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BY

MAGNUS DEGERBØL

København
i kommission hos Ejnar Munksgaard
1952

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Introduction.

In the spring of 1950 some interesting finds of remains of mammals were made in two gravel pits in Seest, about 3 km west of Kolding, Jutland. The gravel pits, which belong to Kolding Mortar Works, are situated west of Seest Church on the slope facing Hylkedalen; the pits are still working. The first find, a brain-case with the lower part of the antlers of a giant deer (*Megaloceros giganteus*), was made by Mr. Oluf Jensen, who took care that the fragment was handed over to Mr. Straarup, teacher, of Vonsild, and thus it was saved from destruction. During the work in an adjacent gravel pit some weeks later the central part of the lower jaw of a large mammal was excavated, and Mr. Karl Rasmussen again informed Mr. Straarup who with fervid zeal attented to the interests of the Zoological Museum. A third fragment, a metacarpal bone (*metacarpus*) of the steppe-living bison (*Bison priscus*) was handed over to Mr. Krog, geologist, who had arrived in order to study the locality more closely. This fragment had been excavated the preceding year by Mr. Aksel Rasmussen, who had kept it since then.—In the same year another large bone was found in the gravel pit, where the mandible had come to light, a tibial bone (*tibia*) of a rhinoceros. When this find was published in the press Mr. Straarup sent in another bone, the metacarpal bone, no doubt of *Bison priscus* from a gravel pit in Grønninghoved, belonging to Mr. Lambert Laursen and situated some ten km SSE of Kolding.

The discovery of so many and not particularly powerful bones in gravel pits is fairly surprising. As such material is deposited by melt water rivers and washed out of moraine deposits it has ordinarily been exposed to so rough a treatment that only the most resistant and hard bones have been able to avoid pulverization. By far the greater part of the bones found in gravel pits in Denmark have therefore belonged to so powerful animals as elephants, notably teeth and single fragments of bones of mammoths (*Elephas primigenius*) to which are added some teeth of forest-dwelling elephants (*Elephas antiquus*). There are only a few other examples showing that weak bones can be found in gravel pits; from Raagelund, situated east of Odense, Funen, a *metacarpus* of red deer (*Cervus elaphus*) and some fragments of antlers of fallow deer (*Dama dama*) and elk (*Alces alces*) which too are polished by water, are known.

Also from the moraine deposits proper in Denmark only few finds are known. Of terrestrial mammals a very powerful brain-case of musk ox (*Ovibos moschatus*) from a marl pit near Helsinge in North Zealand should be mentioned here, and a left frontal bone with its horn-core of steppe antilope (*Saiga tartarica*), found near Ringe on Funen.

I. Find of Merck's Rhinoceros (*Dicerorhinus kirchbergensis* Jäger), new to the fauna of Denmark.

The present fragment consists of the middle part of a left horizontal ramus of a lower jaw (fig. 1–3). Anteriorly it is broken through the alveolus for the first deciduous tooth (dp1), posteriorly through the alveolus for the 2nd molar. Three teeth are present. The two anteriormost of these are in their proper position on the jaw, and their elongate and slender shape and low brachyodontous crowns show that they are milk teeth (dp3 and dp4). The posteriormost tooth sits in its alveolus, it is unworn and in the living animal had not made its appearance above the gum. This tooth will be the first molar (m 1). In front of dp3 the bifurcate alveolus for dp2 is found with the anteriormost broken root still left in its socket. Most anteriorly there is a single alveolus for dp1. Usually this tooth too has a double root; that there is only a single alveolus here may be due to the fact either that the anteriormost socket has been broken or that this tooth in this case had a single root only.—The fracture anteriorly seems to have taken place along the posterior border of the symphysis, which is now marked by a projecting edge. The fragment is surprisingly well preserved, though it has in some degree been exposed to the action of the melt water. The total length is 26 cm.

Since the fragment was found in a gravel pit, it is in a secondary or allochtone position and must have been removed from the place where the animal died. The bones may be lying either in deposits of the same age as that to which it originally belonged, i. e. it has been primary allochtone or may have been dug out from older deposits than that in which it was found, secondary allochtone (cf. Schroeder 1930, p. 107). This means that the present fragment cannot be younger than the last Glacial Period, but may be older, e. g. from interglacial deposits. Theoretically it may belong to one of the following four species of rhinoceros: 1) the cold-loving woolly rhinoceros, *Coelodonta antiquitatis* Blumenbach from the last Glacial Period. (Würm-Glacial Period), or the older interglacial warm-loving rhinoceroses i. e. 2) Merck's rhinoceros, *Dicerorhinus kirchbergensis* Jäger 3) its near relative the steppe rhinoceros, *D. hemitoechus* Falc., from the last Interglacial Period (Risz-Würm Interglacial Period) and finally, though less probable 4) *D. etruscus* Falc. from a still earlier period.

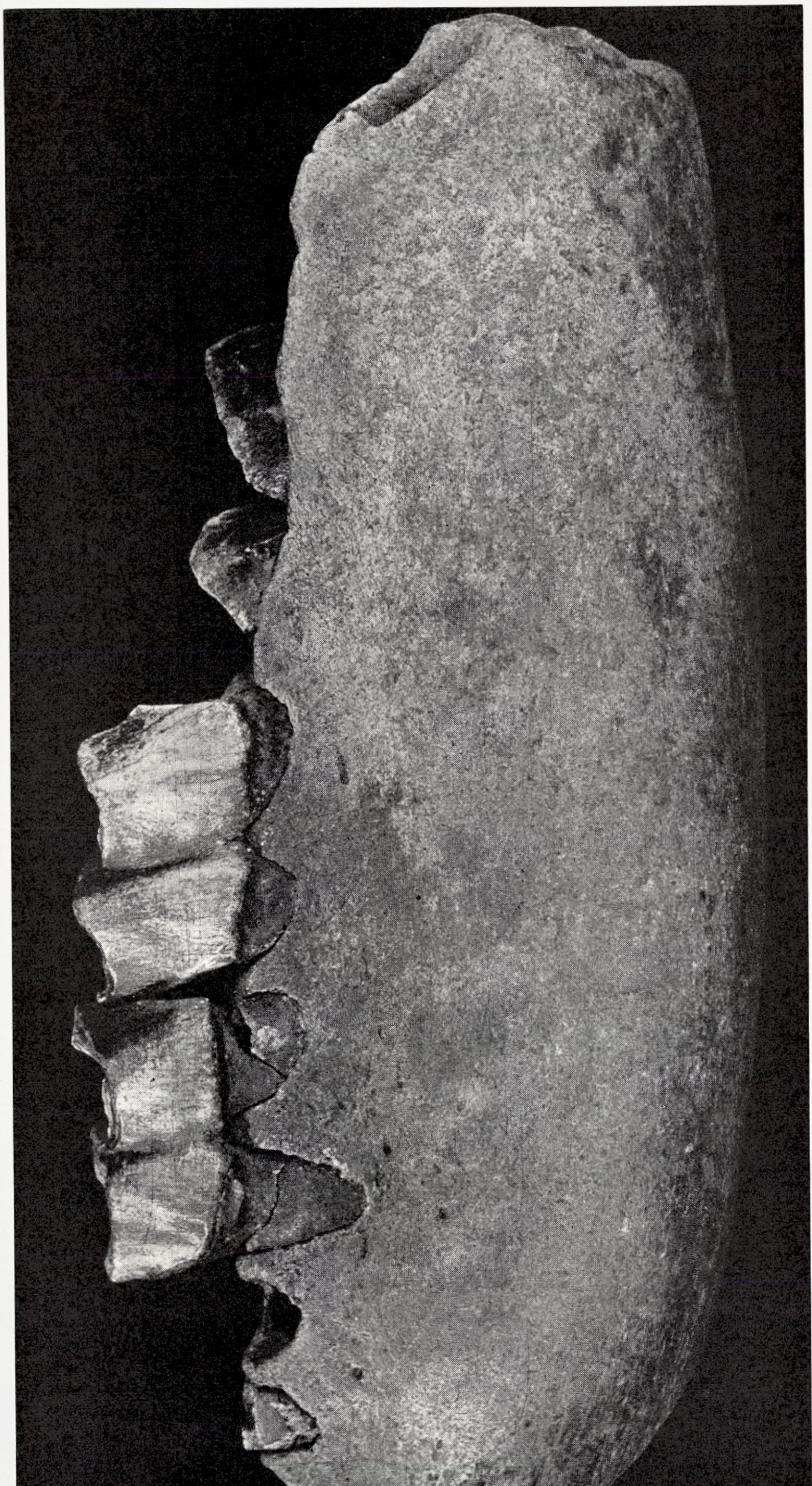
Since there is no material of these species for comparison in Copenhagen, the question as to which species the present fragment belongs can only be answered by

means of the literature. Here I shall not go into the very comprehensive literature available on extinct species of rhinoceros. It should, however, be noted that the older records may contain directly opposing data on the characteristic features in dentition which separate the different species. In this connection I fully agree with HESCHELER, 1917 who writes: "Als ich mich anschickte, die Differenzen zwischen Unterkieferzähnen der beiden diluvialen Nashornarten (*C. antiquitatis* and *D. kirchbergensis*) aus der Literatur festzustellen, ging es mir, wie wohl manchem vor mir, der nicht über ein umfangreiches Vergleichsmaterial verfügte: je weiter man sich in die Literatur vertieft, um so unsicherer wird man. Rhinoserosarten nach Unterkieferresten oder einzelnen Unterkieferzähnen bestimmt zu scheiden, fällt, wie bekannt, allgemein schwer" (p. 322).

An important contribution in this respect was made by SCHROEDER's great work on the German finds of "Rhinoceros mercki" (1930).—The trend of development is clear in the main features; like the mammoth the woolly rhinoceros is a specialized form, adapted to the extreme conditions of life, while Merck's rhinoceros is a more primitive type. Like the woolly rhinoceros the little known *D. hemitoechus* has become grass-eating and therefore in certain features in the dentition reminds of the recent white rhinoceros. *D. etruscus*, which is known right from the end of the Tertiary Period, is the original form of the four forms and is characteristic among other things by its relatively low, brachyodont teeth.

Of relatively good characteristics by which the teeth on the lower jaws of the two species of rhinoceros, *D. kirchbergensis* and *C. antiquitatis*, can be distinguished can be mentioned: 1) that the teeth of the woolly rhinoceros are covered with a thick layer of cement and that the layer of enamel is considerably thicker than in *Dicerorhinus*, 2) that in accordance with this the vertical cleft, which is found on the outer side of the tooth between the two crescentic lobes, in *D. kirchbergensis* is clear and sharply marked right to the base of the crown, whereas this furrow in *C. antiquitatis* is shallow and totally disappears about one cm above the base, 3) that *D. kirchbergensis* has a powerful cingulum which from the anterior edge of the tooth drops steeply towards the base of the outer side. In *Coelodonta* the cingulum is weak and does not extend to the outer side, 4) that in *C. antiquitatis* the most anterior crescent, the foremost half part of the tooth, has a more or less flat outer side, it is more angular and this portion of the tooth is just as broad as the hindmost part of the tooth; in *D. kirchbergensis* this anteriormost crescent is just as rounded, convex as the hindmost one and more narrow than this, 5) the two grooves or valleys of the tooth are deeper, more pointed and more closed on the inner side, i. e. more cone-shaped, in *C. antiquitatis* than in *D. kirchbergensis* which has broader and more open valleys. This is due to the fact that the middle and hindmost of the three inner columns or prominences of the molars, in *C. antiquitatis* on the inner side of the tooth is broader and bent someward forewards.

If we use these characteristics for the identification of the present lower jaw we find that they all tend to show that it belonged to *Dicerorhinus kirchbergensis*. It is



U. MOHL-HANSEN fot.

Fig. 1. *Dicerorhinus kirchbergensis.* Central part of a horizontal ramus of left mandible. From Seest. Lateral view. $\times$ c. $^{4}/_{5}$.

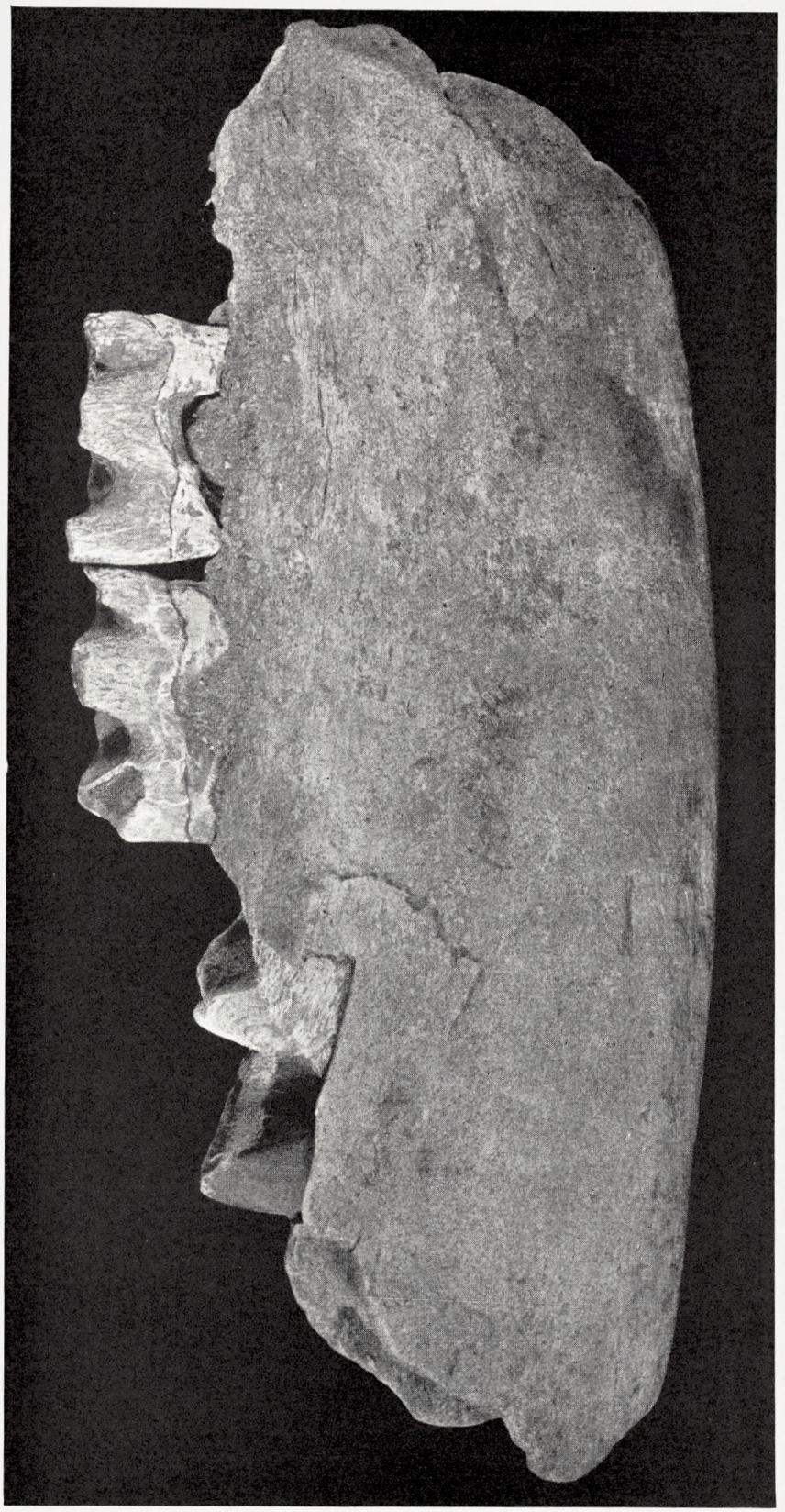


Fig. 2. *Dicerorhinus kirchbergensis.* Same mandible as fig. 1. Medial view. × c. $^4/_5$. U. Mohl-Hansen fot.

Fig. 3. *Dicerorhinus kirchbergensis*. Mandible from Seest. — Seen from above. U. Mohl-Hansen fot.

true that several of the said characters apply only to the permanent teeth, and of these there is only one on the Seest lower jaw; but the evidence is clear. There is no layer of cement on the teeth and the vertical middle furrow on the outer side of the tooth is distinct and sharp right down to the base. It might be supposed that the layer of cement on this lower jaw which has been exposed to the action of the water had disappeared by erosion, but there is no indication of this. An important feature is the primitive shape of the tooth with the more open and broad valleys.— The cingulum can be clearly seen from the outer side.

The position of *Dicerorhinus hemitoechus* is far from clear both as regards its morphology and occurrence, in time and space. The general form of the teeth places is near *D. kirchbergensis*, but as regards the hypsodonti, the coarse sculpture of the enamel, and the more angular shape of the first crescent on the lower molars show agreement with *C. antiquitatis*. It has therefore often been confounded now with one and now with the other of these two species.

Also the possibility that the fragment could belong to *D. etruscus* must be excluded. This form is characterized by lower crowns, and along the whole outer side of the tooth there is a cingulum.

If the Seest fragment is compared with the lower jaws of *D. kirchbergensis* we find the Danish fragment has very large teeth, especially the molar (m 1) is big (cf. table 1).—Milk teeth of *D. kirchbergensis* seem to be rare. Schroeder in his work (1930) describes a lower dp 4 from Schlangenhorstbrücke

a U. Møhl-Hansen fot.

b U. Møhl-Hansen fot.

c U. Møhl-Hansen fot.

Fig. 4. *Dicerorhinus kirchbergensis*. First lower molar (m1). a. Lateral view; b. Medial view; c. Seen from above. × 1.

TABLE 1.

Dicerorhinus kirchbergensis Measurements of mandible	Seest	Schlangenhorstbrücke (Schroeder 1930)	Mosbach (Schroeder 1903)	Taubach (Schroeder 1903)	Britz (Schroeder 1930)	Westerweyhe (Schroeder 1930)	Roter Berg, Saalfeld (Schroeder 1930)	Rabutz (Wüst) 2 specimens	Taubach (Wüst)	Taubach (Freudenberg 1914)	Schaffhausen (Meister)	Fiume, Maspino. Basel Mus. (2 specimens)	San Romano Basel Mus.	Tegelen, Netherland (Bernsen)	The Thames (Dawkins 1865)	C. antiquitatis Eichstätt (Schlosser)	» Lahntal (Schlosser)
dp 2—dp 4 length	128	—	—	—	—	—	—	—	—	128	—	—	—	—	—	—	—
dp 1—dp 4 »	(145)	—	158	158	—	—	—	—	—	—	—	—	—	—	—	—	—
dp 1 length (at base of crown)	—	—	18	—	—	—	—	—	—	—	—	—	—	—	—	16	24
dp 2 » » » » »	(30)	—	32	32	—	—	—	—	—	32 34 (4 sp.)	—	—	—	—	30	26	32
dp 3, greatest length	47,5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36	43
» length at base	46,5	—	41	43	—	—	—	—	—	44 45 (4 sp.)	—	—	—	—	42	—	—
dp 4, greatest length	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	42	45
» length of grinding surface	50	ca.45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
» length at base	47,5	46,5	50	47	—	—	—	—	—	47	—	—	—	—	46	—	—
» breadth ant. lobe, at base	26	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
» breadth post. lobe, at base	28	28	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
» height, ant. lobe, outer side posteriorly	30	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
» post. lobe, outer side, middle	27	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
m 1, greatest length	60	—	—	—	—	—	—	—	—	—	45	—	—	—	—	—	—
» length of grinding surface	60	—	45	—	—	45	—	—	—	—	—	—	—	—	—	—	—
» » at middle	57	ca. 47,5	—	—	50	45	—	—	—	—	—	—	—	—	—	—	—
» » » base	54	53	44	48	50	44	48	53 43	49	—	—	41 44	47,5	46	48	—	—
» breadth, ant. lobe, at base	33	ca.35	28,5	31	33,5	30	—	—	—	—	—	—	—	35	—	—	—
» » post. » » »	35	34	30,5	30	34	31	29	37 33	—	—	30	—	—	—	—	—	—
» » of grinding surface																	
» » anterior	—	25	22,5	—	26	21	—	—	—	—	—	—	—	—	—	—	—
» » middle	—	—	26	—	—	27	—	—	—	—	—	—	—	—	—	—	—
» » posterior	—	27	29	—	28	28	24	—	—	—	—	—	—	—	—	—	—
» height, ant. lobe, outerside	58	49	27	57	43	28,5	58	—	—	—	—	—	—	—	—	—	—
» » post. » »	53	46,5	27,5	48	39	29,5	49,5	—	—	—	—	—	—	—	—	—	—
Greatest thickness of mandible	56	64	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Depth between dp 3—dp 4	90	89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
» behind dp 4	90	—	65	—	—	—	—	—	—	—	—	—	—	—	—	—	—

near Nauen. This tooth is somewhat more worn than in the Seest fragment, so much that the dentine in the first and last crescent is fused. The length at the base is 46.5 mm as compared with that of the Seest fragment which is 47.5 mm. The length of the grinding surface is stated to be 45 mm (measured on the figures it is however 47 mm), while the Seest fragment here measures 50 mm. The width of the foremost crescent at the base in both specimens is 26 mm, and also the breadth of the hindmost crescent is the same, viz. 28 mm. The height of the crown naturally depends on the degree of wear, so the larger measurements of the Danish tooth only show that this is less worn.— SCHROEDER states that these measurements agree well with the corresponding

length and breadth measurements in a couple of dp 4 from Taubach (Wüst 1901, p. 279). The fact that the lower jaw from Taubach is considerably weaker than those from Seest and Nauen only shows that this lower jaw belonged to a younger individual (cf. table 1).

In a previous work (1903, p. 117—118 and table XII) SCHROEDER has described and figured a lower jaw of a young individual from Mosbach belonging to this species with all four milk teeth preserved, while m 1 is still hidden in the jaw. This fragment belonged to a somewhat younger animal than the Seest specimen. The length of these milk teeth is stated to be 158 mm and the same holds good of a specimen from Taubach which SCHROEDER has used for comparison. If however the measurements of the individual teeth are added it makes only 141 mm; this great difference seems somewhat striking, but is presumably due to the fact that the individual teeth were measured at the base, on the inner side. As said above, the Seest specimen has only one root for dp 1, as the foremost root was presumably broken. In the present state the total length of the milk teeth is 143 mm, but to this length should presumably be added the length of the foremost root of dp 1, viz. so that we get a total length of about 150 mm. Table 1 shows that regarding dp 3 and dp 4 which can be directly measured these teeth in the Seest specimen are equally large as in the above mentioned two German specimens.

FREUDENBERG too (1914, p. 480) gives measurements of some milk teeth. The length of dp 2—dp 4 is 128 mm in a *Rh. etruscus* var. *Heidelbergensis*, the same measurements as in the Seest specimen. For 6 dp 2 (table 1, p. 480) belonging to "*Rh. mercki*" is stated that the greatest length varies between 32 mm and 34 mm. In the Seest fragment only the alveolus measurement, 30 mm, can be given for this tooth, which means that the crown presumably was 32 mm long. The greatest length of dp 3 and dp 4 in the Seest specimen is however 47 mm and 50 mm respectively, while the length in the said six individuals, in FREUDENBERG, for dp 3 varies between 41 mm and 45 mm, for dp 4 between 43 and 50 (5 individuals).

In 1865 BOYD DAWKINS has given excellent drawings of the milk dentition of *D. mercki* (*Rh. megarhinus*) from the valley of the Thames (Grays Thurrock). He records the following measurements, taken along the outerside of crowns: dp 2 30 mm (1·22 inches), dp 3 42 mm (1·16 inches), dp 4 46 mm (1·8 inches), m 1 48 mm (1·9 inches).

The foremost molar (m 1) in the Seest lower jaw is, as mentioned above, completely unworn, in the living animal it can hardly have penetrated through the gum. Since the jaw narrows somewhat on the alveolar border this involves that the tooth which sits loose in its socket could not fall out during the rolling of the jaw in the water from the melted ice. By removal of a small part of the upper inner side of the wall of the alveolus the tooth could easily be taken out (fig. 4). It will thus be seen that roots are practically absent, only at the base of the crown are there some faint traces left. Two well defined depressions in the bottom of the alveolus however show that the roots have been partly developed. The crown consists only of a comparatively

thin shell, i.e. that the pulpa cavity has been large. The greatest length of the tooth, 60 mm, is found a little below the grinding surface, and from here decreases strongly towards the base, where the length is 54 mm. It should be born in mind however, that as the enarmel of this tooth is not quite formed, the length with age would probably increase by one or two mm. Tab. 1 shows that these measurements of the Seest molar are considerably larger than the measurements otherwise recorded in *D. kirchbergensis*.

SCHROEDER (1930, p. 96, taf. 18, fig. 75—76) describes and figures a powerful first, lower molar (m 1) belonging to this species from Schlangenhorstbrücke, Nauen. As regards size—length at base 53 mm—this tooth from northern Germany corresponds most closely with the Danish specimen. This holds good too of the structure of the enarmel: "Die Oberfläche des Emails ist zimlich glatt und nur von feinen Fältchen bedeckt, wie sie auch an mitteldeutschen *Mercki*-Zähnen vorkommen" (SCHROEDER).

According to the same author (1930, p. 50) a lower m 1 from Westerweyhe bei Uelzen (Lüneburg) is of so small dimensions—the length of the grinding surface nevertheless is 45 mm—that regarding size it may have belonged to the older and more primitive *D. etruscus*, but as a strong basal cingulum is missing SCHROEDER comes to the result that this tooth should be referred to *D. kirchbergensis*. The sexual dimorphism on this point also may be considered as "ein weiblicher *mercki* könnte in seinen Dimensionen einem männlichen *etruscus* nahe kommen".

From Germany WÜST too gives some records of the dimensions of the lower m 1 in this species (1901, p. 278). From Rabutz two specimens are known; a powerful tooth measures 53 × 37 mm (length × breadth) and a small one 43 × 33 mm. A third specimen, from Taubach, is 49 mm long.—On a mandible from Schaffhausen, Schwitzerland, m 1 measures 45 mm in greatest length and 30 mm in breadth. About this specimen however MEISTER (1898) remarks: "Die sämtliche Zähne des Unterkiefers sind verhältnismässig sehr gross, namentlich sehr breit; die Schmelzlager ist durchwegs dünner als an entsprechenden Stellen bei *Rh. tichorhinus* (= *C. antiquitatis*)".

In the summer of 1950 I had the opportunity in the Zoological Museum in Basel to take some measurements of three mandibles labelled *D. kirchbergensis*. In comparison with the Seest specimen these teeth too are rather small. On two mandibles from Fiume Maspino 1920 (ch. 663 and 599) m 1 measures 41 and 44 mm respectively, and a lower m 1 from San Romano is 47,5 mm long[1].

These records indicate that the teeth of *D. kirchbergensis* from the various localities vary greatly in size. The two greatest, known to me, are from North Germany and Denmark.

The teeth in *Coelodonta antiquitatis* are generally smaller than in *D. kirchbergensis*.

[1] For the permission to examine these animals and for all kindness shown me during my visit to the museum, I beg Dr. S. SCHAUB to accept my most cordial thanks.

a U. Møhl-Hansen fot. b U. Møhl-Hansen fot.

Fig. 5. *Tibia* from Seest. a. Anterior view; b. Posterior view.

The *tibia* from Seest is strongly corroded (fig. 5) especially in its upper half. Only three measurements can be taken with exactness: the maximum length is 42 cm, the maximum breadth at distal end 11 cm and the maximum thickness at distal end 7,7 cm. I think however that these measurements may be sufficient to prove that this *tibia* had belonged to the same species as the mandible, viz. *D. kirchbergensis*.

In *D. etruscus* the *tibia* is rather small. Bernsen (1927, p. 93) has recorded some measurements of two *tibiae* from Tegelen clay belonging to *D. etruscus* and for comparison he has added the corresponding measurements of the *tibiae* of other

species of rhinoceros: *D. kirchbergensis, D. hemitoechus* and *Coelodonta antiquitatis*, 8 specimens in all. None of these has so long a *tibia* as the Seest specimen. The great length then excludes *D. etruscus* and the same holds good of the dimensions of the distal end which considerably exceeds those in the different *etruscus*-specimens. On the other hand, this distal end is too weak for a *tibia* belonging to *C. antiquitatis*. The *tibia* of this species is broader and thicker, hence clumsier.

In the often cited work: "Über Rhinoceros mercki und seine nord- und mitteldeutschen Fundstellen" (1930) SCHROEDER says in the introduction: "*Rhinoceros mercki* Jäger (einschl. *Rh. leptorhinus* Owen — *Rh. hemitoechus* Falc.) ist in West-Mittel- und Südeuropa allgemein verbreitet".—It may seem strange that SCHROEDER who in his work distinguishes sharply between *hemitoechus* and *kirchbergensis* (mercki) here unites these two forms. This may be due to the fact that Schroeder's work is incomplete, because the author died during its preparation, and the work was published unchanged after his death; but rather because these two forms are generally not kept separate in the literature.

The locality nearest Denmark stated by SCHROEDER here is Grünenthal in Schleswig-Holstein in 54°07′ N. lat.—It is however strange that this find is not mentioned later in the work, which otherwise contains very detailed information of the German finding places and their fauna. This might indicate that SCHROEDER in this work does not consider the Grünenthal fragments as belonging to *D. kirchbergensis* proper, but agrees with WÜST who studied this find more closely. WÜST writes as follows on this find (1922, p. 686): "Im Zoologischen Institute der Universität Kiel liegen 2 Nashornzähne, die beim Bau des Kaiser-Wilhelm-Kanales im März 1893 bei km 35,4, d.h. zwischen Grünenthal und Oldenbüttel, in einer Tiefe von 10,6—12,0 m unter dem Kanalwasserspiegel gefunden worden sind . . . . . Es handelt sich um P II u. III max. dextr. von *Dicerorhinus hemitoechus* Falc."

The finding places of *D. kirchbergensis* which are to be found nearest to Denmark are thus at Lüneburg and Menthen (West Prussia).—The Seest fragment thus shows that this species was distributed considerably farther north than hitherto presumed.

It can be mentioned in this connexion that the upper end of the *radius* of a Rhinoceros in 1935 was sent to the Zoological Museum from Højrup in South Jutland. It was found here about fifty years before in a field. This bone is somewhat damaged, e.g. the lateral side of the surface for articulation is missing. The transversal breadth was about 11 cm; the breadth, anteriorly-posteriorly, about 7 cm. This fragment could not be identified with certainty, but owing to its stoutness it had been referred to *Coelodonta antiquitatis* (Degerbøl 1938).

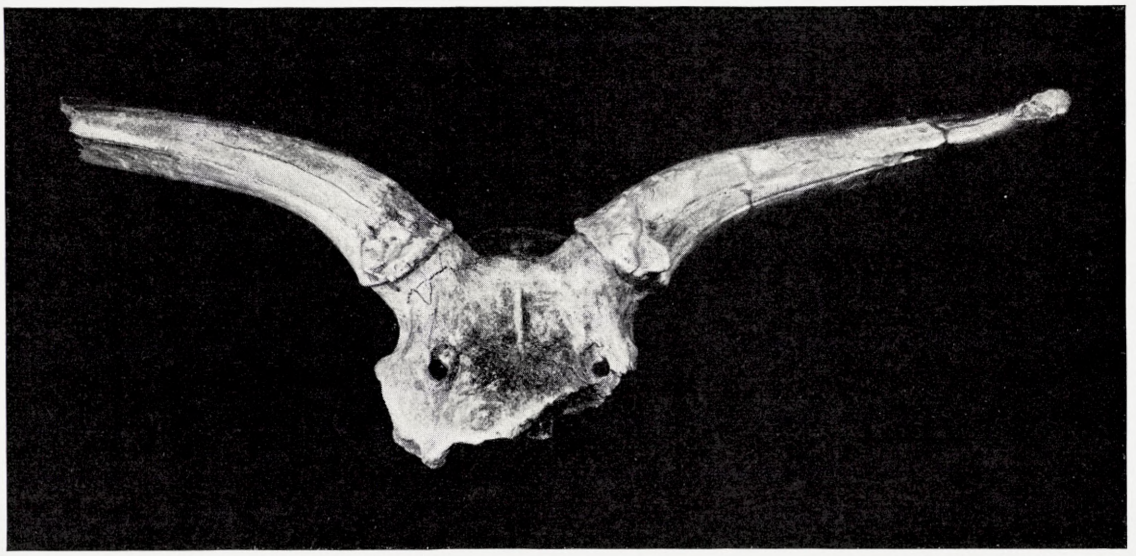
II. The Giant Deer (*Megaloceros giganteus* (Blumenbach)).

The present specimen consists of a brain-case with the lower parts of the antlers (Fig. 6—7). Greatest width of the fragment is now 95 cm. The specimen has been rolled by water, but not so much as to change the original surface. As the fractures too are polished by water this means that the specimen now almost is in the same state as when it was buried in the gravel pit. On the right side the skull is broken just before the lacrymale, on the left side through the orbit. Of the antlers the shafts or beams are complete on both sides and on the left side a small part of the palm is moreover left. Both brow tines are totally broken. They have sprung at the very base of the antler, on the upper side of the rose. On the left antler the base of the broken 2nd tine is marked too.

The present fragment represents a powerful animal. The pedicels, from which the antlers spring, are rather high, which indicates that the animal had reached the prime of its age. In old animals the antlers come off almost directly from the skull-wall. The length of the shaft, from the base of the rose to the middle of 2nd tine, is 44 cm. The circumference immediately above the rose is 30 cm, 10 cm from the rose 22 cm; 15 cm from the rose the shaft is almost circular in circumference with a diameter of 6,5 cm. The measurements of the brain-case also indicate a powerful animal (cf. table 2). With the Seest-specimen the giant deer has for the first time become

TABLE 2.

Megaloceros giganteus Measurements of brain-case and antlers in centimetres	Seest	Hesselagergaard	Ireland (Copenhagen)	» » (cm. 654)	» » (665)	» (After Reynolds) (3 specimens)
1. Least distance between *for. supraorbitales*	12.3	c. 13	11.9	12	11.4	10.3–12.2
2. Greatest width across *orbitae*	c. 25	c. 25	25	24	24.5	—
3. Interorbital constriction, at fronto-lacrymal sut.	21	—	19	18.7	17.8	15.9–18.2
4. Least distance between curvatures between *orbita* and rose	20	21	21	19.5	20	—
5. Least intertemporal width	12	13	11.5	11.7	11.5	—
6. Greatest supraoccipital width	19	19.8	18.5	18.2	19.3	
7. Width across condyles	11	c. 11	10.9	13.5	11.0	9.7–10.7
8. *Meatus acusticus* width	c. 16	c. 18	17.7	16.5	17	15.2–16.0
9. Length of beam from base of rose to middle of 2. tine	44	—	l. 36 r. 33	52 39	38 —	— —
10. Circumference of beam immediately above rose	30	—	31	22.5	26.3	—
11. Circumference 10 cm from rose	22	—	22	18.2		—
12. Diametres of beam 15 cm from rose	6.5×6.5 l. 6.5×6.2 r.		l. 6.8×7.0 r. 6.8×6.8	5.9×6.0 5.7×6.0	5.5×5.7 5.6×5.9	
13. Circumference of pedicle	l. 25 r. 26	26 27	27 27	22.5 22.5	23.2 24	— —



U. Møhl-Hansen fot.

Fig. 6. *Megaloceros giganteus.* Brain-case with fragmentary antlers. From Seest. Anterior view.

known from glacial deposits in Denmark. In the summer of 1951 however another fragment, a distal end of a *metatarsus,* was found in a gravel pit near Svenstrup, 10 km S of Aalborg, North Jutland (Fig. 8). Besides these discoveries, however, remains of this species have been found in 5 other localities in Denmark, but they are all from the time *after* the last glaciation (Fig. 9).—The first record of remains

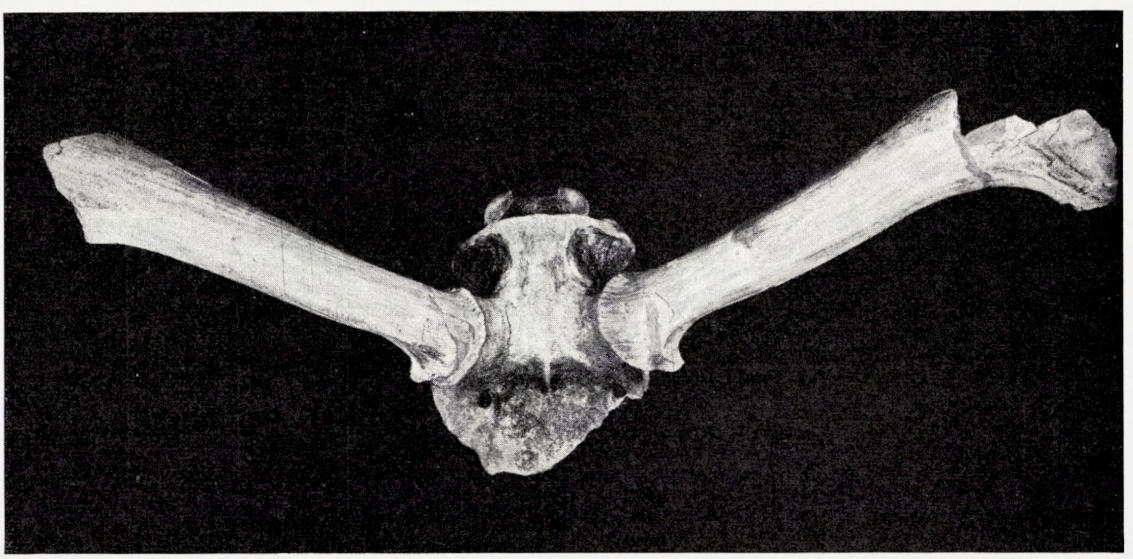


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Fig. 7. *Megaloceros giganteus.* Same brain-case as fig. 6. Seen from above.

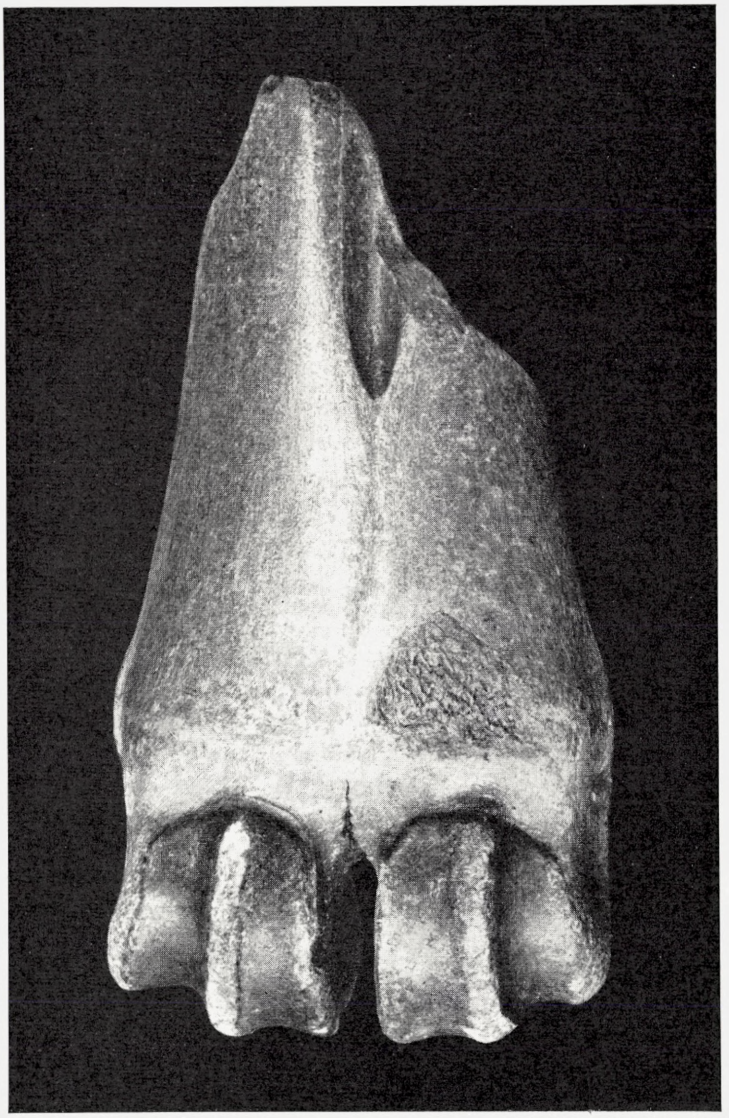

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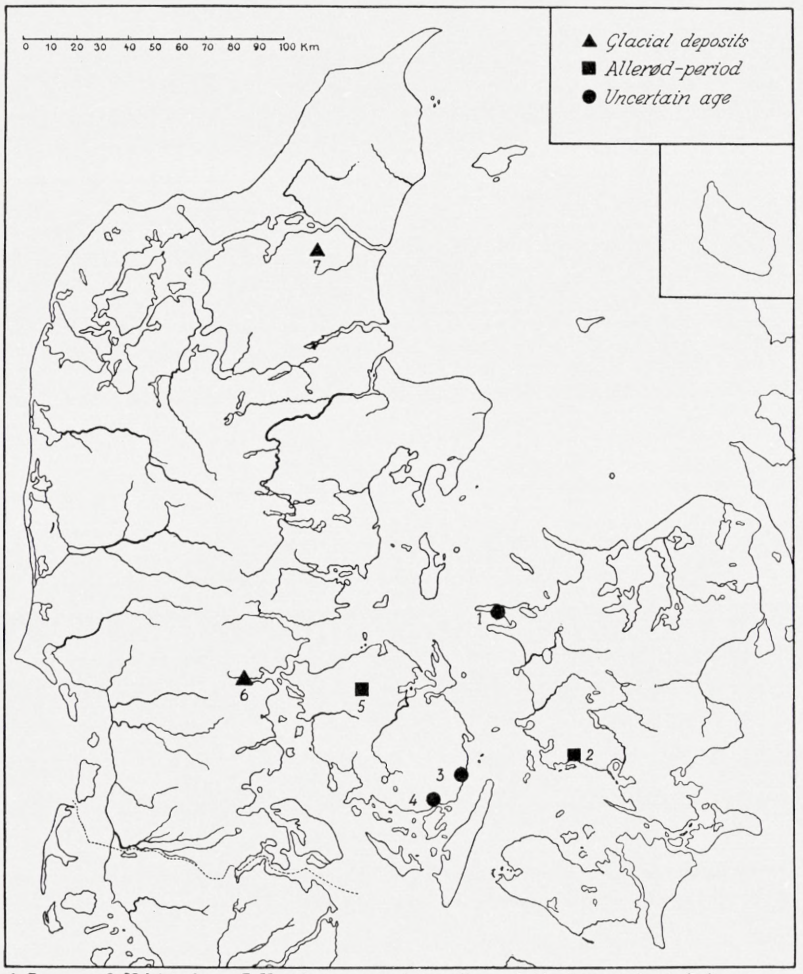
Fig. 8. *Megaloceros giganteus.* Distal end of *metatarsus.* From Svenstrup. × 1.

of the giant deer in Denmark we owe to Japetus Steenstrup, who in 1848 at a meeting of Videnskabernes Selskab was able to demonstrate the lower end of an antler of this species, found 12 years before on Røsnæs, N.W. Zealand. The next find too, a brain-case with pedicels but without antlers, from Hesselagergaard, Funen, was recorded by Steenstrup (1869, p. 162).

Not till 70 years later, in the year 1938, were new remains, a shed antler from a small bog at Vævlinge, Funen, unearthed. While the age of the first two finds was



1. Rosnæs. 2. Holsteinsborg. 3. Hesselagergaard. 4. Svendborg. 5. Vævlinge. 6. Seest. 7. Svenstrup.

Fig. 9. Map showing the discoveries of *Megaloceros giganteus* in Denmark.

uncertain, Dr. Johs. Iversen, Danmarks Geologiske Undersøgelse, by means of a pollen-analytical examination was now able to date the Vævlinge antler to the Allerød-period or pollen zone II. (M. Degerbøl 1938, p. 134—137; M. Degerbøl and J. Iversen 1945, p. 50). According to Mr. H. Krog, the pollen analyst of the Zoological Museum, some skeletal parts of 3 individuals, one adult female and two young animals, excavated in 1943 at Holsteinborg, South Zealand, belong to the same period. This find will be published in detail later. Regarding the age of the fifth find, a shed antler from Tved Nørremark near Svendborg, South Funen, it can only be stated that it belonged to the late glacial times.

As we now know that the earliest settlement in Denmark, Bromme, South Zealand, is dated to the Allerød-period, this means that the giant deer in Denmark has

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Fig. 10. *Megaloceros giganteus*. Antler from Vævlinge, Funen. From the Allerød-period. × $^1/_{10}$.

been contemporaneous with man, just as in Ireland (K. Jessen and Farrington 1938). Denmark is situated at the nothern limit of the area of distribution of *Megaloceros*. From Sweden, Southern Scania, a shed antler curiously enough was found in 1938, the first discovery of this species in Sweden. Here too the giant deer occurred in late glacial times (Berlin und Mohrén 1942).

From a morphological point of view the question now arises whether the Seest fragment agrees with the late glacial Danish animals or with the older interglacial giant deer? Various authors have described several "races" of giant deer, but there has been a great diversity of opinion about the validity of these races and how they should be grouped. Pohlig (1872) has recognized two continental varieties, *Cervus* (*Euryceros*) *germaniae* and *C. italiae*, which he considered worthy of distinction from *C. hibernicus*. *Megaloceros giganteus germanicus* (C. germaniae) is of speciel interest to the comparison with the Seest specimen since it comprises the German examples from interglacial times. The most distinguishing features of this subspecies are the smaller and more upwardly direc-

ted antlers, which consequently has a smaller span than in the Irish elk (*M. g. hibernicus*).

With its strong and outwardly directed antlers or shafts the Seest animal as far as can be seen from the fragment, shows no connection with these interglacial animals, but a comparison with three skulls of the Irish elk in the Zoological Museum in Copenhagen fully indicates the idendity. This may either imply that the *hibernicus*-form was already in existence in interglacial times or that the Seest specimen is younger, belonging to an animal, which has lived in the periglacial area, the icefree landscape in Southwest Jutland during the last glaciation.

It has been claimed too (Soergel) that in the geological later forms the brow tine springs at the very base of the antler, from the rose or immediately above the rose, while it is characteristic of the older, interglacial animals that this tine has moved higher up on the shaft. This character however is of no taxonomic significance. In the Seest specimen from the glacial deposits this tine comes off close to the rose, while in the Vævlinge antler, from Allerød-time, it is placed far from the rose (fig. 10).

III. Steppe Bison (*Bison priscus* H. von Meyer).

The *metacarpus* from the gravel pit in Seest is incomplete, missing the lower end, while the specimen from Grønninghoved is in good condition. Both are a little water-rolled.

It is very difficult to arrive at an exact species-determination of the great bovine metapodials, especially *Bos* versus *Bison*. Several authors have discussed the value of the characters according to which it has been attempted to distinguish between the metacarpals of these two animals. The most recent papers are those by Schertz (1936), Reynolds (1939) and Lehmann (1949). As distinctive features on this point, the size, the shape of the upper end and the distal width, compared with that at the suture for the epiphysis, have been quoted.

Regarding size it has been recorded that the *metacarpus* is tending to be more slender in *Bison* than in *Bos*. The greatest length of the complete Danish metacarpus (Grønninghoved specimen) is considerable, 24,8 cm (table 3). This far exceeds the length of metacarpals of recent bisons. According to Allen (1876, p. 29) the range of variation of the corresponding measurements of nearly one hundred adult American bisons are 17,4 and 21,3 cm, and the same author records the extreme length of a *metacarpus* of the large extinct *Bison antiquus* as 22,3 cm. In the Jalna-district and West Sibiria Tscherski (1892) has unearthed 19 metacarpals which he has determined as belonging to *Bison priscus*, the variation range is here 18,6 and 24,2 cm, measured on the outer side—the corresponding measurements in the Grønninghoved specimen is 23,5 cm—but only two of these Asiatic specimens surpass the Danish specimen: 24,1 and 24,2 cm. The next in size measures 22,8 cm—Reynolds too has quoted very

TABLE 3.

Bison *Metacarpus* In millimetres	Grønninghoved	Seest	*Bison antiquus* (Allen, 1876)	*Bison americanus* (About 100 specimens) (Allen 1876)	*Bison priscus* Windy Knoll (Reynolds, 1939)	» (»)	Forest Bed (Reynolds. 1939)	Gouvern. Irkutsk (Tscherski, 1892)	» »	*Bos primigenius* Grenge. 1942 ♂
1. Greatest length	248	—	223	174–213	234	222	257	—	—	252
2. Length, inner side	236	—	—	—	—	—	—	242*	241*	235
3. Proximal width:										
a) transversal	88	—	82	60–74	89	71	80.5	80	98	87
b) anterior-posterior	52	—	—	—	—	—	—	—	—	52
4. Width at midde of diaphysis:										
a) transversal	51	59	56	35–45	55	42.5	44.5	50	58	52
b) ant.-post.	34	37.5	—	—	—	—	—	31	40	35
5. Distal width, ant.-post., of diaphysis	40	—	—	—	—	—	—	—	—	41
6. Width at suture between diaphysis and epiphysis	82	—	—	—	85.5	75	80	—	—	81
7. Distal width	86	—	84	58–73	88.5	70.5	81.5	84	97	88

* Outer side.

great measurements of this bone. From a locality, Windy Knoll at Manchester, where "an immense number of bones was found associated with horn-cores of *Bison*, but with nothing to indicate the presence of *Bos*", he records: 23,4 and 22,2 cm as greatest lengths and from the Forest Bed 25,7 cm.

Still longer metacarpal cannon bones are however to be found in supposed *Bos primigenius:* 27,0—26,4—25,7 and 22,9 cm (Reynolds, p. 47). In twenty metacarpals of postglacial *Bos primigenius* from Denmark the greatest length varies between 24,3 and 25,8 cm (vide too table 7, Degerbøl 1942), up to now no remains of *B. primigenius* have been discovered in glacial or interglacial deposits in Denmark. It appears from these measurements that the Grønninghoved *metacarpus* is long enough to fall within the range of variation of the Danish *Bos primigenius* and not longer than the longest of the pleistocene *Bison priscus*. An exact determination as regards specific identity can therefore not be based on the length of the *metacarpus*.

There is the same uncertainty and difficulty as to the determination due to the shape of the upper end of the *metacarpus*. It is maintained by SCHERTZ that in *Bos* the upper end tends to be more rectangular than in *Bison*, in which there is a more outward tapering of the articulating surface. REYNOLDS (l.c.), however, has described and figured 17 upper ends of bovine metacarpals and demonstrated that there are specimens of an intermediate character, "there is a tendency for the stouter metacarpals of both *Bos* and *Bison* to be relatively rectangular, the more slender to taper".—As the Grønninghoved *metacarpus* is a powerful specimen it ought to be *Bos*-like in the shape of the upper end, but on the contrary it clearly shows the outward tapering

considered to be typical of *Bison*. It should be noted here too that on this point all the aforementioned metacarpals of the Danish *Bos primigenius* have the shape generally considered to be characteristic of *Bos*, this gives the Grønninghoved specimen a unique position in the Danish material of fossil bovine metacarpals (fig. 11).

Nor does the difference in the shape of the distal end seem to be quite constant. REYNOLDS considers that on the whole "the width of the lower end affords a character which, while not always reliable, is of some value for purposes of discrimination". On the basis of a German material however LEHMANN (l.c., p. 204) more definitely

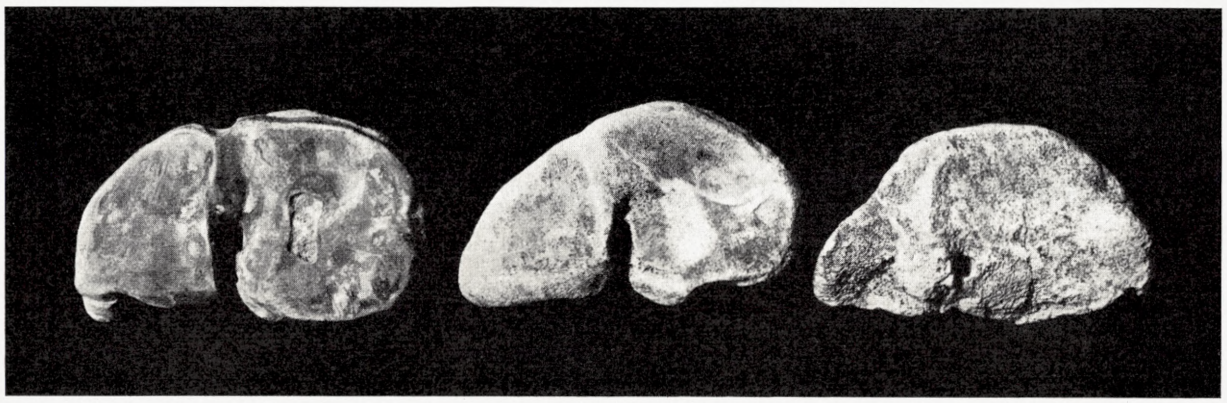

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Fig. 11. Distal ends of metacarpals of *Bos primigenius* (to the left), of Grønninghoved-specimen (middle) and of Seest-specimen (right). × $^1/_2$.

writes: "Stücke, deren Bestimmung nach diesem Kennzeichen zweifelhaft ist, sind ziemlich selten".

Here too the Danish *Bos primigenius* material is uniform. All metacarpals of adult animals are markedly wider at the distal end proper than at the suture between epiphysis and shaft.

This different shape of the epiphyses involves a different appearance of the shafts in the two specimens. In the lower half the lateral curvatures are more curved in *Bison* than in *Bos*. There are other small differences i. a. that the length of the ridges on the trochlea (on the articulating surfaces at the distal ends of the metacarpus) are longer in *Bison* than in *Bos* (fig. 12).

In all these characters: 1) the shape of the upper and lower end 2) shape of diaphysis and 3) length of curvature of ridges on trochlea the Grønninghoved metacarpus is *Bison*-like and quite different from the metacarpals of Danish *Bos primigenius*.—Undoubtedly, this *metacarpus*—and the fragmentary *metacarpus* from Seest—have belonged to *Bison priscus*.

Hitherto nine Bison-discoveries have been made in Denmark (M. Degerbøl and J. Iversen, 1945). With the remains from Seest and Grønninghoved this number has risen to eleven. One of these is from interglacial age, four are found in glacial deposits,

four must be dated to the late-glacial period (Late Dryas), one to the beginning of the forest period (Preboreal) and only one find cannot be dated with certainty.

How and when have the remains of these species found their way to the Seest gravel pit? It may be supposed that the animals lived in the periglacial area, the icefree landscape in front of the icesheet and from here have strolled to the ice-

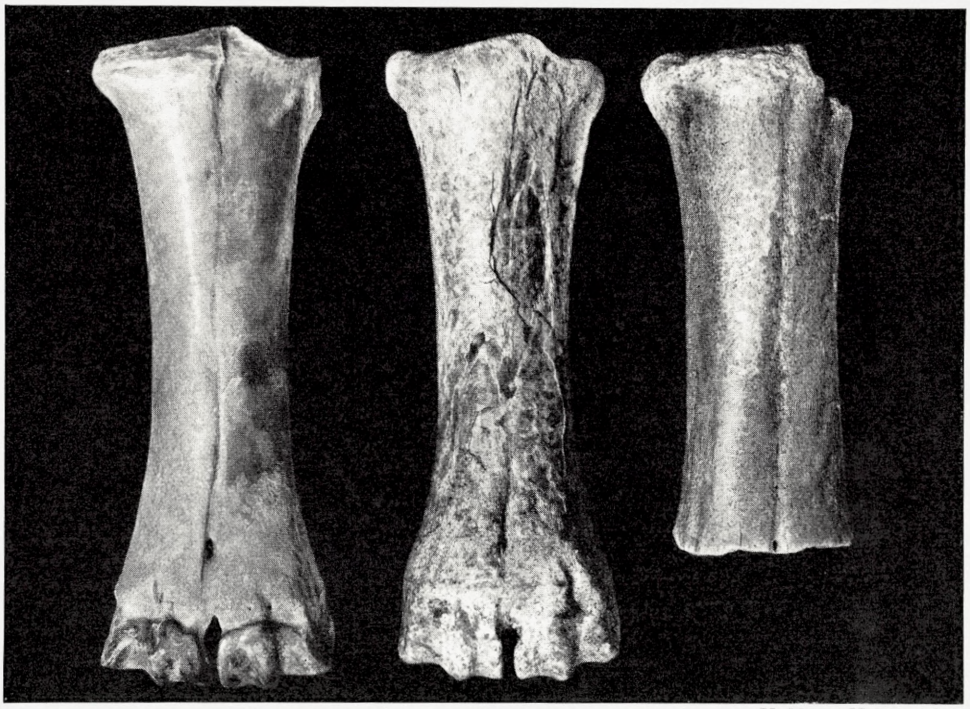

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Fig. 12. Metacarpals of *Bos primigenius* (left), Grønninghoved-specimen (middle) and Seest-specimen (right). $\times$ 1/3.

border and here perished. There skeletal parts have been spread by the meltwater rivers, but in view of the good condition in which they have been discovered they presumably have not been washed far away. If this is the case the animals lived during the ice age proper perhaps in an interstadial period. As we now know that the giant deer lived in the rather cool Allerød time this probability may not be quite excluded. The same holds good of the *Bison priscus*, the remains of which have been discovered in interglacial deposits equivalent to the preboreal period after the last ice age. The late-glacial *Bisons* in Denmark belong to another species or subspecies, *B. bonasus arbustotundrarum* Degerbøl.—Regarding *Dicerorhinus kirchbergensis* however, which is associated with the temperate forest biotope of the interglacial time, this explanation is improbable. The rhinoceros mandible may have been dug out from earlier, interglacial layers. According to information given by Danmarks geologiske Undersøgelse such interglacial deposits have been found by wellsinkings in this district.

Interglacial deposits are known too in several localities in the tracts near Kolding. About 3 km west of the Seest gravel pits the well known interglacial bog at Ejstrup is situated, which has yielded remains of the fallow deer (*Dama dama*). In this bog too a fragment of a pelvis of an elephant has been discovered, but it has not been possible to decide whether this bone is of a mammoth or of *Elephas antiquus* (Nordmann 1921). The last mentioned elephant is a denizen of the forest or parkland and an ordinary companion of *D. kirchbergensis*. Near Egtved, 20 km NW of Kolding, remains of the interglacial *Bison priscus* has been unearthed too in primary position.

Presumably the fragments from Seest mentioned here may be dated back to these interglacial deposits. It should be emphazised however that these 3 species are not generally living in the same biotope. As already mentioned *D. kirchbergensis* prefer the forest country, the bison and giant deer the open landscape. Remains in gravel pits are often of a mixed origin.

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