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Praeovibos priscus (Bovidae, Artiodactyla, Mammalia) from the North Sea and aspects of its paleoecology

Mol, D., De Vos, J. & Reumer, J.W.F., 1999 - *Praeovibos priscus* (Bovidae, Artiodactyla, Mammalia) from the North Sea and aspects of its paleoecology - in: Reumer, J.W.F. & De Vos, J. (eds.) - ELEPHANTS HAVE A SNORKEL! PAPERS IN HONOUR OF PAUL Y. SONDAAR - DEINSEA 7: 223-232 [ISSN 0923-9308]. Published 10 December 1999

Three vertebrae are described and attributed to the extinct muskox *Praeovibos priscus* Staudinger, 1908. The three vertebrae were trawled from the bottom of the North Sea between The Netherlands and England. The vertebrae are surprisingly large and strongly mineralised, such in contrast to bones attributed to the Late Pleistocene muskox *Ovibos moschatus* (ZIMMERMANN, 1780). A late Early Pleistocene or Middle Pleistocene age is inferred for these bones. The faunal elements, with which the species is found associated, indicate that *P. priscus* was not an inhabitant of the cold mammoth steppe. Unlike modern *O. moschatus* it may have had a short-haired pelage.

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Keywords: muskoxen, Praeovibos, Ovibos, North Sea, Pleistocene, paleoecology

INTRODUCTION

The first find of the extinct muskox Praeovibos priscus known from the literature is a nicely preserved skull fragment with the horn cores from the Forest Bed of Trimingham, Norfolk, East Anglia, which was obtained through a fisherman (Fig. 1). This find from the bottom of the North Sea was described in 1883 by the English paleontologist W.B. Dawkins as being from a female specimen of Ovibos moschatus. The skull fragment originates from the Middle Pleistocene 'Forest Bed'. It was later recognised as belonging to the extinct species Praeovibos priscus. The type locality of P. priscus is Bad Frankenhausen in Thuringia, Germany. Staudinger (1908) described a skull fragment with horn cores from this locality

that was clearly to be distinguished from *O. moschatus*. The latter species is known from the Late Pleistocene and is still extant in, e.g., Canada and Greenland. Fossil remains from the Late Pleistocene are also known from The Netherlands and from the bottom of the North Sea (Kortenbout van der Sluijs 1957, 1959; Erdbrink & Kortenbout van der Sluijs 1961; Hooijer 1960, 1984; Bosscha Erdbrink 1983, 1986, 1993a, 1993b; Van Kolfschoten 1981; De Vries 1990; Zijlstra 1991; Kerkhoff & Mol 1991; Mol & Zijlstra 1994; Van Dam-Van Beek & Van Dam 1994; Van den Hoek Ostende & Mol 1997).

A first mention in the literature of the presence of *P. priscus* in the Dutch

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Pleistocene is found in Crégut-Bonnoure (1992), who based this record on an unpublished communication of T. van Kolfschoten. Unfortunately, the material concerned was not mentioned.

NEW FINDS FROM THE NORTH SEA

Thoracic vertebra (Figs. 2A-D, Table 1) In 1995 mr. Piet van Es trawled a thoracic vertebra from the bottom of the North Sea with the vessel SL27. The coordinates of the location are 52° 00' N - 02° 50' E. The vertebra is in the collection of Dick Mol, inv. no. 2030. In Figures 2A-D the specimen is depicted; it is a rather complete vertebra with part of the dorsal spine still present. The relatively narrow neural canal and the generally massive built of the bone are characteristic for muskoxen. The bone is strongly mineralised and some iron concretions are adhering to it. These features characterise fossil land mammals from the late Early and Middle Pleistocene. This thoracic vertebra can be ascribed to a large individual, possibly a bull. It can not be stated with certainty whether it is a second, third or fourth thoracic.

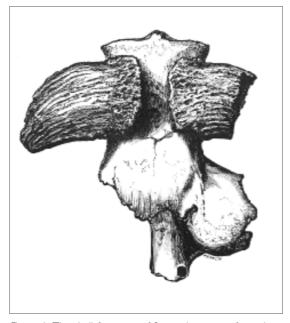


Figure 1 The skull fragment of *Pra* e ovibos priscus from the Trimingham Forest Bed, after W. B. D awkins (1883).

Epistropheus (Figs. 3A-D, Table 1)

A second cervical vertebra (the axis or epistropheus) was trawled by the crew of the vessel ARM20 in May 1996. The location where the specimen (collection Mol inv. no. 2031) was found must have been one of the gullies north of the lightship Noordhinder (Southern Bight). This epistropheus lacks the dorsal arch. It is massively built, and must originate from a large individual. The fossil is strongly mineralized and possesses a reddish-brown colour, most probably as a result of iron deposition. It is a vertebra that is highly characteristic for muskoxen, with a small neural canal.

Cervical vertebra (Figs. 4A-D, Table 1)

This seventh cervical vertebra (collection Mol inv. no. 2032) was trawled in July 1998 by the crew of the ARM20. The exact location is unknown, but it must have been situated in the Southern Bight of the North Sea between England and The Netherlands. It is a very large and strongly built vertebra. Part of the dorsal spine is lost and the lateral processes are slightly damaged. This seventh cervical vertebra too has a relatively narrow neural canal. Its colour is of the same dark brown as the thoracic vertebra found in 1995, and the iron depositions are remarkable.

PRAEOVIBOS IN THE NETHERLANDS AND THE ADJACENT NORTH SEA

The bottom of the North Sea between England and The Netherlands is the source of large quantities of mammal remains dating from the entire Pleistocene. The remains are trawled and brought ashore by fishermen, and they then find their way to collectors and museums in - mostly - The Netherlands. Considerably large collections are to be found in the museums of Middelburg, Leiden and Rotterdam. The material from the North Sea has different ages. It will be evident that such material - which is not found *in situ* - can be difficult to identify. The morphology is of course a primary source of information.

Table I Sizes (in mm) of fossil (*P. piiscus*, numbers 2030, 2031, 2032 from the Collection Mol) and recent (*O. moschatus*) vertebrae.

	2030	recent	2031	recent	2032	recent
anterior height neural canal	26.4	15.5				
anterior width neural canal	21.5	30			23.5	22.5
anterior height of centrum	51.5	45			63.5	52
anterior width of centrum	55.5	47			67.1	54
posterior height neural canal	26.8	17			19.3	2.2
posterior width neural canal	29.3	16				
posterior height of centrum	51	46.1	59.4	55	67.3	5.5
posterior width of centrum	58.1	46.5	80	81	71.5	55
length of centrum	58.8	37			48.5	37
width of centrum			122	116		
width of spine			50	32		

The degree of fossilisation can be a clue to the geological age of the material. Early Pleistocene and early Middle Pleistocene material is characterised by a high degree of fossilisation and by a metallic sound the fossil produces when tapped upon with a hard object. They are mostly of a dark colour (dark reddish-brown, dark brown to pitch black). Such fossils can easily be distinguished from Late Pleistocene and Holocene bones that do not possess the mentioned characteristics, and that are hardly or not mineralized. Marine mammals possessing the same degree of fossilisation are known from the Tertiary/Quaternary transition and from the Early Pleistocene.

WHAT WAS PRAEOVIBOS LIKE?

In *Praeovibos* (which species is also known by the popular name of giant muskox) the horns are less flattened at their base as is the case in *Ovibos*. *Praeovibos* must have been considerably larger than the Late Pleistocene and recent muskoxen that reached a whithers height of about 130-165 cm. Most probably *Praeovibos* was less specialised than *Ovibos*. Kurtén (1968) suggested that *Praeovibos* was

more agile and did not have an intraspecific defensive cooperation such as the modern - and possibly the Late Pleistocene - species. The giant muskox had longer and more massive limbs.

Several ovibovines lived in the Early and Middle Pleistocene of Eurasia. The distribution area of Praeovibos during the late Early and Middle Pleistocene ranged from the East Anglian coast and the Spanish Mediterranean coast eastwards up till northwestern Canada. Three species of Praeovibos are known (McDonald et al. 1991): Praeovibos priscus STAUDINGER, 1908, Praeovibos recticornis (RYZIEWICZ, 1933) and Praeovibos beringiensis SHER, 1971. In addition to *Praeovibos* a steppe goat is known of the genus Soergelia, represented by two species, viz. *Soergelia minor* (Early Pleistocene of Venta Micena, Spain), and Soergelia elisabethae (Middle Pleistocene, e.g. from German localities such as the classic Süssenborn near Weimar (Kahlke 1964, 1969). The Canadian paleontologist Harington (1989) considers Soergelia to be an indicator for the Middle Pleistocene, although Soergelia minor occurred together with Praeovibos in the Early

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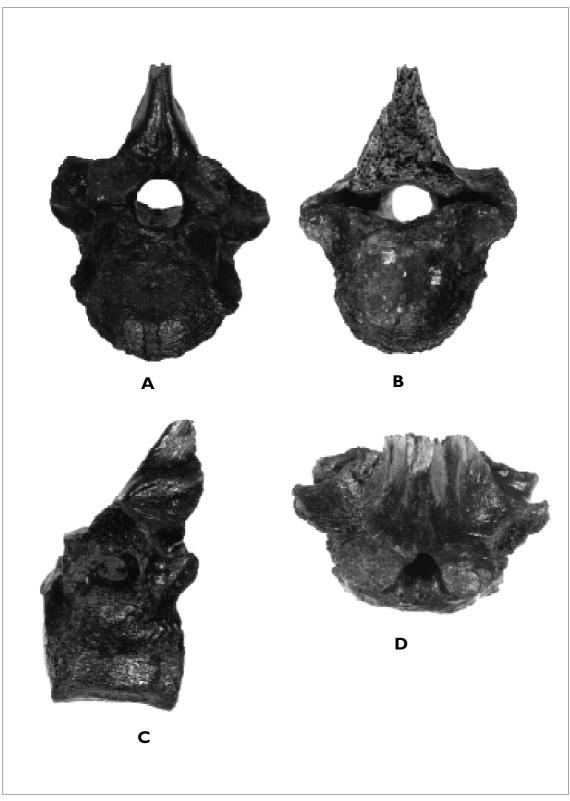


Figure 2 Second, third or fourth thoracic vertebra, coll. Mol inv. no. 2030. $\bf A$ anterior view, $\bf B$ posterior view, $\bf C$ lateral (sinistral) view, $\bf D$ dorsal view.

Pleistocene fauna of Venta Micena. Praeovibos priscus is known in Western Europe from Venta Micena in southeastern Spain (Agusti et al. 1986, Moyà-Solà 1987, Van der Made pers. comm.), from La Caune de l'Arago in southern France (Crégut 1979), from Eccles, Wallcott and Trimingham in East Anglia, England (McDonald et al. 1991), from Casa Frata in the Arno valley in Tuscany, Italy (De Giuli & Masini 1983), from Mosbach, Süssenborn, Wettin and Bad Frankenhausen in Germany (Kahlke 1964, 1969; McDonald et al. 1991). The finds from Venta Micena can be considered to be the oldest, viz. 1.2 My (Agusti et al. 1986), those from the Caune de l'Arago the youngest, viz. about 400.000 y. Other Praeovibos finds are reported from localities in (the former) Czechoslovakia, Poland and the former Soviet Union. A very complete revision of the occurrence of the genus *Praeovibos* and of the known remains is given by McDonald et al. (1991). In nearly all cases the remains concern the skull, the horns or loose dental elements. Postcranial remains are very rare. Complete skeletons have never been found. And, as far as we could discover, postcranial elements have never been found in association or in articulation with the highly characteristic skulls.

ASSOCIATIONS WITH PRAEOVIBOS

Venta Micena

Venta Micena (in the Guadix-Baza Basin, S.E. Spain), yielded a rich mammal fauna correlated to the late Early Pleistocene *Allophaiomys pliocaenicus* range zone, and that has an age of c. 1.2 My. Its faunal content is described by Agusti *et al.* (1986), and contained, among other taxa, *Equus stenonis*, *Mammuthus meridionalis*, *Stephanorhinus etnuscus*, *Hippopotamus antiquus*, *Megaloceros solilhacus*, *Cervus elaphoides*, *Capra* sp., *Bison* sp. and *Soergelia minor*. A range of large carnivores is also present in this fauna, that is clearly of a temperate character.

Trimingham

The first find of *Praeovibos priscus*, as described by Dawkins (1883) is characterized by depositions of iron. As Dawkins (1883: 576) put it: 'red matrix is still adherent in places'. The stratigraphical position of the Trimingham skull fragment is not known, but Dawkins placed it in the 'Forest Bed' (= Cromer Forest Bed, Middle Pleistocene). The three vertebrae mentioned above are characterised by the same 'red matrix'. This may lead us to the suggestion that they originate from sediments similar as from where the Trimingham skull of Dawkins came. Trimingham is one of the many localities on the East Anglian coast. It is stratigraphically placed in the Cromerian Forest-bed Formation, which Formation accumulated during the early temperate substage Cr IIa of the Cromerian (West 1980, Meijer & Preece 1996). The fauna may thus be some 600.000 -650.000 y old. Large herbivores in the locality include Cervus elaphus and C. rhenanus, three species of Megaloceros, Eucladoceros tetraceros and E. ctenoides, Palaeoloxodon antiquus, Mammuthus trogontherii, Equus stenonis, E. suessenbornensis and E. altidens (Azzaroli 1996, Lister 1996).

Caune de l'Arago

The richest locality with postcranial elements of *P. priscus* is the Caune de l'Arago, France. The material from the c. 400.000 y old fauna was described in detail by Crégut (1979). The list of faunal elements from the Caune de l'Arago contained, in addition to *Praeovibos* priscus the following taxa of larger mammals: Canis etruscus, Vulpes cf. praeglacialis and Vulpes sp., Cuon priscus, Ursus deningeri, Panthera cf. pardus, Panthera (leo) spelaea, Felis (lynx) spelaea, Felis syl vestris, Proboscidea gen. et sp. indet., cf. Praemegaceros sp., Cervus acoronatus, Dama sp., Rangifer tarandus, Cervidae indet., Ovis ammon cf. antiqua, cf. Hemitragus bonali, Rupicapra rupicapra, Bos primigenius, Bison priscus, Equus caballus mosbachiensis, Stephanorhinus

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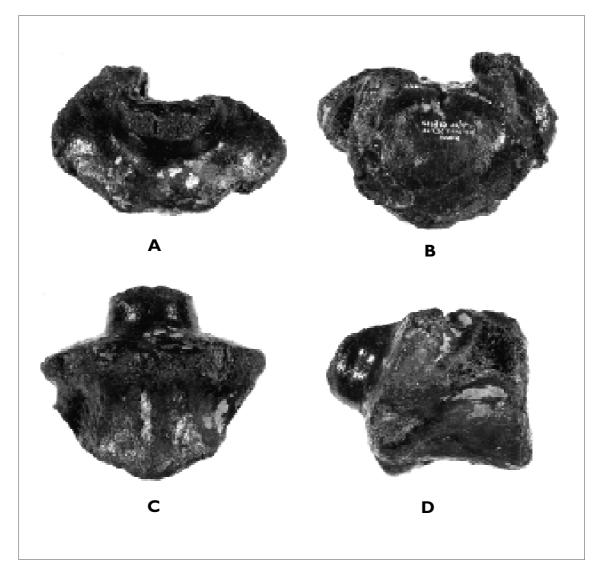


Figure 3 Epistropheus (second cervical vertebra), coll. Mol inv. no. 2031. **A** anterior view, **B** posterior view, **C** ventral view, **D** lateral (sinistral) view.

mercki and Stephanorhinus hemitoechus. In addition to this, the locality got its fame from the presence of early human remains. It will be clear from the composition of this fauna that it is not a cold climate mammoth-steppelike fauna, but a fauna of more temperate climates.

The Netherlands

As stated above, our three vertebrae can be associated with other fossils from the North

Sea that show the same state of fossilization. In the course of the past century, many collections of such Early and/or Middle Pleistocene mammals have been assembled. Typical members of such faunae are: *Mammuthus meridionalis* (the southern mammoth and characteristic for the Early Pleistocene), *Mammuthus trogontherii* (the steppe mammoth we associate with the Middle Pleistocene), *Alces latifrons*, *Eucladoceros ctenoides*, *Bison* sp., *Bos*

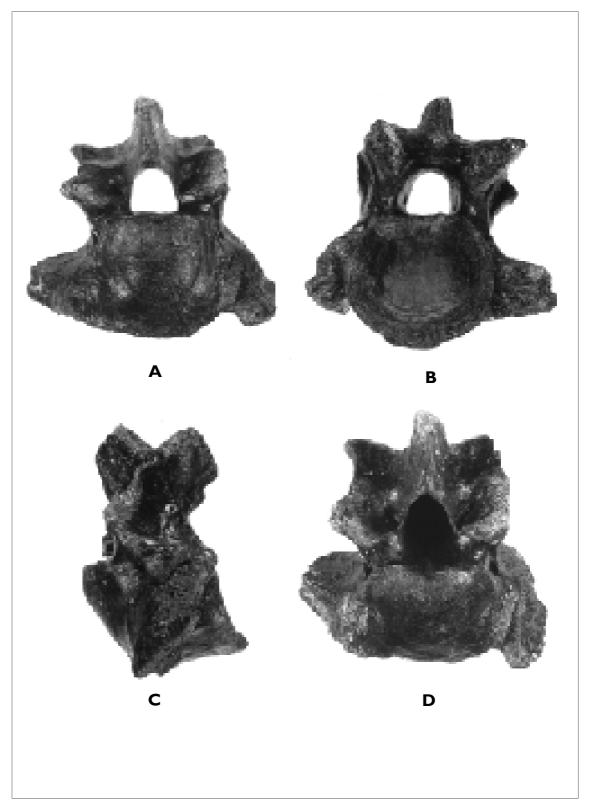


Figure 4 Seventh cervical vertebra, coll. Mol inv. no. 2032. **A** anterior view, **B** posterior view, **C** lateral (sinistral) view, **D** dorsal (dorso-posterior) view.

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primigenius, Hippopotamus antiquus, Sus cf. strozzii, Trogontherium cuvieri, Canis etnuscus, Equus major/stenonis, and Stephanorhinus etruscus.

DISCUSSION

We compared the three vertebrae with skeletal elements of a recent muskox Ovibos moschatus from Alaska (present in the collection Mol). This recent specimen is an extremely large animal, a bull. Table 1 shows that all three North Sea fossils are larger than this recent muskox. We have, on the other hand, been unable to find morphological differences. The three strongly mineralised bones from the North Sea are attributed to the Early and Middle Pleistocene species Praeovibos priscus. During the Early Peistocene the taxon could be placed in a fauna that inhabited northwestern Europe and that also contained the southern mammoth M. meridionalis. During the Middle Pleistocene P. priscus belonged to a fauna that also contained the steppe mammoth M. trogontherii.

The faunal composition of the southern European locality of Venta Micena suggests that the animals were inhabitants of vast grassy areas, the savannahs of the Early Pleistocene. The composition of the rich fauna from the Middle Pleistocene of the Caune de l'Arago (with many large grazers and browsers) also shows that Praeovibos did not live in the cold tundras in which we find the present-day muskoxen. The same conclusion applies to other localities in which the giant muskox has been found. All evidence therefore suggests that Praeovibos must be seen as a representative of a fauna from more temperate climatic stages in the Early and Middle Pleistocene. It is thus not a member of the cold fauna of the mammoth steppe, as could easily be inferred when applying an actualistic principle. Present-day muskoxen are sturdy animals with a thick and furry pelage, adapted to withstand the extreme cold of the Canadian high North. It would, in analogy to the common names 'woolly mammoth'

for Mammuthus primigenius and 'woolly rhino' for Coelodonta antiquitatis, not be strange to speak of the 'woolly muskox' when referring to Ovibos moschatus. The adjective 'woolly' sets these species apart from related, stratigraphically older, species, that are considered not to have had a woolly pelage, animals such as Mammuthus meridio nalis or Stephanorhinus etruscus. In analogy to this, we hypothesise that Praeovibos priscus, being an inhabitant of more temperate stages, also had a rather short-haired pelage.

Praeovibos used to be seen as the precursor of the Late Pleistocene Ovibos moschatus. There are, however, deposits of identical age in which the two species are found (Kahlke 1964, Kurtén 1968). It is thus more likely that the giant muskoxen and the extant muskoxen had a common ancestor.

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received 31 December 1998

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM P.O.Box 23452, NL-3001 KL Rotterdam The Netherlands