Zoo Biology 1:251–261 (1982)

The Skulls of Asian Rhinoceroses: Wild and Captive

Colin P. Groves

Department of Prehistory and Anthropology, Australian National University, Canberra, Australian Capital Territory

Skulls of identified individual Asian rhinos from zoos were compared with wild-shot skulls of the same species to detect any captivity-induced changes. *Rhinoceros unicornis* and *Rhinoceros sondaicus* are typically stunted by captivity, while *Dicerorhinus sumatrensis* is not and may even be affected in the opposite manner, becoming giant. The consequences for husbandry are discussed.

Key words: ***Rhinoceros unicornis, Rhinoceros sondaicus, Dicerorhinus sumatrensis,* growth, skull**

INTRODUCTION

Asian rhinos have always been successfully kept in captivity. Even in relatively poor caging they live for many years, and given the right facilities they will breed—as has become clear (in the case of *Rhinoceros unicornis*) over the last twenty years—not too late, one hopes, to perpetuate the species in captivity.

As the remains, usually the skull only, of a number of Asian rhinos that have died in captivity in the last century and a half have been preserved in collections, it seems worthwhile to compare them with the skulls of wild-shot specimens. This in turn will involve elucidation of sexual dimorphism, which has not been attempted before; although, as will be seen, the evidence is not all it might be, I have measured every specimen in every collection known to me, and the evidence is unlikely to improve dramatically in the near future.

MATERIALS AND METHODS

The collections of wild-shot Asian rhinos have been listed in previous publications [Groves, 1967; Groves and Guérin, 1980]; several additional specimens have been seen since these publications, as will be described below.

On each skull a standard schedule of measurements was taken as follows: occipitonasal length, basal length, toothrow length (maxillary), bizygomatic breadth, nasal breadth, occipital breadth (or mastoid breadth in the case of the genus *Rhinoc-*

Received for publication July 16, 1982; accepted August 14, 1982.

Address reprint requests to Colin P. Groves, Department of Prehistory and Anthropology, The Australian National University, PO Box 4, Canberra, ACT, Australia 2600.

0733-3188/82/0103-0251$03.50

eros), and occipital height. These, as well as a few others not considered here, are described in the above-listed publications. Basal length is here used in preference to condylobasal length because of damage to the condyles in some of the wild-shot specimens.

In each species of rhino, the nasal horn is stouter and heavier in the male than in the female [Groves, 1971]. It would seem, therefore, a good working hypothesis that the breadth of the nasal bones would be greater in males than in females; such indeed was the finding of Pocock [1946], while in an African species the difference was found to be so marked that skulls could be sexed using this character alone [Groves, 1975]. For each of the three Asian species (in one case taking subspecific size groups separately) the nasal breadths were plotted (Fig. 1), and where possible unsexed skulls were thereby allocated. The skulls of the specimens from captivity could now be compared with wild-shot skulls of the same taxon, age, and sex.

The histories of the captive rhinos whose preserved skulls were studied are given by Reynolds [1960]. It is unfortunate that so few specimens, out of the large number listed by Reynolds, appear to have been preserved after death: Material of great importance, for studies of animal husbandry as well as taxonomy, has been irretrievably lost. I would like to urge zoo personnel to arrange for the preservation of the skeleton, at the very least, of every specimen of all rare species dying in their institutions.

RESULTS

Indian Rhinoceros, *Rhinoceros unicornis*

Data on this species have not previously been published by the present author. Guérin [1981] gives some measurements but, with so few sexed specimens, could

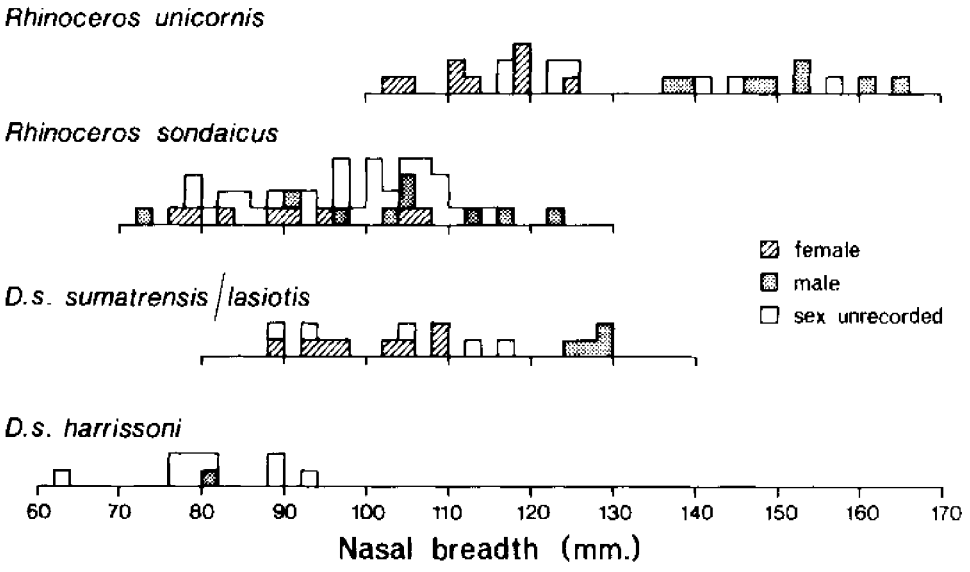

Fig. 1. Sexual dimorphism in skulls of Asian rhinos: distribution of nasal breadth measurements, showing bimodality in *R unicornis* and the larger subspecies of *D sumatrensis*, absence of bimodality in *R sondaicus* and its probable absence in *D s harrissoni*.

only record a negative verdict as far as sexual dimorphism was concerned. The collections of this species, are, in fact, even more slender than those of the other two Asian species—an irony, considering that at the present time it is by far the most numerous—or shall we say, the least endangered—of the three.

Figure 1 shows a bimodal distribution of nasal breadth in this species; skulls of known sex fit into the two respective peaks, with a cutoff point at about 130 mm. If all below this point are female, and all above it are male, then we derive statistics as in Table 1: The 2 SD (95%) limits for nasal breadth do not overlap, and in all other skull measurements males are significantly larger than females ($P < .05 > .01$ for occipitonasal length). The tooth measurements, however, are not significantly different: The female mean is in fact larger than the male, but a t-test shows this to be nonsignificant.

Rather few adult wild-shot specimens are localized; one male and three females are from Assam, one male and four females from Nepal; one female is from Kasmanda, Uttar Pradesh; one male is said to be from Burma. Comparisons on these limited data do not suggest consistent differences between the geographical samples, so all samples are combined, with the exception of the Burma skull, which falls outside the range of other males and has been excluded from the pooled sample.

The skulls of four males and two females from captivity are available in collections (Table 1). They are briefly characterised below.

Owen's rhino. The first rhinoceros in the London Zoo was an Indian rhino, which arrived in May 1834, estimated to be 4 years old, and died in September 1849. In this smug, cantankerous, and invulnerable warrior Sir Richard Own recognised a kindred spirit; he called him "my ponderous and dignified old friend, whose remains will furnish forth an immortal monograph." They did, too [Owen, 1862]. The skeleton, BM 51.11.10.2, is mounted in the Osteology Room of the British Museum (Natural History). It is small for its species ($P < .01$) though not in fact below the minimum for wild males, unusually broad across the zygomata and with a high occipital crest. The zygomata are in fact broader than in any wild specimen, due apparently to an extreme bilateral rugosity.

Felix. This rhino was presented by the King of Nepal to the London Zoo in December 1924, when it was about 3 years old. It died of tuberculosis in November 1941. The skull was at first placed in the Royal College of Surgeons [Pocock, 1946]; it is now BM 1950.10.18.4. The skull is remarkably similar to that of Owen's rhino, with the same high occiput, zygomatic broadening and rugosity, but it is broader across the mastoids.

Hush. The King of Nepal presented a pair of year-old rhinos to Whipsnade Zoo on 29 April 1933. Hash, the female, died in 1938; her remains are not preserved. The male, Hush, lived until 15 March 1945. Like that of his contemporary Felix, his skull was at first placed in the Royal College of Surgeons; it is now BM 1951.10.8.4. It is much larger than those of the previous two specimens, of precisely average size, in fact, for a male of the species. The zygomata are broader than average, but without the extreme development of Owen's rhino and Felix. The mastoids are more pneumatised instead, and the bimastoid breadth is the greatest seen in the species.

Mohan. Caught in Assam, Mohan arrived "half-grown" in Whipsnade Zoo on 7 August 1947, and died on 7 March 1961, having sired several calves on his mate, Mohini, who arrived in 1952 (and is still alive). His skull, BM 1961.5.10.1, is by far the smallest adult skull, of either sex, of this species ($P < .001$ compared to wild males); it is very broad with zygomatic rugosity, and has a high occiput.

TABLE 1. Skull measurements of *Rhinoceros unicornis:* wild and zoo specimens

	Wild males			Zoo males				Wild females			Zoo females	
	Mean	SD	n	Owen's	Felix	Hush	Mohan	Mean	SD	n	Mullick's	Barrackpore
Occipitonasal length	610.7	14.61	6	583	583	10	538	590.4	18.64	10	564	557
Basal length	650.2	12.45	6	(639)	665	647	593	635.4	16.76	9	—	590
Zygomatic breadth	392.8	8.64	6	410	414	405	374	364.6	8.55	11	346	358
Nasal breadth	149.8	9.81	6	152	160	152	138	118.0	5.31	11	105	103
Mastoid breadth	302.4	6.66	5	295	313	328	277	284.6	12.88	11	260	284
Occipital height	195.5	14.28	6	210	204	210	190	185.8	13.37	8	174	175

TABLE 2. Skull measurements of *Rhinoceros sondaicus:* wild and zoo specimens

	Wild males			Zoo male	Wild females		
	Mean	SD	n	Adelaide rhino	Mean	SD	n
Occipital length	509.1	14.37	9	437	532.9	19.20	7
Basal length	562.6	20.67	8	503	577.5	17.82	6
Zygomatic breadth	344.2	10.20	9	318	348.7	13.06	9
Nasal breadth	102.7	13.52	9		88.1	12.56	8
Mastoid breadth	288.6	10.57	8	260	279.9	12.00	8
Occipital height	152.5	8.46	8	192	159.9	9.32	7

Rajah Mullick's. No details are recorded of this rhino during life, except that it was a female that lived for some time in the private menagerie of Rajah Mullick in Bengal in the last century. The skull is ZSI 19240 [see Groves and Chakraborty, in press]. It is smaller than any wild female ($P < .01$) but not abnormally proportioned.

Barrackpore. A female that lived in Barrackpore Zoo, Calcutta, for an incredible 45 or 47 years [Reynolds, 1960]; skull now ZSI 19262. It is very small for its species ($P < .001$), smaller than Mullick's, and broader across both zygomata and mastoids.

It is remarkable how similarly each of these animals was changed from the normal, wild morphology. With the sole exception of Hush, all are notable for their small size, great zygomatic and mastoid breadth, and great occipital height, which could perhaps be explained by being fed from a trough on the floor. Most affected is Mohan, despite being the one who, one would think, had all the advantages: already said to be "half-grown" at capture, living in a garden zoo in the postwar era of scientific animal husbandry. Like so many captive Indian rhinos he spent long hours rubbing his horn down on the horizontal bars of his paddock, until it became a shiny flat disc; he would also rub his cheek against the bars and walls. This latter behaviour could perhaps account for the rugosity of the zygomatic arches; alternatively, it could be due to excessive use of the masseters, perhaps to cope with some unaccustomed dietary staple. His small size is curious. He is most unlikely to have been genetically small: It is surely no coincidence that all but one of the captive Indian rhinos failed to grow to the minimum (skull) size of wild members of their species.

The other noticeable result of these comparisons is that the specimen least affected by captivity was Mohan's predecessor in the same zoo, who was apparently younger at capture. What was the great difference in husbandry that kept Hush pristine yet reduced Mohan to a runt?

Javan Rhinoceros, *Rhinoceros sondaicus*

Guérin [1981], on the basis of rather more specimens than for *R unicornis*, found himself able to confirm the hypothesis of Hoogerwerf [1970] that the female of this species is actually larger than the male: a remarkable conclusion which demands the closest scrutiny. About one-third of the available adult or nearly adult skulls are sexed; there is a large overlap in nasal breadth although the distribution as a whole is weakly bimodal (Fig. 1.) (This is a little surprising, as the male has a well-developed horn, the female little or none [Groves, 1978]). There is therefore no possibility of sexing the rest of the skulls, and comparisons must be between those whose sex is recorded. As the subspecies, which differ feebly in any case, do not differ in the characters used in the tables, they are combined here in order to enlarge the sample: At least one skull of each sex from Java, Sumatra, Malaya, and Bengal is represented. The result (Table 2) confirms that of Guérin: Females are larger than males ($P < .05 > .01$).

The only skull of a captive Javan rhino which appears to have been preserved is that of the Adelaide Zoo rhino, which spent its life masquerading as an Indian rhino; but its skull characteristics, as well as the external features (its mounted skin is on exhibition in the South Australian Museum), confirm that it was *R sondaicus* [Finlayson, 1950]. It arrived in Adelaide in 1886, at an estimated 18 months of age, and lived until 1907. Finlayson reports that the mounted skin is only 4 ft 5 in (135 cm) high, and that the skull is the smallest known for the species ($P < .001$, cf wild

males). I confirm the latter (Table 2): It is remarkably small, only 86% of the mean skull length for wild males (compared to Mohan at 88% of the mean skull length for males of *R unicornis*). Like captive Indian rhinos the skull is relatively broad; the occiput is extremely high.

Sumatran Rhinoceros, *Dicerorhinus sumatrensis*

The previous taxonomic revision of this species [Groves, 1967] noted that "if (any sexual differences) exist, they do not obscure subspecific ones." There are now enough skull data amassed to test whether such differences do in fact exist. It appears (Fig. 1) that, as in *R unicornis*, there is a clear division between males and females in nasal breadth in the large mainland and Sumatran forms, but not in the diminutive Bornean race *harrissoni* in which the single skull of known sex is a male whose nasal breadth falls into the lower half of the distribution. Skulls of the large races can thus be allocated by sex, but those of *harrissoni* cannot. The resulting statistics are given in Table 4.

The difference in size between males and females of *D s sumatrensis* is very marked: wild males are much larger than females ($P < .01$ for occipitonasal length), skull length in females being only 94% that of males with the other measurements (nasal breadth excepted) in proportion. Males are slightly more variable than females (coefficient of variation [CV] for skull length, 3.6 vs 2.7), but the sample is smaller. The combined sample of *D s harrissoni* has a CV for skull length of 4.3, suggesting that there is in fact some sexual dimorphism to be disentangled, but that there would be a considerable overlap between males and females. For *D s lasiotis* there are unfortunately only male skulls available from the wild: Both are smaller than the *sumatrensis* average, although one is not quite mature so might have been a little larger had it lived, and it is likely that the two races are about the same size. The broad high occiput of *lasiotis* is still a valid subspecific character after the sexual dimorphism has been disentangled; the difference in breadth, at least, would seem to increase clinally through Tenasserim via Pegu.

Every one of the zoo specimens whose skulls have been preserved is female. They are as follows:

Jenny. Sent by the Austrian consul in Singapore to Schönnbrunn Zoo, Vienna; she arrived in October 1900 and lived until November 1908. The skull, NMW 3082, is not quite mature (stage 5 of Groves [1967]), but at this age full growth has nearly

TABLE 3. Toothrow lengths of genus *Rhinoceros* (sexes combined): wild and zoo specimens

R unicornis		
Wild	Mean	254.2, SD 12.94 (18)
	Minimum	220
Zoo	Owen's	269
	Felix	268
	Hush	270
	Mohan	241
	Mullick's	214
	Barrackpore	233
R sondaicus		
Wild	Mean	225.6, SD 8.54 (15)
	Minimum	213
Zoo	Adelaide rhino	203

TABLE 4. Skull measurements of *Dicerorhinus sumatrensis:* wild and zoo specimens

	Wild females			Zoo females						Wild males		
	Mean	SD	n	Jenny	Mary	Bettina	Bogor	Subur	*niger*	Mean	SD	n
D s sumatrensis												
Occipitonasal length	518.1	13.43	9	516.5	550	474	486	507	515	551.0	20.52	5
Basal length	502.1	14.68	9	498	535	453	468	457	489	520.6	15.08	5
Zygomatic breadth	283.6	10.03	9	287	297.5	278	256	278	298	298.8	11.97	5
Nasal breadth	98.9	7.28	8	102	107.5	89	83	108	108	118.4	13.81	5
Occiput breadth	122.9	7.96	9	114	123	122	115	118	114	129.6	4.04	5
Occiput height	116.8	5.19	9	109.5	115	103	87	108	117	119.5	4.24	5

	Wild males		Zoo female
	(1)	(2)	Begum
D s lasiotis			
Occipitonasal length	528	525	596
Basal length	513	498	—
Zygomatic breadth	293	295	325
Nasal breadth	112	87[a]	119
Occiput breadth	147	154	167
Occiput height	126	124	130

Other populations	*D s harrissoni* (both sexes)			*D s sumatrensis* ≦ *lasiotis*		
					Pegu females	
	Mean	SD	n	Tenasserim male	(1)	(2)
Occipitonasal length	471.8	20.09	9	542	530	508
Basal length	477.8	13.52	9	—	511	506
Zygomatic breadth	260.8	9.51	9	282	282	—
Nasal breadth	80.8	4.13	8	—	110	105
Occiput breadth	118.7	8.58	10	113	141	141
Occiput height	112.4	3.34	8	127	121	136

[a]Not completely adult.

been achieved: this sets a minimum of eight years for achievement of full size, though we know only that she was very small when she arrived. In general, Jenny's skull is that of a normal specimen; perhaps her occiput is rather narrow, but this could be within normal limits.

Mary. Again procured by the Austrian consul in Singapore (and so doubtless from Malaya), and sent to Schönnbrunn, where she lived from July 1902 until the summer of 1919. Her skull, NMW 5026, is that of an exceptionally large female ($P < .01$) with proportionately a narrow occiput. Both Mary and Jenny were apparently kept in a dry enclosure with no pool [Van Strien, 1974], and perhaps because of this lost all their body hair. The narrowness of the occiput in both of them may be coincidence, or may indicate some defect of their captive conditions, such as positioning of their feeding troughs.

Bettina. In 1959, a Danish/Indonesian joint expedition to Pakan Baru, on the Little Siak River in Riau Province, Sumatra, captured nine females and one male of this species [Andersen, 1961], of which only three females were brought alive out of Sumatra: the male escaped, two females died (their remains are in the Museum Zoologici Bogoriense), and the others were released. The three that were retained went to Basel, Copenhagen, and Bogor, respectively. Bettina was the Basel specimen; she was not in fact wild-caught but was the pet of a planter. She was unfortunately sickly from the very beginning, and died in 1961 of pernicious anaemia. Her skull, NMB 10259, is by far the smallest of this race in any collection, being the size of an average *D s harrissoni,* but is broader and does not have the upright nuchal surface of the latter, and is very light and poorly ossified.

Bogor rhino. The second of the three rhinos brought out of Sumatra in 1959 was presented to the Indonesian government. It was kept in a private zoo in the grounds of the late President Sukarno's residence in Bogor, where it died on 8 August 1961. Its skull, MZB 8440, is of an animal not quite mature (between stages 5 and 6); it is the next smallest skull of this subspecies in collections—after Bettina's—even taking its marginal immaturity into account ($P < .01$ compared to wild females). It is not possible to say whether it was a naturally small specimen or stunted by its two years in (rather cramped) captivity; certainly the skull is not clearly pathological as is Bettina's.

Subur. This was the third of the 1959 rhinos; she lived in Copenhagen zoo until February 1972. Early photos of her [Andersen, 1961] show an animal evidently still immature. Her skull, UZMK 3791, nonetheless shows signs of senility; the only pathology is the rather crowded condition of the cheekteeth. It is a perfectly normal specimen of the subspecies, if somewhat on the small side ($P < .05$).

Type of *Ceratorhinus niger*. This female, shipped to the London Zoo by Jamrach from Malacca, arrived on 21 August 1872 and died exactly one calendar month later. The skull, BM 72.12.31.1, is that of an extremely aged animal, quite normal in every way, as indeed one would expect.

Begum. This famous female rhino was captured near Chittagong (in the far southeast of present-day Bangladesh) in January 1868, but was not sent to the London Zoo until February 1872, at which time Sclater [1872] estimated her age as "at least six years"; and the lifelike painting illustrating Sclater's paper does seem to show a nearly mature specimen. On the arrival of the female listed above as a type of *Ceratorhinus niger,* there was a flurry of excitement among taxonomists; Sclater [1872] identified it as the true *sumatrensis* and described Begum as a new species,

Rhinoceros lasiotis, while Gray [1873] insisted that Begum was the true *sumatrensis* and the aged female described above represented a new species, *Ceratorhinus niger.* Most of these opinions were based on the differences in the color and texture of the hair covering the body and fringing the ears. Begum proceeded to earn the longevity record for this species in captivity; she died in August 1900. Her obituary [Thomas, 1901] reports that her appearance had changed during the course of her life, and that the ill-natured disagreements of nearly 30 years before had in effect been based on differences between youthful and aged animals! The skull, BM 1.1.22.1, is extraordinary in its huge size: it is by 20 mm (occipitonasal length) the largest of the species in any collection. Thomas noted its great size, and Sclater found that even on its arrival in London it was already larger than the aged female described above. As Table 4 shows, wild specimens from the general area, referable to the subspecies *D s lasiotis,* do not differ in overall size from *D s sumatrensis* although proportionately—broad high occiput, very large teeth [Groves, 1967]—like the skull of Begum, so for occipitonasal length Begum's skull may be compared to the fair-sized sample of the nominate race. The difference is highly significant ($t = 17.40$, at 8 degrees of freedom; $P < .001$), and the enormous size seems most likely to be a result of exceptionally favorable conditions in the animal's four-year initial captivity in Chittagong, in the vicinity of her homeland.

Somewhat in contrast to *R unicornis,* therefore, the *D sumatrensis* specimens appear to have been affected by captivity in diverse ways. Eliminating the pathologically dwarfed Bettina and the already aged type of *niger,* we have two specimens whose growth was evidently enhanced by captive conditions (Mary and Begum, the latter extraordinarily so), two apparently unaffected in this way (Jenny and Subur), and only one probably adversely affected (the Bogor rhino).

A further noteworthy point is the sex ratio of captive specimens. As noted above, all those whose remains have been preserved are female. Van Strien [1974] points out that in the list compiled by Reynolds [1960] there are 22 females and only nine males. The Danish/Indonesian expedition to Riau Province caught nine females and only one male. But of wild-collected specimens (all ages) in collections whose sexes is known, there are 15 females and 14 males; the total among the wild-collected specimens, arrived at by allocation as described above, are 18 females and 15 males. The sex ratio of wild-collected specimens thus seems nearly equal; that of specimens in captivity, very unbalanced. Kurt [1970] notes that rhinos killed in Aceh are trapped by spear-falls placed over regularly used trails; and that this method catches mostly females which have smaller home ranges and travel by regular paths, whereas males range much more widely and visit a given area only infrequently. The 1959 capture expedition used stockade traps erected over regular paths, and therefore caught mostly females. We do not know how Sumatran rhinos were caught for zoos in former times, but it seems likely that at least those supplied by dealers, such as Jamrach, would have been caught by this maximum-gain-minimum-effort method.

CONCLUSIONS

Typical "captive morphology" in large mammals was first described by Hollister [1917] for lions, and attributed to the affect of muscle disuse. Groves [1966] drew attention to it in Equidae, where it is certainly correlated with dental and periodontal pathology; no such pathology is detectable in the Asian rhinos, however. The influ-

ence of diet on growth is well documented (for example, Verme and Ogoya [1980]); that nutrition affects final adult size is less clear, but there does seem to be such an effect in some species at least [Robinette et al, 1973].

This study can reach no firm conclusions, but it is strongly implied that Asian rhinos can be affected in unexpected ways by captivity. Particularly unlooked-for is the finding that, while nearly all Indian rhinos from zoos are unusually small, the most runtlike was Whipsnade's Mohan, the very one in whose case an effort was made to provide a more naturalistic setting. It is evident that more attention must be given to what are the essential elements of the "natural habitat," and how best to reproduce these in captivity. Especially so is this the case for the Javan rhino: Successful protection over the last 15 years in Ujung Kulon, Indonesia, has apparently raised their density to carrying capacity level [Anon, 1981], and it is not unlikely that a few will be arriving in zoos at some time in the future. It is vital that optimum conditions, for both reproduction and longevity, should be assured.

As for the Sumatran rhino, matters may be a little different. Only one specimen seems to have been stunted by captivity; and the opposite reaction is evidently not detrimental—Begum's longevity suggests that her large size did her no harm at all, and Mary, also "over-sized," lived 17 years in captivity. It is also worth pointing out that this is the species that was first bred in captivity [Van Strien, 1974].

ACKNOWLEDGMENTS

I thank the curators of collections for access to and assistance with material in their charge: Dr. P. Aitken, Dr. K. Bauer, Dr. B. Biswas, Bp. B. Boeadi, Dr. F.W. Braestrup, Dr. J. Clutton-Brock, Dr. U. Rahm; and Bp. B. Boeadi and Dr. E.M. Lang for helpful discussions.

REFERENCES

Andersen, S. Sumatran rhinoceros at Copenhagen Zoo. INTERNATIONAL ZOO YEARBOOK 3:56–7, 1961.

Anon. SSC in New Delhi. ORYX 16:14–15, 1981.

Finlayson, H.H. Notes on the cranial and dental characters of a specimen of *Rhinoceros sondaicus* Desm. PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON 120:151–4, 1950.

Gray, J.E. On the dentition of rhinoceroses, and on the characters afforded by their skulls. ANNALS AND MAGAZINE OF NATURAL HISTORY 11(4):356–63, 1873.

Groves, C.P. Skull-changes due to captivity in certain Equidae. ZEITSCHRIFT FUR SÄUGETIERKUNDE 31:44–6, 1966.

Groves, C.P. On the rhinoceroses of south-east Asia. SÄUGETIERKUNDLICHE MITTEILUNGEN 15:221–37, 1967.

Groves, C.P. Species characters in rhinoceros horns. ZEITSCHRIFT FUR SÄUGETIERKUNDE 36:238–52, 1971.

Groves, C.P. Taxonomic notes on the white rhinoceros *Ceratotherium simum* (Burchell, 1817). SÄUGETIERKUNDLICHE MITTEILUNGEN 23:200–12, 1975.

Groves, C.P.; Chakraborty, S. The Calcutta Collection of Asian rhinos. RECORDS OF THE ZOOLOGICAL SURVEY IN INDIA (in press).

Groves, C.P.; Guérin, C. Le *Rhinoceros sondaicus annamiticus* (Mammalia, Perissodactyla) d'Indochine: distinction taxinomique et anatomique, relations phyletiques. GEOBIOS 13:199–208, 1980.

Guérin, C. Les Rhinocéros (Mammalia, Perissodactyla) du Miocene terminal au Pléistocène supérieur en Europe occidentale; comparaison avec les espèces actuelles. DOCUMENTS DE LABORATORIE DE GEOLOGIE LYON 79:1–421, 1981.

Hollister, N. Some effects of environment and habit on captive lions. PROCEEDINGS OF THE US NATIONAL MUSEUM 53:177–93, 1917.

Hoogerwerf, A. UDJUNG KULON. Leiden, E.J. Brill, 1970.

Kurt, F. Final report to IUCN/SCC and WWF International of Project 596 LEUSER RESERVE (Sumatra) 1970.

Owen, R. On the anatomy of the Indian rhinoceros (*Rh. unicornis*). TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON 4:31–58,

1962.

Pocock, R.I. A sexual difference in the skulls of Asiatic rhinoceroses. PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON 115:319–22, 1946.

Reynolds, R.J. Asian rhinos in captivity. INTERNATIONAL ZOO YEARBOOK 2:27–42, 1960.

Robinette, W.L.; Baer, C.H.; Pillmore, R.E.; Knittle, C.E. Effects of nutritional change on captive mule deer. JOURNAL OF WILDLIFE MANAGEMENT 37:312–326, 1973.

Sclater, P.L. Report on the additions to the Society's menagerie during the months of June, July, August and September 1872. PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON 1872:789–95.

Thomas, O. Notes on the type specimen of *Rhinoceros lasiotis* Sclater with remarks on the generic position of living species of Rhinoceros. PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON 1901:154–8, 1901.

Van Strien, N.J. *Dicerorhinus sumatrensis* (Fisher), the Sumatran or two-horned Asiatic rhinoceros. MEDEDELINGEN VAN LANDBOUWHOGESCHOOL WAGENINGEN 74:16, 1974.

Verme, L.J.; Ogoya, J.J. Effects of diet on growth and lipogenesis in deer fawns. JOURNAL OF WILDLIFE MANAGEMENT 44:315–324, 1980.