Pleistocene Rhinocerotidae of W. Europe with reference to the recent two-horned species of Africa and S.E. Asia

H. Loose

Palaeontology is too often odontology of necessity, the dentition being the most resistant part of the skeleton. When, as in the genus *Dicerorhinus,* the dentition can be a source of mistaken identity, we must look for species determination based on complete skulls as referents. This leads to problems of ecology when seen in combination with the fluctuating Pleistocene vegetation belts. Some recent species are included to show similarities and dissimilarities within the group.

H. Loose, Rijksmuseum van Geologie en Mineralogie, Hooglandse Kerkgracht 17, Leiden, the Netherlands.

Introduction

Among the fast disappearing large land animals the most threatened are to be found among the Rhinocerotidae.

Today they are represented by the one-horned genus *Rhinoceros* L., the two-horned genus *Dicerorhinus* Gloger (both in S.E. Asia) and the African genera *Diceros* Gray and *Ceratotherium* Gray.

We are concerned here only with the two-horned group, more specifically the Dicerorhininae of the Pleistocene of W. Europe *(Dicerorhinus* Gloger and *Coelodonta* Bronn). This choice was dictated by the need for a re-evaluation of this group. *Dicerorhinus sumatrensis* (Fischer) from Burma, Malaya, Sumatra and Borneo is included as the only living representative; *Dicerorhinus megarhinus* (de Christ.) and other Pliocene species are mentioned to place the complicated nomenclature in its historical context. Other Pleistocene Dicerorhininae of Eurasia, the Near East and (perhaps) Africa are mentioned briefly to indicate the former range of the group. The recent African genera are used as an introduction mainly to show what cannot and what can be inferred from the measurements first used by Zeuner (1934).

The objective of this study is to separate the W. European Pleistocene species, using these measurements, a general description of the skull, especially of the otic region and (if possible) of the mandibular symphysis. Also attention has been given to their ecological niches. Some speculations about the possible origin of the group and putative evolutionary relations within the group have been added.

This study is biological in essence. The general remarks on vertebrate palaeontology have been inserted for two reasons. Neontologists are usually woefully ignorant of the facts of life (and death) that restrict palaeontology. More important, formulating the factors that serve as a boundary for any attempt at palaeobiology helps as a constant warning to stay within one's own limitations.

Large concentrations of fossil vertebrates are (with a few exceptions) thanatocoenoses, graveyards for material from different ecological niches that has been transported by water or predators to this final rest for some length of time.

The first part to drop off during transport by water is the mandible. Usually the cranium is next. Soon decomposition of the bowels reaches the stage where the cadaver loses buoyancy, sinks to the bottom and slowly breaks up as it is dragged by the current over sand or gravel. In this process the ribs, the long bones of the extremities and the pelvic bones are reduced to fragments.

A complete skeleton means instantaneous death and instantaneous conservation in situ, perhaps by volcanic ash that has not been disturbed by rain or a changed watercourse. This would truly be an exceptional case. In palaeontology a 'complete' skeleton means an almost complete skeleton: quite a few parts have been lost or irreparably smashed during transport, however short.

After the material has been covered by sediment, the fragmentation and crushing continues, by pressure of younger sediments or by reworking of the sediment by a river, flash floods, rain or other erosive agents. Only the most resistant parts of the skeleton survive this treatment. The result is that a palaeontologist usually writes about dentition, with a few metacarpals and -tarsals thrown in. The stories about palaeontologists discarding skulls after smashing them to extract the teeth as the only important part can be dismissed as slander. Palaeontology is too

often odontology simply because nothing else is left.

When (as in the Pleistocene Dicerorhininae) it is difficult to assign separate molars with certainty to a species, the only possibility left is comparison with a complete dentition in a complete (or at least identifiable) cranium. To do so, we need a better understanding of the systematical differences between the crania of these species.

At present, species identification on an osteological basis (long bones, hand and foot) is difficult if not illusory. Large bones (and teeth!) of *Dicerorhinus etruscus* (Falc.) have been and still are described as *Dicerorhinus kirchbergensis* (Jäger) because of the persisting notion that the latter species was larger (Bernsen 1927, p. 46, 104, Guérin 1974). This notion is founded mostly on the larger molars of *Dicerorhinus kirchbergensis:* that an animal with larger molars surely must be larger, is a 'truth' held to be self-evident by too many palaeontologists.

METHOD

The skull of the higher vertebrates, being an intricate three-dimensional body, is not exactly an object for unequivocal and precise description unless accompanied by a wealth of illustrations. By using the method of F. Zeuner (1934) of measuring certain angles in the median sagittal plane (m.s.p.), we get a simplified two-dimensional picture. Supplemented by a short description of the cranium and other parts (e.g. mandible), this yields in most cases a usable definition.

It cannot be stressed enough, that the angles used by Zeuner, the basal length of the cranium and the incision in the occipital crest, all apply only to the m.s.p. It is impossible to measure them from a photograph of the cranium in the norma lateralis, because palate, basion, opisthion are not visible.
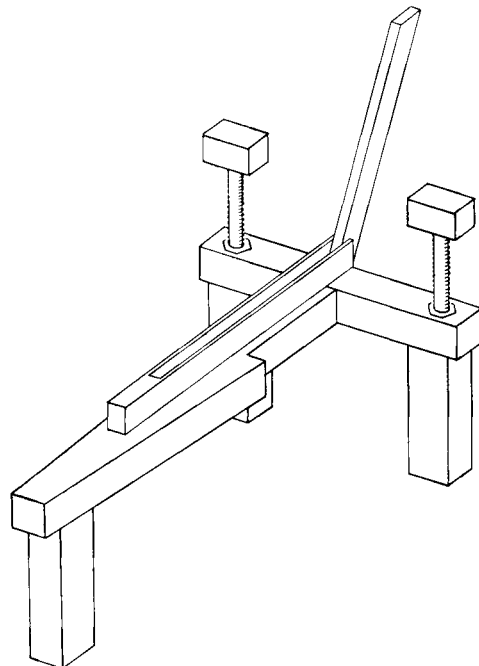

Fig. 1. Tripod with measuring device.

I have used a tripod (fig. 1). The screws supporting the occiput can be adjusted until the palate is parallel with the long arm of the cross and the median sagittal plane bisects the long arm of the tripod at an angle of 90°. If lower and upper side of this cross are planparallel, it is now possible to take all measurements involving the palate by holding one arm of a bevel against either upper or lower side of the cross.

A mean value of 3 - 4 readings was taken as final. If the range was larger than 3°, this set of measurements was discarded. In some cases approximative values are given. A value of ca. 90 means that although no accurate measurements were possible, the value was about 90, with upper and lower limits of 93 and 87 respectively, in other words: 90 ± 3.

In the following definitions the m.s.p. has been omitted, to keep them as simple as possible.

l   basal length (basion-rhinion) (fig. 2)
st   incision in the occipital crest
o   angle between opisthion + occipital crest and parietals (fig. 3)
i   angle between hindmost point of occiput + occipital crest and parietals
n   angle between parietals and tangent of hornbases
p   angle determined by a and b (b = aboral extension of palate; a = perpendicular from opisthion to b).
po angle between opisthocranion + opisthion and palate (aborally extended)
y   angle between opisthion + basion and parietals
x   x = m — o
z   minimum width between cristae temporales
l, st, z in cm; the others in degrees
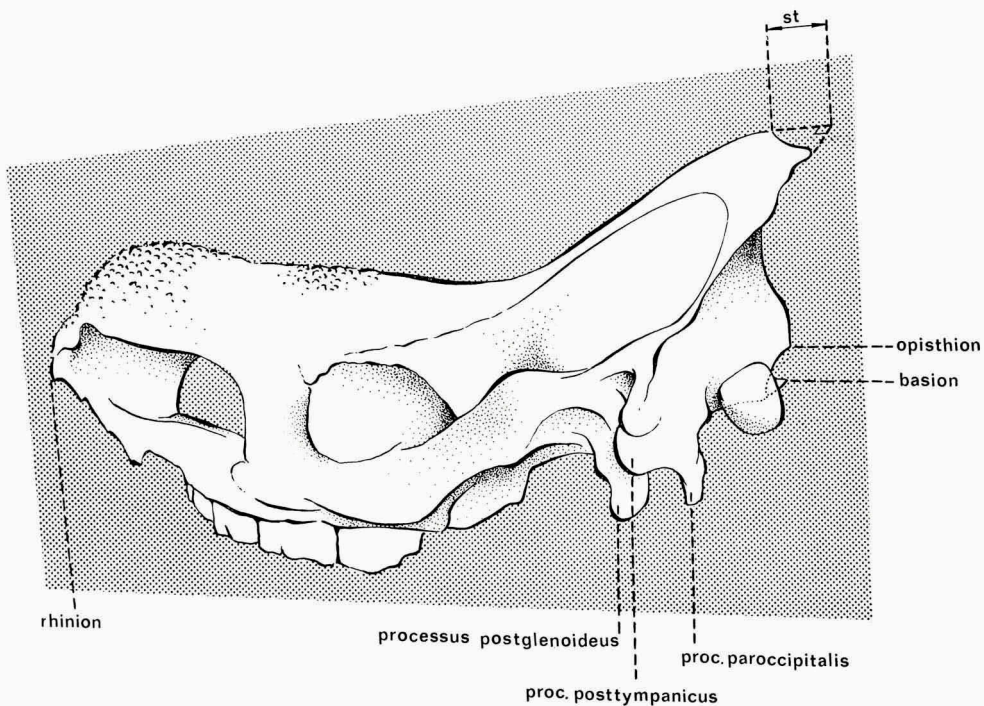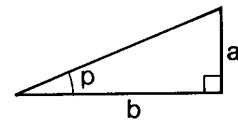
Fig. 2. Rhinoceros-skull bisected in the median sagittal plane (dark background).
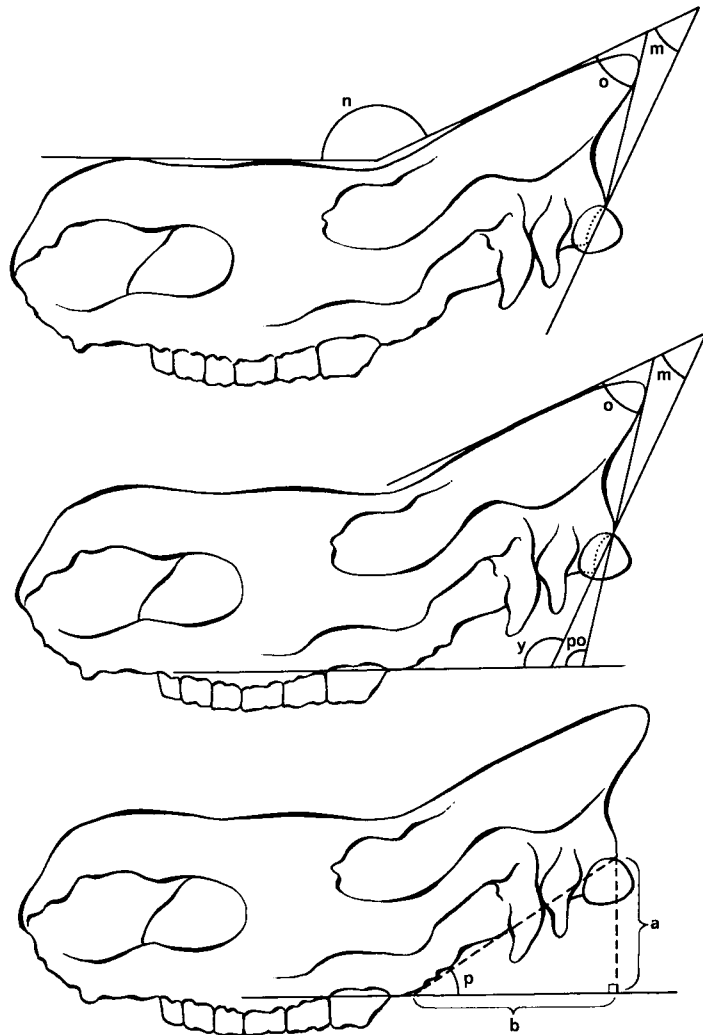
Fig. 3. The angles used by Zeuner.

Problems of dentition are not discussed unless absolutely necessary. The emphasis is on the morphology of the skull, trying
1. to establish clearcut definitions for a number of species (or subspecies)
2. to show the relations between morphology and ecology
3. to propose some views on migrations of *Dicerorhinus*.
Complete lists of synonyms for all species are not given. Only synonyms necessary for strict demarcation or synonyms used by authors cited are mentioned.
    Zeuner's system, its uses and abuses, are discussed in full on p. 9.

RGM	Rijksmuseum van Geologie en Mineralogie	Leiden
Zool M.	Zoölogisch Museum	Amsterdam
Landesmus.	Hessisches Landesmuseum für Naturkunde	Darmstadt
Mainz	Naturhistorisches Museum der Stad Mainz	
SfN	Sammlungen für Naturkunde	Karlsruhe
SMN	Staatliches Museum für Naturkunde	Stuttgart
IGF	Istituto Geologico	Firenze
MGP	Museo Geologico	Pisa
MNB	Museum für Naturkunde	Basel

The Animals

1. SYSTEMATICS

One of the most difficult groups of mammals is the Rhinoceros family.

Little is known about the habits of its living members. Only near-extinct species get some attention, the extinct next to none. As Wood (1949, p. 185) pointed out, we can construct a 'family-tree' for horses with a distinct main line and many branches. For the Rhinocerotidae we get a shrub with many long, nearly parallel shoots. At any time on any of these a combination of several 'typical' features may appear. Most of these are only ecological adaptations.

Little is known about evolutionary relationships in this family. The whole concept of evolution within the group discussed here should be stamped 'handle with care'. The number of patterns for constructing an animal within a given family is limited and, thus, certain patterns are bound to appear several times. Sometimes we will get duplications of certain parts: only a specialist can separate molars of *Dicerorhinus kirchbergensis* and *Dicerorhinus hemitoechus*. Yet their skulls are as different as the skulls of *Diceros bicornis* and *Ceratotherium simum*. In plain words: similar teeth do not indicate a direct evolutionary relationship; at the best they indicate similar feeding habits or food with a similar silica percentage.

Unfortunately palaeontology of the mammals is mostly odontology. For instance the type material of *Dicerorhinus kirchbergensis* consists of two upper molars and one lower molar. This had regrettable consequences when, later in the 19th century, other species were discovered. Part of the following pages will be an effort to contribute to clearing the mudhole in which rhinoceros-palaeontology wallows.

Five species of Rhinocerotidae are still living, these are usually grouped in four genera:

Rhinoceros L.	*Rhinoceros unicornis* L.
	Rhinoceros sondaicus Desmarest
Dicerorhinus Gloger	*Dicerorhinus sumatrensis* (Fischer)
Diceros Gray	*Diceros bicornis* (L.)
Ceratotherium Gray	*Ceratotherium simum* (Burchell)

From a palaeontologist's point of view, the crania of *Diceros bicornis* and *Ceratotherium simum* are no further apart than those of *Dicerorhinus etruscus* and *Dicerorhinus hemitoechus*. I have refrained from splitting the genus *Dicerorhinus* (or, conversely, lumping *Diceros* and *Ceratotherium)* because the systematics of the fossil species, depending on incomplete skeletal remains, does not warrant this.

The recent species are sharply divided into two geographical groups: an African and a S.E. Asian group. Of the latter, the one-horned genus does not concern us here. *Rhinoceros sondaicus* has been treated extensively by Hooijer (1947) and Sody (1941, 1959). Details about the wildlife of *Rhinoceros unicornis* are given by Gee (1959).

The African group is a close-knit unit, with enough distinct morphological characters to make it impossible to maintain the name *Dicerorhinus* as the name for all Rhinocerotidae with one nasal and one frontal horn ('tandem-horned'). Adherers to this lumping (e.g. Arambourg 1959, p. 73, 1962, p. 371) say, that Gloger's description of *Dicerorhinus sumatrensis* is sufficiently vague to allow the inclusion of all tandem-horned species in Gloger's genus; they forget to mention that Gloger also proposed the name *Opsiceros* for the African species, because these were too different to be included in his genus *Dicerorhinus*.

There is wide agreement that probably all 'tandem-horned' species belong to one taxonomical category, though this may range from subfamily to genus.

Too many fossil species have been added to the genus *Dicerorhinus* because it was considered to be inconvenient to create a new genus. Only one species has had its own genus for 140 years: *Coelodonta antiquitatis*. Its only claim for this status is the completely ossified nasal septum. In all other respects it has the skull of a heavy Dicerorhine. As long as our knowledge of fossil Rhinocerotidae is rather scanty it will be better to have as few genera as possible, but this can (and probably will) be carried too far. Merging *Diceros* and *Dicerorhinus* would be the last straw. One subfamily Dicerorhininae with several genera is a better tool than 'the first of the two (or four) lines of Dicerorhine Rhinocerotidae' (e.g. Arambourg 1959).

My personal preference is a variant of Simpson's classification (1945):

Simpson (1945, p. 142)			Present paper			
Subfamily Dicerorhininae			Subfamily Dicerorhininae			
Dicerorhinus	Gloger	1841	tribe Dicerorhinini	genus *Dicerorhinus*	Gloger	1841
Coelodonta	Bronn	1831		genus *Coelodonta*	Bronn	1831
Ceratotherium	Gray	1867	tribe Dicerotini	genus *Ceratotherium*	Gray	1867
Diceros	Gray	1821		genus *Diceros*	Gray	1821

Major differential characters of these two tribes are:

Nasals:

Dicerorhinini Nasals long and slender (fig. 4a); the curvature sometimes dominated by the rugosity of the nasal hornbase (fig. 4b).

Dicerotini   Shortened and bunched nasals with a large, round indentation in the foremost part (fig. 4c).

Premaxillae:

Dicerorhinini The anterior end of the premaxillae is fused partly; the nasal septum is supported by this symphysis (pl. 11, fig. 4).

Dicerotini   The premaxillae also are reduced. I have not found a single cranium of either species, in which the premaxillae meet at the anterior end in a symphysis. In senile animals the opening between the premaxillae is often partly filled with a lattice of bony spicules.

Having thus drawn the line between Dicerotini and Dicerhorhinini we now give a short list of major differential characters between the two African species and their correlation to Zeuner's angles.

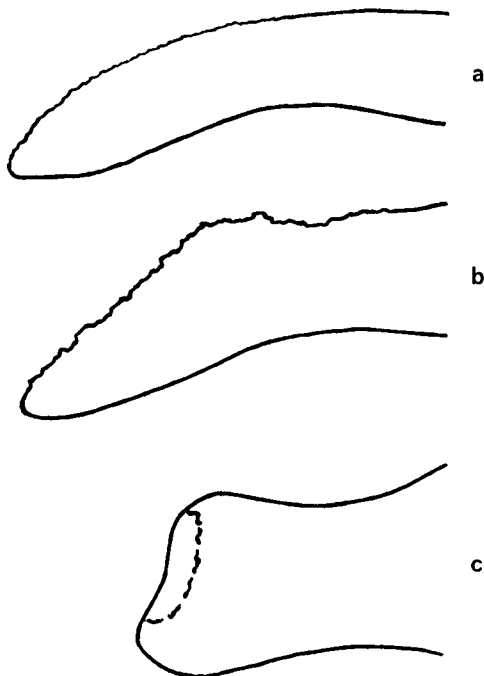| *Diceros bicornis*	*Ceratotherium simum*
7 low crowned molars: p^1 persists; skull base (l) smaller than in *Ceratotherium simum;*	6 extremely large high crowned molars; skull base larger;
parietals rising steeply (n);	parietals low;
occipital crest straight (st);	occipital crest notched;
$y^{med.} = 90°$.	$y^{med.} = 110.5°$.

Fig. 4. Nasals of Dicerorhinini and Dicerotini (schematic).

Table 1

Diceros bicornis
(Zeuner 1934)

	min.	q^1	med.	q^3	max.	number of specim.	arithm. mean
l	51	55	57,5	60	63	42	—
st	0	0,5	1,1	1,6	2,5	43	1,0
o	57	66	70	73	79	44	69
i	59	66	71	75	86	46	70
n	128	138	141	144,5	162	40	142
p	23	29	32	34	39	44	32
po	56	63	67	73,5	88	44	68
y	74	85	90	94	120	42	90
m	27	41	47,5	52	64	40	47
x	- 41	- 26,5	- 21,5	- 17	0	40	- 22

Ceratotherium simum
(Zeuner 1934)

	min.	q^1	med.	q^3	max.	number of specim.	arithm. mean
l	57	—	71	—	75	7	—
st	0	3,1	3,7	4,6	9,3	10	4,1
o	59	61	64	70,5	71	9	65
i	59	62	65	71	79	9	67
n	144	156	160,5	165	167	8	159
p	22	23	25,5	27	32	8	26
po	80	82,5	88	98,5	103	8	90
y	89	106	110,5	119,5	131	8	111,5
m	30	36	50	54	63	9	46
x	- 35	- 26	- 21	- 10,5	- 1	9	- 19

Since for most species his material was insufficient for extensive statistic treatment, Zeuner chose the quartile method. All available measurements for one angle are graded according to size. If there are n measurements, the median is measurement number $\frac{n+1}{2}$, n being an odd number. If n is even, the median lies halfway between measurement $\frac{n}{2}$ and $\frac{n+2}{2}$. In the same way the other quartiles are assigned to measurements half-way minimum and median, and again half-way median and maximum.

There are two objections, not to the method, but to the way Zeuner used it.

1. His material is not homogeneous (Zeuner 1934, p. 23). For the recent species all available material was used, from foetus to senile, also including zoo-animals; distinct subspecies have been lumped.

2. It is a pity that for most species only the quartiles are given; complete figures for separate individuals appear only when the material was insufficient even for quartiles.

Ceratotherium simum has two distinct subspecies, *Ceratotherium simum simum* in South Africa and *Ceratotherium simum cottoni* in N.W. Uganda. In Table 2 are given from left to right: Zeuner's figures for the species, my own for the two subspecies and the combined figures of these for comparison with Zeuner's. The

Table 2

	Ceratotherium simum (Zeuner 1934)						*Ceratotherium simum cottoni* Congo + Uganda				*Ceratotherium simum simum* South Africa				*C. simum cottoni* + *C. simum simum*					
	min.	q^1	med.	q^3	max.	number of specim.	min.	med.	max.	number of specim.	min.	med.	max.	number of specim.	min.	q^1	med.	q^3	max.	number of specim.
l	57	—	71	—	75	7	60.5	71.5	75.5	7	70.1	71	72.5	5	60.5	70	71.25	72.25	75.5	12
st	0	3.1	3.7	4.6	9.3	10	5.0	6.2	7.0	7	1.5	2.5	3.5	5	1.5	2.5	5.1	6.7	7.0	12
o	59	61	64	70.5	71	9	62	73	77	7	55	59	66	5	55	59	66.5	75	77	12
i	59	62	65	71	79	9	67	73	77	7	55	59	72	5	55	59	69.5	75	77	12
n	144	156	160.5	165	167	8	142	156	160	7	150	152	156	5	142	150	153.5	156	160	12
p	22	23	25.5	27	32	8	25	31	43	7	24	25	31	3	24	25	30.5	31	43	10
po	80	82.5	88	98.5	103	8	65	75.5	82	6	85	88	90	3	65	75	79.5	85	90	9
y	89	106	110.5	119.5	131	8	95	104	113	7	108	110.5	111	3	95	99	109	111	113	10
m	30	36	50	54	63	9	35	42	50	7	44	46	50	5	35	42	45.5	49	50	12
x	-35	-26	-21	-10.5	-1	9	-39	-28	-25	7	-20	-11	-9	5	-39	-30	-26	-11	-9	12
z							5.1	5.5	7.2	7	5.5	7.8	7.9	5	5.1	5.3	5.75	7.8	7.9	12

differences between minimum and maximum values are explained by Zeuner's inclusion of immature and zoo-animals. Differences in the median are also caused by a different ratio between the number of specimens of the two subspecies.

Table 3

Diceros bicornis

	Zeuner (1934)						Present paper					
	min.	q^1	med.	q^3	max.	number of specim.	min.	q^1	med.	q^3	max.	number of specim.
l	51	55	57.5	60	63	42	52	55.1	56	58	61.5	26
st	0	0.5	1.1	1.6	2.5	43	0.5	1.5	2.1	3.0	4.0	25
o	57	66	70	73	79	44	55	65	68	70	81	27
i	59	66	71	75	86	46	59	66	67	72	81	27
n	128	138	141	144.5	162	40	131	137	138	140	156	18
p	23	29	32	34	39	44	27.25	30	32.25	33.5	36	17
po	56	63	67	73.5	88	44	54	62	67	71	76	25
y	74	85	90	94	120	42	72	88	89	93	100	25
m	27	41	47.5	52	64	40	35	42	44	47	54	26
x	− 41	− 26.5	− 21.5	− 17	0	40	− 35	− 28	− 23	− 21	− 9	26
z							4.5	6.3	7.4	7.9	9.7	27

According to Hopwood (1939), *Diceros bicornis* has five subspecies. Of these five, two are provisional, without name, being founded on one immature skull each (one from Angola and one from Nigeria).

The three remaining subspecies are based exclusively on material from the British Museum (Natural History) coming from the eastern half of Africa (Abyssinia - Cape of Good Hope).

Later investigators (Zukowsky 1964, Groves 1967) include subspecies from Equatorial Africa (Chad, Central African Rep.).

Diceros bicornis was a fairly common species in all of Africa south of the Sahara, until it was more or less exterminated in the colonies of the western half of the continent in the 19th and the early 20th century. A few isolated animals remain (The Cameroons, Central African Rep., Chad, Congo (Zaïre), Rep. Côte d'Ivoire,? Niger, Nigeria). At present the populations examined by the above-mentioned authors are restricted to East and Equatorial Africa (Chad, Central African Rep.). However, all attempts to recognize different subspecies must be discarded unless the important West African material has been included in these studies.

To understand the nomenclature of European Pliocene and Pleistocene Rhinocerotidae we must examine the history of these names.

Cuvier, in his Recherches sur les Ossemens Fossiles, 1822, II, I, p. 93, distinguishes 'au moins quatre espèces de rhinocéros fossiles'
1. *Rhinoceros tichorhinus* (= *Coelodonta antiquitatis* Blum. 1799)
2. *Rhinoceros leptorhinus*
3. *Rhinoceros incisivus* (= *Rhinoceros Schleiermacheri* Kaup 1832?)
4. *Rhinoceros minutus*

Rhinoceros incisivus is 'celle d'Allemagne de taille ordinaire et munie de dents incisives'. *Rhinoceros minutus* is a provisional name for one or more small

species with incisors from S. France: 'Je laisse aux lecteurs à conclure s'il y a eu dans cet endroit plusieurs espèces de petit rhinocéros'. There remain the first two species. They were the only fossil species without incisors known to Cuvier. Of *Rhinoceros tichorhinus* he had ample material, from France to Siberia. *Rhinoceros leptorhinus* is represented by a skull and some bones found by Cortesi in 1805 near Piacenza. This skull Cuvier never saw himself. All he had was Cortesi's description and a drawing by a young botanist, Adolphe Brogniart. The only thing clearly shown in this drawing is the important fact that there was no bony nasal septum (Rech. s.l. Ossem. foss. 1822 II, I, Rhinoceros pl. IX fig. 7). The bones found with the skull indicated a slender build in contrast to *Coelodonta*. Therefore Cuvier identified all bones from Italy and France that were too large for *Rhinoceros minutus* and too slender for *Rhinoceros tichorhinus* with *Rhinoceros leptorhinus*.

Unfortunately two things happened:

1. In 1834 de Christol erroneously inferred the presence of a nasal septum in *Rhinoceros leptorhinus* from shadows in new drawings of the, now badly mutilated, skull; (like Cuvier, he never examined the original specimen). Therefore he regarded *Rhinoceros tichorhinus* and *Rhinoceros leptorhinus* as synonymous. He described two skulls from S. France and one from Germany *(Rhinoceros Schleiermacheri* Kaup 1832) without bony nasal septum as *Rhinoceros megarhinus*.

2. Worse, the Cortesi skull in Milan, Cuvier's type of *Rhinoceros leptorhinus,* was first badly mutilated and later destroyed by war. There ensued a battle of distinguished palaeontologists, that can be followed best from the list of names and dates in Falconer's Memoir on the European Pliocene and Post-Pliocene species of the genus Rhinoceros (Falconer 1868: 319-320).

All we know with certainty about Cuvier's *Rhinoceros leptorhinus* as opposed to his *Rhinoceros tichorhinus* is:

1. Occipital crest less developed
2. Orbit above M^2 *(tichorhinus* M^3)
3. Bony septum nasale absent

The first two could apply to various species; all that remains is the absence of a bony nasal septum and this is not enough for a positive identification since all Pliocene representatives of this group share this characteristic.

As new species were being introduced there always was a scientist who considered the new name to be a synonym of *Rhinoceros leptorhinus, megarhinus* or *tichorhinus.*

A short list of names and first descriptions:

1799 Blumenbach   *Rhinoceros antiquitatis*
1812 Cuvier   *Rhinoceros tichorhinus* (= *Rhinoceros antiquitatis* Blum.)
1819 de Serres   Rhinocéros de Montpellier (= *Rhinoceros megarhinus* de Christol 1834?)
1822 Cuvier   *Rhinoceros leptorhinus*
1834 de Christol   *Rhinoceros megarhinus*
1839 Jäger   *Rhinoceros kirchbergense*
1841 Kaup   *Rhinoceros Merckii* (= *Rhinoceros kirchbergense* Jäger)
1868 Falconer   *Rhinoceros etruscus*
    Rhinoceros hemitoechus

Although the type specimen of Falconer's *Rhinoceros hemitoechus* (BM 27.836) had an incomplete bony septum, it had been referred to *Rhinoceros leptorhinus* (according to Cuvier a species without a bony septum nasale, according to de Christol with a complete bony nasal septum) by Owen in 1846, who threw in *Rhinoceros kirchbergensis* for good measure. In 1886, in his Catalogue of fossil mammals in the British Museum, Lydekker writes under *Rhinoceros leptorhinus* (Owen): 'Cuvier's name of *Rhinoceros leptorhinus* being inadmissible for the next species [*Rhinoceros hemitoechus*], and *Rhinoceros (Atelodus) aymardi* and *Rhinoceros mesotropus* being uncertain, while *Rhinoceros hemitoechus* is of a later date, Owen's name is adopted for the present species'. This 'present species' turns out to be a combination of *Dicerorhinus hemitoechus* and *Dicerorhinus kirchbergensis*.

Since it is impossible to ascertain that *Dicerorhinus leptorhinus* and *Dicerorhinus megarhinus* are synonyms, modern authors usually discard *Dicerorhinus leptorhinus* Cuvier as uncertain and ambiguous in favour of the younger name *Dicerorhinus megarhinus* de Christ.

This leaves us with the following species:
1. *Dicerorhinus megarhinus* (de Christol 1834)
2. *Dicerorhinus kirchbergensis* (Jäger 1839)
   Dicerorhinus Merckii (Jäger 1841) [should be *Dicerorhinus Merckii* (Kaup)!]
3. *Dicerorhinus etruscus* (Falconer 1868)
4. *Dicerorhinus hemitoechus* (Falconer 1868)
5. *Coelodonta antiquitatis* (Blumenbach 1799)

The fossil and recent species that concern us can be separated with the following key:

|		
1a	No bony septum nasale	2
b	Complete or incomplete bony septum nasale	5
2a	Premaxillae fused	4
b	Premaxillae divided by septum nasale	3
3a	7 low crowned molars	*Diceros bicornis* (L.)
b	6 very high crowned molars	*Ceratotherium simum* (Burchell)
4a	Auditory meatus open	*Dicerorhinus sumatrensis* (Fischer)
b	Auditory meatus closed	*Dicerorhinus megarhinus* (de Christol)
5a	Complete bony septum nasale	*Coelodonta antiquitatis* (Blum.)
b	Incomplete bony septum nasale	6
6a	y > 110	*Dicerorhinus hemitoechus* (Falconer)
b	y < 110	7
7a	Processus posttympanicus and processus paroccipitalis form together a pyramid (fig. 5)	*Dicerorhinus etruscus* (Falconer)
b	The processus posttympanicus is a separate element on the anterior rim of the processus paroccipitalis (fig. 5)	*Dicerorhinus kirchbergensis* (Jäger)
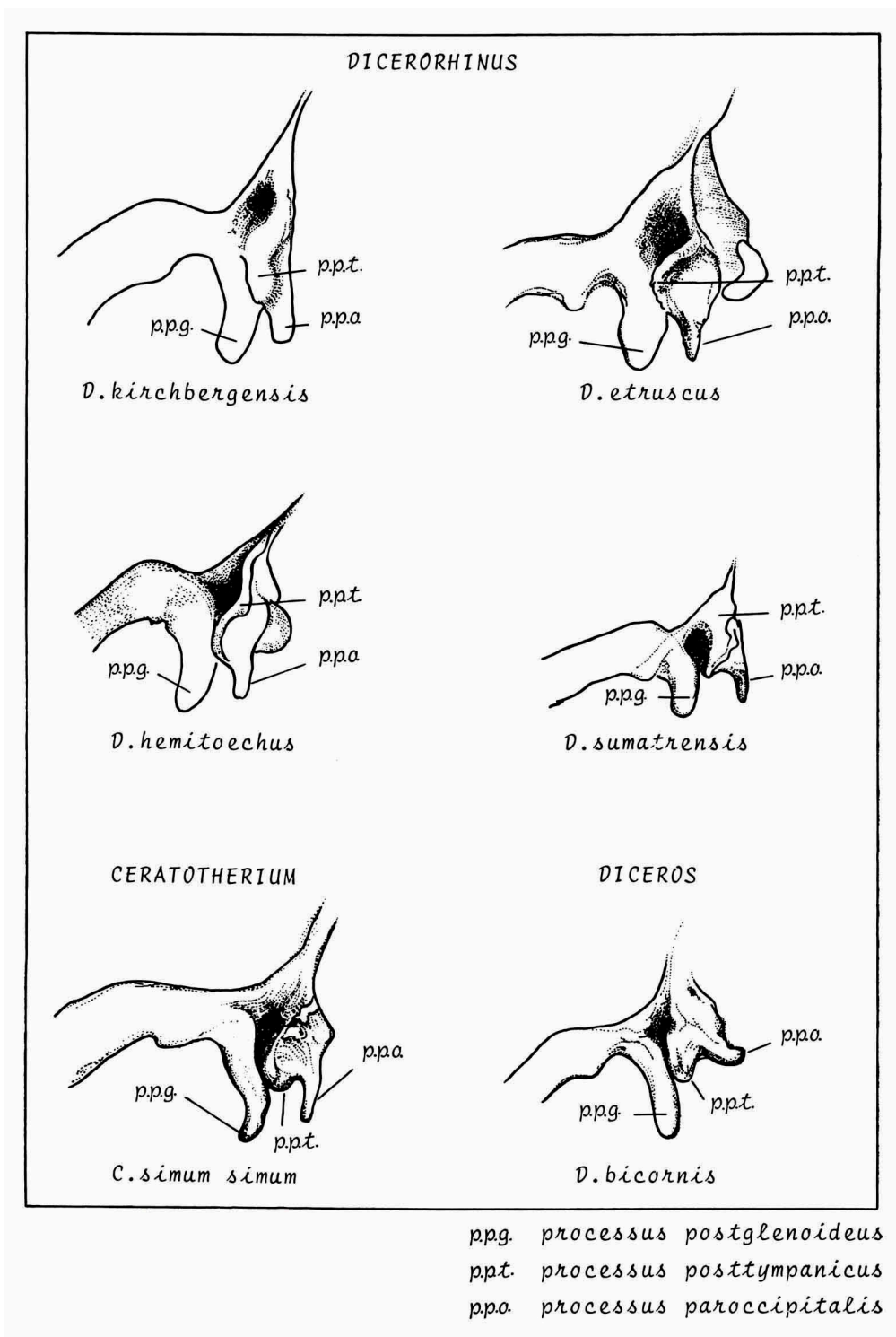
Fig. 5.   Otic region.

Dicerorhinus sumatrensis (Fischer)

Table 4

Dicerorhinus sumatrensis (Fischer)

	Zeuner (1934)				Present paper					
	number of specim.	min.	med.	max.	number of specim.	min.	q^1	med.	q^3	max.
l	7	40	51	52	12	47.5	51	51.5	52.2	54.3
st	7	0.7	1.7	2.2	12	0.5	1.0	1.2	1.3	1.8
o	5	80	88	100	12	70	77	79	88	96
i	7	80	86	100	12	77	77	79	88	96
n	6	145	157	163	12	152	155	155.5	160	162
p	5	24	27	32	11	22	25	27	28	30
po	5	55	64	73	12	54	66	68	72	81
y	5	88	95	100	12	87	94	97	97	107
m	5	52	58	66	12	40	50	55	60	64
x	5	– 44	– 28	– 22	12	– 41	– 31	– 29	– 27	– 14
z					11	4.4	5.7	6.5	7.35	8.4

The first species described as belonging to this genus (Gloger 1842) is also the only living member.

The basal length of the skull is small (l = 47.5 — 54.3). The occipital crest is slightly smaller than the base of the occiput. Sometimes there is a distinct occipital bulge above the opisthion (i $\neq$ 0). The processus posttympanicus and postglenoideus are not fused, leaving the auditory meatus open. Both hornbases are very slight, the frontal hornbase is often only fractionally rougher than the rest of the frontals. For defense the animal does not rely so much on its horns but on the large tusks (probably canines): it bites instead of tossing. The maximum distance between the jugals is large as compared with the length of the skull. There is no bony nasal septum. Keeping in mind the negligible basal length, the minimum distance between the cristae parietales (z) is astonishing ($q^1 — q^3 = 5.7 — 7.35$).

According to British authors, the name *Didermocerus* Brookes (1828) has priority (Boylan 1967). However, in contrast with *Rhinoceros kirchbergensis*, a species-name generally mentioned by 19th century authors as the original name, (although they use the name *Rhinoceros Merckii)*, the genus *Didermocerus* is what Guérin (1974) would call a prime example of a nomen oblitum: after its publication in 1828 it has been in complete disuse until 1939 (Hubback, p. 1). I have used *Dicerorhinus* Gloger as a nomen conservandum. The chaos in rhinoceros nomenclature is bad enough without a new generic name. This may be questionable nomenclature but it strikes me as common sense within the present rules. Also the argument that any animal described by Brookes in the same catalogue with *Didermocerus* would have to be renamed (e.g. *Acinonyx)* if we go on using *Dicerorhinus* fails to impress me.

The holotype of *Didermocerus* [*Dicerorhinus*] *sumatrensis harrissoni* Groves (1965) is an adult by courtesy only. The third molar is just peeking through, all sutures of the skull are very much visible. The animal has been included in table 11 on p. 37, but not used in calculating the quartiles (BMNH 1901.8.15.1).

Although there seem to be certain trends (large animals from the continent), my sample is too small for distinct, reliable subspecies.

Originally found in a large area comprising Burma, Indochina, Malaya, Sumatra and Borneo, as far as known the species is now limited to a small population on N.W. Borneo (?) and Sumatra. Sody ((1941), 1959, p. 165) mentions sightings from the Sumatran coast, viz. a coastal badak and a forest badak. However, in these cases there is no certainty that *Dicerorhinus sumatrensis* was involved and not *Rhinoceros sondaicus*. Certainly *Dicerorhinus sumatrensis* is not, as Guérin et al. (1969, p. 129) seem to believe a swampdweller by preference, turning to the montane forest only as a last refuge.

The determinants for the presence of *Dicerorhinus sumatrensis* (if we disregard the role of man) are shade, food and water. Frequent mud-baths do not make it a swampdweller. Rather, being a browser with a preference for soft food, its normal habitat (however adaptable the animal may be to a broad environmental spectrum) is and has always been the montane forest, from where it descends on the lower plains in the dry season for food and/or water (Van Strien 1975, p. 37).

The handful of animals reported still to be in existence on the Asian continent is a small group spread from Burma, Siam and Cambodia to Malaya. Even if the highest estimates are assumed to be correct, they are too few to perpetuate the species in this farflung and war-torn area.

Dicerorhinus megarhinus (de Christol 1834)

According to de Christol, the type from Montpellier had no trace of a bony septum. This was also the case with Cuvier's type of *Dicerorhinus leptorhinus* (the Cortesi skull in Milan as described by Falconer 1868).

Nevertheless some skulls from N. Italy and S. France attributed to *Dicerorhinus megarhinus* definitely have an incomplete bony septum.

There are two possibilities:
1. *Dicerorhinus megarhinus* is a forerunner of *Dicerorhinus etruscus,* evolving into this animal, and developing a bony septum.
2. *Dicerorhinus megarhinus* has no bony septum. In this case some material will have to be renamed as it does not correspond to de Christol's description. The provisional name *Dicerorhinus* cf. *megarhinus* (Guérin et al. 1969) is unfortunate, as it can be interpreted as an evolutionary relation that is in this case by no means certain.

An evolutionary line *Dicerorhinus megarhinus-etruscus* is improbable. The teeth associated with *Dicerorhinus megarhinus* could never belong to a primitive *Dicerorhinus etruscus*. They could be (and have been) described as belonging to a forerunner of *Dicerorhinus kirchbergensis*. But this species does not appear in W. Europe before the Middle Pleistocene, and *Dicerorhinus megarhinus* stops at the Plio-Pleistocene border.

As the type material of the last century (Milan, Montpellier) has been destroyed or badly damaged, Guérin (Guérin et al. 1969) has designated as neotype for *Dicerorhinus megarhinus* the skeleton from Millas (Pyrenées Orientales), described by Maurette (1910). Guérin's conclusion that the animal was 'a swampdweller, like *Dicerorhinus sumatrensis*' is unfortunate.

Dicerorhinus etruscus (Falconer 1868)

Table 5

Dicerorhinus etruscus

	Zeuner (1934)						Present paper					
	min.	q^1	med.	q^3	max.	number of specim.	min.	q^1	med.	q^3	max.	number of specim.
l	57	61.5	66	70.5	72	12	61	67	69	71	73.5	9
st	0	1.1	1.6	2.0	2.6	17	– 0.2	1.0	1.5	2.4	3.3	9
o	63	70	73	78	83	14	70	74	75	79	81	9
i	63	70	73	78	83	14	70	74	75	79	81	9
n	142	145.5	149	154	157	12	ca. 140	150	150	155	ca. 160	9
p	25	—	27	—	31	3	25	—	30	—	33	3
po	66	—	71	—	90	7	65	—	76	—	78	7
y	80	—	98.5	—	107	6	88	—	93	—	104	7
m	34	43.5	46	55	70	8	42	46	51	52	57	9
x	– 40	– 30	– 25.6	– 22	– 12	8	– 33	– 31	– 24	– 23	– 19	9
z							3.4	3.9	4.7	6.45	9.2	8

Occiput rectangular. No heavy occipital crest.

Processus posttympanicus and paroccipitalis form together an irregular pyramid; the (downward-pointing) apex is the processus paroccipitalis.

The part of the zygomatic arch directly anterior of the glenoid fossa is horizontal, not plunging downward as in *Dicerorhinus kirchbergensis*.

The condylar part of the mandible is ca. 9 cm long.

The symphysis of the mandible is long and slender, the upper surface dropping to a short vertical posterior part that meets the ascending lower surface with a distinct angle.

Both Zeuner's and my own measurements have been given (table 5). Zeuner's inclusion of subadults leads to slightly smaller minimal and median values.

Compared with *Diceros bicornis*, the basal length (61 - 73.5) is greater *(Diceros bicornis* 52 - 60). The incision in the occipital crest is larger. For the other measurements the median and minimum are lower in *Diceros bicornis*, while the maximum is almost the same in both species. The minimum-maximum range of most measurements of *Dicerorhinus etruscus* corresponds with the q^3 - max. range of *Diceros bicornis*.

It is evident that the greater number of skulls *(Diceros bicornis* 25 as compared to 8 of *Dicerorhinus etruscus)* leads inevitably to a wider range of variation. Contributing to this disparity is probably the fact that an old, fully grown adult is most likely to succeed in getting fossilized.

Keeping this in mind we get from the angular measurements the picture of a rhinoceros built essentially as *Diceros bicornis*. The difference in basal length is explained by one of the differences between *Diceros* and *Dicerorhinus:* the short, bunched nasals of *Diceros*.

Certainly the skeleton of *Dicerorhinus etruscus* does not suggest a larger animal than *Diceros bicornis*.

Originally described from N. Italy, *Dicerorhinus etruscus* or closely related species have been found in Lower Pleistocene deposits from W. Europe to China (Chow Ben-shun 1963b, p. 329).

The name *Rhinoceros etruscus,* without an adequate description of the species, is mentioned by Falconer in 1859 in a letter to Anstedt (1859, p. 602). The complete description was published by Murchison after Falconer's death (Falconer 1868, p. 354-368).

The probability of local and/or temporal subspecies remains to be investigated. Zeuner (1934, p. 68-69) gives a few measurements of the development of the hornbase, indicating a larger hornbase (independent of the basal length of the skull) in the late animals (Mosbach) as opposed to Senèze. Most authors only remark that *Dicerorhinus etruscus* is a stable and almost unchanging species.

With the coming of the heavy glaciations (Elster) and the changes in the flora of W. Europe, the species is replaced by *Dicerorhinus kirchbergensis* during the Upper Cromerian (Mosbach, Hauptfundschicht).

Dicerorhinus kirchbergensis (Jäger 1839)

Rhinoceros kirchbergense	Jäger 1839
Rhinoceros Merckii	Kaup 1841
Rhinoceros Mercki	auct.
Rhinoceros merckii	auct.
Rhinoceros mercki	auct.
Rhinoceros merki	auct.
Rhinoceros leptorhinus	Owen 1846
Rhinoceros leptorhinus { *Rhinoceros kirchbergensis* Jäger / *Rhinoceros Merckii* Kaup	Jäger 1850

Table 6

Dicerorhinus kirchbergensis (Jäger 1839)

	Zeuner (1934)				Present paper			
	min.	med.	max.	number of specim.	min.	med.	max.	number of specim.
l	63	67	74	3	62.2	67.75	78	4
st	1.0	1.1	1.4	5	1.0	1.0	2.0	3
o	70	77.5	83	4	67	70	77	3
i	68	76	83	5	67	70	77	3
n	147	152	155	3	145	150	155	3
p	21	27	28	4				
po	67	67	72	3	72	72	80	3
y	82	95.5	109	4	93	97	101	4
m	41	55	66	5	46	50	51	3
x	– 42	– 17.5	– 13	4	– 26	– 21	– 20	3
z					3.5	4.3	5.6	4

The occiput is slightly trapezoidal, larger at the base, usually vertical, without a pronounced occipital crest. The often large bulge leading to the opisthion in *Dicerorhinus etruscus* is absent.

The processus posttympanicus is a distinct separate element, a vertical bar on the upper anterior part of the processus paroccipitalis. The zygomatic arch plunges forward and downward, directly anterior of the glenoid fossa.

The condylar part of the mandible is 12 - 13 cm long. The symphysis of

the mandible is massive, with a high vertical posterior edge. The number of skulls usable for angular measurments is too small for statistical treatment. Only a few tentative conclusions are warranted.

The differences between my figures and Zeuner's are caused by different material (vid. appendix).

The teeth of *Dicerorhinus kirchbergensis* are considerably larger than those of *Dicerorhinus etruscus*. This difference is reflected in a larger, heavier dental apparatus (the maximum distance between the zygomatics, glenoid fossae, maxillae and mandibulae). Especially the wide curve of the zygomatic arch suggests a heavier and larger skull and therefore to many palaeontologists a larger animal. This pars pro toto reasoning is usually reflected in reconstructions (e.g. Kurtén 1968 p. 141) where *Dicerorhinus etruscus* is depicted as a rather pathetic little animal of the order of *Dicerorhinus sumatrensis*. Guérin (1974, p. 64), also wants us to believe that *Dicerorhinus kirchbergensis* is the largest Dicerorhine. However the median of the basal length of the cranium is 69 cm for *Dicerorhinus etruscus*, 67.75 for *Dicerorhinus kirchbergensis*. Keeping in mind our insufficient data, the fact that a colder climate is not necessarily proof of a larger animal and the variability in both species, *Dicerorhinus kirchbergensis* would seem a compacter, heavier built animal - not necessarily a larger animal than *Dicerorhinus etruscus*.

Dicerorhinus kirchbergensis with high-crowned teeth and a heavy mandible, manages to survive in a world changing from temperate to cool vegetation, from open forest to savanna, with more grasses and a larger silicon content in its food.

The original name was *Rhinoceros kirchbergense* Jäger (1839). Only two years later, in 1841, J. J. Kaup invented the name *Rhinoceros Merckii* in a crusade against the latinization of typical germanic words (ächt teutscher Wörter). According to Kaup, his friend Jäger had consented, on Kaup's plea, to change the 'provisional' name *Rhinoceros kirchbergensis* into *Rhinoceros Merckii*, to honour the man who first described remains belonging to this species as *Rhinoceros incisivus*. However in 1850 (p. 909) Jäger is convinced that Owen's designation of the species as *Rhinoceros leptorhinus* is correct. After a spirited defense of the practice of naming a new species after a locality *(Rhinoceros kirchbergensis* is cited as an example) he endorses the name given by Owen and calls the animal:

Rhinoceros leptorhinus Cuvier $\begin{cases} Rhinoceros \ Kirchbergensis \ \text{Jäger} \\ Rhinoceros \ Merkii \ \text{Kaup} \end{cases}$

This disposes of Kaup's claim that his friend Jäger changed the name as a favour to Kaup. As indicated by Jäger, the new name (if used at all) should be *Rhinoceros Merckii* Kaup. Since 1841 the name has been spelled Merckii, merckii, Mercki, mercki and merki.

Not counting his chauvinism, the arguments given by Kaup for the change in the name of the animal are not very convincing: a) *Rhinoceros kirchbergense* is a provisional name; b) remains of the same species had been found earlier near Frankfurt, Chagny, Crozes, Canstadt and Lussheim.

Any name founded on three or four teeth is a provisional name by necessity until the species is established as valid by further finds. Earlier finds, described as belonging to other, established species *(Rhinoceros incisivus, Rhinoceros antiquitatis)* do not affect the description of a new species based on later finds.

In 1947 Hooyer reverted to *Dicerorhinus kirchbergensis* according to the rules of priority (vid. also Schroeder 1903 p. 78-80). In recent years (Mayer 1971) some palaeontologists have advocated the name *merckii*. They argue that *kirch-*

bergensis is a prime example of a 'nomen oblitum'; that besides, there is no Pleistocene mammal (certainly no rhinoceros) that will not be found to have been described under at least one other name, antedating the name in common usage at this moment; that this mania for priority will hamper research by the lack of stability in nomenclature.

Mayer (1971), the man who mentions these arguments as the opinion of Azzaroli and Guérin, is an 'enginer hoist with his own petar'. In his account of the history of the cranium of *Dicerorhinus mercki (kirchbergensis)* (Jäger) var. *brachycephalus* Schroeder from Daxlanden, instead of comparing the skull with other skulls of this species, he has chosen for stability, using 'the name in common usage', var. *brachycephalus* (sic). The well preserved cranium from Daxlanden, found in 1802, was used by Schroeder (1903) as the only complete skull in Germany for his study of the vertebrates of the Mosbach sands (Wiesbaden), since from that locality he only had skull fragments and teeth of this species. In his study Schroeder compares three rhino skulls. The first is the skull from Irkutsk described by Brandt (1877) as *Rhinoceros Merckii* Jaeg. The second is the skull from Daxlanden. The third is a skull from Ilford, Essex, described as *Rhinoceros leptorhinus* Owen by Woodward (1874). Because the second skull is much shorter than the first and third, with higher occipitals and shorter nasal apertures, Schroeder named the Daxlanden skull *Rhinoceros Mercki var. brachycephala*. This difference in length is not surprising since both the Irkutsk and the Ilford skull belong to *Dicerorhinus hemitoechus* (Falc.), a species characterised by a long low cranium with a large occipital crest reaching far backwards. The skull from Daxlanden is a perfectly normal skull of *Dicerorhinus kirchbergensis (Merckii)*. There is no reason whatsoever to refer to it as a separate variety *Dicerorhinus Mercki (Merckii)* var. *brachycephala*. But since Schroeder (1903), this name var. *brachycephala (brachycephalus)* for the Daxlanden skull has been used time and again. Staesche (1941, p. 143), who first gave a complete comparative description of *Dicerorhinus hemitoechus* and *kirchbergensis,* points out Schroeder's error, but uses the name given by Schroeder for the Daxlanden skull, and so does Mayer (1971). A mania for stability will hamper research by lack of interest or excessive respect for authority.

Any publication in which the name *Rhinoceros (*or *Dicerorhinus) merckii* is used, should be read with the utmost caution. The name has been used for a long time in the belief that *Dicerorhinus kirchbergensis* and *Dicerorhinus hemitoechus* were one species (e.g. Schroeder 1903). Also *Dicerorhinus mercki (*or *merckii)* has been used mistakenly for *Dicerorhinus etruscus* (Bernsen 1927 and after him many others). As we tend to take the authority of a specialist for a given locality for granted, his mistakes are perpetuated in handbooks and fauna-lists.

The mandible described as 'Rhinocéros de Merk provenant de Meyrargues (Bouches du Rhône)' by Bonifay (1961) has heavy incisors, in contrast to *Dicerorhinus kirchbergensis*.

In one museum I found a skull of *Coelodonta antiquitatis* Blum., labelled *Coelodonta merckii,* a name given to *Dicerorhinus kirchbergensis* by Abel (1919, p. 857) following Brandt (1877), who lumped the Pleistocene Dicerorhinini in one genus (or subgenus), containing only two species: *Rhinoceros (Tichorhinus) antiquitatis* with a complete bony nasal septum and *Rhinoceros [(Tichorhinus)] Merckii* with an incomplete bony nasal septum. Wherever the name *Dicerorhinus* (or *Rhinoceros) merkii* appears in literature, it will usually be found to have been used either for a composite of *Dicerorhinus kirchbergensis* and *Dicerorhinus*

hemitoechus, or for any other Pleistocene Dicerorhine.

To maintain the name *Dicerorhinus merckii* as a nomen conservandum (Azzaroli 1962b) leads only to uncertainty and confusion as Azzaroli shows himself (op. cit.). According to him the skull from Daxlanden (Samml. f. Naturk., Karlsruhe) does not belong to *Rhinoceros merckii:* its systematic position is uncertain, the skull being too small, nasal apertures reaching not far enough backwards etc.

The mistake of Schroeder (1903, 1930) caused by the lumping of two species is understandable, considering the scarcity of well preserved skulls and the similarity in dentition.

Why a modern palaeontologist, making a study of *Dicerorhinus kirchbergensis and Dicerorhinus hemitoechus* wants to perpetuate this mistake (var. *brachycephala)* and clings to an ambiguous name *(Merckii)* that has been spelled at least in five different ways and used for at least five different species is not readily understandable. If it is stability we want and a name that cannot give rise to any misunderstanding, we might do well by going back to the original name: *Dicerorhinus kirchbergensis* Jäger.

Staesche (1941, p. 103-131) has given an excellent differential analysis of *Dicerorhinus kirchbergensis* and *Dicerorhinus hemitoechus.* He used the two skulls from Steinheim (one of each species) in the Staatliche Museum f. Naturk. Stuttgart. However, the *kirchbergensis* skull has been repaired and restored extensively several times. Unfortunately the *hemitoechus* skull was used as a model, with the result that hardly any difference remains. This already affected the original description by Staesche and the photographs (Staesche 1941, pl. 11).

Appearing first at Mosbach (Hauptfundschicht) *Dicerorhinus kirchbergensis* gradually replaces *Dicerorhinus etruscus.* It disappears at or shortly after the end of the last interglacial.

Until now, *Dicerorhinus kirchbergensis* has not been found in the Netherlands. A few teeth, described as *Rhinoceros merckii* (Rutten 1909), belong to *Dicerorhinus hemitoechus,* while the remains from Tegelen (Bernsen 1927) belong to *Dicerorhinus etruscus,* as shown by the typical slender *etruscus*-type of mandibular symphysis.

From the fossil evidence, *Dicerorhinus kirchbergensis* appears always in lesser numbers than the other contemporaneous *Dicerorhinus.* This could be due to two factors (probably both):

a) Its ecological niche was unfavourable for fossilization.

b) It was a rare animal bound to a vegetation belt that did not occupy much territory in the changing landscape of the Pleistocene.

Often, especially by British authors, *Dicerorhinus kirchbergensis* is called the forest-rhinoceros, in contrast to *Dicerorhinus hemitoechus,* an animal usually associated with a steppe fauna. This cognomen is not entirely justified and leads to contradictions. The first finds of *Dicerorhinus kirchbergensis* (Mosbach, Hauptfundschicht) are from places and times where the forest is receding being replaced by an open landscape.

Dicerorhinus hemitoechus (Falconer 1868).

Table 7

Dicerorhinus hemitoechus

	min.	q^1	med.	q^3	max.	number of specim.
l	63.0	65.0	65.5	69.6	72.5	9
st	– 1.0	0	0.1	0.4	1.2	11
o	47	50	55	55	61	11
i	47	50	55	55	61	11
n	141	145	149	158	ca. 160	9
p	—	—	—	—	—	—
po	—	—	—	—	—	—
y	ca. 110	115.5	118	119	ca. 120	7
m	28	35.5	37.5	39.5	44	10
x	– 23	– 19.5	– 17.5	– 12.5	– 7	10
z	1.8	3.6	4.2	5.0	6.0	11

Occiput not rectangular but trapezium shaped: the length of the occipital crest is ca 2/3 of the basal length.

Processus paroccipitalis and posttympanicus are a single element. The thick, rounded, anterior edge is often a little irregular.

The downward plunge of the zygomatic arch is steeper than in *Dicerorhinus kirchbergensis*.

The articular plane of the glenoid fossa is 10-12 cm. The condylar part of the mandible should, therefore, be slightly smaller than in *Dicerorhinus kirchbergensis*.

The mandibular symphysis has a high, more or less vertical posterior surface, rounded where it passes into the slightly slanting upper surface angular at its lower border. Lower and upper surfaces run almost parallel upwards, meeting at the front in a shallow angle.

Minimum and maximum for y are both approximations. If these two values are discarded we get a minimum of 115, maximum 119, while the median stays the same (118).

The basal length (l) seems to be slightly smaller than that of *Dicerorhinus kirchbergensis*.

The incision in the occipital crest is often absent or replaced by a small posterior protuberance (st negative).

The angle between opisthion + occipital crest and parietals (o) is very small. The median is 54, the minimum for *Ceratotherium simum simum* is 55, for *Ceratotherium simum cottoni* 62. The maximum values for o and m are lower than the corresponding minima for *Dicerorhinus kirchbergensis*. The minimum for m is 42 for *Dicerorhinus etruscus* against a maximum of 44 for *Dicerorhinus hemitoechus*.

These measurements indicate an animal with an occipital crest drawn far backwards, extremely large values for y ('drooping head'), in short, an animal like *Ceratotherium simum*.

Introduced originally as a new species for a few skulls from S. England and Wales that dit not fit the description of *Dicerorhinus kirchbergensis* or *Coelodonta antiquitatis,* this species was rejected by nearly all palaeontologists until 1941 (Staesche). It was usually included in *Dicerorhinus merckii*.

Remains have been found from England to Siberia, also in Italy and the Near East (Lebanon, Syria, Israel), perhaps reaching into N. Africa.

It makes its first appearance at Süssenborn (near Weimar), approximately at the same time as the main fauna of Mosbach (Wiesbaden). However, Süssenborn being farther to the east, the fauna has a colder character. At Mosbach (Wiesbaden) on the border of the Rhine Valley, the decline of *Dicerorhinus etruscus* and the coming of *Dicerorhinus kirchbergensis* indicate the change from temperate woody savanna to a cooler climate, from open forest to steppe. At Süssenborn, in Thüringen, the change is complete. With the open steppe comes *Dicerorhinus hemitoechus*, the only specialized grazer among Pleistocene Dicerorhines in W. Europe.

Like *Dicerorhinus kirchbergensis, Dicerorhinus hemitoechus* is exclusively an interglacial or interstadial animal. However, in contrast to the first species, *Dicerorhinus hemitoechus* is a sign of the following colder periods wherever it is found.

The fauna from Joint Mitnor Cave, Buckfastleigh (Sutcliffe 1960) is an Eemian fauna of the open forest-savanna; *Palaeoloxodon antiquus* (Falconer & Cautley) is commonly regarded as a woodland elephant; also present are brown bear, fox, wild cat, badger. But there are also *Bison priscus* (the steppe bison) and *Megaceros*. In this mixed assemblage the absence of *Dicerorhinus kirchbergensis* against an abundance of *Dicerorhinus hemitoechus* suggests the coming of the steppe and a later date than the warmest part of the Eemian proposed by Sutcliffe (1960).

Rather than intolerance for a cold climate, its dietary specialization led to its final disappearance from W. Europe at the coming of the last glaciation.

Coelodonta antiquitatis (Blum. 1799)

Rhinoceros antiquitatis	Blumenbach	1799
Rhinoceros tichorhinus	Cuvier	1812
Coelodonta Boiei	Bronn	1831
Rhinoceros (Tichorhinus) antiquitatis	Brandt	1877

Table 8

Coelodonta antiquitatis (Blum.)

	min.	q^1	med.	q^3	max.	number of specim.
l	62	69.9	70.9	72	76.8	10
st	– 2	—	– 0.5	—	0	5
o	43	—	52	—	53	7
i	46	—	52	—	53	7
n	150	153	154	155	160	9
p	30	—	32	—	33	3
po	95	—	106.5	—	110	4
y	82	—	94.5	—	102	8
m	43	48	51	53	56	10
x	– 5	– 2	0	+ 3	+ 4	8
z	6.7	8.5	9.8	10.2	12	9

Occiput square. Heavy occipital crest. Processus paroccipitalis and posttym-

panicus are one heavy lumpy entity, the slightly rounded anterior edge firmly fused with the thick processus postglenoideus.

The zygomatic arch curves gradually forward and down; the anterior part thickens with a slight curve of the upper edge.

The condylar surface of the mandible is 8.50-10.5 cm. The septum nasale is completely ossified.

The rugosity of the nasal hornbase is very large. Irregularities are frequent in all parts of the skull (exostoses, bulges on occipital and parietal region, ragged edges on other bones).

The extremely high crowned teeth with their corrugated enamel are unmistakable.

The symphysis of the mandible is of the same general form as in *Dicerorhinus etruscus* but the posterior part is rounded without a distinct edge.

The basal length is great to very great, the minimum corresponding with the third quartile of *Dicerorhinus etruscus* and *Dicerorhinus hemitoechus*.

The incision in the occipital crest is sometimes absent, replaced by or combined with a posterior protuberance (st negative). The angle between opisthion + occipital crest and parietals (o) is even smaller than in *Dicerorhinus hemitoechus* (max. of *Coelodonta antiquitatis* = med. of *Dicerorhinus hemitoechus)*. There are also sometimes differences between o and i (occipital bulge).

The minimum of n corresponds with the third quartile of *Dicerorhinus hemitoechus* and *Dicerorhinus etruscus*.

However, y corresponds with *Dicerorhinus etruscus* and *Dicerorhinus kirchbergensis;* the same holds for m (basion + opisthion and parietals). This results in four out of seven values for x being positive.

Barring *Dicerorhinus etruscus* (min. 3.4, med. 4.7, max. 9.2), the maximum for z (minimum distance between the cristae temporales) is lower for the other pleistocene species than the minimum for *Coelodonta antiquitatis* (7.2): *Dicerorhinus hemitoechus* 6.0, *Dicerorhinus kirchbergensis* 5.6.

The large, massive skull has tempted many authors to compare *Coelodonta antiquitatis* with *Ceratotherium simum* (Viret 1958, p. 456). However, about all the two species have in common are the large skull and the very large values for z (minimum distance between cristae temporales).

In *Coelodonta* st is shallow or absent, o much smaller, n on the large side, y smaller and x small - positive.

A heavy occipital ridge is combined with values for y that are normal for a browser.

There is no need to look for special solutions for such a combination of browsing and grazing characteristics - the angle y = ca. 90 (browsing), combined with an occipital ridge (grazing) - if we do not insist on regarding the species as a typical grazer (e.g., *Dicerorhinus hemitoechus* carried its head drooping like *Ceratotherium simum, Coelodonta* achieved the same effect by pointing skull and neck downward). From the external and internal evidence (stomach contents, conifer twigs between molars), emerges a 'dual-purpose' animal, grazer in the summer, retreating into the protection of the forest in the winter. The reconstructions of *Coelodonta antiquitatis* with its nasal horn horizontal, ploughing the snow before its head in search of food are fanciful but not very convincing in the face of evidence from cave paintings (or engravings) that show an animal with its head drooping a little less than *Ceratotherium simum*. Lowering the head and neck, the represented animals could reach the flora of tundra or cold steppe;

only a little elevation of the head (y, m!) was sufficient for browsing in the forest.

Neontologists are very reluctant to discuss the cause of the large open sores on the flanks of the African species. If the temper of these animals is mentioned usually an embarrassing silence ensues. Too many big game hunters and collectors have used tall stories of 'fights to the death between giants' as a convenient excuse to acquire an illicit trophy. However, quarrelling does occur and accidents will happen in the best regulated families. The scars on the hide of the second woolly rhinoceros from Starunia (Nowak e.a., 1930, pl. 7 fig. 2) are probably the result of an intra-species squabble. Looking for other explanations puts rather a strain on our credibility and credulity.

The original name is *Rhinoceros antiquitatis* Blum., antedating *Rhinoceros tichorhinus* Cuvier. Brandt (1877) advocates the name *Tichorhinus antiquitatis* although using the name *Rhinoceros tichorhinus*. He rejects *Coelodonta* Bronn (1831, p. 61) because the name is not based on the description of a fully adult specimen, an argument used by von Meyer (1831, p. 438) who rejected Bronn's new genus and species as being a young *Rhinoceros tichorhinus* (= *Coelodonta antiquitatis* Blum.) or a near relative.

A satisfactory explanation why *Coelodonta antiquitatis* did not cross the Bering land bridge like *Mammuthus* has yet to be given.

According to Vangengeim (1967), *Mammuthus* is an animal of the northern humid tundra. *Coelodonta* is a periglacial animal but more frequent in the arid, cold Central Asiatic steppe, reaching its maximum frequency in the Transbaikal region, less abundant in the north as opposed to *Mammuthus*.

This only leaves us with the question why several species from the arid zone did migrate to the American continent or at least reached Alaska (Saiga, Yak), while *Coelodonta antiquitatis* reaches N.E. Asia (Chuckchi region, Kamchatka), and stops at the Bering strait (Vangengeim, 1967).

In W. Europe *Coelodonta antiquitatis* is usually associated with a tundra flora in cold, periglacial deposits. It first appears at the beginning of the Elster glaciation in three E. German localities, Bornhausen (Harz), Neuekrug (Harz), Frankenhausen (Kyffhäuser) (Sickenberg, 1962), it is absent in the following interglacials, returns with the cold and it is last seen in W. Europe in the second interstadial of the Weichselglacial (Zeuner, 1959, p. 328).

The Animals

2. ANATOMY

In 1955 Thenius published a study on the systematical value of the ossification of the nasal septum.

Describing sets of nasal bones (not two skulls, as sometimes stated, e.g. Azzaroli 1962a, p. 13), from Ajnacskö (Hungary) and Montpellier, one with and one without traces of an ossified septum, he tentatively starts with the theory that these represent not two different species, but a case of sexual dimorphism. This theory is elaborated. According to Thenius the ossification of the septum develops as a response to the pressure of the nasals. This pressure is a result of a larger nasal horn. The size of the horn can be measured from the rugosity of the hornbase. The male rhino is supposed to have larger horns than the female. There-

fore, Thenius concludes that in *Dicerorhinus etruscus*
a) all males had an (incomplete) ossified septum
b) skulls without ossified septum, or with less advanced ossification belong to females.

Making allowances for different phylogenetic stages, Thenius jumps to the general statement that, in skulls of any single species from synchronous deposits
a) a difference in the rugosity of the hornbase or the ossification of the septum is conclusive proof of sexual dimorphism and
b) sexual dimorphism is the cause of differences in the rugosity of the hornbase or the ossification of the septum.

Thenius goes on to the conclusion that in some species at an early evolutionary stage the male had an ossified septum, while in the female this characteristic was not yet fixed, but fluctuating. Therefore, according to Thenius, the systematical value of the ossification of the nasal septum is doubtful.

Thenius starts with presenting sets of nasals from the same locality with some anatomical differences. At first he postulates as a possible cause sexual dimorphism. At the end he is convinced he has proved that sexual dimorphism is the only possible solution. However, apart from the inconsistencies and flaws in Thenius' arguments, there are several other possibilities he ignores.

In a discussion of his theory some anatomical observations will serve us best.

The rhinoceros horn is a dermal formation. It is anchored at its base in the thick dermal armour. There is no rigid connection with the rugosity that indicates the hornbase on the skull. In fact, the implantation is rather elastic. Thus, in a heavy collision there is little danger of breaking. However, malformations occur frequently.

The hornbase is a rugose patch formed by polygonal warts or pillars. The cause of this configuration is open to speculation. According to some authors, the interstices between the pillars harbour the bloodvessels that feed the epidermis where the horn is formed. This sounds plausible. The rugosity is an area of friction between horn and skull; without this protection local hemorrhage might result. A large rugosity is not necessarily an indication of large horns, rather of frequent use. According to Schack (1958, p. 48), in *Ceratotherium simum* the nasal horn of the female is long and slender (and therefore, liable to malformations), the nasal horn of the male shorter with a larger base. Inspection of a larger population soon shows this generalizing from a few animals to be erroneous. The variability of *Ceratotherium simum* and *Diceros bicornis* due to age and perhaps sex is so large that even within the subspecies it is impossible to correlate in any way the size of the rugosity and the sex of the animal.

I have not been able to find any sex-characters in the skull of these two species (the same holds for *Dicerorhinus sumatrensis*). The fact that, of 56 skulls examined by me, the sex of 6 animals was indicated, was a contributing factor.

While these sad experiences, mainly with animals of another genus *(Diceros)* are not proof, they are in my opinion an indication that sexing fossil rhino skulls is a waste of time. The evidence, or rather lack of it, given by Thenius points in the same direction. His few arguments are either faulty or half truths:
a) If the ossification of the septum is necessary to relieve the pressure on the nasals as the horns grow larger, reaching its peak in *Coelodonta*, then why is there no ossification of the septum in recent species? The largest known horn of *Ceratotherium simum* is 158 cm long. This might be expected to create some response in the septum.

b) Hornsize and rugosity are not related. While there may be some relation between hornsize and sex, there is no evidence for the sweeping statement that in the Rhinoceros family the horns of the male are larger. The largest known horn of *Ceratotherium simum* (158 cm) is from a female (Rowland Ward, 1935, p. 345). As for the sexual differences in the nasals (♀ long and slender, ♂ shorter, more massive), Thenius is simply juggling the material. If the 'male' bony nasal septum (Thenius, 1955, pl. 1, fig. 2) is rotated forward and downward until it fits in its place on the symphysis of the premaxillae, the nasals (consisting mostly of plaster) are as long as the 'female' nasals (ibid., pl. 1, fig. 4).

c) The term nasal septum tends to be misleading. Too often palaeontologists using it ignore bilateral symmetry. Actually the septum consists of a right and left part. This is seen best where ossification occurs: two bony plates are formed that are closely joined in the median sagittal plane (fig. 6d).

As rhino-skinning is slow work, decomposition may set in and in consequence may lead to disruption of the anterior part of the palate by a contracting non-ossified septum after death. This accounts for the fact that the palate in cleaned modern rhino-skulls is mutilated as in fig. 6b.

If we look at the ossified septum in a cross-section we find a situation as in fig. 6d. The interstice is filled with spongy osseous tissue, often lost in fossilisation. It is therefore meaningless to state that 'no trace could be found of an ossified septum in the middle of the nasals'. Instead we should look for two traces.
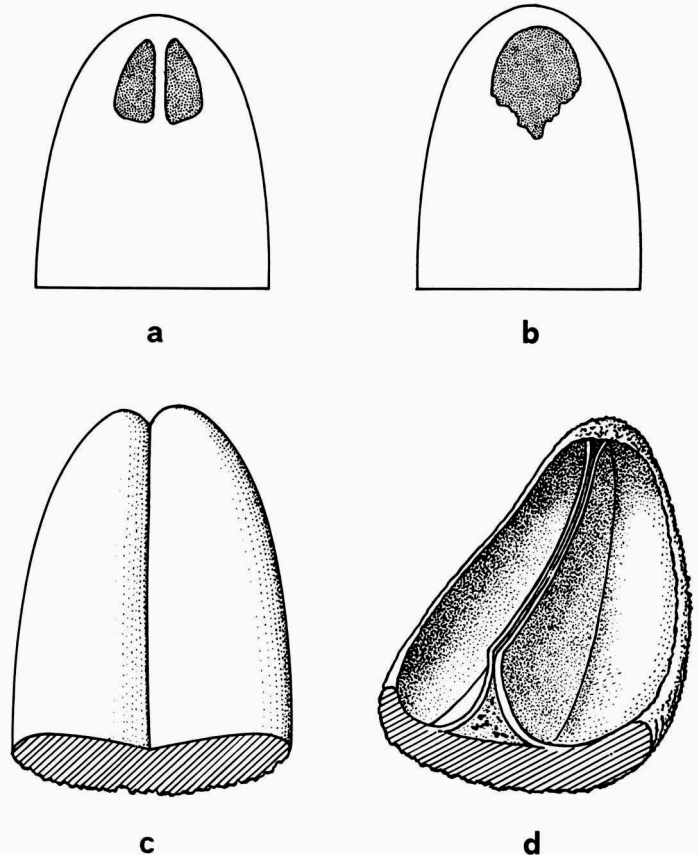

Fig. 6. a, b. palate;   c. nasals with suture (juv.);   d. nasals with septum.

The shallow depression in the median sagittal plane (fig. 6c) is not the groove where a non-ossified septum started; it is the suture of nasals belonging to a sub-adult specimen.

The fairly large suture in nasals, described by Thenius, Azzaroli (1962a) and others as female *Dicerorhinus etruscus* or *Dicerorhinus megarhinus* makes them suspect. Very probably all these fragments belong to young *Dicerorhinus etruscus* of indeterminable sex. The synostosis between the facial bones was not yet complete, resulting in the rupture between nasals and frontals.

The Environment

In a howling blizzard two giants plough their way through an arctic landscape consisting of endless plains filled with deep snowbanks. This is the way *Mammuthus mammuthus* and *Coelodonta antiquitatis* are usually depicted, plodding to their sad end.

Even if we accept these two species as animals of the open periglacial tundra or cold treeless steppe, their extinction is a striking contrast to the ecological success of surviving species of Pleistocene origin from these areas (e.g. *Ovibos moschatus, Rangifer tarandus*).

Tolerance for low temperatures is common among mammals. It is shared by Rhinocerotidae. On a December day in 1966, in cold sleety rain, I saw the herd of *Rhinoceros unicornis* in the Basle Zoo out in the open, active and unconcerned, in better condition than the only visitor in a deserted zoo, myself.

Of course there is a limit to this tolerance. But usually this limit is reached indirectly because the animal's principal food sources disappear, not directly as an effect of the drop in temperature.

The extinction of the lion in Eurasia can be accredited to man in several ways. By overhunting: the lion as a dangerous predator and as a status symbol (game of kings), but also by extermination of its normal prey. Temperature had nothing to do with it.

Kurtén (1968) suggests overkill as an explanation of the disappearance of *Ovibos moschatus* in postglacial Eurasia: A whole herd, defending its young effectively against carnivores and arctic weather by forming a 'living wall' around them, becomes vulnerable to attack by spear or bow and arrow. The species has found a refuge in Northern America and Greenland, in arctic regions where man followed much later.

As mentioned, *Coelodonta antiquitatis* for unknown reasons never crossed the Bering land bridge.

The cave paintings of W. Europe might be an indication that it became extinct by the hand of man, confined to a shrinking ecological niche without a route of escape to the arctic regions of the New World.

If we want to associate our Quaternary rhinoceroses with the changes in temperature we shall have to examine the succession of vegetation belts. If there are indications of close ties between species and vegetation we can evaluate its place in a continually changing landscape.

The feeding habits of modern Rhinocerotidae have been investigated by several authors (Sody 1941, Zeuner 1934, Hoogerwerf 1970).

Diceros bicornis is mainly a browsing animal, stooping to grazing only when browse is insufficient or absent. The food is brought into the mouth by the prehensile upper lip with little or no assistance from the lower lip. The animal has no preferred feeding time (day/night). When hungry it looks for food. Most of its time in between is spent resting in the shade.

Ceratotherium simum is not only different in being an exclusively grazing animal, it is also, in spite of its larger bulk, the more active of the two, resting only in the heaviest heat of the day. At other times it moves around like an oversized lawn mower, both jaws cropping the grass, ingesting it with both lips.

These differences in feeding are reflected in

a) The larger, very hypsodont teeth of *Ceratotherium simum*. According to Dougall, Drysdale and Glover (1964) in Kenya the average silica content of the dry matter of the grasses is 4.95% against 0.56% (leguminous) - 1.46 (non leguminous) of the dry matter of the browse.

b) The sturdier symphysis of the mandible of *Ceratotherium simum*, showing the role of the (heavier) mandible to be much more active.

c) The angle y, 95 - 113 in *Ceratotherium simum* (median 109), 72 - 100 in *Diceros bicornis* (median 89).

Of our fossil species, the mandible of *Dicerorhinus hemitoechus* has about the same symphysis as that of *Ceratotherium simum*. The angle y is even larger (110 - 120, median 118). The teeth are large but not as large as the pillars of *Ceratotherium simum*. This is probably a consequence of the difference in SiO_2 content between tropical and northern steppe. The two species share the form of the large, hanging head and the mandible. Apparently *Dicerorhinus hemitoechus* is the only exclusively grazing species among Pleistocene Dicerorhines. It is sometimes found in the same deposits as *Dicerorhinus kirchbergensis* or *Coelodonta antiquitatis*.

Dicerorhinus kirchbergensis has often been described as an adaption to the open steppe developed from *Dicerorhinus etruscus*. The skull of *Dicerorhinus kirchbergensis* is heavier, but there is no significant difference in size or shape. The mandible however is much heavier.

The size of this species and the heavy mandible suggest an animal much like *Diceros bicornis*. *Dicerorhinus kirchbergensis* was an interglacial animal on the edge of forest and steppe, capable of subsisting part of the year on grass if the browse was no longer sufficient. Its grazing counterpart on the open steppe was *Dicerorhinus hemitoechus*.

The teeth of *Dicerorhinus kirchbergensis* are more like those of *Dicerorhinus megarhinus* than *Dicerorhinus etruscus*. This fact makes any evolution from *Dicerorhinus etruscus* to *Dicerorhinus kirchbergensis* unlikely. A direct evolution however from *Dicerorhinus megarhinus* is impossible: *Dicerorhinus megarhinus* disappears at the Plio-Pleistocene border, whereas *Dicerorhinus kirchbergensis* appears much later. There is in W. Europe no *Dicerorhinus kirchbergensis* in the Lower Pleistocene. The often cited dentition from Tegelen is too small for *Dicerorhinus kirchbergensis* and the mandible has the typical slender *Dicerorhinus etruscus* symphysis (Bernsen 1927, Loose 1960). Nor is *Dicerorhinus etruscus* the 'daughter species' of *Dicerorhinus megarhinus* (Kurtén 1968, p. 142). Again, size and dentition make this extremely unlikely.

This leaves us with only one possibility: all these animals are immigrants from the East, representing a succession of fauna waves. During the Pleistocene, the sealevel drops to its lowest point during a pleniglacial. This makes direct immi-

gration from Africa over landbridges unlikely for typical interglacial species dependent on an interglacial flora as food source.

Dicerorhinus kirchbergensis is the successor of the 'warm' Dicerorhinus etruscus, almost, but not directly accompanied by Dicerorhinus hemitoechus. Just as the African species, browser and grazer are close ecological neighbours. Here also the browser (Dicerorhinus kirchbergensis) was potentially a grazer, as in the case of Diceros bicornis.

The succession of Dicerorhinus kirchbergensis - Dicerorhinus hemitoechus - Coelodonta antiquitatis, three different animals following each other in a short period, living near each other or replacing each other until they disappear before the cold of the Weichsel-glaciation is more than a succession of animals with different feeding habits. In the ratio Dicerorhinus kirchbergensis - Dicerorhinus hemitoechus we see the inverse ratio of areas occupied by woody savanna and open steppe respectively; Coelodonta antiquitatis is the cold successor of both species, disappearing from W. Europe about the Second Interstadial of the last glaciation (Zeuner 1959, p. 328). Unlike his measurements of Ceratotherium simum and Dicerorhinus, Zeuner's measurements of Coelodonta show no adaptation to grazing. Yet it is a typical animal of the cold steppe. Zeuner explained this by postulating that Coelodonta (y = ca. 90) walked with neck and head downward. But Zeuner also knew of the difficulties of life in a cold climate on the steppe. He mentions the conifer needles from the rhinoceros deposits at Starunia (Nowak c.s. 1930). Coelodonta, with its large occipital crest, was a dual-purpose animal, much more so than Dicerorhinus kirchbergensis. It was able to retreat into the conifer forests of the mountains or to cross the mountains where Dicerorhinus kirchbergensis, used to feeding on leaves and grass, could not go. The Alps, Pyrenees or Caucasus are no barrier for a determined rhinoceros. The decisive factor is the kind of food available.

The vegetation and climatological cycles of the Pleistocene (warm, cool, glacial, interstadial, glacial, interglacial) are well documented for the N.W. European area from palynological evidence (v. d. Hammen e.a. 1971). Especially for the second half of the Pleistocene we have a wealth of data about the coming and going of the vegetation belts. A simplified reconstruction of the vegetation and landscape covering W. Europe during an interglacial phase would look as follows: starting in the North there will be a narrow strip of open tundra, grading from shrub tundra into boreal birch-pine forest (taiga), replaced to the South by conifers and eventually deciduous forest. These forests fill W. Europe from the North to the mountain-chains (Pyrenees, Alps, Carpathians) in the South.

During the extreme cold (pleniglacial) the sequence is: polar desert, tundra (steppe- and shrub tundra), with some birch-pine forest surviving in the extreme South in sheltered valleys of local ranges and foothills of the mountain belt (fig. 7).

South of the mountains, the interglacial forest is replaced by steppe. Here a narrow montane forest belt remains between the lower steppe and the alpine steppe belt.

As far as we know the pleniglacial needs a long time to reach its height, while the transition to interglacial conditions is more abrupt: ice melts swiftly - the accumulation of the ice for glacial conditions takes a long time. In this changeover from warm to cold we find the nightmares of palaeontology and stratigraphical geology. Are the Mosbach sands late interglacial or early glacial? Or both?
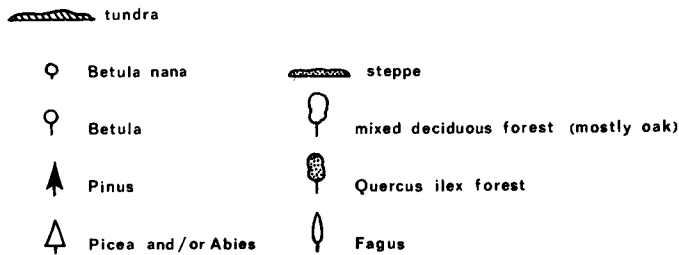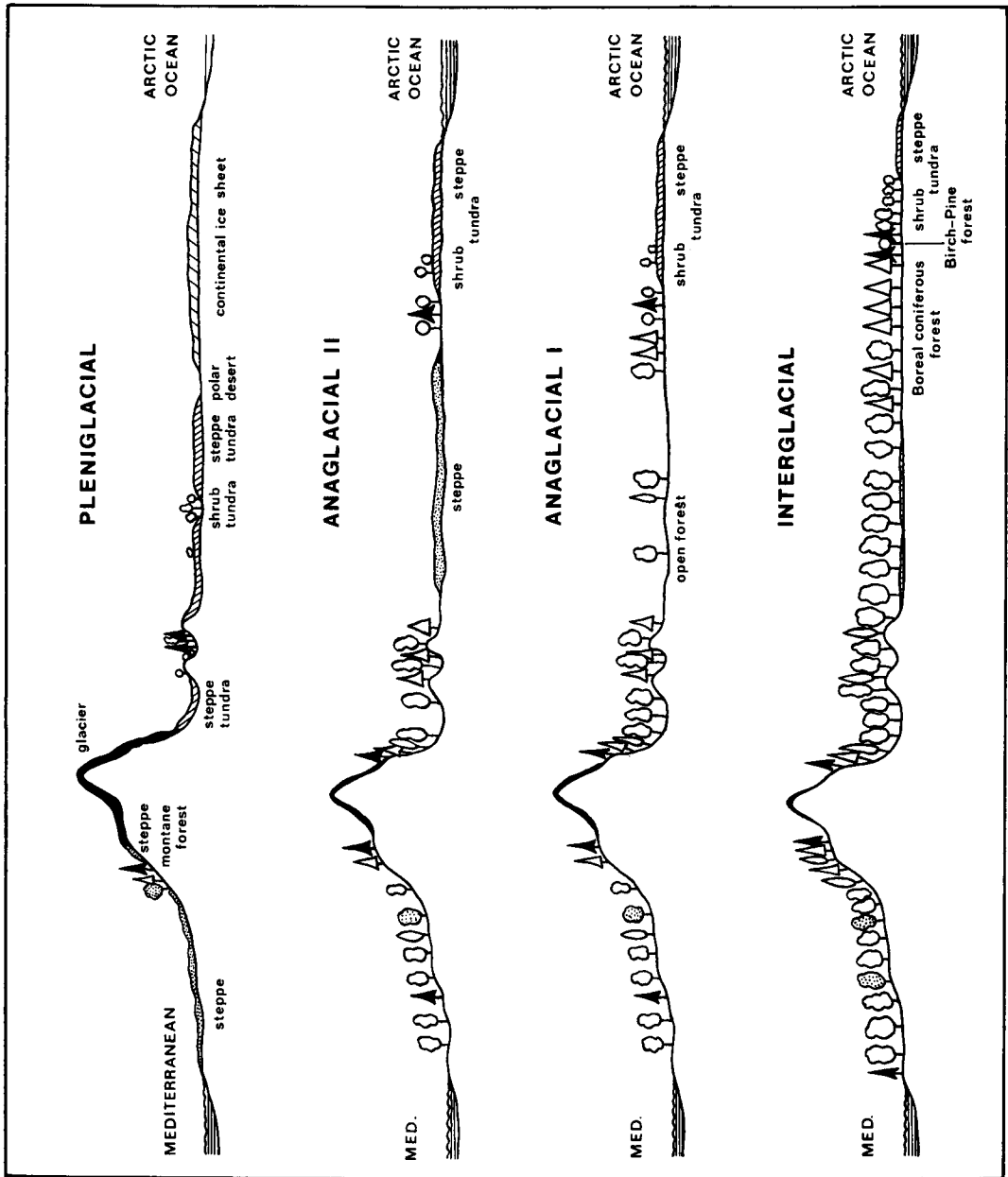
Fig. 7. Vegetation belts and the glacial cycle. Adapted from van der Hammen, Wijmstra & Zagwijn (1971, p. 403, fig. 6).

For this change-over, characterized by a fluctuating climate, decrease of the forest, increase of open vegetation (Ericales, steppe elements, tundra) the name anaglacial has been proposed (Brüning 1972).

During each cold period there is an E - W and a N - S movement of these vegetation belts. Each interglacial (or interstadial) brings the reverse: the steppe and tundra retreat east- and northward, to be replaced by forest, the hardier species (mainly conifers) from groves in sheltered refuges, the others from the southern mountains.

Fig. 8 is an attempt to coordinate the vegetation belts with the succession of rhinoceroses, using the few data known or inferred.

tundra	birch-pine forest	cold steppe	temperate steppe	savanna	open deciduous forest

Fig. 8.   The rhinoceroses and the vegetation belts.

Fig. 9.   Vegetation, stratigraphy and the rhinoceroses. Stratigraphical part adapted from van der Hammen, Wijmstra & Zagwijn (1971, p. 406, table 1).

The range and subdivision of the Pleistocene is largely a matter of personal preference, depending on radiometric (radiocarbon, K-Ar etc.) and palaeomagnetic data. None of these are very dependable. Berggren & Van Couvering (1974, p. 86) quote Van Hinte (1969) observing that 'a succession of phylozones is the most reliable tool in correlation and age determination, because it directly reflects the irreversible evolution of life on earth providing maximum exclusion of the environmental factor'. Even if we accept this teleological tenet, the last six words are not exactly going to help us with the delimitation of an epoch that starts by definition with the first indication of *severe climatic deterioration* (not glaciation as Berggren & Van Couvering seem to think).

The faunules of the Lower Pleistocene abound with local species and subspecies. Correlation is difficult. Their chronostratigraphic position is often uncertain or a matter of geographical ukases. According to Vangengeim e.a. (1966, p. 156) the Tologoj complex of Transbaikalia has a fauna of the Tiraspol type (= 'Alpine Mindel'). Frenzl (1968, p. 140) gives the age of the same fauna as Praetiglian.

Since we are far from reaching any agreement regarding the stratigraphy even of the last three million years, I have kept to the local stages and dates accepted by the majority of the geologists for the Netherlands.
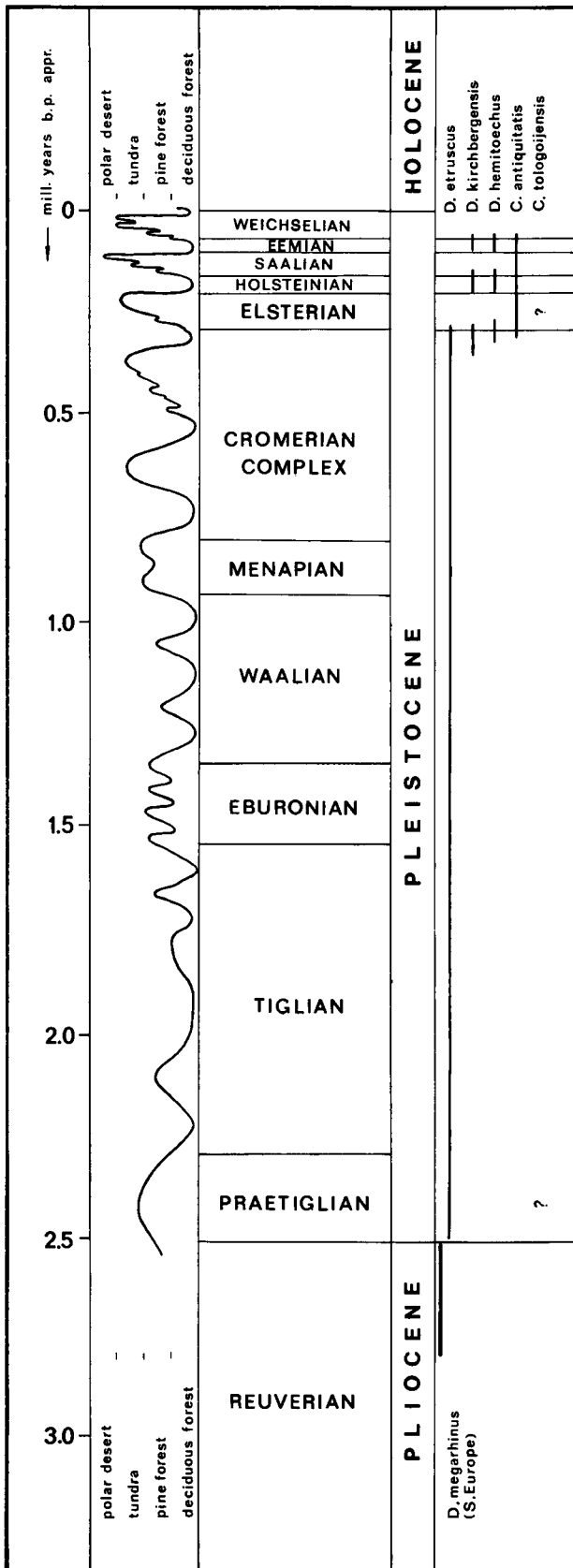
Fig. 9

Specialists on Pleistocene rhino's agree on very few of the facts concerning systematics or evolution.

One of these facts is that *Dicerorhinus kirchbergensis* has been in W. Europe since the lower Pleistocene (Bernsen 1927), an error handed down through the years from handbook to handbook on Pleistocene mammals.

Another is the evolution of grazing species from browsing species, as adaptations to the colder climate. This sounds plausible. However, as has been explained, a direct phylogenetic line *Dicerorhinus megarhinus - etruscus - kirchbergensis - hemitoechus* is improbable, to put it mildly.

Let us consider the evidence.

The angle y is the important factor in distinguishing grazers and browsers. This angle is by definition the angle between palate and basion + opisthion, basion and opisthion being the lowest and highest point respectively of the intersection of the foramen magnum and the median sagittal plane.

Now it is a curious fact that, as y gets smaller, the basion remains in the same position while the opisthion occupies an ever higher position on the occiput. Thus the foramen magnum changes from an ellipse, with the larger axis horizontal (e.g. *Dicerorhinus hemitoechus*), to an irregular triangle, capped by the opisthion halfway the occiput (*Coelodonta antiquitatis*).

When this upper triangular part of the foramen magnum is filled with putty, leaving only the exoccipital part, the angle y becomes as large as in the grazing species. In other words: the large angle y between the palate and the exoccipital region is a constant for the tandem-horned Rhinocerotidae. The angle y is largest in the grazing species (119° in *Dicerorhinus hemitoechus*), where the opisthion is situated on the exoccipitals, and changes to ever smaller proportions as the opisthion lies in a higher position on the more or less vertical supraoccipital region (88° in *Dicerorhinus etruscus*).

We are asked to believe that the evolution from browser to grazer is a process in which the foramen magnum changes from a large acute triangle, with its apex far above the condyles, to its normal size between the condyles, as new bone is formed to close the gap in the occiput. This may be possible, but I find it rather implausible.

Tertiary grazing ancestors with a large angle y and a normal, oval foramen magnum are not unlikely on a warm open steppe of Mio/Pliocene times.

The browsing species in that case are later offshoots, adaptations to the closing in of the woodlands, the change from steppe to open or woody savanna.

However, this remains pure speculation owing to the lack of Tertiary rhinoceros skulls complete enough to allow measurements of y.

Table 9

Ceratotherium simum simum (Burchell)

			l	st	o	i	n	p	po	y	m	x	z
BMNH 1852-12-9-1	South Africa	purch. Brandt	70.1	3	66	72	150	—	—	—	46	-20	5.5
RMNH 19604	Cape Colony		70.5	2.5	64	64	156	24	85	110.5	45	-19	7.8
RMNH 19603	Cape Colony		71	3.5	55	55	150	31	90	108	44	-11	7.9
BMNH 51.12.23.1 type	South Africa	purch. at Stevens Sale	72.5	2	57	57	152	—	—	—	47	-10	7.8
BMNH 1948.1.28.1	South Africa	Rothschild coll.	72.5	1.5	59	59	152	25	88	111	50	-9	5.6

Ceratotherium simum cottoni (Lydekker)

			l	st	o	i	n	p	po	y	m	x	z
RMNH 13120	N.W. Uganda, Obongi, W. Nile Distr.		60.5	6.7	73	73	142	43	65	95	46	-27	5.5
BMNH 1948.1.28.2	Uganda, Lado Enclave	Rothschild coll.	66	5.2	67	67	155	33	—	113	35	-32	5.1
BMNH 25.5.23.1.	Uganda, Lado, Sudan Boundary		70	7	68	72	152	31	75	104	42	-30	5.3
RMNH 13119	Uganda, Obongi, W. Nile Distr.		71.5	6.2	77	77	156	31	76	98	50	-27	5.9
RMNH 13121	Uganda, Obongi, W. Nile Distr.		71.5	6.7	77	77	158	30	73	99	49	-28	5.1
BMNH 1963.8.13.3	Uganda, W. Madi Distr.	Brooks coll.	72.5	5.5	75	75	160	25	79	111	36	-39	7.2
BMNH 30.7.26.1	Congo		75.5	5	67	67	156	28	82	110	42	-25	6.4

Table 10

Diceros bicornis (L.)

	l	st	o	i	n	p	po	y	m	x	z
BMNH 1937.7.23.1	—	2.5	69	69	—	—	71	90	48	– 21	8.3
BMNH 1962.7.6.6.	52	3.5	68	68	138	35	63	88	41	– 27	6.8
BMNH 1918.6.17.1	52.5	2.2	70	70	131	32.5	63	96	35	– 35	5.5
BMNH 1876.9.26.6	53.5	1.5	65	74	—	—	62	89	37	– 28	4.5
BMNH 1876.2.15.5	54.5	3.5	67	69	—	31	70	—	44	– 23	7.5
Private coll. (1)	54.5	2.5	70	70	142	—	60	91	44	– 26	6.8
BMNH 1884.8.1.1	55	1.3	63	63	—	35.25	67	72	54	– 9	7.8
BMNH 1869.2.2.14	55.2	3	64	66	—	—	73	98	43	– 21	9.0
BMNH 1948.1.28.6	55.5	3.0	68	68	138	28	70	96	42	– 26	6.0
BMNH 1874.11.2.2	55.8	2.5	55	59	—	27.25	76	95	45	– 10	6.5
BMNH 1948.1.28.3	56	3	74	79	—	—	58	89	43	– 31	7.6
BMNH 1902.11.18.6	56	1.0	70	70	140	27.5	68	100	37	– 23	6.9
BMNH 1902.11.8.7	56	2.8	69	69	139	30	68	87	47	– 22	7.5
Private coll. (2) young ad.	56	1.5	75	75	139	—	62	96	41	– 34	4.5
BMNH 1962.7.6.3	56	1.8	72	72	132	—	64	88	47	– 25	5.8
BMNH 1962.7.6.1.	56.8	2.0	67	67	140	33.5	67	89	47	– 20	6.3
BMNH 1947.12.29.4. young ad.	57	1.5	64	64	137	—	74	83	52	– 12	9.7
BMNH 1962.7.6.5	57.5	3	67	67	135	36	60	90	44	– 23	6.9
BMNH 1907.2.26.1	58	2.0	67	67	136	32.66	67	87	50	– 17	8.5
BMNH 1948.1.14.3	58	1	61	64	145	31	74	89	47	– 14	8.5
BMNH 1948.1.28.7	58	3.0	75	75	138	34	55	84	43	– 32	7.5
BMNH 1933.4.2.1	58	1.2	74	74	140	—	—	—	—	—	6.3
BMNH 1947.12.29.3	58.5	1.8	78	81	136	32.25	54	86	49	– 29	8.4
BMNH 1962.7.6.4	58.5	4.0	81	81	140	32.5	55	93	46	– 35	7.1
BMNH R3381/67	59	—	63	63	156	27.25	76	91	37	– 26	7.4
BMNH 1919.7.15.511	60	—	65	65	—	—	—	88	44	– 21	8.0
RMNH 19598	61.5	0.5	67	67	—	31.5	73	88	48	– 21	7.6
(Jentink, cat. a)											

Table 11

Dicerorhinus sumatrensis (Fischer)

		l	st	o	i	n	p	po	y	m	x	z
BMNH 1901.8.15.1	B.N. Borneo, Suan Lambah ♀ juv.	46.9	2	86	86	150	27	52	87	56	−30	4.5
BMNH 1461 b	Sumatra	47.5	1.8	80	80	155	25	66	97	50	−30	5.9
RMNH cat. a	Sumatra, Padang Besi ♀ subad.	49	1.2	95	95	162	28	57	87	64	−31	4.8
RMNH cat. c	Sumatra, Tandjung Morawa (Deli)	50.3	1.0	90	90	160	30	67	94	60	−30	7.5
RMNH cat. g	Sumatra	51	1.2	96	96	161	22	69	97	55	−41	6.5
BMNH 1921.2.8.3	Malaya, Ulu Benus, Pahang ♀	51	1.5	77	77	160	27	64	97	42	−35	7.1
RMNH cat. b	Sumatra ♂ young ad.	51.2	0.8	88	88	155	29	54	87	60	−28	5.5
BMNH 1921.2.8.4	Malaya, Ulu Benus, Pahang	51.8	0.5	72	77	154	—	74	105	45	−22	8.4
BMNH 1894.9.24.1	S.W. Sumatra, Siboga ♂	52	1.5	70	78	155	28	81	90	56	−14	6.0
BMNH 1948.12.20.1	Rothschild coll. Tring　subad.	52.2	1.3	74	77	156	23	78	97	55	−19	8.1
BMNH 1949.1.11.1	Rothschild coll. Tring	53	1.3	82	88	156	25	68	94	62	−20	7.2
BMNH 1461a	Burma, Pegu	53	1.2	78	78	152	27	72	102	51	−27	4.4
BMNH 1921.2.8.2	Malaya, Pahang ♂	54.3	0.5	77	77	155	26	68	107	40	−37	ca. 7.5

Table 12

Dicerorhinus etruscus (Falc.)

		l	st	o	i	n	p	po	y	m	x	z
MNB Se561	Senèze	61	2.5	81	81	150	25	—	104	50	−31	3.6
Mainz 1963/156	Mosbach	65	0.2	74	74	150	33	65	93	51	−23	4.7
Landesmus. Darmstadt	Mauer	ca. 67	2.1	79	81	155	—	—	—	46	−33	4.7
StMN Stuttgart 16326	Bammental (Mauer)	ca. 69	2.4	75	75	ca. 160	—	75	ca. 89	52	−23	4.2
Mainz 1945/172	Mosbach	69	−0.2	70	70	150	—	ca. 76	95	48	−27	5.3
Mainz 1956/963	Mosbach	ca. 70	1.0	73	73	ca. 140	—	ca. 75	ca. 93	52	−21	—
Mainz 1956/62	Mosbach	71	1.5	79	79	150	—	78	ca. 100	55	−24	3.4
Priv. coll. Württemberg		72	3.3	76	76	147	30	76	88	57	−19	9.2
Mainz 1958/764	Mosbach	73.5	1.0	75	75	158	—	78	—	42	−33	7.6

Table 13

Dicerorhinus kirchbergensis (Jäger)

		1	st	o	i	n	p	po	y	m	x	z
StMN Stuttgart 16275	Steinheim	62.2	—	—	—	ca. 145	—	—	95	ca. 53	—	ca. 3.5
S.f.N. Karlsruhe	Daxlanden	67.5	1.0	77	77	150	—	72	99	51	−26	5.6
Mainz 1956/962	Mosbach	68	1.0	70	70	155	—	ca. 80	ca. 93	50	−20	4.8
StMN	Altrip	ca. 78	2.0	67	67	ca. 145	—	72	ca. 101	46	−21	3.8

Table 14

Dicerorhinus hemitoechus (Falc.)

		1	st	o	i	n	p	po	y	m	x	z
BMNH 27836		ca. 65	0.3	—	—	ca. 160	—	—	—	—	—	4.0
BMNH 40946	Minchin Hole	—	—	47	47	—	—	—	—	38	−9	5.0
BMNH 112 O.C. Lydekker (1886, p. 120) 'etruscus'		—	0	49	49	—	—	—	—	42	−7	—
BMNH 20013 Falconer 'Northampton skull'		—	0.6	56	56	—	—	—	ca. 120	35	−21	6.0
BMNH 45206	Ilford, Essex	63	0.1	55	55	ca. 160	—	—	ca. 118	41	−14	5.0
IGF 10792		63.9	0	61	61	149	—	—	ca. 113	38	−23	3.5
MGP Pisa 12038		65.0	−1.0	55	55	143	—	—	—	37	−18	3.7
BMNH M 5113	Grays, Essex	65.5	0.2	55	55	145	—	—	—	44	−11	4.8
IGF 1105	Val di Chiana	65.5	1.2	55	55	141	—	—	115	35	−20	1.8
RGM 93302	Zwarte Water	69.6	0.5	47	47	146	24	93	119	28	−19	3.4
StMN Stuttgart 16938	Steinheim	72.0	0	53	53	158	22	—	116	36	−17	5.8
BMNH 45205		72.5	0.1	51	51	ca. 150	—	ca. 110	ca. 110	—	—	4.2

Table 15

Coelodonta antiquitatis (Blum.)

	l	st	o	i	n	p	po	y	m	x	z
Pisa 1852 no. 19 — Kurgan, foce Lena	62	—	ca. 52	ca. 52	155	—	—	—	48	ca. − 4	—
GMIU 1959 P112 — Klompenwaard	68.4	0	48	48	151	32	110	92	52	+ 4	7.2
RGM 12316 — Nieuwe Maas	69.9	—	—	—	154	—	—	92	53	ca. + 1	10.0
StMN Stuttgart 19044 — Stuttgart	70.1	—	—	—	153	—	—	ca. 98	54	—	8.5
RGM 33347 — Botlek	70.8	− 2.0	52	52	155	—	95	96	51	− 1	10.2
RGM 40321 — N.O. Polder	71.0	− 1.0	43	46	160	33	109	102	46	+ 3	9.8
StMN Stuttgart 99 — Stuttgart	71.5	—	53	53	159	—	—	ca. 99	48	− 5	9.1
StMN Stuttgart 1019 — Stuttgart	72	—	53	53	—	—	—	—	56	+ 3	11.5
SfN Karlsruhe — Lampertheim	74.4	− 0.5	45	45	153	—	—	82	42	− 3	6.7
Zool. M. Amsterdam 1004 — Schiermonnikoog	76.8	0	52	52	150	30	104	93	51	− 1	12.0

References

Abel, O., Die Stämme der Wirbeltiere. Berlin, Leipzig. W. de Gruyter: I-XVIII, 1-914, 669 figs.

Adam, K. D., 1961. Die Bedeutung der pleistozänen Säugetier-Faunen Mitteleuropas für die Geschichte des Eiszeitalters. Stuttg. Beitr. z. Nat. a. d. Staatl. Mus. f. Nat. in Stuttgart, 78: 1-34, 17 figs.

——, 1964. Die Grossgliederung des Pleistozäns in Mitteleuropa. Stuttg. Beitr. z. Nat. a. d. Staatl. Mus. f. Nat. in Stuttgart, 132: 1-12.

Ambrosetti, P., 1972. Lo scheletro di *Dicerorhinus etruscus* (Falconer) di Capitone (Umbria meridionale). Geologica Romana, XI: 177-197, 2 figs., 7 pls.

Anstedt, D. T., 1859. On the Geology of Malaga and the Southern Part of Andalusia. Quart. Journ. Geol. Soc., 15: 585-604, 10 figs.

Arambourg, C., 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Publ. Serv. Carte Géol. Alg., Paléont., 4: 1-161, 52 figs., XVIII pls.

——, 1962. Les Faunes Mammalogiques du Pléistocène d'Afrique. In: Problèmes Actuels de Paléontologie (Evolution des Vertébrés), Colloques C.N.R.S., 104: 369-376.

Azzaroli, A., 1962a. Rinoceronti pliocenici del Valdarno Inferiore. Palaeontogr. Italica, 57 (N.S. 27): 11-20, pls. 6-15.

——, 1962b, Validità della specie *Rhinoceros hemitoechus* Falconer. Palaeontogr. Italica, 57 (N.S. 27): 21-34, figs. 1-7, pls. XVI-XX.

Bate, D. M. A., 1937. The fossil fauna of the Wady El-Mughara Caves. In: The Stone Age of Mount Carmel, vol. 1 part II. Palaeontology: 137-240, 8 figs. Oxford, Clarendon Press.

Bernsen, J. J. A., 1927. The Geology of the Teglian Clay and its Fossil Remains of Rhinoceros. 's-Hertogenbosch, C. N. Teulings: 1-108, 12 pls.

Bonifay, M. F., 1961. Etude des Restes de Rhinocéros de Merck provenant de Meyrargues (Bouches du Rhône). Paris, Ann. de Pal., 47: 77-89, figs. 1-9.

Boylan, P., 1967. *Didermocerus* Brookes 1828 v. *Dicerorhinus* Gloger 1841 (Mammalia: Rhinocerotidae) and the Validity of A Catalogue of the Anatomical and Zoological Museum of Joshua Brookes, 1828. Bull. Zool. Nomencl., 24, 1: 55-56.

Brandt, J. F., 1849. De *Rhinocerotis antiquitatis*, seu *tichorhini*, seu *Pallasii* structura externa et osteologica observationes, e reliquiis, quae in museis Petropolitanis servantur erutae. Mém. Ac. Imp. Sci. St. Pétersbourg, ser. VI Sci. Math. Phys. Nat. VII, 2, Sci. Nat. V, Zoologie et Physiologie: 161-416, pls. I-XII, XIIa, XIII-XXIV.

——, 1877. Versuch einer Monographie der Tichorhinen Nashörner nebst Bemerkungen über *Rhinoceros leptorhinus* Cuv. u.s.w. Mém. Ac. Imp. Sc. St. Pétersb., Sér. VII, XXIV, 4: 1-135, XI pls.

Bronn, H. G., 1831. Über die Fossilen Zähne eines neuen Geschlechtes aus der Dickhäuter-Ordnung: *Coelodonta, Höhlenzahn*. Jahrb. für Mineralogie, Geognosie und Petrefaktenkunde, 2: 51-61, pl. I. Heidelberg, Georg Reichard. (In the index: Coelodonta, Hohlzahn)

Brüning, H., 1972. Das Rhein-Main-Gebiet in den quartäreiszeitlichen Periglazialbereichen. Jbr. u. Mitt. oberrh. geol. Ver., NF54: 79-100, 14 figs.

Chow Ben-Shun, 1963a. On the skull of *Dicerorhinus choukoutiensis* Wang from Choukoutien Location 20. Vertebr. Palasiat., 7, 1: 62-70, 1 pl.

——, 1963b. A new species of Dicerorhinus from Yushe, S. E. Shansi, China. Vertebr. Palasiat., 7, 4: 325-330, figs. 1-3.

Christol, J. de, 1834. Recherches sur les grandes espèces de rhinocéros fossiles. Montpellier, J. Martel: 1-70, 31 figs. (non vidi)

Crusafont Pairó, M., 1961. El Cuaternario Español y su fauna de mamíferos. Ensayo de síntesis. Speleon, 12, 3-4: 3-21, figs. 1-3.

Czyzewska, T., 1962. Upper dentition of *Dicerorhinus mercki* (Jäger) from Szczesliwice near Warzawa, Poland. Acta Palaeont. Pol., 7, 1-2: 223-234, 1 fig., 1 pl.

Dawkins, W. B., 1867. On the dentition of *Rhinoceros leptorhinus* Owen. Quart. Journ. Geol. Soc., 23: 213-227, pl. X.

——, 1868. On the dentition of *Rhinoceros etruscus* Falc. Quart. Journ. Geol. Soc., 24: 207-218, pl. VII-VIII.

——, 1880. The Classification of the Tertiary Period by means of the Mammalia. Quart. Journ. Geol. Soc., 36: 379-405.

Dietrich, W. O., 1953. Neue Funde des Etruskischen Nashorns. Geologie (Berlin), 2: 417-430, 1 fig.

Dollman, G. & J. B. Burlace (eds.), 1935. Rowland Ward's Record of Big Game. African and Asiatic Sections giving the distribution, characteristics, dimensions, weight, and Horn & Tusk Measurements. 10th ed. London, Ward: I-XII + 1-408, ill.

Dougall, H. W., V. M. Drysdale & P. E. Glover, 1964. The chemical composition of Kenya browse and pasture herbage. E. Afric. Wildlife Journ., 2: 86-121, figs. 1-5.

Falconer, H., 1859. vid. Anstedt, D. T., 1859: (Appendix)

——, 1868. On the European Pliocene and Post-Pliocene Species of the Genus Rhinoceros. In: Palaeontological Memoirs and Notes of the late Hugh Falconer, A. M., M. D., compiled and edited by Charles Murchison, II: 309-404, pls. 15-32.

Frenzl, B., 1968. Grundzüge der pleistozänen Vegetationsgeschichte Nord-Eurasiens. Wiesbaden, Steiner Verl.: 1-326, 66 figs., 17 pls.

Freudenberg, W., 1914. Die Säugetiere des älteren Quartärs von Mittel Europa mit besonderer Berücksichtigung der Fauna von Hundsheim. Geol. u. Pal. Abh., N. F. 12 (16), 4/5: 1-219 (455-674), figs. 1-69, pls. 1-20 (29-48).

Gee, E. P., 1959. Report on a survey of the rhinoceros area of Nepal. Oryx, 5: 59-85.

Gerth, H., 1923. Neue Funde von Rhinoceros antiquitatis in der Maasmündung. Verh. Geol. Mijnb. Gen., geol. ser. 7, 2: 99-104, figs. 1-4.

Gloger, C. W. L., 1842. Gemeinnütziges Hand- und Hilfsbuch der Naturgeschichte 1: 1-496. Breslau, Aug. Schulz & Comp.

Groves, C. P., 1965. Description of a new subspecies of Rhinoceros from Borneo Didermocerus sumatrensis harrissoni. Säugetierkundl. Mitt., 13, 3: 128-131.

——, 1967. Geographic variation in the black rhinoceros Diceros bicornis (L., 1758). Zeitschr. f. Säugetierk., 32 (5): 267-276, 2 figs.

Guérin, C., 1974. Les trois espèces de rhinocéros (Mammalia, Perissodactyla) du gisement pléistocène moyen des Abîmes de la Fage à Noailles (Corrèze). Nouv. Arch. Mus. Hist. Nat. de Lyon, Ann. 1973, 11: 55-84, pls. 5-17.

Guérin, C., R. Ballesio & H. Meon-Villain, 1969. Le Dicerorhinus megarhinus (Mammalia, Rhinocerotidae) du Pliocène de Saint-Laurent-des-Arbres (Gard). Docum. Lab. Géol. Fac. Sci. Lyon, 31: 55-145, 19 figs.

Hammen, T. van der, T. A. Wijmstra & W. H. Zagwijn, 1971. The Floral Record of the Late Cenozoic of Europe. In: The Late Cenozoic Glacial Ages, Karl. K. Turekian ed.: 391-424, 12 figs., 1 tabl. Yale Univ. Press.

Hilzheimer, M., 1924. Eine neue Rekonstruktion von Rhinoceros antiquitatis Blbch., zugleich ein Beitrag zur Morphologie, Biologie und Phylogenie dieses Tieres. N. Jahrb. f. Min. Geol. Pal., Beil. Bd 50: 490-519, pl. 16.

Hinte, J. E. van, 1969. The nature of biostratigraphic zones. Proc. 1st Int. Conf. Planktonic Microfossils, Geneva, 1967, 2. Leiden, E. J. Brill: 267-276.

Hoogerwerf, A., 1970. Udjung Kulon. The land of the last Javan Rhinoceros. Leiden, E. J. Brill: 1-512, 83 pls., 3 maps.

Hooijer, D. A., 1947. Notes on some fossil mammals of the Netherlands. Arch. Mus. Teyler, Ser. 3, 10, 1: 33-51, 1 pl.

——, 1961a. The fossil Vertebrates of Ksâr 'Akil, a palaeolithic Rock Shelter in the Lebanon. Zool. Verh. Rijksmus. Nat. Hist., 49: 68, 2 pls.

——, 1961b. Middle Pleistocene mammals from Latamne, Orontes Valley, Syria. Ann. Archéol. Syr., XI: 117-132, 24 figs.

——, 1962. The Middle-Pleistocene fauna of the Near East. In: Evolution und Hominisation, G. Kurth ed.: 81-83. Stuttgart, G. Fischer.

——, 1972. A Late Pliocene Rhinoceros from Langebaanweg, Cape Province. Ann. S. Afr. Museum, 59, 9: 151-191, pls. 21-34.

Hooijer, D. A. & B. Patterson, 1972. Rhinoceroses from the Pliocene of Northwestern Kenya. Bull. Mus. Comp. Zool. (Harvard), 144, 1: 1-26, figs. 1-11.

Hopwood, A. T., 1939. Contributions to the study of some African Mammals II. The subspecies of the Black Rhinoceros, Diceros bicornis (L.) defined by the proportions of the skull. Journ. Linn. Soc. London, Zool., 40, 273: 447-457, pls. 10-11.

Hubback, Th., 1939. The Asiatic Two-Horned Rhinoceros. Journ. Mamm., 20, 1: 1-20, 5 figs.

Jäger, G., 1850. Übersicht der fossilen Säugethiere welche in Württemberg in verschiedenen Formationen aufgefunden sind. Verh. Kaiserl. Leopold. Carol Akad. der Naturf., 14: 767-932, 5 pls.

Jentink, F. A., 1887. Catalogue Ostéologique des Mammifères. Muséum d'Histoire Naturelle des Pays-Bas, 9: 1-360, 12 pls.

Jernakov, V., 1958. Exhibition of Pleistocene Mammals of the Heilungchiang province in Harbin. Vert. Palasiat, II, 2/3: 171-172, 1 fig.

Jörg, E., 1971. Ein Cranium von *Coelodonta antiquitatis* (Blumenb.) (Perissodactyla, Mamm.) aus pleistozänen Neckarkiesen von Mannheim-Käfertal. Abh. hess. L.-Amt Boden-forsch., 60: 83-88, 1 pl.

Kaup, J. J., 1841. Akten der Urwelt oder Osteologie der urweltlichen Säugethiere und Amphibien. Darmstadt, publ. by the author.

Klingel, H. & U., 1966. The Rhinoceroses of Ngorongoro Crater. Oryx, 8, 5: 1-5, 1 fig., pls. 7-8.

Krumbiegel, I., 1965. Das Kopenhagener Sumatranashorn, Säugetierk. Mitt., 13, 3: 97-100, figs. 1-6.

Kubiak, H., 1969. Über die Bedeutung der Kadaver des Wollhaarnashorns von Starunia. Ber. deutsch. Ges. geol. Wiss., A. Geol. Pal., 14, 3: 345-347.

Kurtén, B., 1968. Pleistocene Mammals of Europe. London, Weidenfeld & Nicholson: 1-317, 111 figs.

Lamprey, H. F., 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. E. Afr. Wildlife Journ., 2: 1-46.

Loose, H., 1960. Dicerorhinus kirchbergensis in the Tiglian? Proc. Kon. Ned. Akad. Wetensch., (B) 63,3: 380-382.

——, 1961. Dicerorhinus hemitoechus (Falc.) in the Netherlands. Proc. Kon. Ned. Akad. Wetensch., (B) 64, 1: 41-46, figs. 1-5.

Lydekker, R., 1886. Catalogue of the Fossil Mammalia in the British Museum (Natural History), III: 90-161, figs. 12-20, (Rhinocerotidae)

Martin, P. S., 1967. Prehistoric Overkill. In: Pleistocene Extinctions. The Search for a Cause. P. S. Martin & H. E. Wright jun. ed., Proc. VII Congr. Int. Ass. Quat. Res., 6: 75-120, figs. 1-4. New Haven/London, Yale University Press.

Maurette, L., 1910. Etude paléontologique du Rhinoceros leptorhinus du Pliocène inférieur de Millas (Pryrenées orientales) et des faunes du Pliocène inférieur en général. Ann. Soc. Linn. Lyon, 57: 1-26, 1 pl. (non vidi)

Mayer, G., 1971. Beiträge zur Geschichte der Badischen Landessammlungen für Naturkunde in Karlsruhe, III. Der Schädel des *Dicerorhinus mercki (kirchbergensis)* (Jaeger) var. *brachycephalus* Schroeder von Daxlanden und seine Geschichte. Beitr. naturk. Forsch. Südw. Dtl., 30, 2: 157-163, 1 fig.

Meyer, H. von, 1831. Letter in: Jahrb. Min. Geogn. Geol. Petrefaktenk. 2: 432-438. Heidelberg, Georg Reichard.

——, 1864. Die diluvialen Rhinoceros-Arten. Palaeontographica, 11: 233-283, pls. 35-43.

Nowak, J., E. Panow, J. Tokarski, W. Szafer & J. Stach, 1930. The second woolly Rhinoceros *(Coelodonta antiquitatis* Blum.) from Starunia, Poland. (Geology, Mineralogy, Flora and Fauna). Bull. Internat. de L'Acad. Pol. des Sci. et des Lettres, Classe des Sc. Math. et Nat., Série B, Suppl. 1930: 1-47, figs. 1-2, pls. 1-10.

Osborn, H. F., 1900. Phylogeny of the Rhinoceroses of Europe. Bull. Amer. Mus. Nat. Hist., 13, 19: 229-267, figs. 1-16.

Owen, R., 1846. A History of British fossil mammals and birds. London, Joh Van Voorst: I-XLVII + 1-560, 1 pl.

Piveteau, J., 1958. Représentations de Périssodactyles dans l'Art du Paléolithique Supérieur. In: Traité de Paléontologie VI, 2: 493-498, 14 figs.

Portis, A., 1878. Über die Osteologie von Rhinoceros Merckii Jäger und über die diluviale Säugetierfauna von Taubach bei Weimar. Palaeontographica, 25, 4: 141-162, pls. 19-21.

Ringström, T., 1924. Nashörner der Hipparion-Fauna Nord-Chinas. Pal. Sinica, Ser. C, 1, 4: 1-158, 92 figs., 12 pls.

——, 1927. Über quartäre und jungtertiäre Rhinocerotiden aus China und der Mongolei. Pal. Sinica, Ser. C, 4, 3: 1-23, 1 fig., pls. 1-2.

Rowland Ward, 1935. vid. Dollman, G. & J. B. Burlace.

Rutten, L. M. R., 1909. Die diluvialen Säugetiere der Niederlande. Berlin, Friedländer & Sohn: 1-116, 2 maps, 2 pls.

Schack, W., 1958. Ich jagte das Weisse Nashorn. Frankfurt/Main, Umschau Verl.: 1-87, ill.

Schaurte, W., 1960. Vom südafrikanischen Breitmaul-Nashorn, *Ceratotherium simum simum.* Natur und Volk, Senckenb. Naturf. Ges., 90: 389-397, 9 figs.

Schenkel, R. & E. M. Lang, 1969. Das Verhalten der Nashörner. Handb. Zool. (Kükenthal), 8, 10, 25: 1-56, 25 figs. Berlin, W. de Gruyter.

Schroeder, H., 1903. Die Wirbelthierfauna des Mosbacher Sandes, I Gattung Rhinoceros. Abh. Kön. Preuss. Geol.L andesanst., N.F. 18: 1-143, 14 pls. in Atlas.

——, 1930: Ueber *Rhinoceros merckii* und seine nord- und mitteldeutschen Fundstellen. Abh. Preuss. Geol. Landesanst., N.F. 124: 1-114, 26 pls.

Sickenberg, O., 1962. Die Säugetierreste aus den elsterzeitlichen Kiesen (Pleistozän) von Bornhausen am Harz. Geol. Jb., Hannover, 79: 707-736, pls. 34-37.

Sidney, J., 1965: The past and present distribution of some African ungulates. Trans. Zool. Soc. London, 30: 1-397, 94 maps, 39 figs.

Simpson, G. G., 1945. The Principles of Classification and a Classification of Mammals. Bull. Am. Mus. Nat. Hist., 85: VII-IX + 1-350.

Slaughter, B. H., 1967. Animal Ranges as a Clue to Extinction. In: Pleistocene Extinctions. The Search for a Cause. Martin, P. S. and H. E. Wright jun. ed. Proc. VII Congr. Int. Ass. Quat. Res., 6: 155-167, figs. 1-2.

Sody, H. J. V. (1941) 1959. Das javanische Nashorn. Zeitschr. Säugetierk., 24, 3/4: 190-240, figs. 1-13, pls. V-VIII.

Staesche, K., 1941. Nashörner der Gattung Dicerorhinus aus dem Diluvium Württembergs. Abh. Reichsst. f. Bodenf., N.F. 200: 1-148, 2 figs., 14 pls.

Stehlin, H. G., 1930. Bermerkungen zur Vordergebissformel der Rhinocerotiden. Eclog. geol. Helv., 23: 644-649,fig s. 1-3.

Strien, N. J. van, 1975. Dicerorhinus sumatrensis (Fischer). The Sumatran or Two-horned Asiatic Rhinoceros. A study of literature. Neth. Comm. Intern. Nat. Prot., 22: 1-82, 2 figs., 2 maps, 1 photogr.

Sutcliffe, A. J., 1960. Joint Mitnor Cave, Buckfastleigh. Trans. Torquay Nat. Hist. Soc. 13, 1: 1-28, 10 pls.

Thenius, E., 1955. Die Verknöcherung der Nasenscheidewand bei Rhinocerotiden und ihr systematischer Wert. (Zum Geschlechtsdimorphismus fossiler Rhinocerotiden). Schweiz. Palaeont. Abh., 71: 1-17, figs. 1-21, 1 pl.

Toula, F., 1902. Das Nashorn von Hundsheim Rhinoceros (Ceratorhinus Osb.) hundsheimensis nov. form. Mit Ausführungen über die Verhältnisse von elf Schädeln von Rhinoceros (Ceratorhinus) sumatrensis. Abh. k.k. geol. Reichsanst., 19, 1: 1-92, 25 figs., 12 pls.

Van Couvering, J. A. & W. A. Berggren, 1974. The late Neogene. Palaeogeography, Palaeo-climatology, Palaeoecology, 16, 1/2: 1-216.

Vangengeim, E. A., 1967. The Effect of the Bering Land Bridge on the Quaternary Mammalian Faunas of Siberia and North America. In: The Bering Land Bridge., Hopkins, D. M. ed.: 281-287. Stanford University Press.

Vangengeim, E. A., E. I. Beliajeva, V. E. Garutt, E. L. Dmitrijeva & V. S. Zazhigin, 1966. Eopleistocene Mammals of Western Transbaikalia. Acad. Sc. USSR, Geol. Inst., 152: 1-163, figs. 1-78. (Russian only)

Venzo, S., (1953) 1956. Stadi della glaciazione del 'Donau' sotto al Günz ed al Mindel nella serie lacustre di Leffe (Bergamo). Limite tra Pliocene e Pleistocene. Rome, Actes du IV Congrès Intern. du Quatern., 1: 65-85, 4 figs.

Vialli, V., 1956. Sul rinoceronte e l'elefante dei livelli superiori della serie lacustre di Leffe (Bergamo). Mem. Soc. Ital. Sci. Nat. e Mus. civ. Stor. nat. Milano, XII, 1: 1-71, fig. 1-4, pls. I-VI.

Villalta Comella, J. F. de, 1952. Mamíferos fósiles del Plioceno de Villaroya. Bol. Inst. Geol. y Min. de Esp., 64: 1-203, figs. 1-13, pls. 1-27.

Viret, J., 1958. Perissodactyla. In: Traité de Paléontologie, J. Piveteau ed., VI, 2: 368-475. Paris, Masson & Cie.

Ward, R., 1935. vid. Dollman, G. & J. B. Burlace.

Weber, W., 1963. Heimische Eiszeitfunde und ihre Deutung. Natur und Museum, Senckenb. Naturf. Ges., 93, 2: 60-64, 5 figs.

Wernert, P., 1957. Stratigraphie paléontologique et préhistorique des sédiments quaternaires d'Alsace, Achenheim. Mém. Serv. Cart. Géol. d'Alsace et de Lorraine, 14: 1-259, 108 figs., 25 pls.

Wood II, H. E. 1949. Evolutionary rates and trends in Rhinoceros. In: Jepsen, Mayr & Simpson. Genetics, Palaeontology and Evolution.

Woodward, H., 1874. On the Remains of *Rhinoceros leptorhinus* Owen *(Rhinoceros hemi-toechus* Falconer), in the Collection of Sir Antonio Brady, F.G.S. from the Pleisto-cene Deposits of the Valley of the Thames at Ilford, Essex. Geol. Mag., XI: 398-403, pl. XV.

Wright Jr., H. E. ed., 1969. Quaternary Geology and Climate, Proc. VII INQUA Con-gress, 16: IX + 1-162. Washington, D.C., National Acad. of Sciences.

Wüst, E., 1911. Zwei bemerkenswerte Rhinoceros-Schädel aus dem Plistozän Thüringens. Palaeontographica, 58: 133-138, pl. 10.

——, 1914. Rhinoceroszähne aus dem Sande von Mauer bei Heidelberg. In: Freudenberg, W., 1914: 23-26 (475-478).

——, 1922. Beiträge zur Kenntnis der Diluvialen Nashörner Europas. Centralbl. f. Min. Geol. u Pal., 1922: 641-656, 680-688, figs. 1-5.

Zagwijn, W. H., 1974. Palaeogeographic evolution of the Netherlands during the Quater-nary. Geologie en Mijnbouw, 53, 6: 369-385, maps.

Zeuner, F. (E.), 1934. Die Beziehungen zwischen Schädelform und Lebensweise bei den re-zenten und fossilen Nashörnern. Ber. Naturf. Ges. zu Freiburg i. Br., 34: 21-80, pls. 1-8.

——, 1959. The Pleistocene Period. 2nd. ed.: 1-447, 80 figs. London, Hutchinson.

Zukowsky, L., 1964. Die Systematik der Gattung Diceros Gray. Der Zoologische Garten, N.F., 30, 1, 4: 1-178, 81 figs.

Plate 1

Fig. 1. *Ceratotherium simum simum* (Burchell). Lateral view. RMNH 19604 (Jentink cat. b). Approx. × 1/6.
Fig. 2.   *Ceratotherium simum cottoni* (Lyd.). Lateral view. RMNH 13119. Approx. × 1/6.
Fig. 3. *Diceros bicornis* (L.). Lateral view. RMNH 19598 (Jentink cat. a). Approx. × 1/6.

Plate 2

Fig. 1. *Ceratotherium simum simum* (Burchell). Upper view. RMNH 19604 (Jentink cat. b). Approx. × 1/6.
Fig. 2. *Ceratotherium simum cottoni* (Lyd.). Upper view. RMNH 13119. Approx. × 1/6.
Fig. 3. *Diceros bicornis* (L.). Upper view. RMNH 19598 (Jentink cat. a). Approx. × 1/6.

Plate 3

Fig. 1. *Dicerorhinus sumatrensis* (Fischer). Lateral view. RMNH 19596 (Jentink cat. g). Approx. × 1/6.
Fig. 2. *Dicerorhinus etruscus* (Falc.). Lateral view. Mainz 1958/764, loc. Mosbach. Approx. × 1/6.
Fig. 3. *Dicerorhinus kirchbergensis* (Jäger). Lateral view. Mainz 1956/962, loc. Mosbach. Approx. × 1/6.

Plate 4

Fig. 1. *Dicerorhinus sumatrensis* (Fischer). Upper view. RMNH 19596 (Jentink cat. g). Approx. × 1/6.
Fig. 2. *Dicerorhinus etruscus* (Falc.). Upper view. Mainz 1958/764, loc. Mosbach. Approx. × 1/6.
Fig. 3. *Dicerorhinus kirchbergensis* (Jäger). Upper view. Mainz 1956/962, loc. Mosbach. Approx. × 1/6.

Plate 5

Fig. 1. *Dicerorhinus kirchbergensis* (Jäger). Lateral view. SfN, loc. Daxlanden. Approx. × 1/6.
Fig. 2. *Dicerorhinus hemitoechus* (Falc.). Lateral view. RGM 93302. Approx. × 1/6.
Fig. 3. *Coelodonta antiquitatis* (Blum.). Lateral view. SfN, loc. Lampertheim, Hessen. Approx. × 1/6.

Plate 6

Fig. 1. *Dicerorhinus kirchbergensis* (Jäger). Upper view. SfN, loc. Daxlanden. Approx. × 1/6.
Fig. 2. *Dicerorhinus hemitoechus* (Falc.). Upper view. RGM 93302. Approx. × 1/6.
Fig. 3. *Coelodonta antiquitatis* (Blum.). Upper view. SfN, loc. Lampertheim, Hessen. Approx. × 1/6.

Plate 7

Fig. 1. *Ceratotherium simum simum* (Burchell). Lower view. RMNH 19604 (Jentink cat. b). Approx. × 1/6.
Fig. 2. *Ceratotherium simum cottoni* (Lyd.). Lower view. RMNH 13119. Approx. × 1/6.
Fig. 3. *Diceros bicornis* (L.). Lower view. RMNH 19598 (Jentink cat. a). Approx. × 1/6.

Plate 8

Fig. 1. *Dicerorhinus sumatrensis* (Fischer). Lower view. RMNH 19596 (Jentink cat. g). Approx. × 1/6.
Fig. 2. *Dicerorhinus kirchbergensis* (Jäger). Lower view. Mainz 1956/962, loc. Mosbach. Approx. × 1/6.
Fig. 3. *Dicerorhinus kirchbergensis* (Jäger). Lower view. SfN, loc. Daxlanden. Approx. × 1/6.

Plate 9

Fig. 1. *Dicerorhinus hemitoechus* (Falc.). Lower view. RGM 93302. Approx. × 1/6.
Fig. 2. *Coelodonta antiquitatis* (Blum.). Lower view. SfN, loc. Lampertheim, Hessen. Approx. × 1/6.
Fig. 3. *Ceratotherium simum cottoni* (Lyd.). Occipital view. RMNH 13119. Approx. × 1/6.
Fig. 4. *Ceratotherium simum simum* (Burchell). Occipital view. RMNH 19604 (Jentink cat. b). Approx. × 1/6.

Plate 10

Fig. 1. *Diceros bicornis* (L.). Occipital view. RMNH 19598 (Jentink cat. a). Approx. × 1/6.
Fig. 2. *Dicerorhinus sumatrensis* (Fischer). Occipital view. RMNH 19596 (Jentink cat. g). Approx. × 1/3.
Fig. 3. *Dicerorhinus etruscus* (Falc.). Occipital view. Mainz 1958/764, loc. Mosbach. Approx. × 1/6.
Fig. 4. *Dicerorhinus kirchbergensis* (Jäger). Occipital view. Mainz 1956/962, loc. Mosbach. Approx. × 1/6.
Fig. 5. *Dicerorhinus kirchbergensis* (Jäger). Occipital view. SfN, loc. Daxlanden. Approx. × 1/6.

Plate 11

Fig. 1. *Dicerorhinus hemitoechus* (Falc.). Occipital view. RGM 93302. Approx. × 1/6.
Fig. 2. *Coelodonta antiquitatis* (Blum.). Occipital view. SfN, loc. Lampertheim, Hessen. Approx. × 1/6.
Fig. 3. *Diceros bicornis* (L.). Front view. RMNH 19598 (Jentink cat. a). Approx. × 1/4.
Fig. 4. *Dicerorhinus sumatrensis* (Fischer). Front view. RMNH 19596 (Jentink cat. g). Approx. × 1/4.

Plate 12

Fig. 1. *Ceratotherium simum simum* (Burchell). Otic region. RMNH 19604 (Jentink cat. b). Approx. × 1/3.
Fig. 2. *Ceratotherium simum cottoni* (Lyd.). Otic region. RMNH 13119. Approx. × 1/3.
Fig. 3. *Diceros bicornis* (L.). Otic region. RMNH 19598 (Jentink cat. a). Approx. × 1/3.
Fig. 4. *Dicerorhinus sumatrensis* (Fischer). Otic region. RMNH 19596 (Jentink cat. g). Approx. × 1/3.

Plate 13

Fig. 1. *Dicerorhinus kirchbergensis* (Jäger). Otic region. SfN, loc. Daxlanden, Approx. × 1/3.
Fig. 2. *Dicerorhinus kirchbergensis* (Jäger). Otic region. Mainz 1956/962, loc. Mosbach. Approx. × 1/3.
Fig. 3. *Dicerorhinus hemitoechus* (Falc.). Otic region. RGM 93302. Approx. × 1/3.
Fig. 4. *Dicerorhinus etruscus* (Falc.). Otic region. Mainz 1958/764, loc. Mosbach. Approx. × 1/3.

Plate 1

1

2

3

Plate 2
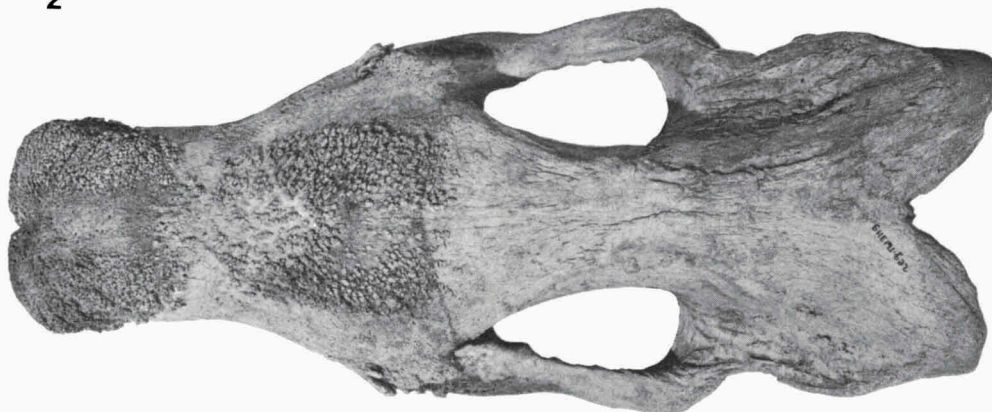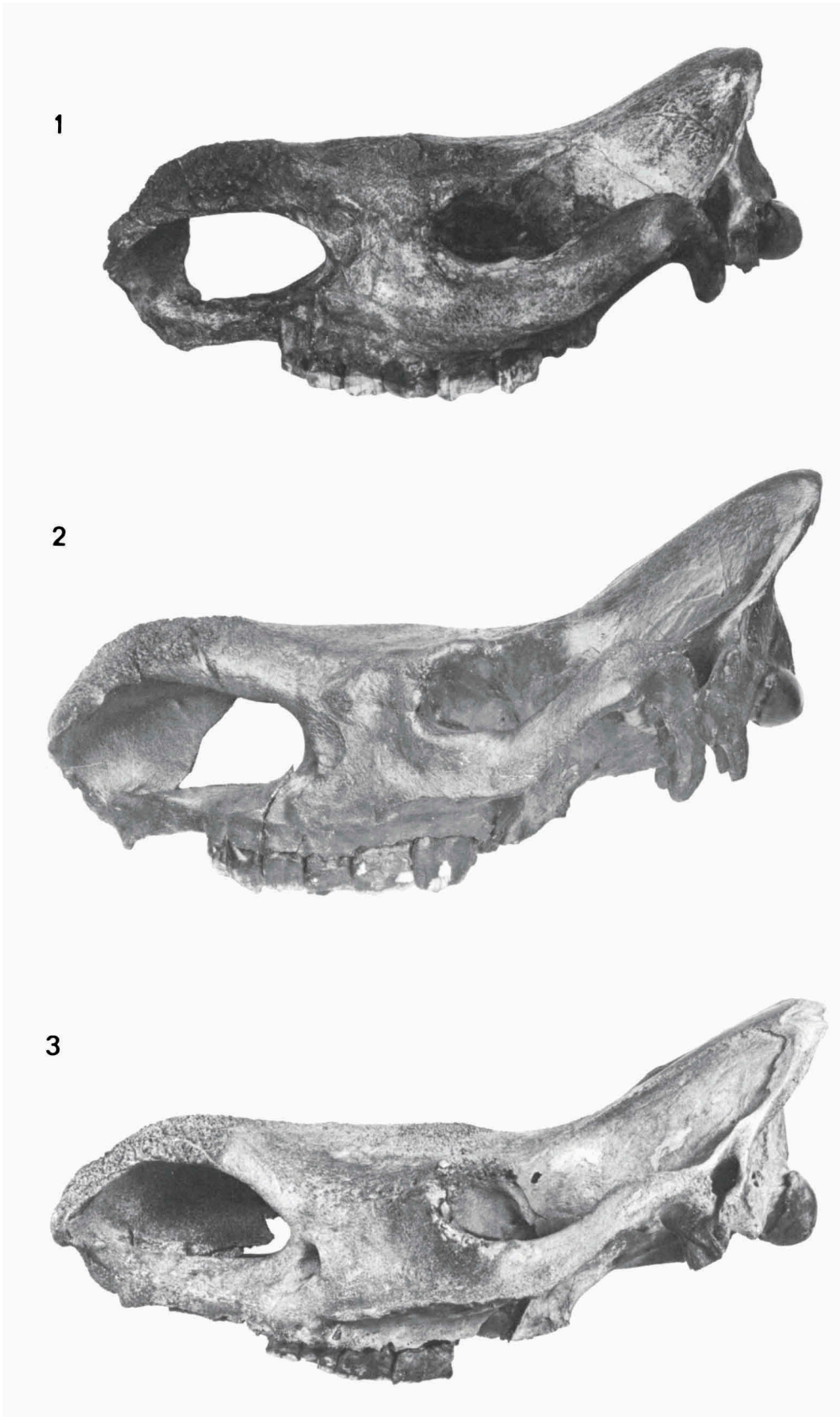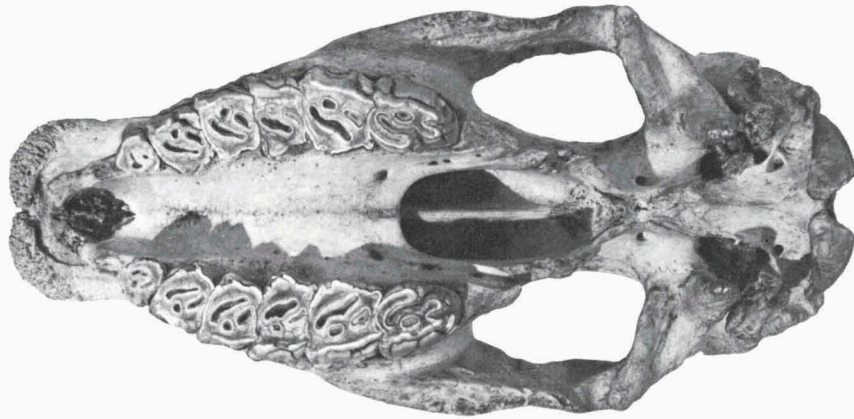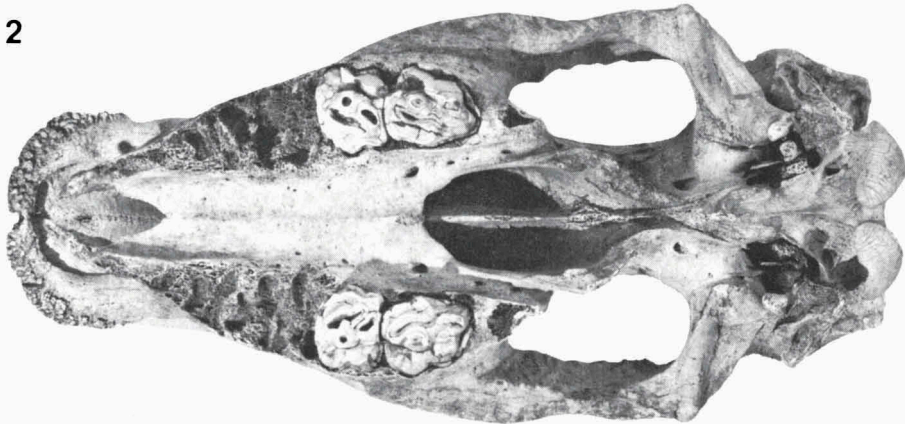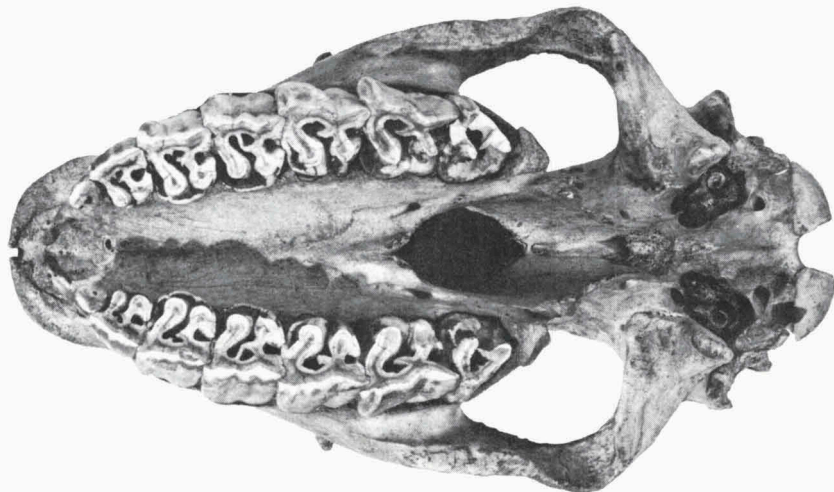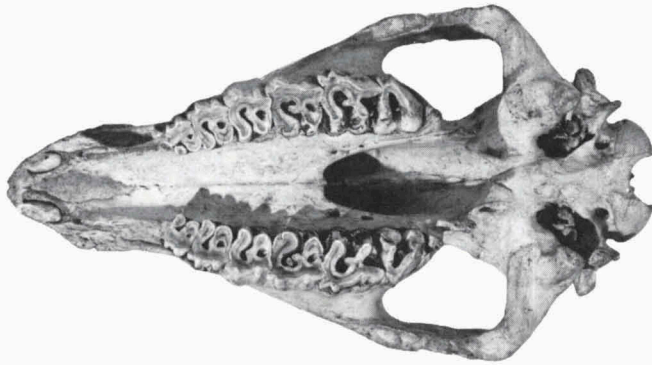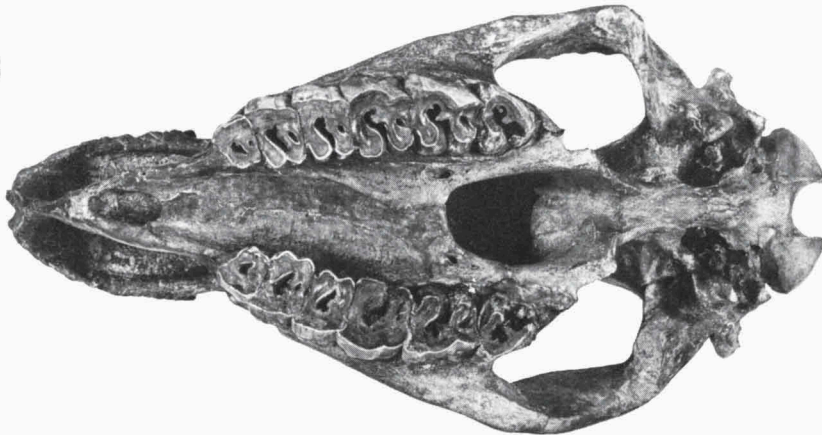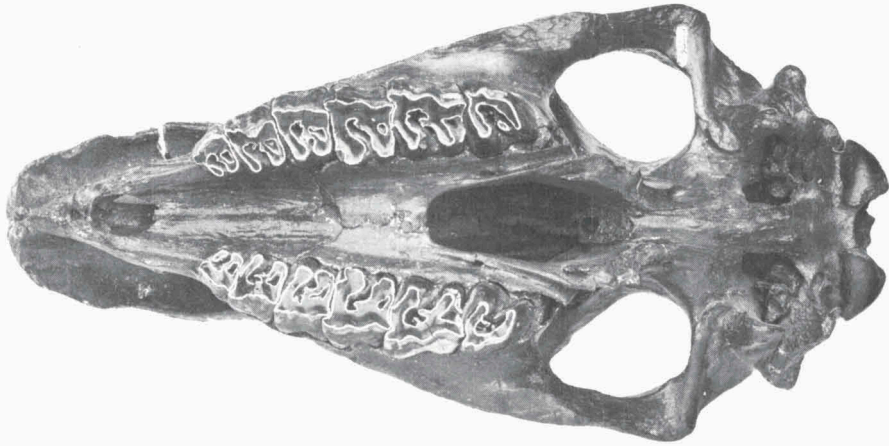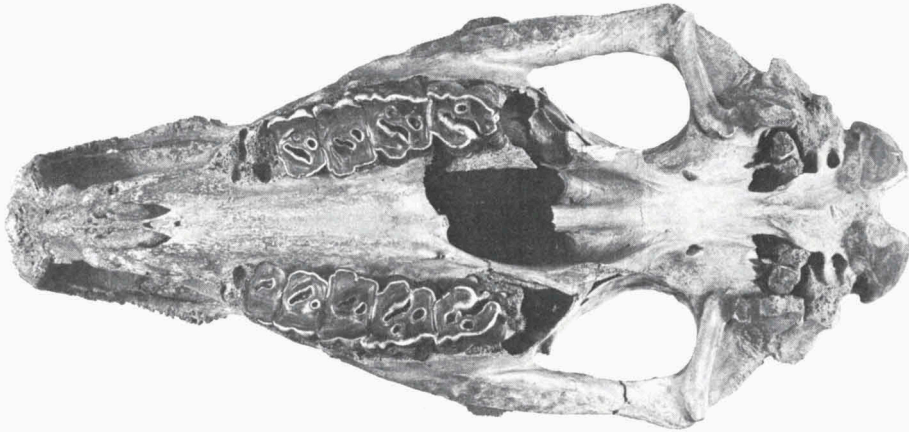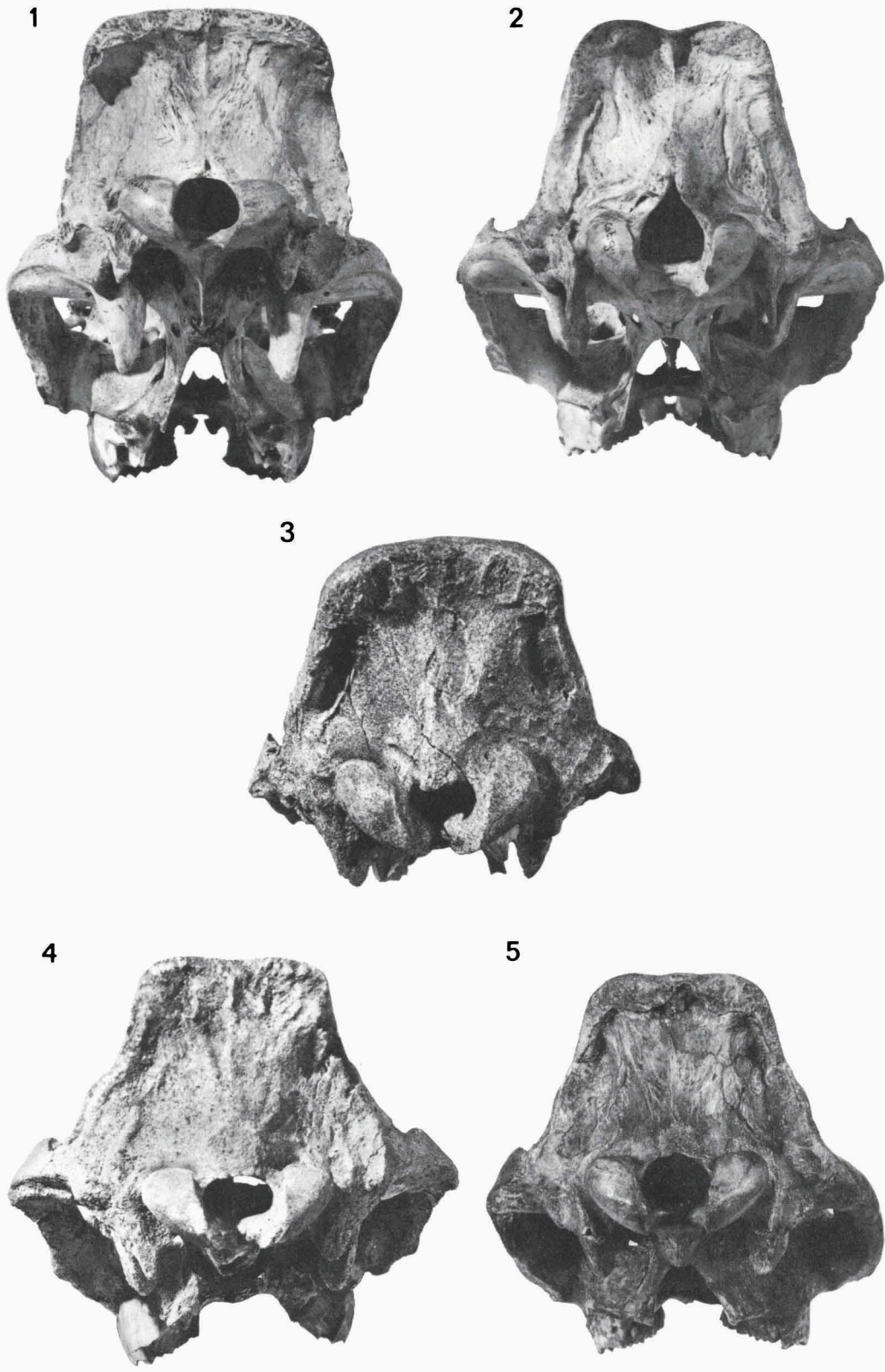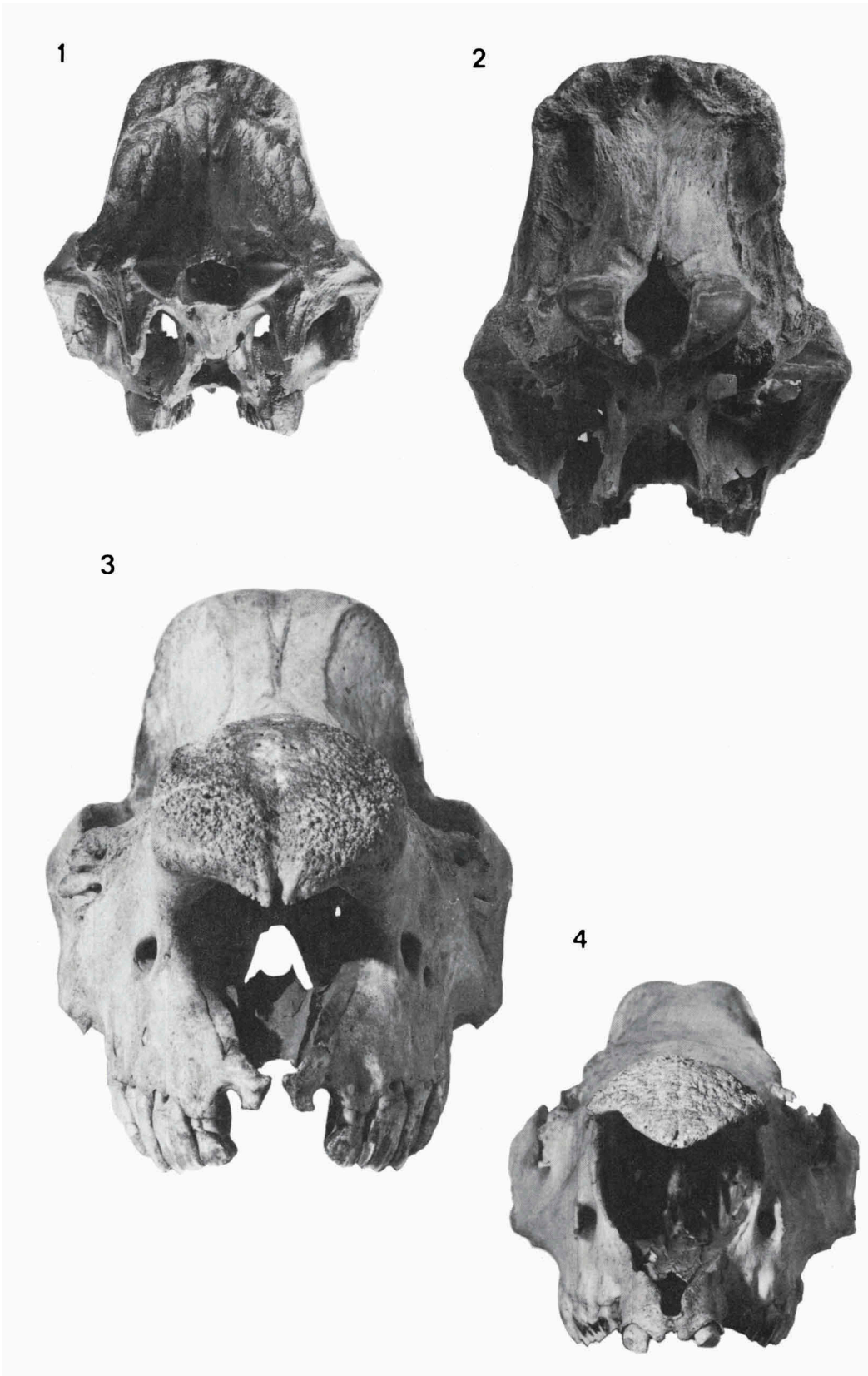
Plate 3

Plate 4
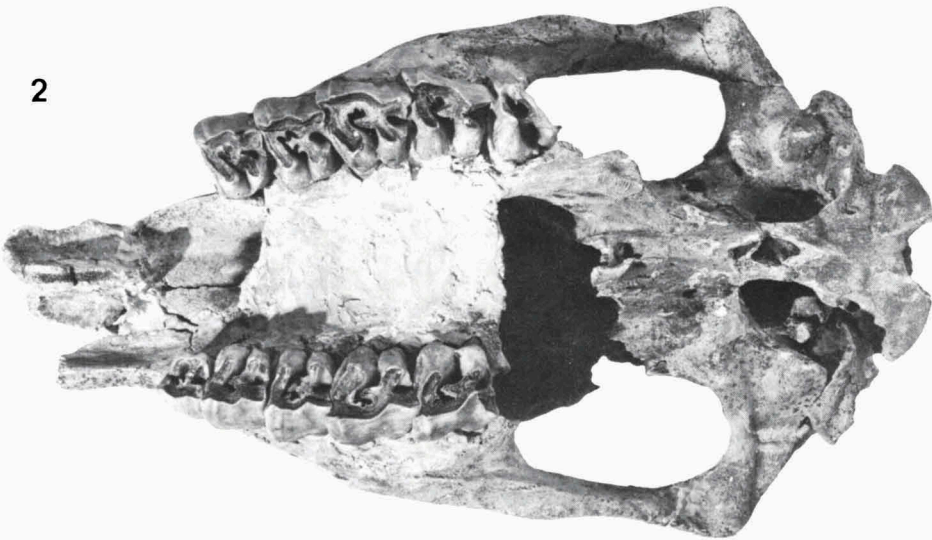
Plate 5

Plate 6

Plate 7

Plate 8

Plate 9

Plate 10

Plate 11

Plate 12

Plate 13
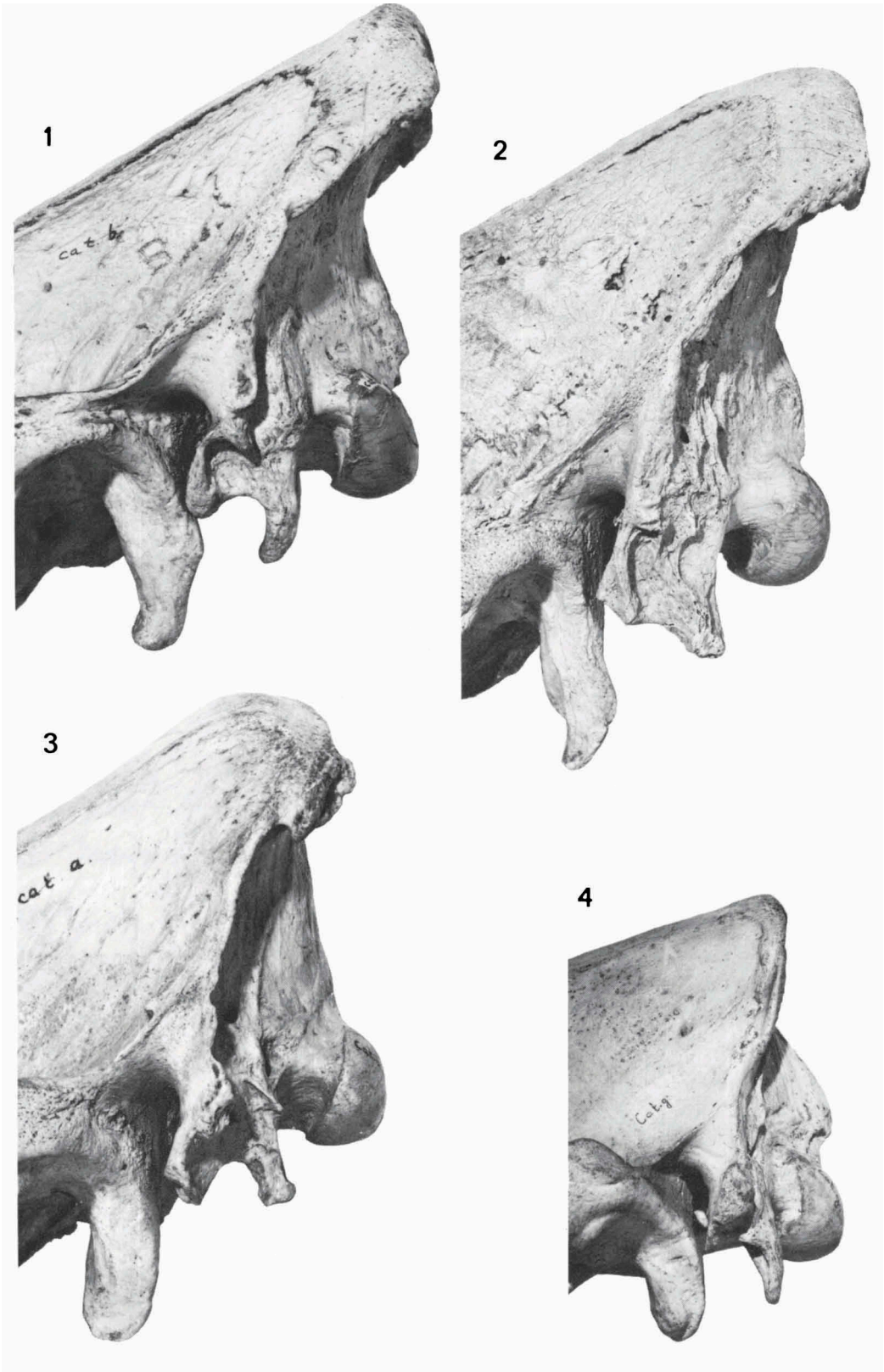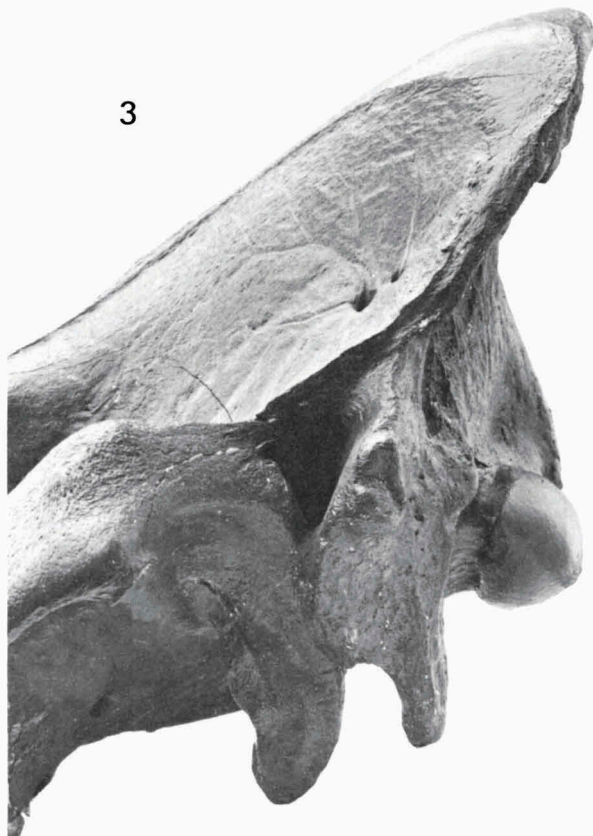
Errata

p. 4, line 23
   for: y angle between opisthion + basion and parietals
   read: y angle between opisthion + basion and palate
         m angle between opisthion + basion and parietals

p. 7, line 16/17
   read: *Rhinoceros sondaicus* has been treated extensively by Hooijer (1946),
         Sody (1941, 1959) and Hoogerwerf (1970).

p. 18, line 21 and p. 19, line 34,

   read: *Rhinoceros leptorrhinus* Cuv. } *Merkii* Kaup.
                                        } *Kirchbergensis* Jäg.

p. 28, line 7 from below
   read: . . . arctic regions of the New World (Piveteau 1958, p. 498, fig. 14).

p. 29, line 28
   for: adaption,
   read: adaptation

p. 29, line 30
   for: . . . in size or shape,
   read: in size.

p. 41 (references),
   add: Hooijer, D.A., 1946. Prehistoric and Fossil Rhinoceroses from the
        Malay Archipelago and India. Zoologische Mededelingen XXVI:
        1-138, 10 pls.