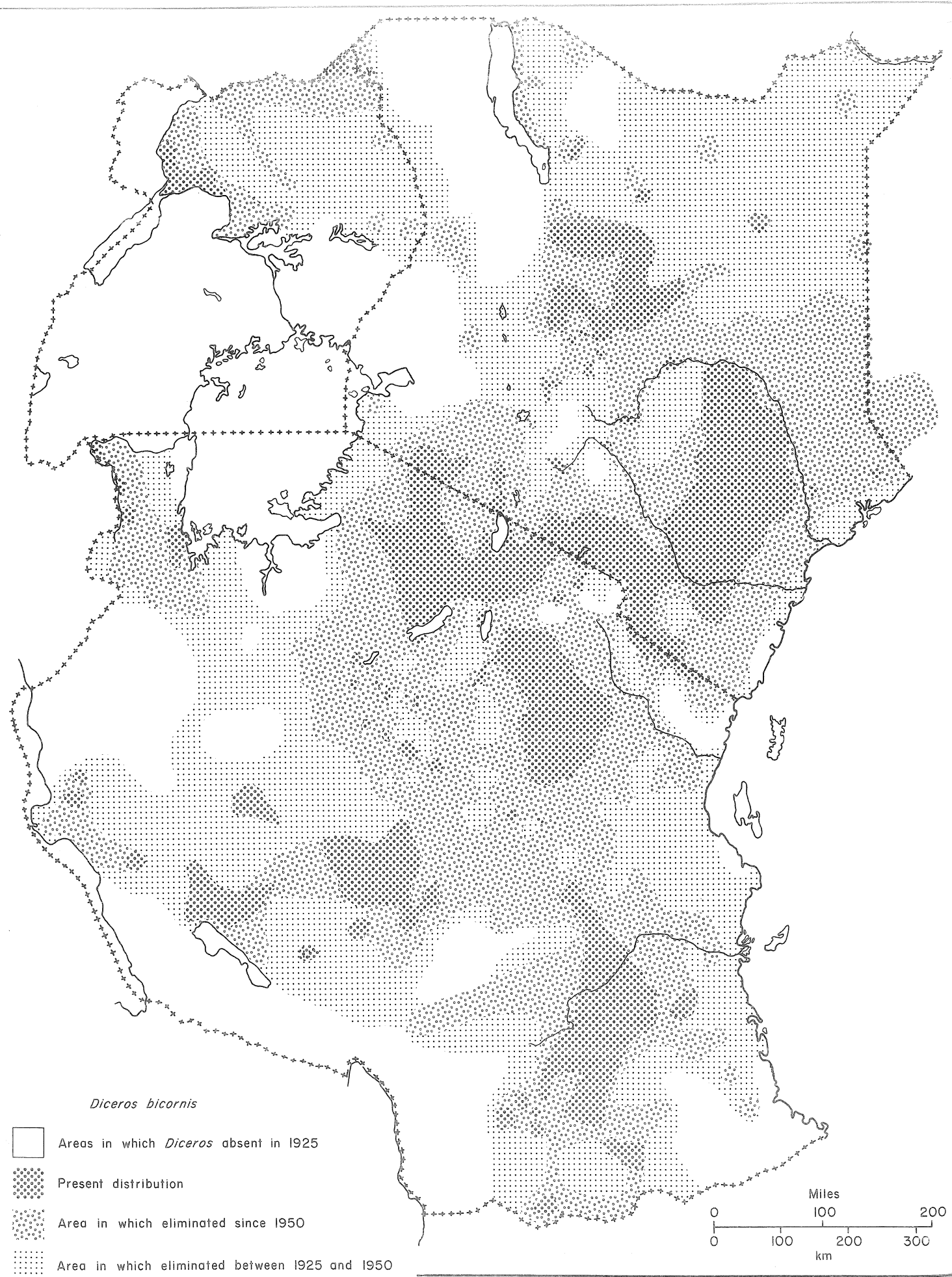
**Black rhinoceros,
Browse rhinoceros
(*Diceros bicornis*)**

This rhinoceros is subject to considerable variation, some of which may represent local genetic traits; animals from the more arid habitats tend to be smaller and the highly variable skull proportions may also tend to show some degree of regional consistency. However, it is doubtful if any racial subdivision is justified.

This species probably ranged over a large part of sub-Saharan Africa at one time and it was found in practically all but the very driest areas of East Africa until relatively recently, commonly at altitudes up to 2,700 metres. It seems to be absent from the hot, humid lowland forest belt from Nigeria to Uganda but small population pockets were reputed to exist in the forests of the Middle Congo and Cameroon (Blancou, 1954). Because it needs to drink regularly it is only found within range of permanent water. Although it disperses into a wider area in the rains, its maximum dry season range is about 25 km from water. On open grassland and in closed canopy areas of the *Brachystegia* woodlands rhinos have always been very scarce or absent, and their favoured habitats are along the edges of thickets and wherever there are extensive areas of short woody growth, the thin regenerating twigs of which provide, together with legumes, their main food, however these may be heavily augmented by grass in some marginal habitats. Where there is a permanent source of water and plenty of shrubs and herbs growing within easy reach, the rhinoceros is capable of becoming a major animal in the ecological community because its diet includes resources which are used by few other animals except elephants. The black rhino was therefore very common and widespread until recently and it is still capable of reaching astonishing densities when protected in suitable habitats. In the Ngorongoro crater twenty-three rhinos live in the 2.6 sq km of Lerai Forest, a grove of *Acacia xanthophloea* trees with thin canopy and continuously regenerating undergrowth which provides the animals with ideal conditions. Of these twenty-three rhinos, Goddard (1967a) never saw seventeen outside this area in three years of intensive study. Pointing out its unique dietary niche and ecological role, Frazer Darling (1960a) considered that this animal might be a key species in the management of indigenous African vegetation.

Some 200 species of food plants from 50 families have been recorded by Goddard (1970b) and some of the commonest foods are dominants in the thicket, hard-pan Acacia and riverine communities that are favourite rhinoceros haunts. Thus *Acacia*, *Commiphora*, *Grewia*, *Cordia*, *Lansea*, *Euphorbia*, *Adenia*, *Sansevieria* and *Aloe* are commonly observed rhino foods. Shenkel (1969) also lists *Aerva persica*, *Bauhinia*, *Blepharis*, *Ehretia titensis*, *Sericomopsis* spp. and *Crotalaria*. In spite of being uncommon, *Caesalpinia trothae* is a favourite food; also green clover, *Trifolium*, is greatly favoured while certain dominant plants such as *Boscia* and *Thylachium* are never eaten at all. Salt may be a factor in the rhino's liking for *Suaeda monoica*, a shrub growing in saline soils. Rhinos are soon regular visitors to the artificial salt licks that have been set up beside many tourist lodges.





The importance of the prehensile upper lip in gathering twigs into the mouth has been mentioned and it is interesting that rhinos on the floor of the Ngorongoro crater, where grass is normally an important food, took to picking up gnu dung for some days when the grass was only 7—8 cm long following a fire. Klingel and Klingel (1966c) suggest that this may have been to correct a mineral deficiency but, more simply, it may have been due to the difficulty the rhinos faced in cropping short grass. As several hundred gnu were in the area, their dung would have answered the rhinos' need for bulk food more effectively than attempting a task for which their mouths are ill-adapted.

Various fallen fruits are readily picked up and the large sausage-like fruit of *Kigelia* are favoured, as are those of various *Acacia* and *Grewia* species. Roots, particularly those of succulents, are occasionally eaten. The horns have been seen to dig them out as well as to break branches above the reach of the mouth. Rhinos have even been seen to balance on the backlegs to reach twigs nearly 3 m off the ground.

Digging for water is not uncommon in rhinos and in the sand of river beds they use their forelegs quite effectively to this end. Water is needed in some quantity as sweating is the principal cooling mechanism of the rhinoceros. Notwithstanding the habit of hanging around waterholes, they generally drink rapidly and finish in less than five minutes. I have followed rhinos over 10 km back to their regular haunts, which they reached in less than three hours with very little feeding on the way. Well-worn tracks, usually shared by a variety of other animals, lead to and from water to wallows. In areas where many rhinos are concentrated there is a maze of subsidiary tracks running parallel to the main ones. In thickets rhinos can become important path-makers for other animals if they use a track often enough but many of the plants such as *Lansea* and *Commiphora* are sufficiently pliant to spring back after the rhino's passage. Following a rhinoceros in such country can sometimes mean crawling on hands and knees for long periods.

Resting and sleeping in mud wallows is common, but the heat of the day is normally spent sleeping under shade, while the most intense feeding periods are in the earlier part of the morning and evening. In areas where they are persecuted they become largely nocturnal. Wallowing in mud or water is a conspicuous habit. During the 1960—61 drought when hundreds of rhinos died of nutritional anaemia (Tremlett, 1961), a high proportion ended up in the shallow waters of the Athi River, where they presumably found some relief from the heat and biting flies. Schenkel and Schenkel (1969) have suggested that wallowing protects the skin from flies as well as conditioning it. As wallows are most commonly used during or after the hottest part of the day, cooling is likely to be the most direct incentive for the individual's behaviour. Incidental effects might include protection from sun and insects, also the blazing of pathways with flakes of scented mud, which are probably valuable identity tokens for the scent-orientated rhinoceros.

Rhinos so frequently pass under or through bushes when they could just as easily have skirted them, that one suspects that scraping and scratching must be a rewarding sensation for the animal; shedding flies and mud flakes could be incidental benefits of this behaviour. As well as using mud wallows, rhinos will roll in fine dust or the ash of burnt trees or branches. They are



often attracted by bush-fires and have even been known to scatter burning logs with their horns. I once found the impression of a rhinoceros that had rolled in ash so perfectly recorded that the animal could be recognized by its scars and creases. Such impressions also show that the depression immediately behind the shoulder may miss being coated in ash or soil. As this spot is the commonest area for "rhino sores" the protective function of mud and ash seems evident.

Exposed areas of skin are very thick and inflexible—the effect is of armour plates. Between these plate units movement demands more flexible and thinner skin and lions attacking rhinos have been seen to seize the throat and chest, after which they can easily unbalance the top-heavy animal and bite the softer underparts.

Rhinoceroses cannot roll across their sharp spines from side to side but lie down with hindquarters resting on one leg and then roll sideways until the spine throws them back. They will generally half rise or even get up and turn round before rolling on the other side. Abrupt rising and a few brisk movements, even interrupting a period of complete immobility or preceding a long sleep, are characteristic of rhinos. A rhino may sleep lying on its brisket, chin or cheek on the ground or it may doze standing with its head hanging. The ears continue to move even when it is asleep.

Rhinos are not slow and can make sharp turns even in the middle of a charge at some 50 km per hour. An alerted rhino tries to focus its ears on a source of alarm and may swing from side to side with the head up and nostrils flaring as it sniffs.

Although eyesight plays an inferior role to hearing and smell, the common claim that rhinos are half blind is misleading. Long-distance vision is of little importance to them but they give every sign of responding to visual stimuli at



close quarters. In some encounters, swinging movements seem to have the character of ritualized head-flagging. Bulls, particularly, raise their fore-quarters in a stiff-legged walk with erect head, in which they turn with some deliberation and posture in profile. It has been suggested that this is in order to see better out of one eye than ineffectively out of two, but head-on vision is functional in spite of a broad muzzle and horns (see drawing). However, myopic the rhinoceros seems to be, it is certainly capable of perceiving the silhouette of a massive neck, head and horns. Bulls tend to meet at wallows and waterholes and encounters are characterized by mutual displays which may or may not develop into sparring matches.

Alarms and threats are accompanied by short snorts but it is evident that snorts probably have shades of meaning for the rhino. A male approaching a female punctuates his slow progress with a series of three or four snorts, pausing momentarily after the first before giving two more in quick succession; the effect is somewhat like morse. When excited they also make a deep wheeze, which has been likened to a man gasping for breath. I have heard a similar call in a captive when approached by his keeper; it may imply pleasurable excitement or it could be an adult modification of the high-pitched noises of very young rhinos at play. These are different to the squealing distress call of the young. During his immobilization and tagging programme, Goddard (1970a) witnessed a calf attract an adult male from over a kilometre away in response to its squealing. Another very high-pitched call is uttered by mothers calling their young. When threatening or fighting one another, rhinos grunt loudly or else scream.

