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A Zoological and Geological Investigation of the Finds in Danish Pleistocene Deposits

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With 7 Plates.

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Contents.

I. Introduction.

Whereas we have a very comprehensive and, to a great extent, dated find-material for the Aurochs *(Bos primigenius* Boj.) from Danish bogs, there were only three known Danish Bison finds up to a few years ago, and their age was furthermore quite uncertain. The first find — a brain-case — came from Baldersbrønde near Roskilde and was published in 1852 by JAPETUS STEENSTRUP, who moreover in the year 1869 mentions still another find, but without saying anything about the finding-place. V. NORDMANN (1915) has shown that from all the evidence STEENSTRUP in the case of the second find was referring to a skull fragment from Mjang Mose, on the island of Als, which in STEENSTRUP's time was already in the museum of the Sorø Academy. The third Bison find was made in 1902 in a bog near the town of Hjørring — again a brain-case (V. NORDMANN 1930).

To these three long-familiar finds it is now possible to add several new ones. In two instances, however, it is not the find but the identification that is new: Two finds made in the 1920's, a very fragmentary skull from an interglacial bog at Egtved, which previously was identified as that of Aurochs, and a number of bones from Akkerup Præstegaardsmose at Haarby, Funen, which only now have been thoroughly examined. Four finds of Bison are of the past few years. A fragmentary frontal bone was found in 1936 below Lysabild Klint on Als (V. NORDMANN 1943); a lower molar was found in a gravel pit at Pindsminde, Randers; and finally, last summer two incomplete skeletons were unearthed from a small bog at Harndrup, Funen, and Jarmsted Mose at Tranum in Han Herreder respectively.

Thus we have quite a number of Bison finds, but the only one dated was the interglacial find from Egtved (K. JESSEN 1929). In the following, one of us (MAGNUS DEGERBØL) will present the zoological examination of the bone material and the conclusions to be drawn from it, whereas the other (JOHS. IVERSEN) will give an account of the pollen-analytical examination of the finds that were datable by this means and discuss the conditions of life for the large herbivorae in late-glacial times.

II. Examination of the Bone Material.

The Bison *(Bison bonasus arbustotundrarum subsp. nov.,* and *B. b. priscus* (H. v. M.)) in Denmark.

a. New Finds.

The Bison from Akkerup.

Some years ago I discussed the question of the sexual dimorphism of the Aurochs (DEGERBØL 1942), and on that occasion went through the large number of skeletal remains of *Bovidae* which, dating from prehistoric times and found in settlements and bogs, were preserved at the Zoological Museum in Copenhagen. While doing so I came across a find which HERLUF WINGE in 1921 had placed together with the other material of Aurochs *(Bos primigenius* Boj.), but from the information accompanying it I gathered that the identification was quite tentative, and that the remains were possibly of Bison.

A closer examination of the bones — some vertebrae and costae, a fragment of humerus, and a scapula, quickly showed that the material was a somewhat mixed one; most of the bones undoubtedly belonged to a Bison, but the humerus fragment was that of a stag, and the scapula had belonged to a very large domestic ox. To all appearances, bones had been collected from various parts of the bog.

As only three Bison finds from Denmark were known at that time 1941, and their age moreover was unknown, it was obvious that the new find might prove to be of the greatest interest if, by its means, it were possible to obtain a geological determination of the time when the Bison lived in Denmark, and therefore I decided to subject this find to a thorough examination.

From the information obtainable from the records of the Zoological Museum it appeared that some bones (one atlas, two dorsal vertebrae, one costa and one scapula) "found during draining operations at Akkerup Præstegaard Mose in Funen" in August 1921 had been sent to the Museum by Mr. A. Møller, a farmer at Akkerup, E. S. E. of Assens. On receiving the bones the Zoological Museum requested Danmarks Geologiske Undersøgelse to make an investigation of the finding place, which that institution suggested doing in the following spring. In October of the same year, 1921, the Museum received nine more vertebrae and five costae "found at the same place as the vertebrae previously received from Akkerup". With this the matter seems to have been left in abeyance by the Museum.

When the matter was revived after twenty years the obvious course to pursue was to approach the Geological Survey again; and on this

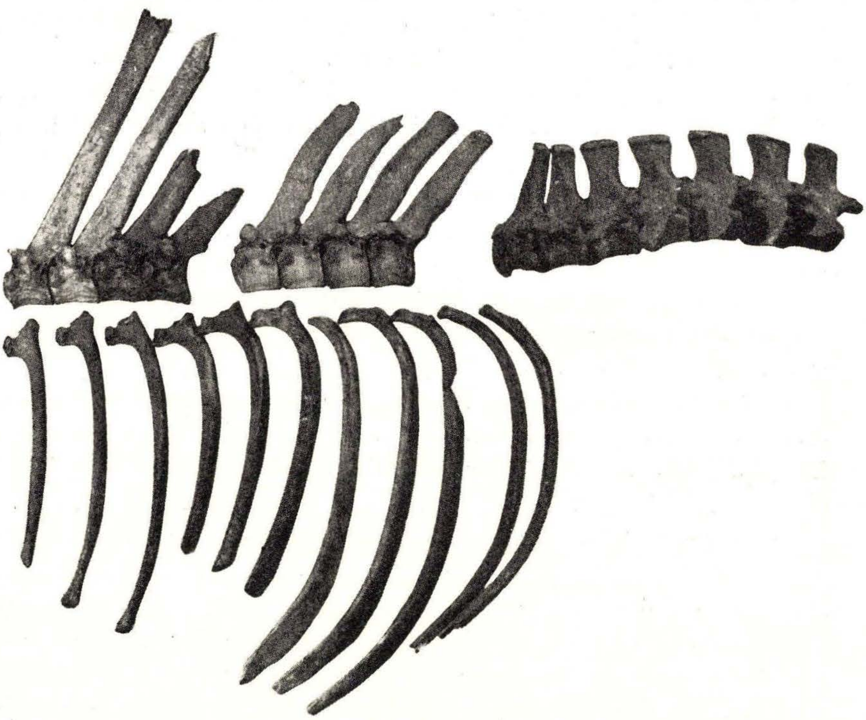

Fig. 1. Skeletal parts of Bison from Akkerup. Late Dryas time.
U. Møhl-Hansen phot.

being done I was happy to find that the institution had in fact made an examination of the Bison locality and still was in possession of the soil samples then taken, in addition to which some more bones of the animal, a scapula, some costae and vertebrae had been recovered.

On the basis of these samples and the soil still removable from the bones, Dr. IVERSEN succeeded in determining that the Akkerup Bison dated from late-glacial time, Late Dryas period (cfr. Dr. IVERSEN's paper). As it had generally been assumed in this country that the Bison lived together with the Aurochs in the Maglemosean Period, this result at first caused some surprise. Since then, however, it has turned out that three more Danish Bison finds are from late-glacial time. When dealing with the distribution of the Bison I shall revert to this point, but first shall describe the material.

From Akkerup we have the following skeletal parts: 1 atlas, 10 dorsal vertebrae, 5 lumbar vertebrae, 19 fairly intact costae, 3 proximal and 5 distal ends of costae — which means that in all we have 14 right and 12 left whole or fragmentary costae, a part of a sternum and a scapula; all these undoubtedly belong to a Bison (Fig. 1). In addition there is, as stated, a right scapula which does not belong to this individual but represents a large domestic cow, as well as a fragmentary stag humerus.

At this juncture I shall confine myself to the Bison bones. It may often be difficult, or even impossible, to decide whether certain bones are of Bison or Aurochs, or even the domestic cow. The features which characterize the Bison in comparison with other members of the bovine family are the enormous head and high shoulders. As there are no cranial bones in the Akkerup find, we must first and foremost be guided by the high shoulders, as represented by the very high spinous processes of the foremost dorsal vertebrae, though the scapula is also affected by it.

The Bison usually has 14 thoracic vertebrae, but there are exceptional cases where the number is only 13. This means that for the Akkerup Bison we lack 4, or possibly 3, dorsal vertebrae. Commencing from the front we find that No. 1 is missing, Nos. 2, 3, 4 and 5 are present; then one or two are missing, and then follow 4 continuous vertebrae, then another gap in the series, and finally the two rearmost dorsal vertebrae. As already stated, the crucial point in determining to what species these vertebrae belonged is particularly the height of the spinous processes on the foremost dorsal vertebrae, but unfortunately not one is undamaged. The least injured are the spinous processes of the 2nd and 3rd vertebrae, which are pronouncedly long and slender, but are short of the distal end. In judging these processes we must give due consideration to the age of the animal, as the height increases very rapidly with age, as W. Koch (1932) has shown. All our vertebrae have fused epiphyses, which shows that the animal was fully grown; according to Koch it must therefore have been at least seven years old.

Some measurements of these two dorsal vertebrae compared with those of the corresponding vertebrae of a complete Aurochs skeleton, which likewise is that of an adult animal, will make the difference clear[1]). Although the distal end of the spinous process of the 2nd dorsal vertebra of the Akkerup animal is broken off, the height of

[1]) It may be observed that the Aurochs vertebrae here measured are particularly long; others are much shorter (cfr. fig. 2).

this vertebra, measured from the inferior side of the *corpus* to the end of the spinous process is just as great as that of the Aurochs, 450 mm compared with 445 mm, and in addition the Akkerup vertebra was originally larger, no doubt about 40 mm higher. Taking the height of the spinous process itself, measured along the anterior aspect and from the surface of the anterior articular process, we find that even on the broken Akkerup vertebra it is greater than on the intact Aurochs vertebra, 392 against 370 mm; and here again we must

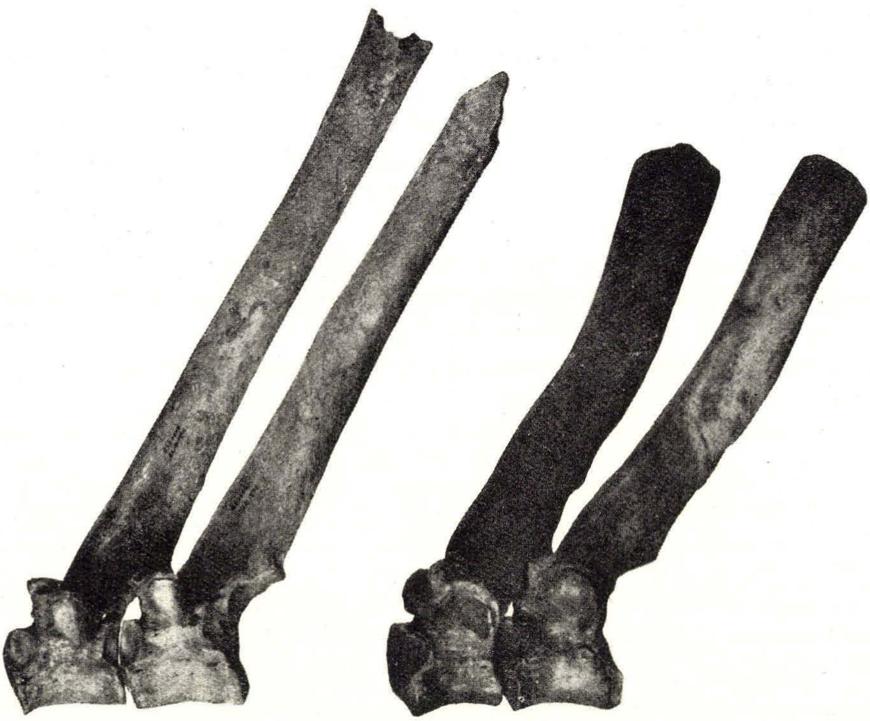

Fig. 2. 2nd and 3rd. *vertebra thoracica* of Bison from Akkerup (left) and of *Bos primigenius* (right).
U. Møhl-Hansen phot.

add about 40 mm to the Akkerup specimen, on which the spinous process must originally have had a total height of about 430 mm.

The width or length of the spinous process, measured from front to back, is much smaller on the Akkerup specimen than on the Aurochs, 36 mm against 43 mm, just as the corpus vertebra of the Aurochs is longer, 66 and 57 mm respectively.

We find rather similar proportions as regards the 3rd dorsal vertebra, though more of the spinous process is broken off. For the Aurochs the total height of the intact vertebra is 435 mm, whereas the height of the damaged Akkerup vertebra is 420 mm, but, judging from the shape, the latter was about 50 mm longer, or 470 mm in all. On both vertebrae the spinous process now measures 370 mm, so that on the Akkerup specimen the original height must have been about 420 mm.

Comparison between the dorsal vertebrae of the Akkerup Bison and the Aurochs will also show that the spinous processes of the former have a greater rearward incline than that of the latter. One peculiarity of the Akkerup vertebrae is that, with the exception of the first two, *foramina intervertebralia* are divided, whereas in the Aurochs this is the case only with the foremost vertebrae. Furthermore, the inferior part of the corpus of the Akkerup vertebrae forms a fairly sharp keel.

Turning now to the lumbar vertebrae, the number is worth noting — 5 in all. Most *Bovidae* have 6 lumbar vertebrae, the sole exception in fact being the Bison, which normally has only 5. W. Koch (l. c., p. 639) states that of a large number of skeletons of the European Bison he only once found one animal with 6 lumbar vertebrae. That there really were only 5 of these in the Akkerup animal is clear from the fact that anteriorly the foremost lumbar vertebra fits well into the rearmost dorsal vertebra, whereas the shape of the posterior articular process on the 5th lumbar vertebra actually signifies that it is the last vertebra[1]).

The Bison scapula also presents certain peculiarities, most of which taken separately do not suffice to characterize the species but when viewed collectively are all-important. I have been able to compare the Akkerup scapula with half a score of Aurochs scapulae and, on the basis of this comparison, must say that the scapula of the Bison differs from that of the Aurochs by its higher and more slender form. In some cases this difference is very conspicuous, in others it is much less so. — There is a fairly outstanding difference in the modelling of *collum scapulae*, which in the Bison is weaker, being narrower anterior-posteriorly. As in addition the coracoid process is much thinner in the Bison, the width of the collum measured across this process will be specially small. Disregarding quite young animals, the Aurochs on this point will have much larger measurements than the old Akkerup Bison (cfr. Table 1, measurement No. 4). If the widths are expressed as a percentage of the total scapula length this

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[1]) It may be remarked here that a skeleton of the European Bison set up in the Zool. Mus. in Copenhagen has 15 dorsal vertebrae and 15 pairs of costae, but only 4 lumbar vertebrae. Thus this specimen has the same deviation as the first skeleton of the American Bison which was described by Cuvier, and which had the result that for many years it was thought that the American Bison thereby differed from the European species (cf. Allen 1876 p. 2).

Table I.

Scapula.	*Bison bonasus*					*Bos primigenius*								
	Akkerup Late Dryas period	Harndrup Late Dryas period	*B. b. bonasus* C. N. 292 ♀ Zool. Mus.	*B. b. bison* C. N. 1396 Zool. Garden	*B. b. bison* C. N. 704 Zool. Garden	Bønnelykke	Møen	Sorø	Brendstrup	Locality unknown	Grærup	Tinglev	Taastrup	Gøderup
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Greatest width of *cavitas glenoidalis*, anterior-posteriorly	77	81	60.5	80	78	87	87	85	85	85	80	79	80	78
2. Greatest width of *cavitas glenoidalis*, transversely	67	68	48.5	68	—	70	68	75	71	79	74	63	66	67
3. Least width of *collum*, anterior-posteriorly	76	76	61.5	80	76	84	82	84	87	84	82	80	70	74
4. Greatest width of *collum*, from *proc. coracoideus* to rear border of cavitas	88	87	78.5	91	98	102	110	107	106	100	95	95	97	99
5. Width of upper end, greatest	267	ca. 295	220	275	248	275	295	303	305	272	—	260	ca. 255	—
6. Greatest length, from middle of *cavitas glenoidalis* to *margo dorsalis* at top of *spina scapulae*	482	495	405	535	486	463	505	450	490	ca. 480	440	465	410	ca. 400
7. $\frac{5 \times 100}{6}$	55.4	—	54.3	51.4	51.0	59.4	58.4	67.3	62.2	—	—	55.9	—	—
8. $\frac{4 \times 100}{6}$	18.3	17.6	19.4	17.0	20.2	22.0	21.8	23.8	21.6	—	21.6	20.4	23.7	—

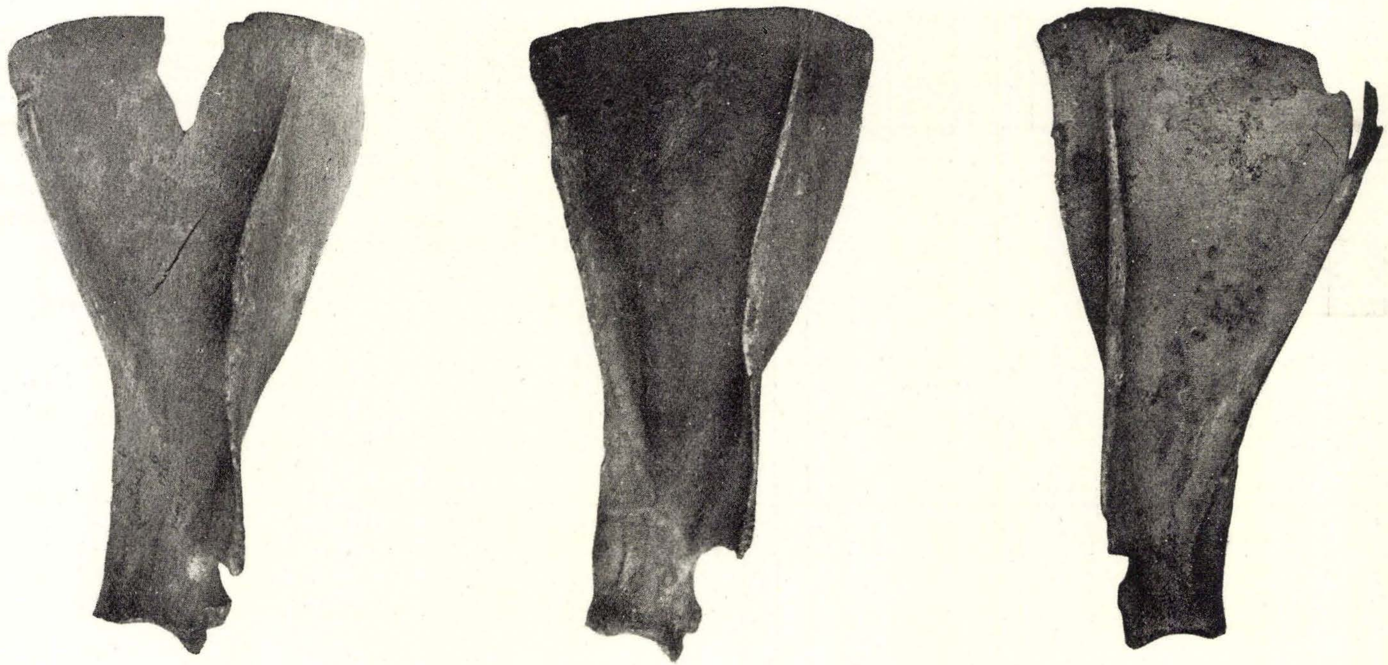

Fig. 3. *Scapulae* of *Bos primigenius* (left) and of Bison from Akkerup (middle) and Harndrup (right). In the Bison the width of the *collum* across *proc. coracoideus* is smaller and the inferior part of *spina scapulae* inclines more anteriorly than in *Bos primigenius*.

U. Møhl-Hansen phot.

becomes even more distinct. For example, in the younger Aurochses from Taastrup and Gøderup, Nos. 13 and 14, the collum is narrower than that of the Akkerup Bison, 70 and 74 mm respectively against 76 mm, but the width across the coracoid process is greater, 97 and 99 mm compared with 88 mm.

The length or height of the Akkerup scapula is greater than that of most Aurochses, whereas the length of the upper edge is less. Only two Aurochses, No. 7 and No. 9, have a higher scapula, but they are also wider, so that if we express the length in relation to the maximum width, the Bison falls right outside the variation limits of the Urus. It may also be pointed out that in the Bison the inferior part of *spina scapulae* inclines more anteriorly than in the Aurochs; this becomes clear when the two bones are laid upon a table with the medial side downwards (Fig. 3). More superiorly the same spina seems to be more vigorously modelled in the Bison than in the Aurochs. On the Akkerup scapula it reaches out to the dorsal margin, whereas on Aurochses of the same age it is shorter, or is less vigorously marked. On the whole, however, this feature is not particularly prominent. Here, as in so many other characteristics, due consideration must be given to the changes accompanying age.

Among other more varying and less conspicuous peculiarities the posterior margin of the Bison scapula runs almost straight, whereas on the Aurochs it is concave.

Finally, the costae are of great value in determining species. Curiously enough, the ribs of the *Bovidae* are among those skeletal parts that are most characteristic of the species. In the Bison the ribs are not nearly so flattened as in the Aurochs, being more rounded in cross-section (fig. 1).

From what is described in the foregoing it must all in all be held that these skeletal parts from Akkerup undoubtedly belonged to a Bison and, judging from the relatively gracile bones, a cow.

The Harndrup Bison.

This paper having been completed in all essentials, the remarkable thing happened that the Zoological Museum received two more Bison finds, from Harndrup and from Tranum. From Mr. Herluf Nielsen, a schoolmaster at Harndrup, North Funen, came some large bones: a scapula, a sacrum, half a pelvis and three lumbar vertebrae, found in the course of peat-cutting in a small bog belonging to the smallholder Alfred Andersen, of Harndrup. — The high and narrow scapula made it likely at once that another Bison was represented (cfr. fig. 3, right). I therefore wrote to Mr. Nielsen, drawing his attention to this possibility and at the same time suggesting that most probably there were other parts of the animal in the bog; at the same time I requested more particulars about the circumstances of the find. The result was that more bones were sent in a few days later: 13 dorsal vertebrae, 2 lumbar vertebrae, 17 costae, a fragment of a sternum and another half pelvis (Fig. 4). It was further reported that the bones were found "2—5 inches down in the clay under the peat". On the chance of finding the rest of the skeleton, the skull and the extremity bones, the Museum sent Taxidermist MØHL-HANSEN

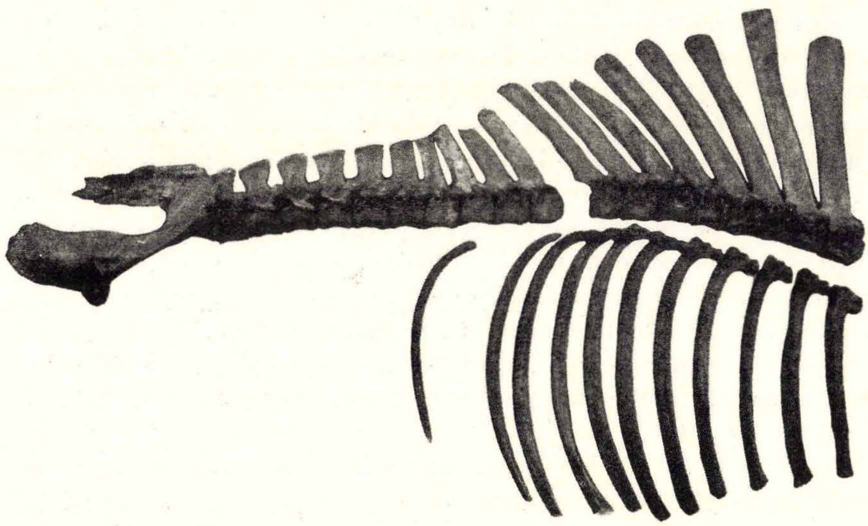

Fig. 4. Skeletal parts of Bison from Harndrup. Late Dryas time.
U. Møhl-Hansen phot.

to make a further investigation on the spot, but all that was recovered after extensive excavations was three more costae.

The measurements of the scapula are shown in Table I. Here again we find the special features already singled out in respect of the Akkerup Bison. Very remarkable is the slight breadth across the coracoid process, 87 mm, despite the fact that this scapula is higher than the Akkerup specimen. As on the latter, the height of the collum measured from the articular surface to *spina scapulae* is slight; in most Aurochses this distance is greater than in the Bison.

The vertebral column also shows clearly that these are the remains of a Bison. Of the dorsal vertebrae only one, from the middle, is missing. The total length of the second dorsal vertebra measured from the underside of the corpus to the top of the spinous process is 490 mm. The height of the spinous process, measured along the anterior margin, is 440 mm. For comparison I may add that on a fossil Bison skeleton from Scania, now in the Zoological Museum at Lund, the height of this spinous process is 450 mm (LILLJEBORG 1874, p. 881). This Swedish skeleton was that of a very powerful bull, as can be seen i. a. by the skull, which is the only one of the subfossil skull known that can compare with the large brain-case from Baldersbrønde (see below). In the Harndrup Bison the length of the spinous process, anterior-posteriorly, is 42 mm. The total height of the third dorsal vertebra is 448 mm, but here unfortunately the upper end of the spinous process is missing, so that in its complete state the vertebra must have been still higher; the spinous process measures 404 mm in height, but must thus have been higher.

With the exception of the two posterior ones all the dorsal vertebrae have double holes for the passage of the spinal nerves. The Harndrup specimen also has five lumbar vertebrae, the number characteristic of the Bison. In contrast to what was the case with the Akkerup Bison, we have here the entire pelvis. To those who are familiar with the form of this skeletal part of the ox, both Aurochs and domestic ox, there is an outstanding feature which at once distinguishes the present pelvis from that of the ox: On the inferior aspect of *collum ossis ilium*, just anterior to the *acetabulum*, is a conspicuous, deep oval depression such as that to be seen on the stag, whereas in the ox it is very shallow or open. — As in the Akkerup Bison the costae are not nearly so flat as those of the Aurochs. The skeleton from Harndrup is that of an adult animal; the epiphyses are missing from only two of the dorsal vertebrae; otherwise they have fused completely with the corpus.

After the foregoing it will thus appear that the Harndrup skeleton is that of a Bison and, judging from the robust bones, a bull. — According to Dr. IVERSEN the find may be placed to the end of the late-glacial age, Pollen Zone III, Late Dryas time.

The Tranum Bison.

In July 1944 the press contained references to the finding of a complete Bison skeleton in Jarmsted Mose in Vendsyssel, Jutland. The Zoological Museum made immediate inquiries, but unfortunately only few of the bones were then recoverable. Inspector SVENNING P. SVENNINGSEN, of Ø. Svenstrup, alone had secured some of them, and these he kindly presented to the Museum. Altogether they comprise: broken parts of right and left horn-core with small portions of *os frontale*, fragment of *basioccipitale*, two upper cheek teeth, parts of two dorsal vertebrae and a lumbar vertebra, *os sacrum*, fragments of both halves of the pelvis, and three costae. (Regarding the deposits see Dr. IVERSEN's paper).

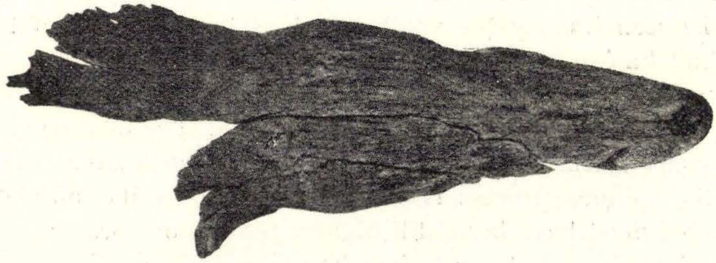

Fig. 5. Horn-core of Bison from Tranum. Late Dryas time.

Contrasting with the Bison finds described above, in which the bones were in an excellent state of preservation, the condition of

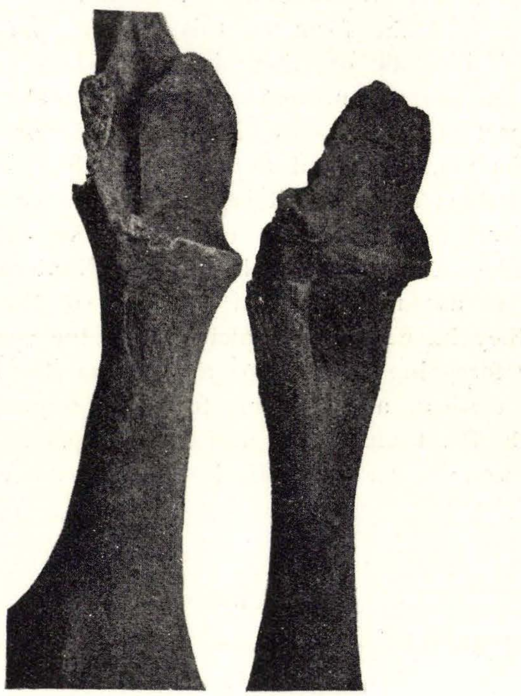

Fig. 6. Part of os *ilium* of *Bos primigenius* and of Bison from Tranum. Ventral view.
U. Møhl-Hansen phot.

these bones was very bad; they are thin, light and decomposing. No doubt this too explains why so little of the skeleton was recovered, although Mr. SVENNINGSEN afterwards tried excavating at the site.

Several features make it obvious that these bones are of a Bison: 1) the shape of the relatively short and thick horn-cores with parts of the domed and broad frontal bone (Fig. 5), 2) the narrow and high spinous process of the dorsal vertebra, though it is broken at the top, 3) the large and deep depression in the inferior aspect of the *collum ossis ilium* anterior to the *acetabulum* (Fig. 6), and 4) the narrow costae.

The following measurements are possible on the fragmentary horn-cores, which are badly eroded. The maximum and minimum diameters at the base are 93 and 70 mm respectively; the circumference of the base is 260 mm; the chord to the inner side (from the base of the horn to the apex) 187 mm, and the inner curvature measures 205 mm.

This find too is from the Late Dryas (see Dr. IVERSEN's paper).

The Pindsminde Bison.

In a gravel pit at Pindsminde near Randers a tooth was found in 1941 and sent to Dr. THAMDRUP, the Museum of Natural History at Aarhus, which in turn forwarded it to the Zoological Museum in Copenhagen for identification. The tooth is a lower molar, probably the second, from the right side, of a large species of ox (Fig. 7).

Fig. 7. 2nd right lower molar from Pindsminde. Interglacial time. View from inner side (left) and from the grinding surface (right). Natural size. U. Møhl-Hansen phot.

In conformity with its being found in a gravel pit the colour is a faint yellowish-brown, and the tooth itself is water rolled, massive and heavy. The specific gravity is 2.35, whereas that of a corresponding Aurochs tooth is 1.89.

Here again the question of Bison or Aurochs arises. Definite identification of this tooth is scarcely possible. It is true that early authors, especially RÜTIMEYER, have explained the difference between the teeth of the Bison and those of the Aurochs; and when one has an entire set for inspection, a definite specific determination can undoubtedly be made. But the position is different with a solitary tooth like the present. In any case, the following sceptical pronouncement of an expert on prehistoric mammals so eminent as STEHLIN suggests caution: "Quelques auteurs se font forts de distinguer *Bos primigenius* et Bison d'aprés les molaires ou d'aprés les os isolés. Je n'ai pas cette prétention et préfère m'abstenir d'une détermination précise toute les fois que je ne dispose pas de la partie frontale de la crâne" (1933 p. 130).

On the other hand, it must be said that several features suggest that this tooth belonged to a Bison. I have compared it with i. a. 12 loose, lower m 2. of Aurochs *(Bos primigenius)* cfr. DEGERBØL 1942 Table 12, p. 94. From this comparison it appears that the Pindsminde tooth is very massive; along the inner side of the grinding surface it measures 36.4 mm in length and has a maximum breadth, likewise measured on the grinding surface, of 18.3 mm; at the base of the tooth the maximum width is 22 mm. As the measurements of the grinding surface depend on the amount of wear, it should be added that the length given above is the maximum length of the tooth. The tooth is relatively much worn, as appears from the fact that the maximum height, measured from the base of the crown, is 42 mm.

Of the twelve Aurochs teeth referred to, only two are comparable with this one. Moreover its considerable size shows that the Pindsminde tooth cannot have belonged to any Bison that lived after the Ice Age, but is a very suitable match for the powerful interglacial Bison, *Bison priscus* (cfr. e. g. measurements by FREUDENBERG, p. 83). It is true that the tooth cannot be identified by means of tooth measurements; but the compact and more rectangular form, in conjunction with the slight constriction between the two columns of which the tooth consists, and the somewhat less undulating course of the enamel bands, all make it probable that it is that of a Bison. In this connection the course of the enamel band on the lingual side of the tooth seems to be of special interest. On the Pindsminde tooth it does not describe such a pronounced wave in the middle of the tooth, between the two enamel columns, as on the Aurochs teeth.

As it was found in a gravel pit, this tooth must be that of an animal that lived in interglacial time. This fact too agrees very well with the supposition that the tooth belonged to a Bison. The presence of the Aurochs in Denmark or north of Central Germany in interglacial time has not been demonstrated with certainty.

The Egtved Bison.

I will make use of this opportunity to correct a somewhat earlier find which at the time, especially on account of a very fragmentary and incomplete frontal bone, that was only little convex, was at once considered to be Aurochs, but which through a later examination proved to represent a Bison.

The find consisted of cranial parts unearthed in 1928 at Egtved and, according to K. JESSEN (1929), dated from interglacial time, but otherwise has not previously been dealt with zoologically. From the now reconstructed skull it appears that the Bison it represents was a powerful specimen (plate II, plate I, Table 2). Characteristic features of the Bison as compared with the Aurochs are the large, very prominent, cylindrical or nozzle-shaped orbits, which lie relatively close to the horn-cores, the large nasal bones, the shape and size of the horn-cores, all features which are distinct on plate II. Furthermore, the occipital part of the Bison projects a good distance behind the horns, whereas on the Aurochs the superior occipital line is straight. (On the Egtved skull, however, this occipital area is missing, so that it cannot be applied in this instance). In addition, the frontal bones of a Bison are usually convex like a shield, but on the Egtved specimen this feature is little conspicuous.

Table 2 contains some measurements from the Egtved skull, and corresponding measurements from *Bison priscus* and *Bison bonasus* for comparison, including a skull of *B. priscus* from Lutschka on the Volga, about 20 km S. of Sarepta, presented in 1878 to the Copenhagen Zoological Museum by Consul General PALLISEN. Some measurements are also given of the other Danish Bisons. These measurements show that on the Egtved skull the horn-cores are not so strong as those of the Volga Bison, the span is 105 and 122 cm respectively, and the circumference of the cores is also less. On these points by the way the Egtved specimen lies entirely within the variation limits of *Bison priscus*, which is now known through a relatively large number of skulls. According to H. v. MEYER (1835) and M. PAVLOW (quoting from FREUDENBERG (1914)), the span of the horn-cores of *Bison priscus* varies between 1382 and 950 mm. On the other hand, a feature that is peculiar to the Egtved Bison is the very broad forehead. Measured between the constrictions which separate the orbits from the base of the horn-cores, the width on the Egtved Bison is 332 mm against only 305 mm on the Volga specimen. This measurement lies on the border of what *Bison priscus* can reach (cfr. Table 2 No. 1). True, the Egtved frontal bone is reconstructed of several fragments, but this has no influence whatever on the accuracy of the measurement, because the edges of the various fragments clearly join well together. Other measurements also show the considerable width of the Egtved skull: the maximum breadth across the orbits is 405 mm and the mastoid breadth 330 mm, which is also the maximum measurement of *Bison priscus*.

Fig. 8. 2nd and 3rd right upper molars of Bison from Egtved. m 3 at right. Lateral view.

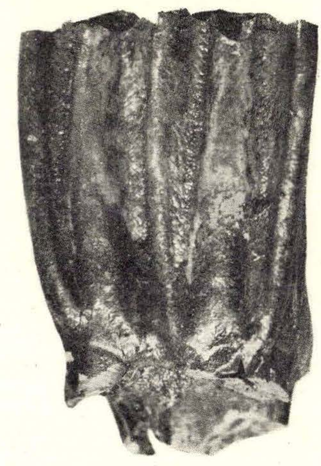

Fig. 9. 3rd upper molar of *Bos primigenius* from Sværdborg. Boreal period. Lateral view. Natural size.
U. Møhl Hansen phot.

Fig. 10. The same teeth as in fig. 8. View from the grinding surface. Natural size.
U. Møhl-Hansen phot.

Of teeth the find includes 4 upper molars, m 2 and m 3 from the right side and m 1 and m 2 from the left. m 1 measures 20 mm in length and 29 mm maximum breadth, measured at the base; for m 2 the corresponding measures are: 35.5 (along the grinding surface) and 31 mm, m 3: 37.3 and 30.7 mm. For the rest, what was said above about the form of the lower molar from Pindsminde applies to these. The medial groove on the buccal side of the teeth is wide and open, curving smoothly in both halves, i. e. limited by fairly parallel sides, whereas in the Aurochs this groove is unsymmetrical, with one side steeper or even leaning in over the groove (fig. 8—9).

b. Previously published finds.

Besides the five Bison finds discussed above we know of four other ones made in Denmark; they will be named in the order in which they were recovered from the ground (cfr. fig. 11).

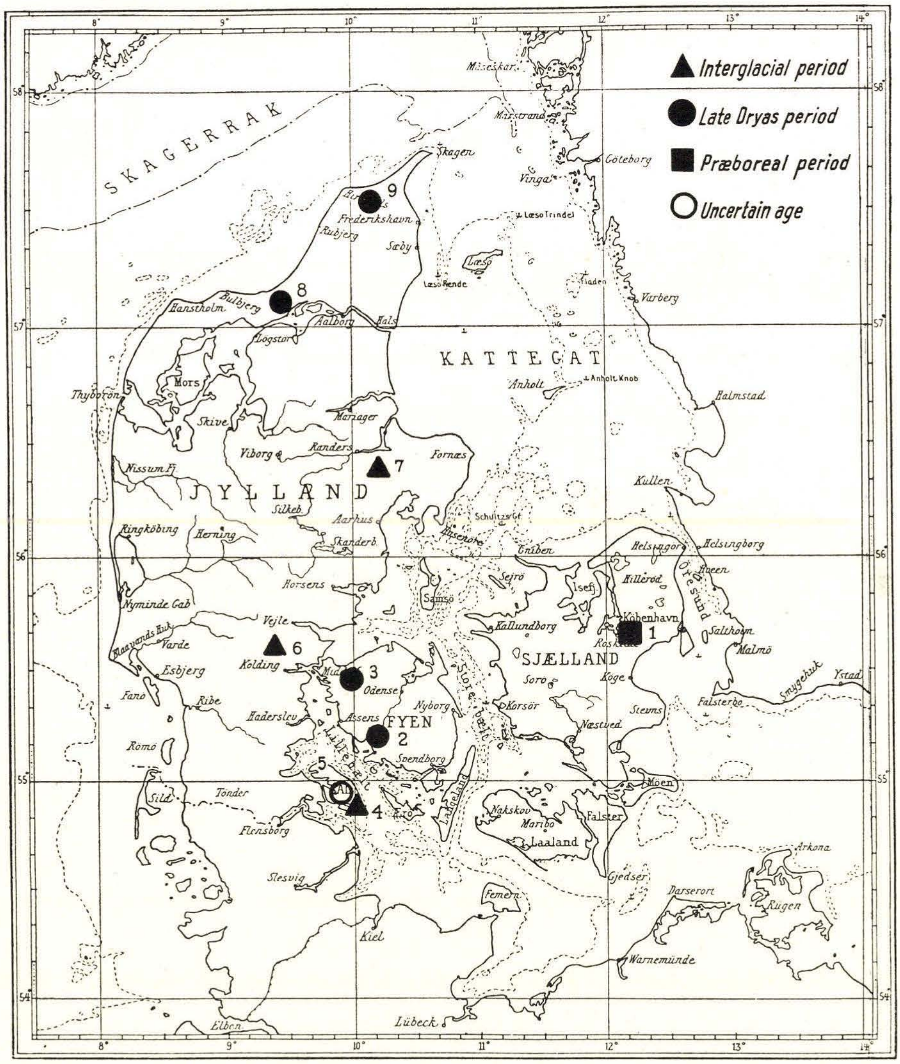

Fig. 11. Map showing the finds of Bisons in Denmark.
1. Baldersbrønde, 2. Akkerup, 3. Harndrup, 4. Lysabil, 5. Mjang, 6. Egtved, 7. Pindsminde, 8. Tranum, 9. Mygdal.

1) A part of a skull was found in Langkær Skovmose at Baldersbrønde, east of Roskilde, Zealand. "It lay at a depth of 24 feet below the surface of the bog basin and at least 14 feet down in the peat". (STEENSTRUP 1852). (Plate III).

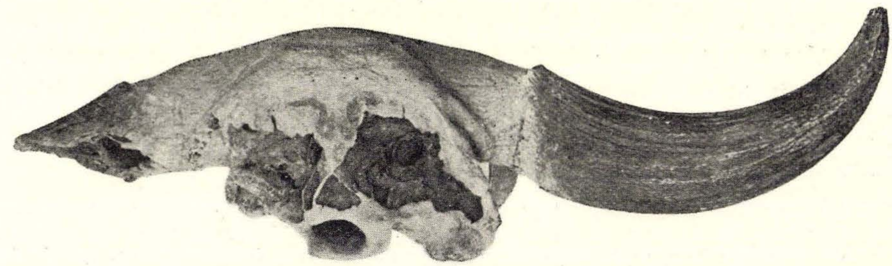

Fig. 12. Bison skull from Baldersbrønde. Occipital or posterior view.
U. Møhl-Hansen phot.

Remarkably enough, NOACK (1905, p. 755) formed the curious opinion that the Baldersbrønde specimen was nothing but a hunting trophy, probably imported in the Middle ages. The deposits, and now the pollen analysis too, show that this skull was discovered in its primary position. Otherwise the considerable size of the

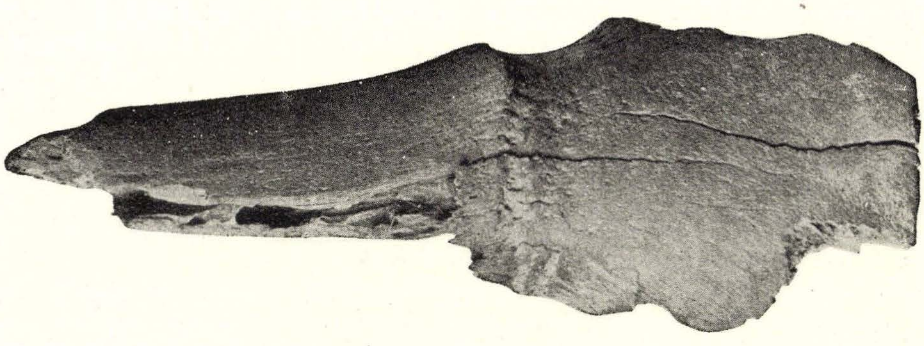

Fig. 13. Part of frontal and right horn-core of Bison from Lysabild.
Interglacial time. Frontal view.
U. Møhl-Hansen phot.

specimen (cfr. p. 30) shows that the Baldersbrønde Bison cannot date from historic time.

It may be pointed out that in this specimen the ascending part of the supraoccipitale, which is usually of powerful shape, is pressed in, and the area around *foramen magnum* is somewhat damaged and brightly polished. It looks as if this part has been water-rolled. The explanation may be that the skull was frozen into the ice, carried by it to the shore and there rolled in the brash-ice (fig. 12).

According to Dr. IVERSEN, this specimen dates from pre-boreal time.

2) Part of skull from Mjang Mose on Als, Jutland. Found about 1864) (NORDMANN 1915). (Plate III).

3) Part of skull found at the bottom of the bog on the property of farmer MARINUS JENSEN in Mygdal Parish, 9 km NE of Hjørring, Vendsyssel, Jutland, in the year 1902 (NORDMANN 1941).

This brain-case also dates from Late Dryas (cfr. IVERSEN p. 35). (Plate III).

4) Part of frontal bone with fragmentary right horn-core, found in 1936 on the beach at the foot of Lysabild Klint on Als, enclosed within a lump of moraine clay which had fallen from the cliff (NORDMANN 1943). (fig. 13).

Judging from these finding conditions the specimen must date from interglacial time. Its size (the circumference of the horn-core is about 385 mm, and the breadth of the forehead between the bases of the cores is about 340 mm (170 × 2)) also shows that it is undoubtedly a *Bison priscus*.

After this presentation of the Danish Bison material we shall consider the placing of these finds in space and time, as well as the taxonomic position of Danish Bisons.

c. Other Bison Finds in Northern Europe.

It may be said that whereas finds of *Bison priscus* all in all are fairly numerous in Europe-Asia, finds of *Bison bonasus*, i. e. animals from the time after the last Ice Age, are rare on the whole.

As recently as 1926 only one find was known in Northwest Germany. On this subject HILZHEIMER (1926, p. 68) writes: "Nur ein einziger Rest eines alluvialen Wisentes aus dem Binnenlande ist bekannt geworden. Es ist das der von mir als *Bison bonasus major* beschriebene Schädelteil aus dem Hermsdorfer Fliesz in der Mark".

However, HILZHEIMER's paper had the effect that several old finds were now recognized and published. He himself adds particulars of two horn-cores from the Roman "Kastell Hofheim" at Taunus, and in the following year (1927) of a brain-case with the horn-cores from Mark Brandenburg ("bei Oranienburg aus der Havel"). In 1929 POHLE was able to give a short account of a mandible fragment of Bison from "Nitzow (Westprignitz) aus der Havel". — In the same year KOCH published two finds, a brain-case and a horn-core, from "Oberbayern und Oberösterreich. Durch diese beiden Stücke ist das Vorkommen des Wisents nunmehr auch für das südlichste Deutschland nachgewiesen", Koch concludes his communication; so that there too finds of Bison are uncommon. A part of a powerful brain-case with horn-cores, from Hinterpommern, was described by MERTENS in 1932. When we go farther east in Europe the Bison finds become more numerous, though it must be said that, considering that the Bison lived in these regions in historic time, they are remarkably few. On the Bison in West Prussia LA BAUME wrote an account of the finds up to 1909. But even here they are relatively few. The Bison is better represented in Transsylvania (JICKELI 1927) and Russia.

None of these skeletal parts of Bison have been dated, for which reason they can tell us nothing about the natural conditions under which the animals lived. It is therefore unusually interesting that certain fragmentary Bison bones have been recovered from the well-known Stellmoor settlement near Hamburg (KRAUSE and KOLLAU, 1943). These fragments belong to the so-called "Ahrensburger Stufe", i. e., they are of the same age as the Danish late-glacial Bison finds: Late Dryas period.

Nor are there many Bison finds in Sweden. ISBERG (Naturens Liv p. 662) writes on the subject: "As regards the Bison subfossil finds are even more uncommon than those of the Aurochs, as only four or five have occurred in Scania and two in Östergötland."

Only as regards one of these can anything be said of the geological age. According to MUNTHE (1922) the brain-case from Hagebyhöga is more or less contemporary with (perhaps a little earlier or later) than the "Ancylus marginal ridge", i. e. the beach ridge which signifies the highest water level of the Ancylus sea at the close of the Boreal Age. This Swedish find is much later than the Danish specimens; but there is no doubt that in those days there was also more or less open landscape in Östergötland.

Much thought has been devoted to the question of why so few Bison finds have been made for the time after the last Glacial Period, whereas contemporary remains of the other large wild ox, Aurochs, *Bos primigenius*, are common; here we find a remarkable contrast to conditions in the interglacial period: We have a large number of diluvial Bison finds, whereas the Aurochs of the same period is not known north of the German Mittelgebirge. In explanation HILZHEIMER advances the theory that the two species lived under different natural conditions, in separate biotopes. The Aurochs made its way predilectively to low-lying regions with forests, lakes and bogs and therefore had a greater chance of perishing in these bogs and lakes, where the skeleton did not decompose. It was different with the Bison, which lived on more open and higher ground; after death the carcase there would be exposed to wind and weather and would disappear completely.

This may sound very plausible; but it should be remembered that in recent time the Bison lived in the rather wet Bialowies forest, for which reason it was considered almost as an arboreal animal. On the other hand it is a question whether the natural conditions in that forest were particularly favourable for the Bison. It is in fact maintained by several authors that the power of procreation of the Bialowies Bison was reduced, while several so-called traits of domestication have been interpreted as signs of degeneration, expressing that these animals lived under less favourable conditions, even if they frequented the more open parts of the forest.

This brings us to the question of Steppe Bison versus Woodland Bison, a problem that also has a bearing on our judgment of the Danish late glacial Bison or Tundra Bison. In the opinion of several scientists (SOERGEL, HILZHEIMER, FREUDENBERG and others) there are two main forms: the large Steppe Bison, *Bison priscus*, with long, slightly out-turned horns, and the Woodland Bison with shorter and more curved horns. The early form of this Woodland Bison, *Bison schoetensacki*, lived at the same time as *Bison priscus* and by several authors is regarded as the progenitor of the alluvial European Bison, *Bison bonasus*, whereas *Bison priscus* became extinct in the diluvial period.

Now where shall we place the Danish Bison?

From Dr. IVERSEN's investigations we know that in the Late Dryas period the soil of Denmark was nutritious and covered with a rich vegetation of *Gramineae*, *Cyperaceae*, *Artemisia* etc. interrupted here and there at the end of the period by copsewood of willow and birch. This bushy tundra sheltered a rich fauna; from it have been recovered remains of reindeer, *Rangifer tarandus*, wild horse, *Equus caballus ferus*, elk, *Alces alces*, Irish elk, *Cervus gigantus*, wolf, *Canis lupus*, Alpine hare, *Lepus timidus*, mouse hare, *Ochotona*, ground squirrel, *Citellus* (*Spermophilus*) *rufescens*[1]), ptarmigan, *Lagopus sp.*, and in the lakes lived the gwyniad, *Coregonus lavaretus*, pike, *Esox lucius* and perch, *Perca fluviatilis*. And now to this fauna we must add the Bison. The above list, however, does not exhaust the animals living on the tundra, as is shown by the late glacial finds at Meiendorf and Stellmoor. From the Early Dryas ("Hamburger Stufe"), which represents the tundra proper, we know of animals such as wolverine, *Gulo gulo*, and desman, *Desmana moschata*. From the Late Dryas ("Ahrensburger Stufe"), when there was a bush vegetation on the tundra, i. e. corresponding to Danish conditions as described

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[1]) In the summer of 1945 bones of wolverine, *Gulo gulo*, have been found from this period; at Bromme, Zealand.

above, lynx, *Lynx lynx*, beaver, *Castor fiber*, and very surprisingly, wild boar, *Sus scrofa ferus* (KRAUSE & KOLLAU, 1943) have been demonstrated.

In other words, in this open landscape, which was of a certain steppe-like character, we meet what is evidently a part of the rich steppe fauna which from Central Europe made its way northwards, possibly driven on by the advancing forest.

Accordingly we might assume the Danish Tundra Bisons to be Steppe Bisons. But are they?

In order to answer the question we must subject the Danish material to a closer examination.

d. The Taxonomic Positions of the Danish Bisons.

To enable us to form an opinion on the taxonomic positions of the Danish Bisons the only real material we have is the three skulls, from Baldersbrønde, Mjang and Mygdal. A glance at these skulls will show immediately that they are very different as to both shape and size. The two latter, from Mjang and Mygdal, are not larger than they can be placed among recent European Bisons — the largest of them (see e. g. the large bull from Lithuania (plate I, Table 2)), — or among the subfossil animals from West Prussia; and yet, the Mygdal Bison has larger horn-cores than even these large Bisons. The Mjang specimen, which has a flat and broad forehead with an inconspicuously developed occipital protuberance, has relatively small horn-cores. — The Baldersbrønde brain-case occupies a position of its own by its considerable size; the cores are unusually large, their measurements being well outside the variation limits of the recent and subfossil Bison, and the same holds good, though to a lesser degree, of other features, cfr. Table 2. For the sake of comparison this table also includes a number of measurements of the three diluvial forms of Bisons: *Bison priscus*, *Bison schoetensacki* and *Bison bonasus mediator* as well as of some subfossil Bison skulls: from West Prussia (LA BAUME 1909), North Germany, including HILZHEIMER's *Bison bonasus major*, and from Sweden; in addition there are the corresponding measurements of some recent Bisons. Particularly interesting among these are the measurements of a very large bull and of a cow from Lithuania, which had already been incorporated in the collections of the Berlin Zoological Museum before the year 1820, and those of five old animals, taken from ALLEN (1876).

From these we shall take some measurements to illustrate the relative size. The distance between outer borders of horn-cores, a measurement that can be taken with exactness, is on the Baldersbrønde Bison 87 cm. On the large Lithuanian bull the distance is 65 cm, on the cow 45,5 cm; the last two measurements once again emphasize the considerable sexual dimorphism observable in the Bison. Nor can the West Prussian subfossil skulls, which as a whole are larger than the recent ones, compare with the Baldersbrønde specimen: 69, 67, 62 and 71 cm. Even for *B. b. major* the greatest distance is only 69.5 cm. The brain-case from Hinterpommern has an unusually large measure· 78 cm. On *B. b. mediator* the distance between the tips of the horns may be estimated at 70 cm, and according to FREUDENBERG the same measurements for three *Bison schoetensacki* from Mauer, early Diluvium, are 87, 87 and 72 cm. — The circumference of the base of the horn-core, measured along the elevated basal margin, is 32 cm on the Baldersbrønde specimen. On the bull from Lithuania it is 25.5 cm, a measure which is not exceeded by the subfossil West Prussian cores, whereas the Hinterpommern specimen measures 29 cm, and the three Swedish Bisons for which measurements are available have similar values: 28.7, 28.5 and 28 cm. Taken by various authors, however, these measurements cannot be credited with any great accuracy. On *B. b. major* the circumference is 28.8 cm, on *B. b. mediator* 34.8 and on *B. schoetensacki* 39 and 33 cm.

The length of the outer side of the horn-core of the Baldersbrønde Bison is 38 cm, on the bull and cow from Lithuania 22.5 and 14.5 cm, on the subfossil West Prussian: 30, 30, 23 and 28 cm. With a length of 30 cm the Hinterpommern specimen again approaches the Baldersbrønde Bison, and the largest of the three Swedish brain-cases has practically the same measurement, 37.5 cm. On *B. b. major* the length is 33.3, on *B. b. mediator* 32.9 and on *B. schoetensacki* 38.5, 37 and 44 cm. Along the inner side of the horn the respective measurements are: 30 (Baldersbrønde), 19.5 and 13.5 (Lithuania), 25, 24, 20 and 22.5 (West Prussia), 25.5, 29, 30, 33, 33, 33, 52 (*schoetensacki*). ALLEN records an unusually large measure for a recent bull: outer curvature 27 cm. The length of the horn-core, taken as a chord from apex to base of horn, is 27.5 on the Baldersbrønde animal, 18 and 12.5 on the two Lithuanian, 20.5, 20.5, 18 and 20 cm on the West Prussian, 18.8 on *B. b. major*, 23 on *B. b. mediator*, and 19, 21, 23, 29.4 and 30 cm on *B. schoetensacki*. Here again ALLEN gives a large measurement for a recent animal: 24 cm.

As the difference between the interglacial *Bison priscus* on the one hand, and the recent and subfossil *Bison bonasus* on the other, is manifested especially in the size of the horn-core, it is obvious that the unusually large cores of the Baldersbrønde specimen, and in so far the Mygdal Bison too, are of considerable interest.

Accordingly, these finds show that as far as the Bison is concerned Denmark had a large *subfossilis* form, as was the case with several other prehistoric Danish mammals: Pine marten *(Martes martes subfossilis* Degerbøl), common bear *(Ursus arctus nemoralis* Degerbøl) and the wild cat *(Felis silvestris magna* Schmerl.), among which the difference between subfossil and recent animals is so great that the former were reckoned as belonging to separate races; other subfossil animals were also of considerabe size, including the lynx, the pole-cat and the wolf (DEGERBØL 1933).

From what has been stated above it will appear that at any rate the Baldersbrønde skull, *inter alia* by its long horn-cores, is clearly different from *Bison bonasus* as we know it from recent animals and the large subfossil forms in Prussia; the Baldersbrønde Bison is most closely approached by a subfossil skull from Hinterpommern and the Swedish animals.

But what is the position of the Baldersbrønde skull in relation to the diluvial Bisons? As the Danish Bisons lived in open country, we shall first compare them with the Steppe Bison, *Bison priscus* (cfr. Table 2). It will be seen that there is a very pronounced differenee in the sizes of *B. priscus* and the Baldersbrønde specimen. In judging between them, however, we must make allowance for a possible sexual dimorphism between these animals, as is the case with the Bison of today. Unfortunately, we know very little about this in connexion with *B. priscus*, though POHLE recently (1943) described the skull of a supposed cow of this form. It appears from this that though the cow is considerably smaller than the bull, it still has the long horn-cores that are characteristic of the species. For the sake of comparison I have after POHLE selected a few of the measurements which can also be taken on the Danish material.

The maximum width at rear of orbits on this cow is 297 mm, on the Baldersbrønde Bison 339, on Mygdal 300, on Mjang 330; on a "typical" bull of *Bison priscus* POHLE gives this measurement as 361 mm. The minimum frontal breadths, measured between orbits and horn-cores, given in the same order are: 231, 282, 250, 253 and 317 mm. The length of horn-core along the greatest curvature is 290 mm on the cow, and for the specimens from Baldersbrønde, Mygdal and Mjang respectively: 380, 330, 220. On the cow the circumference of the core is 220, Baldersbrønde 320 and Mygdal 240 mm. This shows that the frontal breadth is greater on the Danish animals than on the *B. priscus* cow; the length and circumference of the horn core too are greater on the Baldersbrønde and Mygdal Bisons, but much smaller on the Mjang specimen. Accordingly it must be held that the Danish Bisons cannot be regarded as cows of *Bison priscus*, but that this latter species on the whole comprises animals that are much larger than the Danish Bisons. On the other hand it must be said that the Baldersbrønde skull at any rate is so large that it partly bridges the gap which, as regards size, has hitherto separated *Bison bonasus* from *Bison priscus*.

Judging from their size the Danish Bisons thus come nearer to the smaller diluvial Bisons, the pre-glacial and diluvial *Bison schoetensacki* and the later diluvial *Bison bonasus mediator* of the last glacial age. The latter form was set up on the basis of half a frontal bone with its horn-core; and, as thus described, this horn-core is a little shorter, but thicker than that of the Baldersbrønde specimen, while the shape too is different, though in view of the great variation displayed by Bisons, too much weight should not be attached to this. For the rest there is not much to be done with such a solitary specimen; HILZHEIMER gave this sub-species the name of *mediator*, "weil sie zeitlich zwischen *B. schoetensacki* und *B. bonasus* vermittelt und sie so zwischen beiden vielleicht auch stammesgeschichtlich vermitteln kann. Die besondere Bedeutung des Stückes erblicke ich in dem jungdiluvialen Alter, sowie im Vorkommen (Phoeben)". HILZHEIMER also considers that *B. schoetensacki* should be regarded as a sub-species of *B. bonasus*.

As will also be seen from the measurements given above, *B. schoetensacki* varies somewhat in size; in many specimens the horn-cores are not larger than those of the Baldersbrønde Bison, but on an average thicker. According to FREUDENBERG (1914), *B. schoetensacki* had a considerable geographical range, from South Russia to England, and according to the same author this form is "als die Ahnform der mittel- und jungdiluvialen auch der rezenten Bison-Formen unseres Kontinents anzusehen" (p. 82). It may be mentioned in this connection that among the animals occurring together with *B. schoetensacki* is the desman, *Desmana moschata;* as already stated this species was found with Bison remains as close to Denmark as at Stellmoor, east of Hamburg and in so late a period as "Ahrensburger Stufe", i. e. Late Dryas.

If now we proceed to summarize what was shown above about the relation of the Danish Bisons to the diluvial forms, the result is that judging from the size the Danish Bisons most closely approximate *B. schoetensacki*, but ecologically they are associated with *B. priscus*. As the Danish Bisons, as far as we now know, were such decidedly open-country animals that they were unable to adapt themselves to life in the woodlands, but perished when the forest advanced, it will be difficult to imagine the Danish animals as having derived from *B. schoetensacki*. Accordingly, we must take it either that *B. schoetensacki* was not such a decidedly arboreal animal as has been assumed, or that both *B. schoetensacki* and *B. priscus* were specialized forms, whereas the Danish animals come nearest to their original form. To settle this question, however, it will require still more and better material. Until we have this material we must be content to place the Danish Bisons into relation with the recent and subfossil European Bison, *Bison bonasus.*

In respect of these — and also of *B. b. major*, whose geological age is unknown — the Baldersbrønde Bison differs by a size so remarkable that it lies quite outside the variation limits of these animals. The other Danish skulls are larger too, but no larger than that they can be matched by recent animals. Accordingly there may be grounds for setting up these large, late-glacial and pre-boreal Danish Bisons as a separate sub-species: *Bison bonasus arbustotundrarum* subsp. nov. In this case *Bison priscus* must naturally be regarded as another sub-species of *B. bonasus: B. b. priscus.*

Diagnosis of Bison bonasus arbustotundrarum subsp. nov.:

Larger than *B. b. bonasus.* Measurements taken from type specimen, Baldersbrønde, Zealand, lie quite outside the variation limits of recent European Bisons: Distance between outer borders of horn-cores 87 cm, circumference of base of horn-cores 32 cm, length of horn-core along posterior curve 38 cm., width at rear of orbits 34 cm, width at constriction between bases of horn-cores and orbits 28.2 cm.

The measurements of the smaller animals, however, are within those of the largest recent animals. It may be mentioned that the Baldersbrønde skull was previously referred to by Brandt (1867), who on p. 113 writes: "Er gehört, ebenso wie auch die in Schonen gefundenen Schädel, dem grössern Stamme der fraglichen Thierart an." He placed all existing Bisons, European, American and subfossil to one and the same species, but described *B. priscus* as the large race. Brandt, however, knew the specimen only from Steenstrup's brief communication. It should also be added that in the following lines Brandt refers to still another Danish Bison find mentioned by Steenstrup in Overs. Vidensk. Forh. 1853, p. 24, but that in this he is mistaken, for here again it is the Baldersbrønde Bison.

As the smaller brain-cases from Mjang and Mygdal as regards both form and size differ somewhat mutually and also from the Baldersbrønde specimen, it might seem less satisfactory to place them to the same subspecies; but bearing in mind the great variation displayed by the Bison, and as in all probability they are both late-glacial, it would be inadvisable to attach much weight to these deviations until we have a larger material available. Nevertheless there is a possibility that the Baldersbrønde Bison belongs to an eastern, *priscus*-like race which via Sweden, where there is a similarly large form, made its way from East and Southeast Europe towards the west as far as Zealand, whereas the other Danish Bison finds may be placed to a southern race which comes closest to *B. schoetensacki*.

If in conclusion we compare the Baldersbrønde skull with the many extinct Bison species described from America, we shall find that in respect of the size of the horn-cores our specimen comes nearest to *Bison antiquus* Leidy and *B. occidentalis* Lucas. One characteristic feature of the former is the fact that the horn-cores are "directed outward in a plane at right angles with the midline of the skull. In all the other specimens of North American and apparently also of European bisons the axis of the base of the horn-core is directed more or less toward the orbit of the opposite side." (HAY 1913, p. 165).

In *B. occidentalis* "in both the type and in the American Museum specimen the axis of the horn-cores is directed pretty nearly toward the orbit of the opposite side. Also in both a line joining the extremities of the horn-cores passes somewhat behind the occiput."

In the Baldersbrønde Bison the horn-cores are directed so much out to the sides that a line from the tip of the horn-core, drawn at right angles to the median plane of the skull, will meet the occiput; but they do not form an angle of 90^0 with the skull, being directed a little posteriorly, though not so much as in *B. occidentalis*. In the Baldersbrønde specimen the horn-cores furthermore have a more downward direction, as a line connecting the two tips of the horn-cores will not reach up over the skull, whereas in *B. occidentalis* this line will lie over the occipital crest. Thus the Baldersbrønde Bison shows no particular association with the American Bisons.

As already stated, we know nothing of how long the Bison lived in Denmark; but as no remains of it have ever been observed in the large settlement finds of the Maglemose Period or later, it is presumable that it disappeared fairly early, at any rate from the islands; the forests had become too dense. It may have survived longer in the more open country in Jutland, but of this we know nothing. Nor have we any record of the Bison in historic time in Denmark like those in Germany. According to ADAM of BREMEN, Bisons — and indeed Aurochses too — were still roaming the dense forests in Skandinavia in the 11th century. But even if this report s often mentioned, it is so strange that it cannot be correct, as in fact earlier authors, for instance NILSSON (1849), have also held. A few years ago PRELL (1939) attempted to give a new interpretation of this ancient text, and the following brief summary of the matter is taken from his work.

When dealing with Norway ADAM of BREMEN states that in the mountain forests, and even in Lapmarken, there are such great hordes of wild beasts that the population live chiefly on them, and he continues: "Ibi capiuntur uri, bubali et elaces, sicut in Sueonia; ceterum bisontes capiuntur in Sclavonia et Ruzzia: sola vero Nortmannia vulpes habet nigros et lepores, martures albos, eiusdem coloris ursos, qui sub aqua vivunt quemadmodum uri" (lib. IV, Cap. 31) (quoted here from PRELL). It was the words uri, bubali and elaces that caused particular difficulty. It is obvious that buffaloes (bubali) have never lived in Scandinavia, and therefore the word bubali was translated with Bison; but most authors have for the rest picked out of these lines just what they wanted to use, disregarding the absurdities as being something with which Adam of Bremen had been hoaxed. But it is obvious that the text must be understood in its entirety. (In translation it reads: Here are caught uri (aurochses), bubali (buffaloes or bisons?) and elaces (elks) just as in Sweden; for the rest bisons are caught in the land of the Slavs and in Russia: only in Norway are there black foxes and hares, white martens and bears of the same colour, they live under the water in the same manner as the uri (aurochses)). It is clear that having regard to the last sentence, uri cannot be translated with aurochses. And the good Adam of Bremen cannot have been so credulous or ignorant. — I shall not pursue this matter further, but merely add that PRELL has uri = Uria (troile L.) i. e. Guillemot, elaces = Alca (torda L.) i. e. Auk, and bubali = Fratercula, i. e. Puffin. However, be this as it may, I shall merely underline the fact that these sentences cannot provide any evidence that the Bison lived in Sweden in Adam of Bremen's day. The sub-fossil finds also argue against it. Remains of Aurochs in Sweden have been found only in the South, Scania; but in those days Scania belonged to Denmark and it is mentioned by Adam of Bremen only under Denmark, but he makes no mention of the Aurochs there; if this animal really lived in Scania then, there would have been good reason for mentioning it.

III. The Dating of the Bison Finds.

The geological evidence shows that three of the nine Bison remains found in Denmark, date from the time prior to the last glaciation. Two of these, the tooth from the gravel pit at Pindsminde (see p. 17) and the fragmentary frontal bone from Lysabild Klint, Als (see NORDMANN 1943), cannot be dated more exactly. The skull from the interglacial bog at Egtved has already been examined geologically by KNUD JESSEN (1929), for which reason I shall merely refer to that publication. The other six finds will be dealt with below in the order in which they were found.

1. The Bison from Baldersbrønde, Roskilde.

According to STEENSTRUP in "Oversigt over det kgl. danske Videnskabernes Selsk. Forhandl. i Aaret 1852", this skull was found in a bog called Langkjær, where it lay 24 feet below the surface of the bog basin and at least 14 feet down in the peat. This means that it is younger than the last Glacial Age, but so far this is all it has been possible to say about its age. However, some small pieces of peat could be removed from the inner cavities of the bone and, besides various fruits of *Potamogeton* and seeds of *Nymphaea*, they were found to contain a rich pollen flora. A pollen count gave a total of 1337 tree pollen with the following pollen spectrum[1]):

0.3 % *Salix*	5.0 % *Gramineae*	8.6 % *Dryopteris* sp.
60.3 % *Betula*	1.6 % *Cyperaceae*	0.7 % *Dryopteris Linnaeanum*
34.4 % *Pinus*	0.5 % *Ulmaria*-type	0.9 % *Sphagnum*
3.1 % *Alnus*	0.1 % *Artemisia*	0.3 % *Equisetum*
0.7 % *Ulmus*	0.1 % *Chenopodiaceae*	0.1 % *Pteridium aquilinum*
0.1 % *Tilia*	0.1 % *Empetrum*	0.3 % *Nymphaea*
1.0 % *Quercus*	0.1 % *Vaccinium*-type	0.1 % *Myriophyllum spicatum*
100 % AP	0.1 % *Umbelliferae*	0.1 % *Typha latifolia*
2.5 % *Corylus*		

[1]) The percentages calculated on the sum of tree pollen ("AP").

This pollen spectrum belongs to Zone IV, the Birch-Pine period. It is true that there are small frequencies of alder, hazel, oak and elm, but many of these pollen grains are clearly distinguishable by their marked signs of destruction and their occurence must be due to contamination with some slight quantity of alder peat. In pure gyttja the pollen is usually in a good state of preservation, and this is actually the case with the birch pollen. The main characteristic of the spectrum, the preponderance of birch over pine and the very low hazel percentage, is not at all compatible with the occurrence of alder, and it is noteworthy that destruction is farthest advanced among the alder pollen, involving the greater part of the grains. Naturally, such slight contamination will easily occur if a peat find is not handled with particular care, and in many cases the reliability of the analysis will be reduced considerably. However, this cannot be said to be the case here; there can be no doubt that the spectrum of this gyttja must belong to Zone IV. Accordingly the Bison from Baldersbrønde must be dated to this earliest phase of the post-glacial period, the Birch-pine period. At this time the forest had covered Denmark, but it was still rather open and rich in grasses and herbs.

2. The Bison from Mjang Mose, Als.

According to V. Nordmann (1914, p. 231) this brain-case was unearthed during the survey of Mjang Mose in the middle of last century, being brought to light when one of the surveying poles was pulled up. Nordmann continues: "Small lumps of mud with plant remains still are to be seen in the cavities of the skull. Some of this earth has been examined by the botanist Knud Jessen of Danmarks Geologiske Undersøgelse, but the result was somewhat meagre. Most of it consisted of root fibres of *Carex* sp., but an examination of about ten slides revealed 1 pollen grain of *Betula* sp., 1 of an *Ericales* of some kind, 2 grains and possibly fragments of a third of *Pinus* sp., 3 spores of *Sphagnum* sp. as well as fungus hyphae and spores. This suggests that the bone was scarcely deposited in peat, but rather in mud or wet earth; moreover, the rather light colour of the bone and its tendency to scale indicate that it lay in a somewhat clayey substance, and, as its position was rather near the surface (it was unearthed when the surveying pole was pulled up), the probability is that it had been deposited near the shore of the bog. This is perhaps the reason why the skull is so badly injured below and why large parts are missing. As to the geological age of this Bison skull, it is obvious that one cannot say very much from the above sparse information."

NORDMANN's opinion is still valid. The geological evidence indicates that the bone was most probably found in a late-glacial deposit, i. a. because one pollen grain of birch, and two of pine only were found in the preparations. *Sphagnum* spores and *Ericales* pollen also are not likely to be found in the rich environment of Mjang Mose in post-glacial time; *Sphagnum* and *Ericales* are totally absent in the locality today. However, the examination of the soil took place at a time (1914) before the method of pollen statistics had been developed, and it goes without saying that it would be desirable to have another sample from the skull cavities. With the kind help of Dr. NORDMANN the find was made accessible for a renewed examination, with the result that considerable pieces of mud were found still attached to it. Nevertheless, the prospects did not look very bright, as the peat had a very heterogeneous appearance which suggested contamination. The spectrum was very surprising:

4 % *Betula*	1 % *Cerealia*	4 % *Polypodium*
10 % *Pinus*	1 % *Artemisia*	
36 % *Alnus*	1 % *Rumex* cfr. *acetosa*	
1 % *Quercus*	1 % *Plantago lanceolata*	
1 % *Fraxinus*	2 % *Gramineae*	
47 % *Fagus*	2 % *Calluna*	
100 %	1 % *Cyperaceae*	
3 % *Corylus*	1 % *Caryophyllaceae*	

This spectrum is sub-Atlantic and is quite different from the earlier analysis. This again suggests contamination, so that there is no possibility of dating this Bison geologically.

3. The Bison from Mygdal, Hjørring.

On the subject of this skull, now in the Vendsyssel Historic Museum at Hjørring, V. NORDMANN (1941 p. 197) writes:

"According to the Museum's acquisition register the brain-case was found in 1902 by the farmer MARIUS JENSEN of Vestergaard, Mygdal parish, 9 km NE of Hjørring, in his own bog. It lay on the bottom; an elk tine was found in the same bog, also on the bottom. Unfortunately, there is no information on the depth of the bog and the thickness of the peat."

The Geological Survey had a peat sample which Dr. NORDMANN had taken from the bone for pollen analysis, and this was now examined[1]). A characteristic feature of the sample is its marked poverty in pollen, for in spite of a thorough treatment with HF and $(CH_3 CO)_2 O$, only 3 pollen per slide were found.

It has therefore been impossible to calculate a pollen spectrum with the percentages of the various plants, so that I can merely publish the numbers of the pollen grains and spores (6 slides 24 × 32 mm).

Betula	1	*Selaginella*	4
Pinus	8	*Botrychium*	1
Cyperaceae	4		
Gramineae	1		
Liguliflorae	2		

The find of chitin remains from a Chironimid larva suggests a limnic sediment, presumably detritus dy. In so far this is favourable, as limnic sediments are less influenced by local over-representation of pollen than peat.

A priori the remarkable poverty of tree pollen in conjunction with the absence of the pollen of thermophile trees indicate that the sample is late-glacial. The circumstance that the pollen of herbaceous plants has almost the same frequency as tree pollen points in the same direction. The decisive factor in the dating, however, is the presence of the four *Selaginella* microspores and the spore of *Botrychium*. Both are common in Danish late-glacial deposits, but are extremely rare in post-glacial strata. Another point is that as regards these spores we can dismiss the possibility of later contamination in the Museum. It may be objected that five spores of *Selaginella* and *Botrychium* are not much upon which to base a dating; but it must be remembered that the number is large, considering the unusual poverty of microfossils. Without hesitation I therefore date this sample to late-glacial time. A more precise dating is impossible, apart from the fact that it may be assumed that the sample cannot date from the Allerød period with its wealth of birches (only one birch pollen grain in six slides!), but must be referred to Early or Late Dryas (Zone I or Zone III). Normally the peat digger does not go deeper than to the upper

[1]) By a slip of the memory Dr. Nordmann (l. c. 1941 p. 197) writes that no peat sample could be obtained for pollen analysis. The present writer, however, received the sample about ten years ago; it was put aside, as the first examination gave no result. The improved technique of recent years in the treatment of samples very poor in pollen made it possible to come to a positive result at the renewed examination, though it took several days' work for this one fragmentary analysis.

edge of Zone III, and therefore the sample most probably belongs to Zone III.

Thus the analysis seems unequivocally to date this Bison to a cold section of the late-glacial period, characterized in this northern region by tundra vegetation. All the same, the lack of information regarding the find-conditions has the effect that the certainty of the dating cannot be called absolute.

4. The Bison from Akkerup Mose, Funen.

The particulars of the find-conditions are taken from Danmarks Geologiske Undersøgelse's bog department record for 1923 as reported by Dr. KNUD JESSEN, the head of the department at that time. The main points of this report are given below in translation:

"In 1921 Mr. MØLLER, the farmer at Akkerup Præstegaard, sent in some ox bones found in a bog, according to Mr. H. WINGE perhaps belonging to a Bison.

Dr. NORDMANN and I made some excavations at the spot in the bog where Farmer MØLLER had found the bones.

Section where the scapula was found:

A. 0— 42 cm. Rubbish.
B. 42— 60 cm. Yellowish-brown *Amblystegium* peat with rhizomes of *Menyanthes trifoliata* and *Equisetum limosum*. Seeds of *Menyanthes* common.
C. 60— 75 cm. Brown detritus gyttja, becoming greyish brown downwards; leaves of *Myriophyllum spicatum*, *Salix cinerea*.
D. 75—107 cm. Grey snail gyttja. In this was found a scapula of a large ox between 78 and 90 cm below the surface. $1^1/_2$ m from the bone was a pine branch on the boundary between Strata C and D.
E. 107—119 cm. Dark greyish brown gyttja with shells of snails and of *Sphærium corneum*. Fragments of *Potamogeton* cfr. *natans*.
F. 119—135 cm. Grey-yellowish brown gyttja with numerous *Sphærium corneum*.
G. 135—144 cm. Brown detritus gyttja, elastic plankton gyttja with *Sphærium corneum* below.
H. 144—150 cm. Yellowish brown gyttja.
I. 150—182 cm. Greyish-blue, sandy, stoneless clay.
K. Boulder till."

Regarding the position of the various bones Professor JESSEN states furthermore that the scapula and a rib lay respectively a little below and at the upper edge of the snail gyttja, Stratum D. Another rib lay quite near the one mentioned, but 26 cm lower, 101 cm below the surface of the bog. The sternum, which lay about 30 cm below the latter rib, must have been found in Stratum F.

It is clear from these particulars that the bones lay at very different levels, but all in the limnic deposits below the peat. According to Dr. DEGERBØL, there is no reason to doubt that they belonged to the same animal, so that the question arises as to how this scattering of the bones can be explained. Now it must be remembered that a bison is a large and heavy animal, and this fact would mean that the lower part of the body would be pressed far down into the gyttja when the animal fell into the pond. Thus there is nothing unnatural in the sternum's being found at the deepest level, about $^1/_2$ m lower than the scapula. Naturally, the dating should be based on the bones that lay highest, in the uppermost part of the grey snail gyttja. Nevertheless we must face the problem of whether these bones were also too low, having been pressed down into the gyttja strata. This would have to take place while the skeleton was still intact, and therefore it is an interesting point that the scapula and the bones recovered in 1921 (including dorsal vertebrae) lay so far from the sternum that they must have been moved from their original position after the death of the animal. Therefore as regards these bones we cannot assume that they sank down through any other agency than their own weight, which experience shows is not at all great. It should be observed, however, that among the vertebrae are two which differ from the others by their rather darker colour. They were among Farmer MØLLER's collection, so that we know nothing positively about their situation; it is presumable, however, that they were surrounded by a darker sediment than the other bones. It is impossible now to determine whether they came from one of the dark strata in the section (B, C, E) or merely from a darker zone of Stratum D which (see later) is darkest at the middle.

When I made the first attempt at dating the Akkerup find I knew nothing of the excavation made by Danmarks Geologiske Undersøgelse in 1923. At the Zoological Museum Dr. DEGERBØL had brought out the old collection from Farmer Møller again, found that it actually consisted of Bison bones, and sent two dorsal vertebrae to the D. G. U. for a pollen-analytical dating. Two lumps of gyttja were picked out of the foramen of the vertebrae and proved to contain a lot of well-preserved pollen. Afterwards the box containing the other bones unearthed by the D. G. U.s excavations was recovered from the base-ment store where it had been placed twenty years before, together with some soil samples taken for macrofossil analysis. A new analysis was then made of a gyttja sample taken from a vertebra of this collection.

The resulting three pollen spectra (see Table 3 Nos. 1—3) agree well and have a distinctly late-glacial character. This might seem surprising, inasmuch as these bones lay high up in the gyttja, and as it has been customary in Denmark since the classical investigations in the brickworks pits at Allerød and elsewhere to place the boundary

Table 3.

	1	2	3	4	5	6	7	8
Betula	38	38	47	49	74	58	4	2
Pinus	10	14	15	10	11	11	34	37
Salix	3	1	2	4	3	5	—	0.5
Empetrum	1	1	1	0.5	—	0.5	1	—
Vaccinium-type	1	1	—	0.5	—	1	—	—
Gramineae	6	4	8	12	3	9	21	34
Cyperaceae	36	39	26	19	8	12	40	26
Artemisia	2	1	1.5	1	—	1.5	1	—
Rumex	1	1	—	0.5	0.5	1	—	—
Thalictrum	1	—	1	0.5	1	0.5	—	0.5
Chenopodiaceae	1	1	—	1	0.2	0.5	—	—
Pollen total	374	159	266	315	589	234	136	225
Rosaceae-type	1	—	1	0.5	1	1	—	—
Liguliflorae	—	—	—	—	—	0.5	2	0.5
Tubuliflorae	—	—	—	—	—	—	—	—
Cerastium-type	—	1	—	—	—	0.5	—	—
Ranunculus-type	—	—	0.5	0.5	—	2	—	—
Chamaenerium	—	1	—	—	—	—	—	—
Myriophyllum spicatum	—	—	—	—	—	1	—	—
Lycopodium annotinum	—	—	—	—	—	—	—	0.5
Selaginella selaginoides	—	—	0.5	—	—	×	—	—
Dryopteris Linnaeanum	1	—	—	—	2	2	—	—
Botrychium	—	—	—	—	—	×	—	0.5
Sphagnum	—	—	—	0.5	1	—	1	1
Equisetum	0.5	1	1	3	58	3	4	6

1—3: Pollen analyses from 3 different vertebrae of the Akkerup Bison.
4: Analysis from the snail gyttja (Stratum D) in Professor KNUD JESSEN's section in the bog at Akkerup.
5: Analysis from the deeper dark gyttja (Stratum E).
6: Pollen analysis from a vertebra of the Harndrup Bison.
7—8: Pollen analysis from two vertebrae of the Tranum Bison.

between the late-glacial and the post-glacial period at the contact between clay (Upper Dryas clay) and gyttja. Pollen-analytical investigations have shown, however, that in many basins no "Upper Dryas clay" is developed, as throughout the whole of the Late Dryas period the sediment was gyttja, exactly like that in the foregoing and the subsequent period. In such cases the boundary between the late-glacial and the post-glacial periods can only be found with certainty by means of pollen analyses, as it manifests itself by a great and final fall in the curves of the herbaceous plants. Two analyses of a sample from the snail gyttja (Stratum D) and the dark gyttja below (Stratum E) strengthened the author's supposition that the mud series was late-glacial and that the dark sediments below represented the Allerød gyttja (cfr. Table 3 Nos. 4—5).

Complete certainty could only be assured by means of a diagram from the bog. Unfortunately, the pollen samples collected 1923 could no longer be found, and therefore I made another examination of the bog in April 1943. I was able to find the man who had done the digging during the investigation in 1923, so that it was possible to identify the finding-place of the Bison fairly accurately.

This small bog lies a few hundred metres southeast of the village of Akkerup (Haarby parish) at the foot of the remarkable stationary-line region known as "Fynske Alper", and it is surrounded by diluvial sand and boulder clay (cfr. MILTHERS 1940). Undoubtedly the basin of this bog arose through the melting of buried masses of ice (subsidence holes). In late-glacial time the bog was a small well-protected lake without much influx.

A row of borings (Hiller's peat sampler) was made in a line across the bog. The section showed fairly regular stratification. At the bottom was a deposit of late-glacial clay up to $^3/_4$ m thick, passing upwards into a thin layer of sandy gyttja. As will be shown, these deposits were laid down in Early Dryas time. In the entire bog the Allerød gyttja is divided exactly as in Professor JESSEN's section description, there being a dark-brown, at the bottom elastic lower detritus gyttja (Stratum G), an intermediate layer of light-coloured calcareous gyttja (F) and an upper dark detritus gyttja (E). The sediments from Late Dryas time (D) are formed of light-coloured diatom-gyttja which is strongly calcareous at the top and the bottom, but has no lime and is a little darker in the middle (brownish and peaty near the margin of the bog). The brown detritus gyttja at the top of the section in 1923 (Stratum C) was found in a few places only; in most borings the peat followed directly on the top of the calcareous gyttja.

The distribution of the microflora through the series is very interesting. In the Allerød bed various green algae dominate (*Scenedesmus*, *Pediastrum, Tetraëdron* v. a.) and are so numerous that they constitute a large part of the sediment. On the other hand the diatoms characterize the microflora in the sediments from both Early and Late Dryas time. This curious distribution actually is undoubtedly — directly or indirectly — climatically conditioned. I have observed and to some extent examined statistically the alternation between diatom flora and *Chlorophyceae* flora in other late-glacial sections, for example in Bølling Lake, where the upper, "warmest", part of the Allerød gyttja and the preboreal gyttja have *Chlorophyceae* flora, whereas the remainder of the late-glacial sediments have diatom flora. The change-over from the one microflora type to the other is quite abrupt. There is no doubt that microfossil diagrams through late-glacial sediments will provide an excellent supplement to pollen analysis, and indeed in some cases react more distinctly to climatic changes.

The samples for the pollen analysis came from a boring almost in the middle of the bog. At this spot the sequence was as follows (cfr. the sequence p. 37 and Plate IV, left):

A.	0— 30 cm.	Rubbish.
B.	30— 78 cm.	*Amblystegium* peat with seeds of *Menyanthes*. Stratum C (Detritus gyttja) was lacking in this boring.
D.	78—112 cm.	Grey lime gyttja, rich in snails and small mussels. Microflora diatoms.
	112—133 cm.	Greyish-brown (non calcareous) diatom gyttja.
	133—152 cm.	Grey lime gyttja with small mussels. Microflora diatoms.
E.	152—162 cm.	Brownish-grey — brown detritus gyttja. Microflora *Chlorophyceae*.
F.	162—172 cm.	Greyish-green, calcareous gyttja. Microflora as in E.
	172—179 cm.	Grey lime gyttja with snails and small mussels. Microflora as in E.
G.	179—187 cm.	Greenish-brown detritus gyttja with small mussels. Microflora as in E.
	187—192 cm.	Dark brown elastic fine detritus gyttja. Microflora as in E.
H.	192—206 cm.	Greenish-grey, partly very sandy and somewhat clayey diatom gyttja.
I.	206—210 cm.	Stoneless clay.
	210—213 cm.	Clay containing gyttja.
	213—283 cm.	Stoneless, grey, downwards greasier and bluish-grey clay with sand stripes.

The pollen diagram (Plate IV) is drawn according to the principles which I explained fully in a previous paper (Iversen 1942). In order that the tundra vegetation may also be represented in the diagrams I have, in addition to the usual types of tree pollen, included pollen of the wind-pollinating herbaceous land plants (*Gramineae*, *Cyperaceae*, *Artemisia*, *Rumex*, *Thalictrum* and *Chenopodiaceae* and of *Ericales* incl. *Empetrum*). The pollen of water plants is naturally omitted from the pollen total, and the same applies to the pollen of insect-pollinated herbs — which by the way always occurs in very low percentages only except *Helianthemum* pollen, which it might have been of advantage to include. Spores too are reckoned separately in relation to the pollen total[1]).

The diagram shows the interchanges in the mutual relations between the pollen of the three most important types of vegetation: Woodland and scrub (white area), grassland (hatched area), and heath (stippled area). The area of woodland and scrub is formed of the pollen sum of *Pinus*, *Betula* and *Salix*, i. e. the very sum that forms the "classical" diagram. As the area for this type of vegetation is in white, the curves of the various elements can be plotted in the usual manner, and it will be easy to undertake a comparison with late-glacial tree-pollen diagrams. No doubt *Hippophaë* ought to have been included here, but it has been omitted, mainly on account of its low pollen production.

The area for the herbaceous vegetation corresponds of course to the pollen sum of the aforesaid wind-pollinated herbs. To the right of the diagram are the pollen curves for the most frequent of them (*Cyperaceae*, *Gramineae* and *Artemisia*), whereas the others (*Rumex*, *Thalictrum* and *Chenopodiaceae*) as well as *Empetrum* are plotted as silhouettes. The frequency of the pollen and spore types not included in the pollen total is also shown in silhouette form on the extreme right (Col. C).

[1]) As is always the case in Danish late-glacial deposits, the stoneless clay at the bottom of the bog contains a large quantity of re-deposited pollen. They were washed into the late-glacial lake together with the clay particles and, like these, come from boulder clay; originally these rebedded pollen grains came from Tertiary and interglacial sediments. I have previously shown (1936, 1942) that it is possible to segregate the "secondary" pollen, which otherwise of course quite distort the spectra. Some of them can be recognized directly as secondary, the others can be subtracted by a somewhat lengthy process which, besides comprehensive counts, requires a knowledge of the pollen flora in the boulder clay of the region. I shall not describe the method here but merely refer to the papers cited above. In the Akkerup section it was necessary to apply the method to the lowest analyses only, as these alone were mixed with the rebedded pollen. Column D shows the relative frequency of the primary and secondary pollen throughout the section. The basis of the subtraction is a pollen analysis of boulder clay from Helnæs.

Looking at the diagram we shall see at once that the relation between tree pollen and herb pollen alternates in a characteristic manner. It will also be seen that pine and willow take no great part in these alternations, but that the changing frequency of the birch is the determining factor: on the whole the rule is that a rise in the birch pollen curve causes a fall in the pollen curves of the most important herbaceous plants, and vice versa.

The clay strata in the lower part of the section are characterized by the preponderance of the pollen of the herbaceous plants[1]), which is a definite evidence that the region was treeless. In the following light-coloured, sandy diatom gyttja the birch curve rises somewhat, but it is only with the brown detritus gyttja that the birch pollen becomes so predominant that we may assume that the forest birch has made its appearance in the region and has occupied the favourable growing places. At the same time the microflora changes, as already stated; the diatoms are displaced by *Chlorophyceae*. Both bear witness of a rise of the temperature, though it was not lasting. At the transition between the upper, brown detritus gyttja (Stratum E) and the thick deposit of grey gyttja at the top of the section (Stratum D), the microflora changes back to diatom flora and at the same time the birch pollen curve falls rapidly. The tundra is once again the predominant type of vegetation, though without doubt some birches held out in the most favourable places. Uppermost in the diagram comes the final ascent of the tree curves, whereas the curves of the herbaceous plants fall correspondingly, and the lake grows over.

We thus see that the pollen diagram reflects the well-known Allerød oscillation. And the double peak that marks this oscillation of temperature stands out clearly in the pollen curves of the birch, the grasses and *Artemisia*, while the change in the sediments themselves (calcareous gyttja between two beds of detritus gyttja!) is also evidence of it. Nevertheless, the climatic depression in the middle of the Allerød period was not deep enough to affect the microflora.

A very remarkable feature in the vegetation of the Early Dryas period is the common occurrence of *Artemisia*, *Hippophaë* and *Helianthemum*. We may take it that these three heliophile plants grew on the south-exposed slopes. Besides being sunny, these localities are particularly warm and were undoubtedly the first which the birch forests were able to occupy in the Allerød period. As *Artemisia*, *Hippophaë* and *Helianthemum* will not tolerate the least shade, they

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[1]) This is true, however, only after the rebedded (Tertiary and interglacial) pollen are subtracted. Cp. Col. D and the note page 42.

disappear entirely with the coming of the birch. *Artemisia* comes back when the birch forest in its turn has to give way in the Late Dryas period, whereas *Hippophaë* and *Helianthemum* remain very sparse. On the other hand, at this time another plant community appears, the *Empetrum* heath, though it never reaches any great distribution. During all the late-glacial period the herbaceous plants characterize the open vegetation.

To return now to the Bison find: The important, dating bones lay uppermost in the calcareous gyttja. From the diagram it appears that this deposit corresponds to the end of the Late Dryas period. The pollen spectra from the three vertebrae examined should also be placed to the later part of that period.

Accordingly the Bison find at Akkerup should be dated to the transition between late-glacial and post-glacial time. Unless the uppermost bones had also sunk a little way into the gyttja, we may make the dating more precise and fix it to the end of the Late Dryas period. The vegetation was still very open and rich in grasses and other herbaceous plants.

5. The Bison from the Bog at Harndrup, Funen.

The particulars regarding the find conditions were secured by Mr. ALFRED ANDERSEN, M. A., who at the end of June 1944 went to the locality together with Mr. MØHL-HANSEN and took a series of samples for pollen analysis.

The Bison bones were found in the course of peat-cutting in the bog, immediately under the peat. No skull was found, and the further examination of the spot by Mr. MØHL-HANSEN and Mr. ANDERSEN resulted merely in the discovery of two ribs, which are of little value only to a geological dating as they may be pressed deep down into the gyttja to a level lower than the actual find-stratum, as we saw in the case of Akkerup. The factors decisive to the dating are the account of the peat cutters as to the position of the bones, and a pollen analysis from the inner cavities of a vertebra.

The bog in which the bones lay is very small. Three metres north of the finding-place there was the following sequence:

A	0— 24 cm.	Mouldered peat
B	24— 71 cm.	Fen-peat, mainly alder fen-peat.
C	71— 97 cm.	Rather loose mossy sedge peat.
D	97—105 cm.	Detritus dy, but uppermost more like *Equisetum* peat.
E	105—168 cm.	Yellowish-brown, alga-gyttja, light in the middle, above and below darker.

F	168—188 cm.	Dark-brown, rather coarse detritus gyttja, passing downwards into brown, elastic gyttja.
G	188—205 cm.	Light-grey, lime gyttja with molluscs.
H	205—207 cm.	Light-brown calcareous gyttja.
J	207—208 cm.	Lake marl.
K	208—212 cm.	*Amblystegium* peat.
L	212—214 cm.	Terrestrial peat.
M	214— cm.	Boulder clay.

This section displays close agreement with that in the bog at Akkerup and a pollen diagram calculated by Mr. BRORSON CHRISTENSEN (Plate V) further verifies this resemblance. First and foremost the diagram proves that the entire gyttja series is late-glacial. The only difference from conditions at Akkerup is that sedimentation begins in the Allerød period only, as above boulder clay the first to be formed is terrestrial peat ("Allerød mould") and thereafter *Amblystegium* peat, which in turn is overlain by the gyttja series. From this we may conclude that the basin was not yet in existence in Early Dryas time; it was first formed in the beginning of Allerød time by subsidence in conjunction with the melting of a buried block of ice (cfr. HARTZ 1912).

The double peak in the Allerød oscillation is suggested in the sequence and stands out clearly in the pollen diagram, *Artemisia*, *Gramineae* and *Cyperaceae* displaying the usual two minima simultaneously with the maxima of the *Betula* curve. To some extent the boundary between the late-glacial and the post-glacial periods is camouflaged by a change in the sedimentation. The little lake fills up and the *Cyperaceae* become over-represented, which again involves a depression of the birch curve. The uppermost analysis in the diagram (70 cm below the surface), however, belongs without doubt to the post-glacial period (Zone IV), and the uppermost analysis in the alga-gyttja (105 cm below the surface) is naturally still late-glacial (Zone III). The aforesaid boundary must thus lie somewhere between these. It is probable that the filling up of the lake, which at first manifests itself by the change in the sedimentation at 105 cm below the surface, is connected with the beginning improvement of the climate. The boundary between the late-glacial and the post-glacial periods, however, must evidently be laid higher up. Even if we leave out the locally over-represented *Cyperaceae* pollen from the pollen total, the actual rise of *Betula* does not begin until the analysis at 80 cm below the surface, so that it will be reasonable to place the end of the late-glacial period there. It is not until we reach the uppermost analysis that the absolute density of tree pollen reveals the violent increase (cp. col. E) which usually takes place at the transition to the post-glacial period.

According to the accounts of the peat diggers the Bison remains lay "2—5 inches down in the clay" under the peat. Consequently they lay in deposits of the end of the late-glacial period. The pollen analysis of the mud fragments from the inner cavities of a vertebra, reproduced in Table 3 No. 6, gives the same result. The low *Pinus* percentage in conjunction with the occurrence of 2 % *Dryopteris Linnaeanum* spores as well as pollen of *Artemisia*, *Thalictrum*, *Rumex* and *Chenopodiaceae* seem to place the analysis below the marked *Pinus* increase that sets in at the contact between the alga-gytja and the detritusdy. The occurrence of a *Botrychium* spore as well as a *Selaginella* spore in the same sample also points in the same direction. Thus there can hardly be any doubt that the vertebra actually belongs to the top of the late-glacial gyttja.

The Harndrup Bison must accordingly, like the Akkerup find, be placed to the transition between the late-glacial and the postglacial periods, probably the end of the Late Dryas period. The landscape was in the transitional stage between tundra and woodland ("park tundra").

6. The Bison from Jarmsted Mose, East Han Herred.

This Bison skeleton was found towards the end of July 1944 during peat-cutting operations in Jarmsted Mose. Inspector SVENNING P. SVENNINGSEN gives the following description of the find conditions: "The skeleton lay under about 50 inches of peaty soil, 5 inches of marine clay and 10 inches of turf. A little to the west there were only 40 inches of peaty soil on a very firm sandy bottom, so firm that many thousands of years ago the Bison was able to walk on it; it appeared quite clearly that it has stuck fast in a hole, a place where the bottom was so soft that my thin iron probes were unable to reach bottom."

Jarmsted Mose lies in a valley which was once flooded both by the late-glacial Yoldia Sea and the Litorina Sea. From the time of the Yoldia Sea there is a terrace-like plane with late-glacial beach sand between the bog and the hills (AXEL JESSEN 1905 p. 111). In Littorina time the valley was a well-sheltered fjord, and the marine transgression is manifested by the thin layer of alluvial clay-mud in the upper peat deposits as mentioned in the above description of the section at the find-spot.

As will be seen from Mr. SVENNINGSEN's description, the Bison lay 50 inches under the bed of marine clay from the Litorina period and almost on the boundary between the peaty soil and the underlying mud. Accordingly it dates from the time between the two great transgressions, Yoldia Sea and Litorina Sea, and it must be much earlier than the latter. For pollen analyses samples of peat were picked out of the foramen of the two bison vertebrae sent in, a dorsal vertebra and a lumbar vertebra. The pollen spectra are shown in Table 3 Nos. 7—8; the pollen of the *Ericaceae* and wind-pollinated herbs is included in the total. The spectra are characterized by the dominance of the pollen of herbaceous plants and by the absence of other tree pollen than that of *Betula* and *Pinus*. The *Betula* percentage is strikingly low, and the spectra suggest that the region as a whole was timberless.

For a more specific dating it was necessary to correlate the spectra with a pollen diagram from the bog. I therefore requested Mr. Svenningsen to cut a continuous column through the bog deposits by means of some zinc gutters, after preparing a clean-scraped wall. Mr. Svenningsen did this with great care, though the sample column had to be taken 10 or 12 metres from the exact finding-place, as peat-cutting had been continued in the mean-time. The sequence of the section proved to correspond exactly to that communicated by Mr. Svenningsen (see above), only the deposits under the peat were hard sand, except for a few cm thick layer of softer and more muddy character, corresponding to the softer stratum in which the bison bones had lain.

The diagram is given in Plate VI. It will be observed that *Pinus* dominates well over *Betula* in the peat, undoubtly a result of selective pollen destruction. The point is that the pollen is in the poorest state of preservation in the peat; quantities of pollen grains reveal signs of destruction, from which it may be concluded that many have disappeared entirely. As *Pinus* pollen is more resistant than other pollen, the *Pinus* pollen percentage rises automatically with increasing pollen destruction. To some extent this makes the zone determination difficult.

The pollen destruction is due to the fact that the sediments are not limnic, but were laid down under relatively dry conditions. This entails the further drawback that the pollen spectra are strongly influenced by the local vegetation of *Cyperaceae*, *Gramineae* and *Ericaceae*. The transition between the late-glacial and the post-glacial periods (Zone boundary III—IV), which in limnic sediments appears clearly in a fall of the pollen of the herbaceous plants, is here camouflaged by the prolific supply of pollen from the *Gramineae* and *Cyperaceae* growing on the spot.

In spite of these difficulties it seems justifiable to place this zone-border, which is decisive for our dating, between the analyses 120 cm below the surface and 125 cm below, for the following reasons:

1) At this place in the diagram the falling *Salix* curve separates from the rising *Betula* curve. A diagram from a bog at Fjerritslev, 12 km from Jarmsted Mose, shows clearly that this curve figuration begins at the transition between late-glacial and post-glacial times (see IVERSEN 1933, p. 11).

2) Microspores of *Selaginella* were found to a number of 7 in the analysis 125 cm below the surface. This indicates that this analysis still belongs to Zone III (cfr. p. 36).

3) The *Gramineae* curve falls rapidly, *Thalictrum* disappears from 125 to 120 cm below the surface. The *Cyperaceae* curve must presumably be quite locally conditioned, so that we need not credit the slight rise with any importance.

Apart from here the boundary between Zones III and IV can only be placed at one spot, at 133—134 cm below the surface, where the first rise of the *Betula* curve begins. This rise, however, seems rather to be governed by fluctuations in the local herbaceous vegetation, as it runs parallel with a *Salix* rise and is followed by a slight decline.

But whether we lay the zone boundary at one or another place, the pollen spectra from the Bison vertebrae are clearly late-glacial, as they are both prior to the first rise of the birch curve. And the very small content of tree pollen in these samples, especially of birch pollen, proves the same thing: on an average there were only two birch pollen per slide compared with 74 in analysis 120 cm and 121 in analysis 115 cm below the surface, although pollen destruction was much greater in the last two analyses. Eventually I may add that it is not likely that the scull and vertebrae have sunken in the relatively firm deposit.

Thus the Bison find in Jarmsted Mose may definitely be dated to the late-glacial period, and, judging by all the signs to Late Dryas (Zone III). The vegetation consisted entirely, or at any rate preponderantly, of timberless tundra; there may possibly have been a little birch scrub in the most favourable places.

IV. Conditions of Life for the Large Herbivorous Mammals in the Late-Glacial Period.

It has been shown in the foregoing that five of the six late-Quaternary Danish finds could be dated by pollen-analysis, and that four of them belong to the Late Dryas Period (Zone III), whereas one only can be dated to the earliest Forest Period (Zone IV, the birch-pine period). It is a remarkable fact that the four late-glacial finds seem to be almost contemporary and at the same time not very much earlier than the one post-glacial find. One might be inclined to believe that there was a large immigration of Bisons in the transitional time between late glacial and post glacial. Such an immigration might very well find its explanation in the incipient rise of the temperature, which caused the landscape on the south to become less open because conditions for forests to grow became better. If that was the case, steppe animals like the Bison and the Wild Horse would move northwards, where the country was still open.

However, there may also be another explanation for the many finds of large mammals in the transitional time. The majority of bog-found mammals are discovered by peat-cutting. Late-glacial peat is rare; generally the formation of peat begins only with post-glacial times. The result is that the peat-cuttings are carried down through post-glacial deposits alone, so that the only chance of late-glacial animal skeletons being discovered is when they lie immediately under the post-glacial peat. Four of the Bisons lay in that very situation, and three of them were unearthed by peat-cutters; had they been one spit lower, they would not have been found. Consequently, it is not improbable that the Bison was just as common at an earlier phase of the late-glacial period, even if none have ever been found to prove it. On the other hand it may confidently be said that the animal soon became rare once the forest had covered the whole country.

Like the Wild Horse and the Irish Elk[1]), the Bison accordingly was a denizen of the open, late-glacial landscape, and it would be reasonable to try to form an idea of the conditions under which these large grass-eating mammals lived.

It is superfluous to say that our knowledge of the vegetation of late-glacial times is imperfect. This in particular was the case when we knew it only from the finds of macroscopical plant remains (leaves, fruits, etc.). The study of the pollen flora in late-glacial deposits has greatly supplemented our knowledge, so that it is now possible to form a certain picture of the vegetation of those times.

On considering the pollen diagrams one is involuntarily moved to credit the various plants with an importance in the vegetation corresponding to their pollen percentages. Naturally this is wrong, as the pollen production of the various plants varies considerably. In order to have a working basis for the valuation of late-glacial pollen diagrams I have analysed the pollen from the recent gyttja of two Greenland lakes in the inland region of Godthaab Fjord and compared these analyses with the actual vegetation in the environment of the same lakes. Each of the two lakes lies in its own valley, and much time was spent on a careful determination of the relative frequencies of the various plants expressed by their density. A large number of sample plots (circle plans) of 1/10 sq. m. each were investigated from all over the field, 1000 in one valley (Lake I), 200 in the other (Lake II). The degree of covering of each species and category was determined for each sample plot, and the relative frequency of the more important plants in the two areas was calculated on this basis.

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[1]) A find at Vævlinge, Funen, could be dated to the Allerød Period (see Degerbøl 1939). I take this opportunity to draw attention to a confusing slip in Dr. Degerbøl's article. On page 135, 5th last line the text reads: "The pollen-analytical investigation proved that Stratum 4 is Allerød gyttja, birch-forest pollen being much more sparse here than in the other strata". The word should of course have been "abundant", not "sparse". The complete documentation of the dating of the Irish Elk will be published later; for the present I shall merely give a pollen spectrum from a lump of clay-gyttja taken from the root of the antler: *Salix* 2 %, *Betula* 58 %, *Pinus* 16 %, *Gramineae* 5 %, *Cyperaceae* 17 %, *Artemisia* 1 %, *Chenopodiaceae* 1 %, *Thalictrum* 1 %, *Vaccinum* ½ %. In the diagram from the bog this spectrum can only be placed either at the beginning or at the end of the Allerød Period. The occurrence of 1 % *Helianthemum*, ½ % *Hippophaë* and 1 % *Selaginella*, which in the Vævlinge diagram, exactly as in the Akkerup diagram, all disappear a little way up in the Allerød zone, proves that the analysis belongs to the beginning of the Allerød Period. The *Cervus giganteus* find from Ö. Grevie in Scania is placed by Mohrén (Berlin & Mohrén l. c.) to the same time. However, the pollen diagram from Ö. Grevie is very difficult to correlate with other Scanian and Danish diagrams; on the basis of a comparison with my Bornholm and Zealand diagrams I am certainly more inclined to place the Scanian find to the Early Dryas Period.

Table 4.
Comparison between the pollen content of recent gyttja in two Greenland lakes and the composition of adjoining vegetation areas (cp. p. 50).

	Valley I		Valley II	
	Pollen analysis from recent lake mud	Real composition of the vegetation Area %	Pollen analysis from recent lake mud	Real composition of the vegetation Area %
Alnus viridis	13	3	10	5
Salix	6	13.5	6	12
Betula nana	56	19	58	33
Empetrum hermaphroditum	6	6	5	5
Ericaceae	5	26	4	18.5
Gramineae	3	11	5	13
Cyperaceae	10	22	12	17
Artemisia	1	×	0.5	×
Rumex acetosella	0.5	×	1	×
Pollen total	451		226	
Sphagnum	2	5	2	10
Selaginella	2.2	×	—	0
Lycopodium annotinum	23	1	4	1
do. complanatum	3	×	0.4	0
do. selago	0.4	×	—	0
Pinus + Picea (long-distance wind transport)	2	0	2	0

The table 4 provides a comparison between the recent pollen spectra and the actual frequency (relative degree of covering) of the plants in the two valleys. It will be observed that willows (*Salix glauca* and *S. arctica*), grasses (*Gramineae*), sedges (*Cyperaceae*) and especially *Ericaceae* are much more common than one would be entitled to expect from their pollen percentages, whereas the distribution of the crowberry (*Empetrum hermaphroditum*) corresponds to its pollen frequency. On the other hand the birch (*Betula nana*) is heavily over-represented in both pollen analyses; the same would seem to be the case with *Artemisia borealis*[1]), though in this case the material is so small that there is a certain margin of chance. A remarkable feature is the colossal spore production of *Lycopodium*; on the other hand *Sphagnum* is under-represented in the analyses of the recent gyttja.

[1]) This harmonizes with ERDTMANN'S figures for *Artemisia* (l. c. 1943 p. 52).

On this basis I have calculated the relative pollen supply at the same area of covering, and in the following list the plants are arranged according to the size of that value. It is a curious fact that the order of the plants was the same in both areas of investigation.

1. Alder (*Alnus viridis*) 134 %[1]).
2. Birch (*Betula nana*) (100).
3. Crowberry (*Empetrum hermaphroditum*) 47 %.
4. Sedges (*Cyperaceae*) 27 %.
5. Willow (*Salix*) 22 %.
6. Grasses (*Gramineae*) 16 %.
7. *Ericaceae* (*Vaccinium*, *Ledum*, *Rhododendron*) 10 %.

It is clear that the results of this isolated investigation in Greenland have only a limited application; but as far as I know there is no corresponding comparison between the pollen frequencies in recent gyttja and the actual vegetation of other Arctic or sub-Arctic regions[2]).

The necessary conclusion to be drawn from the above is that in our late-glacial diagrams the *Betula* curve lies much too high, whereas the curves for *Ericaceae*, *Salix*, *Gramineae* and *Cyperaceae* are too low in proportion to the real frequency of these plants at the time. In other words, grassland and willow scrub covered greater areas than one should think after seeing the diagrams.

With the pollen diagrams and the macroscopic finds to guide us we shall now try to give a picture of the more important types of vegetation and their approximate distribution in late-glacial time.

Among the pollen of the herbaceous plants the *Cyperaceae* and *Gramineae* have the highest frequency. *Cyperaceae* grow by preference in wet soil, and there can scarcely be any doubt that the high *Cyperaceae* frequencies are due particularly to the fen vegetation.

Grasses occur on both dry and wet soil, but as *Phragmites* was missing in the late-glacial period (cf. SCHÜTRUMPF 1943 p. 16), it may perhaps be assumed that most of the *Gramineae* pollen came from the higher soil. Considering to the relatively moderate pollen production of the arctic *Gramineae* we must conclude that the grass vegetation — compared with present-day tundra — was either more

[1]) The percentages indicate the pollen supplies of the plants per area in proportion to that of the birch (the mean of the percentages of the two valley areas).

[2]) The important investigations of FIRBAS (1934) and AARIO (1940) into the recent pollen flora of the various vegetation regions in Lapland are less applicable to the present purpose, as they were made on recent peat or förna. Both authors indeed point out that for this reason the pollen analyses are strongly affected by the local vegetation. Nevertheless, the tendency is clear enough: *Ericaceae*, *Salix* and *Gramineae* were very weakly represented only in the pollen flora when they were not growing on the actual spot where the sample was taken (FIRBAS l. c. p. 134, AARIO l. c. p. 85 ff.).

luxuriant[1]) or more widespread, such as we find it in the Alps above the timber line (see AARIO 1944). The most luxuriant grass vegetation must have been the tall, herbiferous meadows; a characteristic element of this type of vegetation is *Saussurea alpina* (cfr. NORDHAGEN 1943), the easily recognizable pollen of which was found at Tranum and Akkerup in Late Dryas strata.

Grassland was undoubtedly of the greatest importance as a source of food for the herbivourous late-glacial mammals, whereas heath vegetation was of no value whatever. This applies equally to the calciphile communities that are characterized by *Dryas octopetala, Saxifraga oppositifolia, Salix polaris*[2]), *S. reticulata* and other plants, and the oligotrophous *Empetrum* and *Vaccinium* heaths.

In Early Dryas time the warmer slopes with a southern exposure had a very interesting plant community, with *Hippophaë*, *Artemisia* and *Helianthemum* as character plants. This community is quite unknown in present-day Arctic and sub-Arctic regions and gives the late-glacial vegetation its character. GAMS (1943) points out that *Hippophaë* and *Artemisia campestris* require hygric (not thermic!) continentality and regards them as steppe elements in the late-glacial flora. Unfortunately, as far as *Artemisia* is concerned species determination is uncertain[3]). Most curious is FÆGRI's find in West Norway, which is difficult to reconcile with *A. campestris* (cfr. FÆGRI 1943 p. 81). It is also surprising to see the common occurrence of *Helianthemum* pollen in Danish late-glacial deposits (cfr. IVERSEN 1944); judging from the shape of the pollen grains we must assume that the majority belongs to the North European *H. oelandicum*, nowadays known in three small, isolated regions only (England, Öland and Pinegal in North-east Russia). Nevertheless, this species comes very close to the alpine *H. alpestre*, in which connection it is interesting to see that WELTEN (1944) and LÜDI (1944) have demonstrated that *H. alpestre*, like *Hippophaë* and *Artemisia*, characterize the late-glacial timberless period in Switzerland. This agreement makes it probable that the alpine features in the late-glacial vegetation of Denmark were more prominent than has hitherto been thought likely, more prominent perhaps than the Arctic ones. It will therefore be natural to pay more attention

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[1]) LÜDI & VARESCHI (1936) have shown that luxuriant, manured meadows ("Fettwiesen") have a very large production of pollen.

[2]) According to kind information from Dr. KNUT FÆRGI the very similar *Salix herbacea* is a valuable food plant for the Norwegian reindeers. The same therefore may be the case for *S. polaris*.

[3]) On the other hand there is no longer any reason to doubt the correctness of the genus determination. The pollen of no other northern plant — at any rate no wind-pollinator — can be confused with *Artemisia*.

to the alpine regions, from which very valuable pollen-statistical papers have appeared quite recently.

One peculiar difference between the appearance of *Helianthemum* and *Hippophaë* in the region of the Alps and in Denmark is that in Switzerland the *Hippophaë* stage does not occur until after the *Helianthemum* maximum (WELTEN, l. c.), whereas in Denmark the position is almost the reverse (cfr. Plate IV). The maximum late-glacial pollen frequency of *Hippophaë*, *Artemisia* and *Helianthemum* seems to show a distinct decrease from south to north. For *Hippophaë* this was demonstrated by GAMS (l. c., p. 76). There is a possibility, unfortunately, that the *Hippophaë* curves published in the literature are sometimes based on pollen of both *Hippophaë* and *Helianthemum*. Quite evidently the latter plant too attains to higher pollen frequencies in Switzerland (WELTEN l. c.) than in Denmark. The same applies to *Artemisia*, which according to LÜDI (l. c.) dominates in the late-glacial herbaceous pollen flora in the Lugano area, whereas everywhere north of the Alps the pollen frequency of the genus seems to be inferior to that of grasses and sedges (see LOSERT 1940, IVERSEN 1942, FÆGRI 1943, STEINBERG 1944). It is worth to remember that *Hippophaë*[1]) and the insect-pollinated *Helianthemum* were presumably more widespread than their pollen frequencies indicate, whereas *Artemisia* on the other hand is presumably over-represented in the pollen diagrams.

In the early part of the Allerød period the habitats of *Hippophaë*, *Helianthemum* and *Artemisia* were quickly occupied by the large-leaved birches, and the whole of the characteristic heliophile plant community disappeared almost completely. *Artemisia* advanced again when the birch forests were once more forced back in the Late Dryas time, but *Hippophaë* and *Helianthemum* were never able to assert themselves again. The *Artemisia* pollen curve reacts more readily to climatic changes than most other pollen types, for instance better than that of the *Cyperaceae*, which is also affected by local conditions (desiccation tendencies in the Allerød period and at the transition to the late-glacial period, cfr. Plate IV and V). This applies to southern Denmark, whereas in North Jutland *Artemisia*, *Hippophaë* and *Helianthemum* persist throughout the Allerød period — perhaps the best evidence that the landscape there remained very open in the Allerød period.

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[1]) Regarding the pollen production cfr. FIRBAS 1934 p. 129. It should, however, be remembered that *Hippophaë* is wind-pollinator and therefore presumably has an effective pollen dispersal. FÆGRI (1943, p. 77—78) justly expresses a word of warning against ignoring the possibility of long distance transport when endeavouring to explain finds of quite isolated *Hippophaë* pollen in sediments of a timberless epoch.

Willow scrubs were more widespread in the late-glacial period than the diagrams indicate, for the willow is a poor pollen-disperser. Unfortunately, it is impossible to distinguish between dwarf willows (*Salix polaris* etc.) and shrub willows; some of the *Salix* pollen in Early and Late Dryas times must be from dwarf willows.

Of paramount interest is the question of the density and distribution of the forest, in space and in time, during the late-glacial period. In the first place the fact must be established that even in southernmost Denmark the forest never was very dense. We have seen that birch and pine have a large pollen production compared with willow, *Ericaceae* and most herbs, so that in lake deposits (not in peat) the pollen of the forest will be much over-represented in relation to the area it covers. Furthermore, it must be borne in mind that some of the birch pollen comes from *Betula nana*, which ought to be placed in the category of tundra vegetation. Unfortunately, the pollen of the dwarf birch can be separated from the large-leaved birches by means of comprehensive statistical measurements only, and even then with certainty in non-calcareous sediments only (see FÆGRI 1940 and 1944). In unpublished investigations in Bølling Lake I have separated small-pollen birch (mostly *B. nana*) from large-pollen birch (mostly *B. pubescens* etc.) in the analyses. There proved to be a considerable dominance of large-pollen birch over small-pollen birch[1]), particularly in the birch maxima, though even there about 20 per cent. of the birch pollen was of the size that is characteristic of *Betula nana*. From this it is evident that the birch maxima in Denmark may really be regarded as forest maxima, but that the birch curve should be reduced if it is to be taken as a right expression of the relation between the forest and the tundra.

In Late Dryas time the birch curve does not ascend so high that it would be reasonable to ignore the question of whether the forest-birch pollen could not have been transported from a long distance. AARIO's investigations of recent peat samples in Lapland show that in the narrow tundra region there, pollen values for herbs and *Ericaceae* only rarely attain to such heights that they exceed the quantity of tree pollen, despite the fact that one would expect much higher values for herb pollen in peat than in lake deposits. Howewer, AARIO has suggested (and the suggestion has later been asserted by FIRBAS 1944), that the high relative contents of tree pollen in the samples from the Finnish tundra may be due to the fact that the tundra belt is 20 to 30 km broad only and adjoins a woodland which is more than 1000 km deep and is covered with trees having a prolific

[1]) Early Dryas clay deposits were not examined.

pollen production. On the whole the Finnish Arctic tundra is a special case; the very close situation of the isotherms along the coast means that there is an almost complete absence of the transitional belt, several hundred kilometres wide, which for example in East Russia and in Siberia inserts itself between the forest and the tundra (see NEHRING 1890). This transitional zone ("park tundra"), where the trees grow in the favourable, sheltered localities while the tundra covers the exposed and cold ones, is of particular interest for our understanding of the late-glacial conditions, as it is quite obvious that in late-glacial Europe the boundary between forest and tundra was just of this diffuse character. For this reason we cannot simply conclude from a relatively high herbaceous-pollen percentage that a region consisted of treeless tundra, even when the sample consists of deposit; on the other hand it would be justifiable to conclude that the forest covered only the most favourable localities. Therefore there is no reason to suppose that the forest birch was forced back from southern Denmark in Late Dryas time; at any rate, the finding of a fruit in Late Dryas clay at Snertinge (KNUD JESSEN 1924) shows that *Betula odorata* coll. was still growing in Zealand. Matters are more uncertain with regard to the pine. The very rapid rise of the *Pinus* curve in the Akkerup section at the transition between the late-glacial and the post-glacial periods, and especially Professor KNUD JESSEN's discovery of a pine branch at the transition between the shell gyttja (Stratum D, Late Dryas) and the brown detritus gyttja (Stratum C, pre-boreal) seems to show that the pine too was represented in Funen in the late-glacial period; the pollen diagrams suggest that the immigration took place towards the end of the Allerød period. This assumption receives additional support from SCHÜTRUMPF's find of a pine cone in Late Dryas sediments at Hamburg; the *Pinus* percentage was about the same as in our southern-Danish analyses from the Late Dryas period.

To summarize, it may be said that the late-glacial vegetation in Denmark differed on vital points from the conditions now prevailing in Arctic regions. The grass grew more luxuriantly, the ericaceous heaths were less frequent, and a plant community quite unknown in the Arctic region, with *Helianthemum*, *Hippophaë* and *Artemisia*, had made its appearance. It may therefore be questioned whether one is justified in using the apellation Arctic or sub-Arctic of late-glacial vegetation. The points of similarity with the Central-European alpine vegetation are in reality more prominent.

There is another question to be discussed in this connection. GAMS regards *Hippophaë* and *Artemisia* as steppe elements in the late-glacial vegetation, and he also interprets the high pollen percentages of *Gramineae* as an indication of a steppe-like vegetation. Gross (1937) likewise speaks of sub-Arctic steppe and forest-steppe in conjunction with late-glacial vegetation in East Prussia. There is also no doubt that there were certain analogies between late-glacial vegetation and steppe vegetation, just as there are certain botanic parallels to the much-discussed steppe animals (*Spermophilus rufescens*, Wild Horse, Bison and Irish Elk). All the same, the fact should not be overlooked that the points of resemblance with present-day East European steppe regions are not many in comparison with the profound climatic and botanic differences. Matters are different when we compare with the Central European glacial-age steppes, for here the similarity is beyond doubt as regards climate, flora and fauna. From this angle the view propounded by Gross and Gams has a certain justification. To avoid misunderstanding, however, one should always employ the term "sub-glacial" or "late-glacial" in connexion with steppe if the latter is used in conjunction with late-glacial conditions.

In Denmark the steppe elements were never so prominent as to provide reasons for preferring the term "late-glacial steppe" to "late-glacial tundra". Here it would be natural to introduce the term "park tundra" (or perhaps "bush tundra") for the curious open country that spread over immense regions at the close of the glacial age, and with its mixture of grassland and tree-islands provided ideal living conditions for the rich late-glacial fauna.

Summary.

Nine Bison finds have been made in Denmark; five of them are published here for the first time. An attempt is made to classify the material taxonomically and to date the six late-Quaternary finds pollen-analytically. Three of the Danish finds are inter-glacial, four may be dated to the late-glacial period (Late Dryas), and only one to the beginning of the post-glacial period (preboreal); the remaining find cannot be dated with certainty.

The pollen-analytical investigations show further that the late-glacial bisons lived in an open, park-like landscape where grassland mingled with willow scrub and a little birch forest in the favourable places. In certain important respects the late-glacial vegetation differed from that prevailing today in arctic regions, and it resembled the Central European alpine vegetation. Besides this it had a certain steppe-like character. There can be no doubt that the large herbivorous mammals lived under very favourable conditions in this "park tundra", which extended as a transitional belt several hundred kilometres wide between the tundra proper in the north and the woodland zone in the south (see Plate VII).

In recent years several authors have voiced the opinion that the difference between *Bison priscus* on the one hand and Bison *schoetensacki* and *Bison bonasus* on the other is chiefly caused by different ecological adaptations, *Bison priscus* is a steppe form, the other two are woodland animals. As the Danish late-Quaternary Bisons occured in an open country, (with Wild Horse, Elk, Reindeer, etc. see page 25), ecologically they are more closely related to *Bison priscus*. In the question of size, however, they are more like *Bison schoetensacki*. In comparison with *Bison bonasus*, both recent and sub-fossil, the Danish bisons must be characterized as very large. The measurements of the Baldersbrønde brain-case fall outside the variation limits of these animals, and only one animal is comparable with it, the specimen from Lund, Sweden. Accordingly, Danish bisons of the period after the Glacial Age are established as a separate sub-species: *Bison bonasus arbustotundrarum* subsp. nov. (cfr. diagnosis p. 30).

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Plate I. Table 2. Measurements of skulls.

Dimensions taken	Denmark						Sweden (subfossil)			Germany (subfossil)						
	Late- and postglacial				Inter-glacial											
	Baldersbrønde (Preboreal)	Mygdal (Late Dryas)	Mjang	Tranum (Late Dryas)	Egtved	Lysabil	Lund	Hagebyhøga	Mjølby	Hinterpommern (After Mertens)	Gallnauer See (After La Baume)	Osieczek (La Baume)	Gorrenschin (La Baume)	Strasburg, W. Pr. (La Baume)	Weichsel (La Baume)	B. b. major Hilzheimer
1. Postorbital constriction ..... (Width of frontals between orbits and horn-cores)	282	250	253	—	332	—	292	290	—	265	264	248	256	278	253	295
2. Width at rear of orbits	339	300	330	—	405	—	343	345	—	310	342	302	316	335	310	352
3. Width between bases of horn-cores, least	295	—	—	—	—	—	320	—	—	—	265	273	277	290	288	—
4. Width across forehead, middle	330	260	290	—	360	340	340	c. 320	c. 315	310	—	—	—	—	—	328
5. Width, greatest	367	—	—	—	—	—	348	—	—	—	327	315	337	345	310	—
6. From outside to outside of horn-cores, greatest.........	c. 870	—	625+	—	1050	—	840	—	—	780	670	—	620	710	690	695
7. Distance between tips of horn-cores	c. 850	—	—	—	990	—	830	—	—	—	635	—	600	680	670	650
8. Circumference at base of horn-core	320	240+	—	260+	345	385	300	285	280	290	240	230	220	255	240	288
9. Length along the anterior curve of horn-core	300	—	—	205	420	—	285	—	—	290	240	—	200	225	250	—
10. Length along the posterior curve of horn-core	380	330	220	—	520	—	355	330	330	360	300	—	230	280	300	333
11. Distance from tip of horn-core to base, straight line........	275	—	—	187	350	—	252	—	—	—	205	—	180	200	205	188
12. Greatest diameter of base of horn-core	100	—	73	93	109	—	103	—	—	—	—	—	—	—	—	89
13. Least diameter of base of horn-core	95	—	61	70	99	—	95	—	—	—	—	—	—	—	—	81
14. Basinasal bength .... (Distance from lower border of *foramen magnum* to rear of nasals)	253	—	—	—	—	—	275	—	—	—	276	262	(272)	264	267	—
15. Length from rear of occipital crest to rear of nasals	262	—	251	—	—	—	288	—	—	—	270	252	260	266	265	{275 282
16. Length from rear of base of horn-core to rear of orbita ..	170	—	—	—	197	—	167	—	—	—	167	137	148	163	148	—
17. Height of occipital crest, from lower border of *foramen magnum*	c. 140	—	—	—	—	—	—	—	—	—	153	140	150	152	144	—
18. Height of occipital crest, from upper border of *for. magnum*	96	—	—	—	—	—	105	—	—	—	110	107	113	118	107	—
19. Mastoid breadth	260	—	270	—	330	—	275	—	—	—	—	—	—	—	—	—
20. Distance between hinder-ends of temporal fossae.........	170	—	—	—	—	—	160	—	—	—	190	185	171	180	177	—
21. *Meatus acusticus*-breadth	250	—	—	—	340	—	260	—	—	—	273	242	255	262	253	—

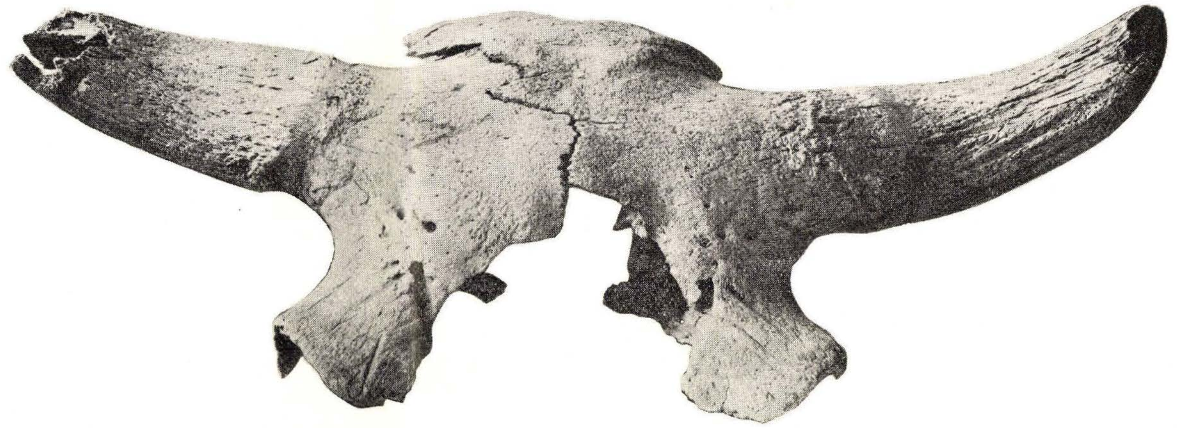
Dimensions taken	*Bison bonasus* (recent)									*Bison priscus*												*Bison schoetensacki*		B. b. mediator Hilzheimer
	No. 1870 (Tscherski)	Lithuania ♂ (La Baume)	Lithuania ♀ (La Baume)	Lithuania (La Baume)	After Allen ♀	After Allen ♂	After Allen ♂	After Allen ♂	After Allen ♂	Wiluiriver (Sibiria) (La Baume)	Wologda (Russia) (La Baume)	Rixdorf b. Berlin (La Baume)	Rhine (La Baume)	Vistula b. Kulm (La Baume)	Rondsen b. Graudenz (La Baume)	Marienburg (La Baume)	Lenzen b. Elbing (La Baume)	Irkutsk (Tscherski)	Jana (Tscherski)	After Pallas	Lutschka (Zool. Mus. Copenhagen)	Mauer ♂ (Freudenberg)	Mosbach ♂ (Freudenberg)	
1. Postorbital constriction ..... (Width of frontals between orbits and horn-cores)	253	271	217	262	206	270	245	231	267	323	292	(333)	283	294	—	—	—	290	321	306	305	—	—	—
2. Width at rear of orbits	323	335	278	343	230	310	328	310	312	367	344	—	353	350	—	—	—	355	379	369	360	—	—	—
3. Width between bases of horn-cores, least	266	296	226	(275)	—	—	—	—	—	374	376	335	343	305	(355)	—	—	—	—	—	—	—	—	—
4. Width across forehead, middle	—	—	—	—	205	278	282	230	270	—	—	—	—	—	—	—	—	338	328	300	370	300	340	310
5. Width, greatest	—	332	270	—	—	—	—	—	—	418	420	427	406	360	—	—	—	—	—	—	400	—	—	—
6. From outside to outside of horn-cores, greatest.........	—	650	455	—	395	647	622	—	560	—	—	1080	(1060)	1070	—	—	—	—	—	—	1220	—	—	—
7. Distance between tips of horn-cores	—	635	440	—	—	—	—	—	—	—	—	1010	—	1050	—	—	—	—	—	—	1070	870	870	700
8. Circumference at base of horn-core	—	255	175	(250)	178	240	242	—	200	—	310	380	305	315	350	350	320	—	—	—	430	—	—	348
9. Length along the anterior curve of horn-core	—	195	135	—	—	—	—	—	—	—	390	470	445	460	—	(300)	450	—	—	—	520	255	—	—
10. Length along the posterior curve of horn-core	—	225	145	—	153	190	230	—	270	—	470	530	530	495	—	(340)	520	—	—	—	620	—	—	329
11. Distance from tip of horn-core to base, straight line........	—	180	125	—	127	177	—	—	240	—	330	375	400	415	—	(290)	375	—	—	—	430	—	—	230
12. Greatest diameter of base of horn-core	—	81	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	143	118	110	105
13. Least diameter of base of horn-core	—	77	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	129	98	100	96
14. Basinasal bength .... (Distance from lower border of *foramen magnum* to rear of nasals)	—	279	235	274	—	—	—	—	—	285	300	—	292	276	—	—	—	—	—	—	296	—	—	—
15. Length from rear of occipital crest to rear of nasals	—	275	234	265	208	285	257	250	265	284	306	—	284	273	—	—	—	—	—	—	315	—	—	—
16. Length from rear of base of horn-core to rear of orbita ..	151	166	145	162	—	—	—	—	—	191	188	—	190	183	—	—	—	195	226	195	215	—	—	—
17. Height of occipital crest, from lower border of *foramen magnum*	129	152	121	146	—	—	—	—	—	152	165	—	160	168	162	—	—	—	—	—	180	—	—	—
18. Height of occipital crest, from upper border of *for. magnum*	—	114	85	122	—	—	—	—	—	118	123	—	128	135	119	—	—	—	—	—	—	—	—	—
19. Mastoid breadth	245	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	276	300	295	291	—	—	—
20. Distance between hinder-ends of temporal fossae.........	—	204	150	168	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21. *Meatus acusticus*-breadth	238	278	213	268	193	254	258	240	245	295	292	—	285	300	305	—	—	293	318	293	292	—	—	—

Plate II.

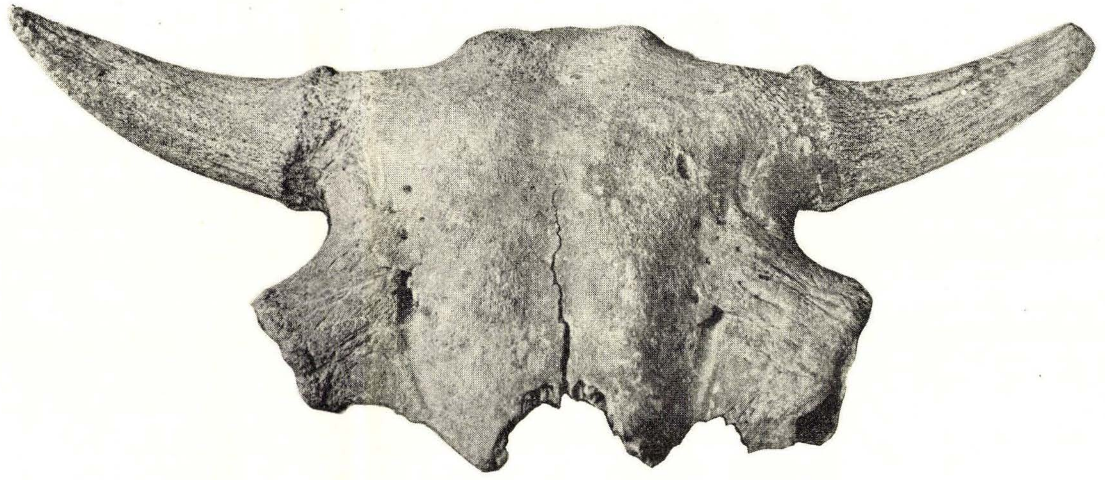
Bison priscus. Skull from Egtved. Interglacial time. Frontal view.
× 1/8. U. Møhl-Hansen phot.

Plate III.

Skull of *Bison bonasus arbustotundrarum* subsp. nov. Type. From Baldersbrønde, Zealand. Preboreal time. Frontal view. × 1/4. U. Møhl-Hansen phot.



Skull of Bison from Mygdal. Late Dryas. Frontal view. × 1/4. U. Møhl-Hansen phot.



Skull of Bison from Mjang. Frontal view. × 1/4. U. Møhl-Hansen phot.

Plate IV. Bog near Akkerup, Funen.

The diagram is divisible into four parts, all of which correspond, however, analysis by analysis. The basis of calculation for all the pollen curves is the total pollen of the trees and the shrubs, the anemophile herbs and the *Ericales* (including *Empetrum*).

A. This part of the diagram shows the proportions between the pollen of the above three categories, the pollen of trees and shrubs (white area) representing forest and scrub, the herb pollen (hatched area) grassland, and *Ericales* pollen (stippled area) the oligotroph heath (*Empetrum-Vaccinium* heath). The curves for birch (including *Betula nana*), pine and willow are inserted on the left, and together they form the collective curve for trees and shrubs.

B. Contains the curves or silhouettes for the more important anemophile herbs and for *Empetrum*.

C. Silhouettes for *Hippophaë*, *Helianthemum* and *Selaginella*, which are not included in the pollen total that forms the basis of calculation.

D. The hatched area represents the percentage of rebedded pollen (cfr. footnote page 42). Here the basis for the calculation of the percentages is the total pollen sum, the rebedded pollen in this case being — exceptionally — included.

n Pollen total (rebedded pollen subtracted).

N Pollen total (rebedded pollen included).

On the extreme left is the zonal division according to KNUD JESSEN's system (l. c. 1935). I Early Dryas, II Allerød, III Late Dryas, IV Pre-boreal.

Plate IV.

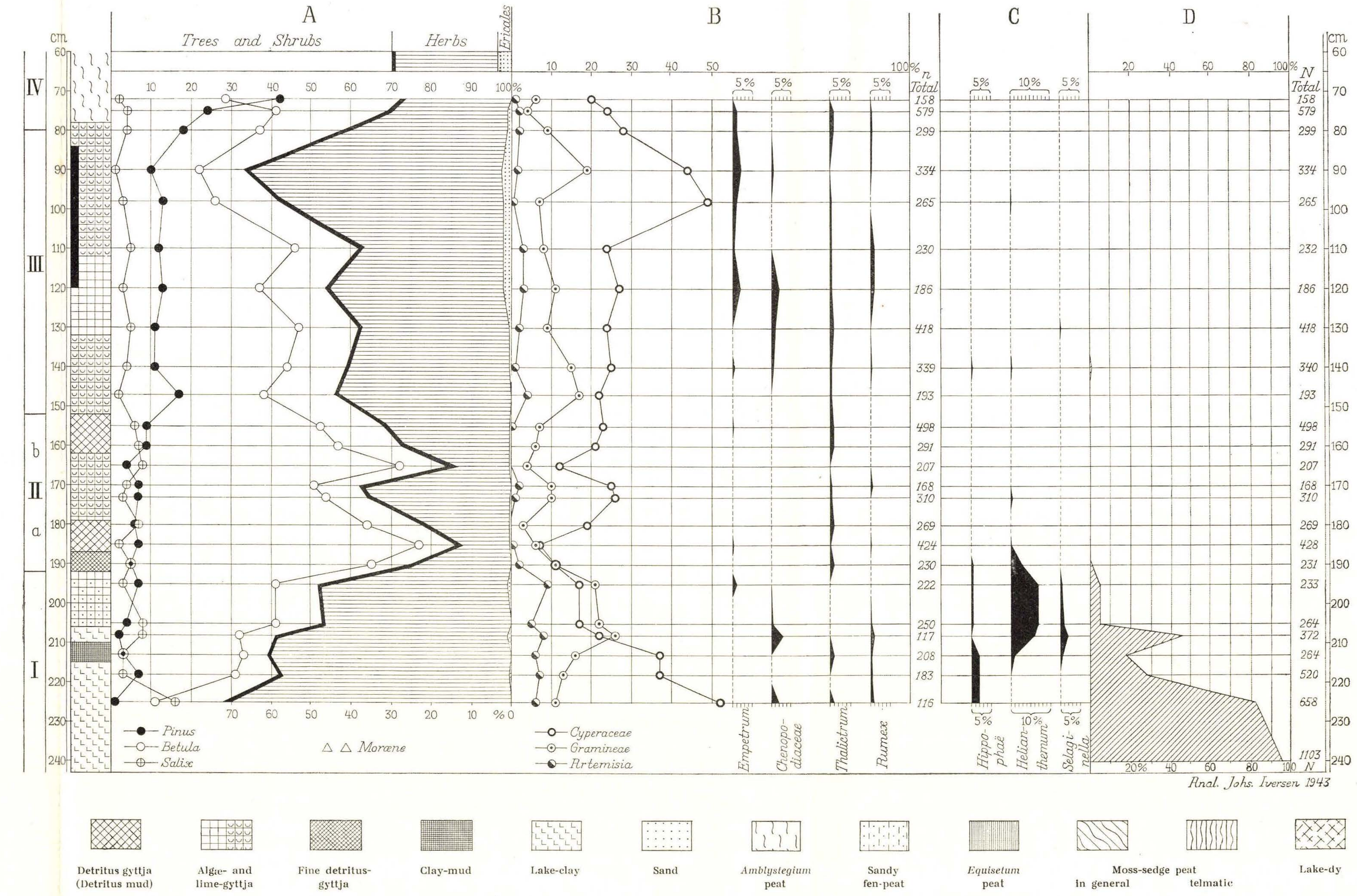


Plate V. Bog near Harndrup, Funen.

See explanations to Plate IV.
C. Silhouette for *Dryopteris Linnaeanum.*
E. Number of tree pollen (*Betula* + *Pinus* + *Salix*) per slide.

Plate V.

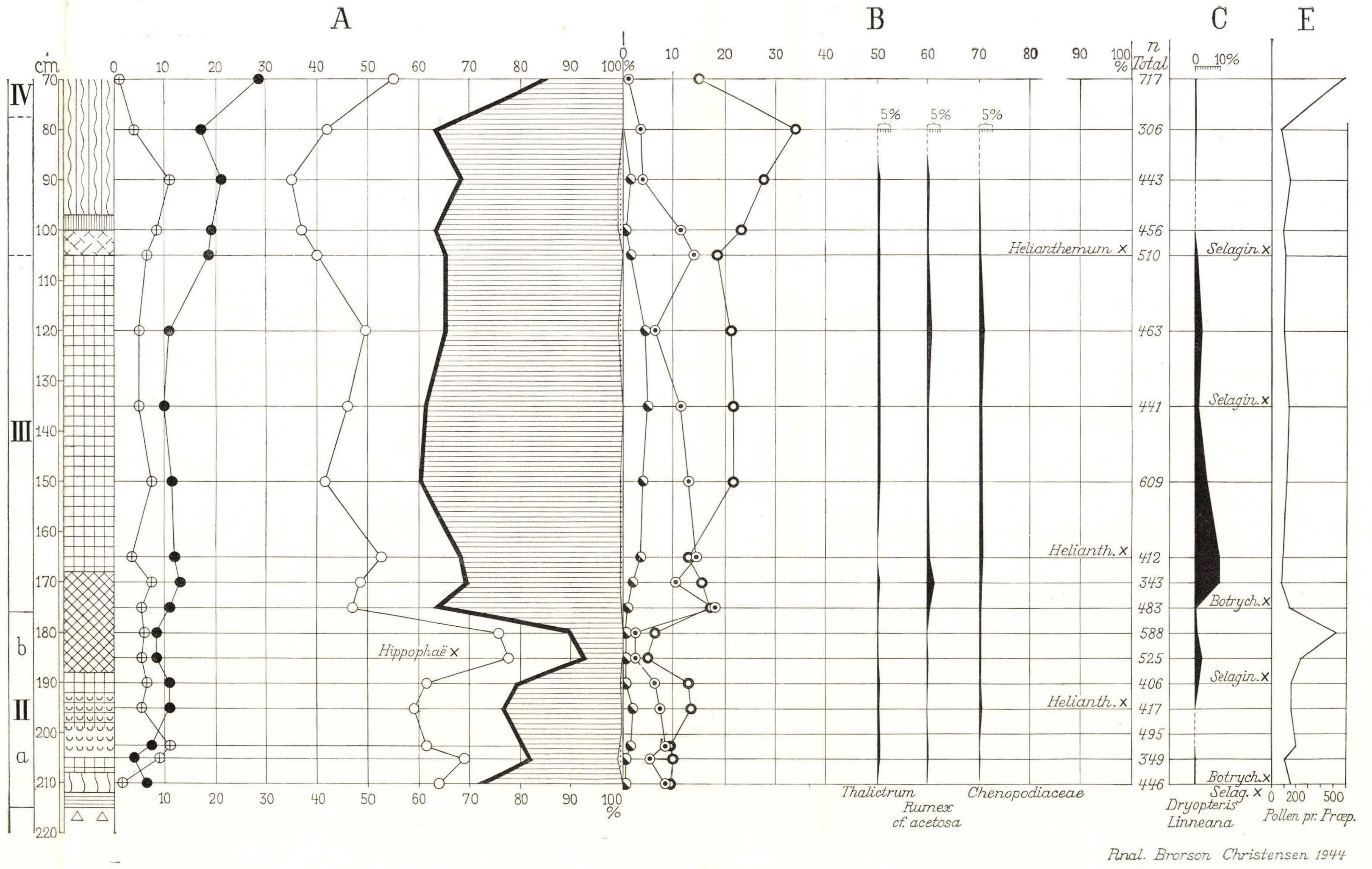


Plate VI. Bog near Tranum, Han Herred (North Jutland).

See explanations to Plate IV.

C. Silhouettes for *Botrychium*, *Equisetum* and *Dryopteris Linnaeanum*.

Below the diagram is an analysis from the Bison vertebrae (cfr. Table 3 Nos. 7 + 8); on the diagram it must be placed at the point shown by the arrow. At the bottom is an analysis from the find-spot of the Bison.

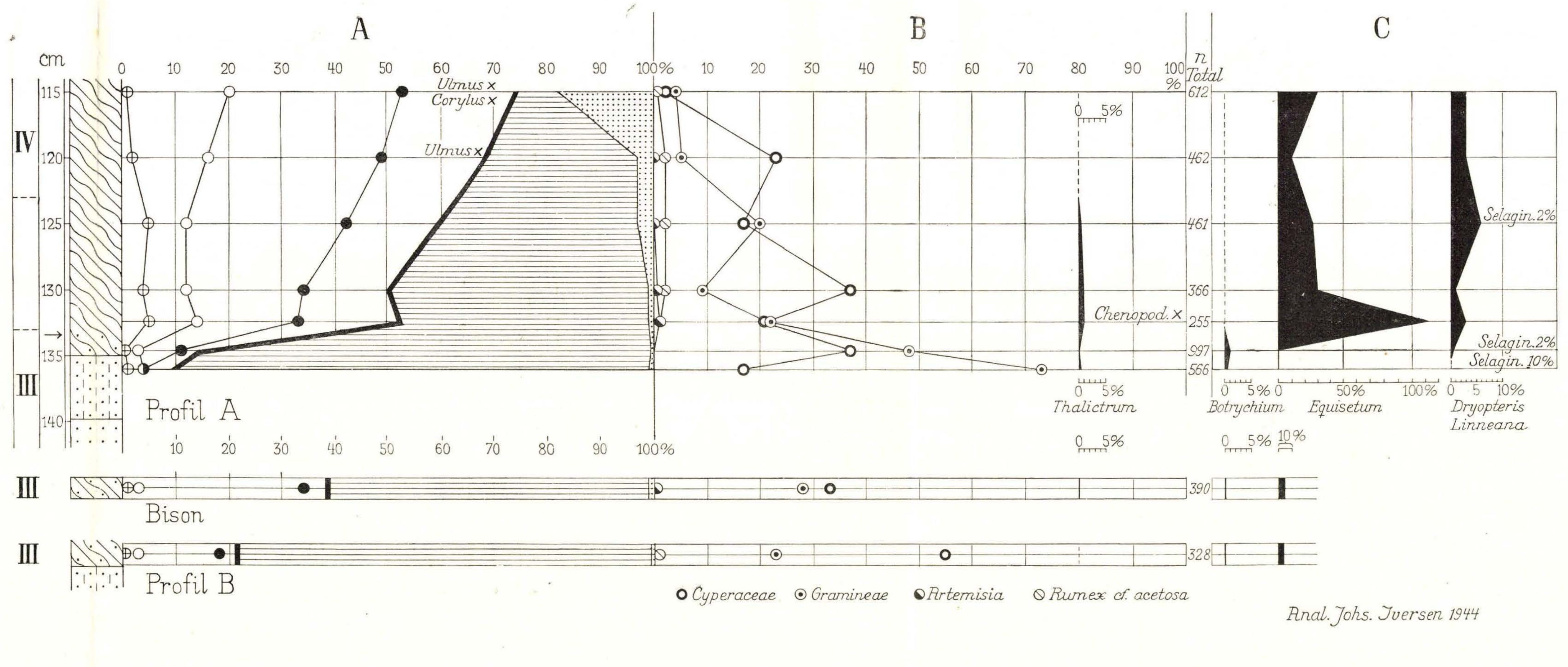


Plate VII.

The plate provides a scheme of the late-glacial vegetal development in different parts of Denmark and in Holstein.

Plate VII.

<table>
<tr><th colspan="2">Zones</th><th rowspan="2">Climatic periods</th><th colspan="5">Development of vegetation</th><th colspan="2">Land mammals</th></tr>
<tr><th>Holstein (Schütrumpf 1943)</th><th>Denmark (K. Jessen 1935, Iversen 1942)</th><th>Holstein (Hamburg)</th><th>Bornholm</th><th>Funen, Zealand</th><th>Bølling Lake (Mid Jutland)</th><th>Northernmost Jutland</th><th>Denmark</th><th>Holstein (Ahrensburg- and Meiendorf-Cultures)</th></tr>
<tr><td rowspan="2">VI
V</td><td rowspan="2">IV</td><td rowspan="2">Pre-boreal</td><td>Pine forest</td><td rowspan="2">Birch-pine forest</td><td rowspan="2">Birch-pine forest</td><td rowspan="2">Birch forest</td><td rowspan="2">Birch forest</td><td rowspan="2">Aurochs, elk, bison, reindeer, brown bear</td><td rowspan="2"></td></tr>
<tr><td>Birch-pine forest</td></tr>
<tr><td>IV</td><td>III</td><td>Late Dryas Period</td><td>Park tundra</td><td>Park tundra</td><td>Park tundra</td><td>Tundra or Park tundra</td><td>Tundra</td><td>Wild horse —
Bison, reindeer, wolf, alpine hare, field mouse, Spermophilus rufescens, Lagomys</td><td>Reindeer, wild horse, bison, elk, beaver, wild boar, hare, Lemmus lemmus, field mouse, wolverine, Vulpes sp., Lynx, Desmana mochata</td></tr>
<tr><td rowspan="3">III</td><td rowspan="3">b
II
a</td><td rowspan="3">Allerød oscillation</td><td rowspan="3">Birch-pine forest</td><td>Birch-pine forest</td><td>Birch forest</td><td rowspan="3">Park tundra</td><td rowspan="3">Park tundra</td><td rowspan="3">Elk, beaver, brown bear, Irish elk, wolverine</td><td rowspan="3"></td></tr>
<tr><td rowspan="2">Park tundra</td><td>Park tundra</td></tr>
<tr><td>Birch forest</td></tr>
<tr><td rowspan="2">II</td><td>I c</td><td>Earlier Dryas Time</td><td rowspan="2">Park tundra</td><td rowspan="2">Tundra</td><td rowspan="2">Tundra</td><td>Tundra</td><td rowspan="2">Tundra</td><td rowspan="3">Reindeer</td><td rowspan="2"></td></tr>
<tr><td>I b</td><td>Bølling oscillation</td><td>Park tundra</td></tr>
<tr><td>I</td><td>I a</td><td>Earliest Dryas Time</td><td>Tundra</td><td>Ice?</td><td>Ice?</td><td>Tundra</td><td>Ice?</td><td>Reindeer, wild horse, Spermophilus rufescens, Lemmus lemmus, hare, wolverine, Vulpes sp.</td></tr>
</table>