Ovibus pallantis rhenanus nov. subsp., an extinct Ovibos of Weinheim, Rhine Valley, Germany

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Zusammenfassung

Der recht gut erhaltene Ovibos-Schädel, den Prof. Dr. W. FREUDENBERG im Jungpleistocan von Weinheim an der Bergstraße gefunden hatte (Sammlung München 1965 I 172; vgl. Dehm, S. 143—153), wird beschrieben und auf Grund einiger besonderer Merkmale als neue Unterart von Ovibos pallantis HAM. SMITH betrachtet. Die Beziehungen von Ovibos zu Ovis und Bison werden an Hand der Schädelmerkmale diskutiert; danach gehört Ovibos eher zu den Bovinae als zu den Caprinae und verdankt die an Ovis erinnernden Merkmale einer gewissen Konvergenz.

Abstract

A fairly complete skull of Ovibos, found by Prof. Dr. W. FREUDENBERG in the Upper Pleistocene of Weinheim, Rhine Valley (Munich collection Nr. 1965 I 172; Dehm S. 143—153) is an interesting object. The skull belongs to an almost seven years old male animal (Allen, 1913, Pl. 15, fig. 9). The sutures are unobliterated by anchylosis except for the fronto-parietal and the median of the frontals. The exostosis extending from the base of the right horn-core appears to have overlapped that of the left in the centre though the coronal interspace is 16 mm wide. Taking as a whole the skull has more similarity with that of Ovibos pallantis rather than Ovibos moschatus wardi in being large in size, having comparatively short tooth-row and broad base of horn-cores in proportion to their length. But, it differs from both by the presence of well developed median pillars (both, accessory column and basal tubercle are present [RÜTIMEYER, 1867—1868, pp. 78—79]) in the upper molars (M2-3) and the parietals being less arched posteriorly.

In regard to its relation with Ovis and Bison, detailed comparative investigation reveals that the characters of the dorsal surface of the skull are more Antilo-

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pine type (LÖNNBERG, 1900, p. 697) rather than Bovine or Caprine type, while the characters of the occipital and palatal surfaces agree more with those of *Ovis* than *Bison*. But, the author agrees with Allen (1913, pp. 164—167) that *Ovibos* has greater similarity with *Bison* on the basis of the external characters and ontogenetic similarities, and differs from Dawkins (1872, pp. 1—30) that *Ovibos* is a musk-sheep rather than a musk-ox. The characters of *Ovibos*, which are alike to *Ovis* are mostly primitive and partially adaptive. The antilopine characters of the dorsal surface of *Ovibos* skull are not primitive but are of later development.

Introduction

In December 1965, the skull was brought by Prof. Dehm for his Institute and he very kindly permitted me to describe it. He has given the locality and horizon etc. in a separate note (p. 143). Letters were sent to the Directors of the American Museum of Natural History in New York, the Mineralogisk-Geologiske Institute in Denmark and Arctic Institute of Canada to find out the presence of the median pillars in the upper molars of *Ovibos*. The replies received from these places are as follow:

"I have looked at all the *Ovibos* in the Museum and have found no specimen with such an accessory pillar ... but I have found nothing very close to Dr. Khan's specimen" (McKenna, 13th Jan. 1966). "Ich habe 130 Schädel aus N. O.-Grönland (zwischen 70 und 82 nrd. Br.) untersucht und eine kleinere Anzahl zeigt, mehr oder weniger ausgesprochen, dasselbe Verhältnis betreffend das Vorhandensein von 'Accessory column' und 'basal tubercle,' wenn auch es mir in gewissen Fällen (vgl. Phot. CN 989) schwierig war, diese variierenden Zahnpfeiler zu deuten." (U. Mohl, 19th Jan. 1966). "However, I there refer to styles (= pillars) on M². To refresh my memory I have looked at a few of the skulls in the National Museum of Canada, and it appears that styles are commoner on M² and M¹ than on M³, and amongst those I looked at there were none with a style on any molar approaching the size of that in your photograph; neither can I recall seeing any so well developed when I examined collections in other museums. Also, your specimen has a fold inside the style. This fold resembles the styles on some of the worn teeth of Wardi." (T. H. Manning, 10th Feb. 1966).

The skull has been compared with the skulls of *Ovis ammon karelini* (No. 1909/207), *Bison bonasus bonasus* (No. 1952/308) and *Bison priscus* in order to find out its relation with them. Comparison has also been made with a skull of *Ovibos moschatus wardi* (No. A. M. 634) and with the photographs of the skull of *Ovibos pallantis* described by Ryziewicz in details (1955, pp. 1—72), for tracing out its greatest affinity with one of the two. Some lights have also been thrown on the probable origin of *Ovibos* and the criteria to create new species or subspecies adopted by several workers.

Description

Order-Artiodactyla Bovidae Family-Subfamily-Caprinae Tribe-Ovibovini

Genus-Ovibos, DE BLAINVILLE, 1816 Ovibos pallantis HAM. SMITH, 1827 Species-Ovibos pallantis rhenanus nov. subsp. Subspecies-

Diagnosis: A large Ovibos; doral surface of skull nearly flat; broad base of horn-cores in proportion to their length; distance between tips of horn-cores less; comparatively short tooth-row, upper molars with prominent median pillars (rudimentary or absent in M1).

The characters of the skull mostly agree with those of others of the species described so far, but some characters appear to be characteristic of this; therefore, a brief description is given as follows.

The skull is well preserved except for the posterior walls of the orbits, tips of the horn-cores and dentition. Only right M3-P3 and left M2 are present and they are also not in good condition. The premaxillae and nasals are missing.

Cranium: The skull is narrow and long similar to Ovis; its length is almost double of the maximum width which falls at the orbits.

Orbits: The orbits are large and more out of profile of the face than are in Ovis and Bison; their cross-sections are circular as in Ovis, not oblong anteroposteriorly similar to those of Bison.

Nasals: The nasals are missing, but the fronto-nasals suture shows that they are broader posteriorly and meet the frontals at right angles to the median line similar to Ovis, not narrow posteriorly as in Bison.

Lachrymals are short and broad with large larmiers or lachrymal fossae similar to Ovis, not long and narrow without larmiers as in Bison.

Frontals: The frontals are long and narrow; slightly arched behind the orbits as in Bison, not strongly arched similar to Ovis. The supraoccipital pits are deep and far behind the orbits, shallow and broad furrows run anteriorly to join the larmiers, and thus the orbits are made completely out of profile of the face. Such type of supraoccipital pits are neither found in Ovis nor in Bison.

Horn-cores are compressed dorso-ventrally and curve sharply downward, dissimilar to Ovis and Bison; the exostosis extending from the right horn-core appears to have overlapped that of the left (now broken) in the centre though the coronal interspace is 16 mm wide; it also extends to the orbits anteriorly and in the posterior hangs over the occiput.

Parietals: The fronto-parietal suture has been obliterated by anchylosis; therefore, the length of the parietals cannot be found out, but according to Allen (1913, P. 139) they are 1/3rd of the frontals on the median line throughout life. The temporal fossae are long and open posteriorly as in *Ovis*, not closed due to development of temporal crest as in *Bison*. The zygomatic arches are strong and straight, not weak and taking sharp downward curve posteriorly as in *Bison*.

S q u a m o s a l s: The squamosals are long, broad posteriorly and narrow anteriorly.

O c c i p u t: The occiput is slightly broader (174 mm) than high (112.5 mm), though the mastoids take very little part in the formation of the occiput as in *Ovis*, while in *Bison* the mastoids take a major part in the formation of the occiput. The supraoccipital has deflected towards the occipital plane; occipito-parietal suture is unobliterated. The nuchal spine is thin but well marked. The occipital condyles are in contact with the exoccipital processes through the accessory condyles as in *Ovis*. Contrary to this in *Bison* there are deep valleys, between the condyles and processes instead of the accessory condyles. The basioccipital is quadrate, tuberosities are weak and the keel is prominent in the centre and turns into grooves in the anterior and posterior as in *Ovis*, while in *Bison* the keel is prominent throughout its length. The tympanic bullae are weak and small as against strong and big as in *Bison* and *Ovis*. The external auditory meatus open backward as in *Ovis*, not forward as in *Bison*.

The alisphenoids and pterygoids are strong and high as in *Ovis*, not weak and low as in *Bison*.

Palates: The palates appear to extend upto the posterior end of M² anteriorly and not far behind the molar series posteriorly, but as a whole the palates are more similar to *Ovis* rather than *Bison*.

M a x illa e: On the superior surface, the maxillae are well developed due to the compression of the lachrymals as in *Ovis*, not weak as in *Bison* and, between the teeth, are broader posteriorly and narrow anteriorly as in *Ovis*, whereas in *Bison* the width of the maxillae between the teeth is nearly the same.

Teeth: The molars are without cement as in *Ovis*, not completely covered with cement as in *Bison*, are longer than broad and have a median small lake in each molar as in *Ovis*, but have well developed median pillars (absent or rudimentary in M¹) as in Bovinae (present in M¹-³). Both, accessory column and basal tubercle are present (RÜTIMEYER, 1867—68, 78—79). The buccal sides of the lobes are nearly flat as in *Ovis*, not convex as in *Bison*. The para-, meso - and metastyles are prominent as in *Ovis*, not weak as in *Bison*.

LÖNNBERG (1900, pp. 712—715) and Allen (1913, p. 167) have referred the presence of the accessory columns in the upper molars of *Oribos* though less developed. But in most of the cases these columns are not seen in the photographs.

Only a small fold from anterior lobe projects in the median valley and is visible only in the molars of young animals whose molars do not contain the small median lakes. It seems that these folds in the later part of animal's life join with the posterior lobes and a small lake is formed in the median of each molar.

The skull has been compared with that of Ovibos moschatus wardi (No. A. M. 634) and with the photographs of the skulls of Ovibos moschatus moschatus, Ovibos moschatus niphaecus and Ovibos pallantis. The skull of Ovibos pallantis, referred here, was collected in 1897 from the Pleistocene clay deposits near the Zbranki village and has been described in details by Ryziewicz (1955, pp. 1—71). One can easily realise that on such scanty materials thorough comparison cannot be done with certainty when the minor individual variations due to age are so great that they exceed the subspecific differences (Allen, 1913, p. 152). But this difficulty can be overcome when attention is paid only to the subspecific characters (1. size,

Tab. 1: Comparison of measurements in mm of 5 Ovibos skulls with Ovibos skull of Weinheim, Rhine Valley, Germany

,	Rhine	Zbranki	Barren Ground	Grant Land Ovibos m. wardi		Hudson Bay
	Present skull	Ovibos pallantis	Ovibos m. moschatus			Ovibos m. niphaecus
	I 172		16604	28072	29960	19490
	3	3	ð	3	9	3
Total length	?488*	?495⊕	479	492	446	485
Basal length	?450*	467	450	465	404	445
Mastoids breadth	174	?195⊕	183	177	150	167
Orbital breadth	239	248	260	258	214	254
Post orbital breadth	132	135	134	142	114	133
Nasal-length	?135*	?132⊕	148	159	147	154
Nasal-greatest breadth	75	? 75⊕	80	73	62	69
Maxillary tooth-row length	138	132	128	148	145	136
Breadth of palate opposite M ²	83	83	81	78	80	73
Horns-distance between			1000			
tips	220	?225⊕	564	_	548	665
Horns-breadth at base	106	100	250	205	213	241
Horns-length on outer curvature	?235*	240	551	627	612	595
Horns-distance between bases of sheadth	16	8.5	7	_	17	11

[⊕] approx. (taken from figs.) * approx. (not well preserved)

Note: Precautions have been taken to compare the measurements of the present skull with those of the recent male ones which are nearly of the same sage in order to eliminate the individual variations due to age and sex.

2. length of the tooth-row and 3. breadth of horn-cores at base in proportion to their length, Allen, 1913, p. 180). Having the above points in view the present skull agrees more with those of *Ovibos moschatus moschatus* and *Ovibos pallantis* and differs from those of *Ovibos moschatus wardi* and *Ovibos moschatus niphaecus* in being large in size, having comparatively short tooth-row and broad base of the horn-cores, in comparison to their length. Though the present skull has greater similarity with *Ovibos pallantis* and *Ovibos moschatus moschatus*, yet is distinguished from them by the presence of the well developed median pillars (both, accessory column and basal tubercle are present, RÜTIMEYER, 1867—68, 78—79) in the upper molars and the distance between the occipital and the hanging part of the extention of the exostosis being 14 mm as against generally 40 mm in the males of the same age.

In order to throw more lights on the similarities and dissimilarities in different skulls of *Ovibos* measurements of several characteristic parts are given as below.

Probable origin of Ovibos

The foregoing description of the skull of *Ovibos* clearly shows that the skull of *Ovibos* has greater similarity with that of *Ovis* rather than *Bison*. This similarity has also been observed by DAWKINS (1872, pp. 1—30) and RÜTIMEYER (1877 to 1878, pp. 103—104 etc.). In *Ovibos* the tail is short as in *Ovis*, not long as in *Bison*.

LÖNNBERG (1900, pp. 142—167) on the basis of the observations made on the soft parts of *Ovibos* advocates that *Ovibos* totally differs from Caprinae and Bovinae: "But, to judge from its soft anatomy, the Musk-ox is entitled to form a subfamily of its own, at least pro tempore, as well defined as the Caprinae or the Bovinae (p. 167)." He, by making comparative study of the skull of *Ovibos* with those of Antilopinae, Bovinae and Caprinae, shows that *Ovibos* retains many primitive characters and thus has no close affinity either with the Bovinae or the Caprinae since last two are advanced forms.

ALLEN (1913, pp. 164—167) states that the general form of body, heavy limbs, occasional presence of the accessory columns in the upper molars and four instead of two teats of *Ovibos* are more similar to *Bison* rather than *Ovis*. He further says that upto about two years of age the structure and relation of component bones of the skulls of *Bison* and *Ovibos* have far closer similarity than that exists between *Bison* and *Bos*.

The author does not accept the view that the antilopine type (parietals and frontals are horizontal and are nearly in the same plane) of the dorsal surface of *Ovibos* skull (Lönnberg, 1900, pp. 696—697) is primitive, since this condition has developed due to down curving of the horn-cores. The posterior arching of the frontals is seen in the young animals before the down curving of the horn-cores. The parietals are short which has already been observed by Lönnberg (1900, p. 700) and the shortening of the parietals is an advanced Bovinae character. The occasional presence of median pillars in the upper molars of *Ovibos*, though less

developed, is also an advanced Bovinae character. The above points lead to the conclusion that *Ovibos* originated from some advanced form of animal, not from a primitive one as has been advocated by Lönnberg (1900, pp. 686—718).

The presence of four mammary glands and production of a single calf at a time after a gestation of nine months (Flower and Lydekker, 1891, p. 359) separates *Ovibos* widely from *Ovis* which has only two mammae and brings forth more than one young at a time after a gestation of five months (Lydekker, 1898, p. 158).

In the opinion of author, *Ovibos* and *Bison* originated from the same stock. Later on, *Ovibos* acquired some characters of *Ovis* through convergent evolution besides retaining most of the primitive characters. It, therefore, is more reasonable, to include it into the Bovinae rather than into the Caprinae, though recently SIMPSON has included it into the Caprinae (1945, p. 162). It is also possible that the American species has its immediate ancestor some one similar to *Bootherium* (LEIDY, 1852), while *Boopsis* (TEILHARD DE CHARDIN, 1936) or some one alike to it is the more nearer form of Eurasian species.

On the varieties of Ovibos

First record of recent musk-ox is found in the description of JÉRÉMIE (1720). ZIMMERMANN (1780) included it in the genus Bos as a species, Bos moschatus.

BLAINVILLE (1816) created a new genus, *Ovibos*, for it, since he considered it as an intermediate form between *Bos* and *Ovis*. This stand was accepted by DAWKINS (1872—1885) and RÜTIMEYER (1877—1878) etc.

For the fossil form collected by Pallas from Siberia, Hamilton-Smith proposed a new species, Ovibos pallantis (1827). Lydekker (1900) gave the fossil forms a subspecies designation, Ovibos moschatus pallantis. Staudinger (1908) created a new genus and species, Praeovibos priscus, on a female skull of Ovibos from Frankenhausen. Kowarzik (1908) recognised four subspecies and one species (O. m. wardi Lydekker, O. m. niphaecus Elliot, O. m. melvillensis Kow., O. m. mackenzianus Kow. and O. moschatus Blainville) of recent forms and two species (O. fossilis Kow. and O. mackenzianus Kow.) of fossil forms (1912).

From the above brief historical background it is quite clear that it was the trend of the period to create a new subspecies or species on minor variations. Allen (1913) after detailed investigations proved that the minor variations were within the limits of the individual differences depending upon the age, sex and abnormalities. He, after giving full consideration to the numerous differences, retained three subspecies (O. m. moschatus, O. m. wardi and O. m. niphaecus) of the recent forms and two species (O. pallantis, Pleistocene of Eurasia and O. yukonensis, Pleistocene of America) of the fossil forms, but he (1913, p. 180) considered the possibilities of existence for more than a single form in the Pleistocene of Eurasia.

Andrée (1933) proposed a new species, *Ovibos kahrsii* for the specimen of Mülheim-Ruhr described by Edinger (1931) as *O. fossilis* Kow. He further div-

RYZIEWICZ (1933) created a new species, Ovibos recticornis on a single male skull of Prague Museum. Schwarz (1937) described a new species, Praeovibos schmidtgeni. Very recently Ryziewicz (1955, pp. 24—37) recognises two genera, Praeovibos Staudinger (1908) and Ovibos Blainville (1816) and five species (P. priscus, P. schmidtgeni, O. pallantis, O. recticornis and O. kabrsii).

After going through the previous works it is evident that now the major problem is how to distinguish the individual differences from the specific characters when these are defined only on the taste of individual worker. However, the author is convinced to propose a new subspecies, *O. p. rhenanus* for the present specimen since the presence of well developed median pillars in the upper molars is a qualitative difference rather than quantitative. This is quite in agreement with SIMPSON (1943, p. 1956) that appearance of wholly new structures and the total loss of old are the qualitative differences.

The presence of the accessory column (median style or median pillar) in the upper molars of *O.m.wardi* is, no doubt, an important point and it may lead to conclude that the presence of the accessory column is within the individual differences. But it may also be considered as the individual difference of *O.m.wardi* only, not of other species or subspecies of *Ovibos* till the evidences prove it i.e.it cannot be generalised. When it is accepted that *O.pallantis* is a distinct species having many primitive characters it is more plausible to look the presence or absence of the accessory column in the upper molars of *O.pallantis*, not in other species or subspecies.

Recently Ryziewicz (1954, pp. 242—252) has distinguished *Ovibos pallantis* forma *abbreviata* as a variety of *O.pallantis* having relatively shorter core bases and the horn-cores being very close to the skull. But he has made no reference to the presence or absence of the pillar in the upper molars. Therefore, the author thinks that in the light of the present knowledge the correct stand is to create a new sub-species as referred above.

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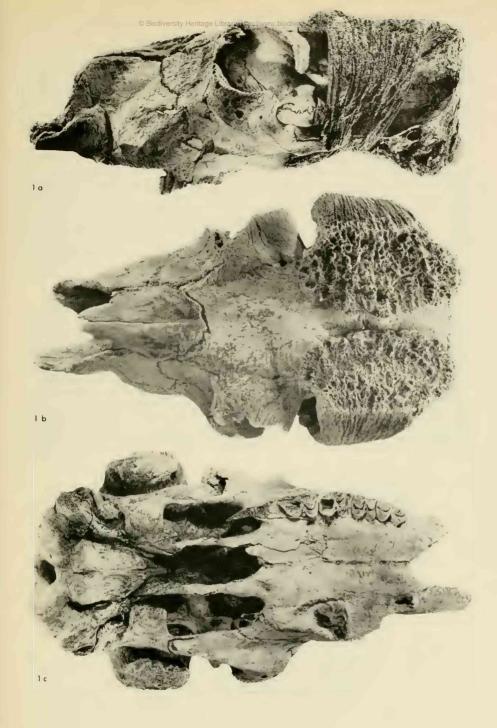
Explanation for plates 11-12

Plate 11

Fig. 1 a-c: skull of Ovibos pallantis rhenanus subsp., from Weinheim, Rhine Valley, Germany; type. Nasalia restored. ca × 0,24. 1 a) left side; 1 b) from above; 1 c) from below.

Plate 12

Fig. 1 a—d: same as plate 11. 1 a—b) right P_3 — M_3 ca 0,9; 1 c) right m^{2-3} ca \times 1,5. 1 d) skull from behind ca \times 0,3



Tafel 11











Tafel 12

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