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LATE WISCONSIN WOODLAND MUSK OXEN IN ASSOCIATION WITH POLLEN AND INVERTEBRATES FROM MICHIGAN

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ABSTRACT—Examination of 2 *Symbos* skulls, from 2 new localities, indicates that *Symbos* and *Ovibos* had long independent histories. Cranial and post cranial elements indicate that *Symbos cavifrons* was taller and more slender than *Bison bison*. Mollusks associated with the White Pigeon specimen indicate permanent ponded water. The pollen spectrum from the Scott's specimen shows a dryer and possibly warmer climate than either spruce maximum or present Michigan climate. The White Pigeon spectrum suggests a more moist and cooler climate. Spectra imply different ages for the specimens and reaffirm a woodland situation for *Symbos cavifrons*, the woodland musk ox. A radio carbon date of 11,100±400 years BP was obtained for the Scotts specimen.

INTRODUCTION

IN AUGUST, 1961, parts of the skeleton of a woodland musk ox were recovered from a calcareous peaty silt in an excavation for a swimming pool near Scotts, Kalamazoo County, Michigan. In August of the following year a skull and tibia of a woodland musk ox were collected from excavations in Marl Lake near White Pigeon, St. Joseph County, Michigan. Sediment samples obtained from the brain cavities, sinuses, and foramina of the 2 skulls proved to be rich in pollen. Also, fossil invertebrates were collected from matrix adhering to both specimens. Therefore, the pollen and invertebrates can be assumed to be contemporaneous, or nearly so, with the skulls.

The purpose of this report is to record the 2 additional localities; figure and describe a complete skull of *Symbos cavifrons* (Leidy), the woodland musk ox; and give a more complete picture of the environment of the woodland musk ox as interpreted from associated pollen and invertebrates. The section in which the localities are described and the osteology discussed is the work of H. A. Semken. The discussion of the fossil mollusks and pollen is by B. B. Miller and J. B. Stevens, respectively.

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MUSK OXEN IN MICHIGAN

Bootherium sargenti Gidley was described from Muskegon County, Michigan (J. W. Gidley, 1908). To this date no additional specimens of *Bootherium* have been identified from the state. The barren ground musk ox, *Ovibos moschatus* (Zimmermann), is still unknown from Michigan, but specimens have been recorded in Ohio and Indiana to the south (Hay, 1923); in Pennsylvania and New York to the east (Kitts, 1953); in Ontario, Canada, to the north (Bensley, 1923); and in Minnesota and Iowa to the west (Hay, 1923). Therefore, *Ovibos* is to be expected in Michigan. Kitts (1953) plotted the distribution of Recent and Pleistocene musk oxen in North America.

The woodland musk ox, *Symbos cavifrons* (Leidy) originally was recorded from Michigan by E. C. Case (1915, 1921) and subsequent specimens were reported by Hibbard and Hinds in 1960. Benninghoff and Hibbard (1961) elaborated on fossil pollen associated with one of the specimens.

Recorded occurrences of *Symbos cavifrons* and *Bootherium sargenti* in Michigan are listed below and are shown in text-figure 1. Undoubtedly, many other musk ox specimens have been found in Michigan but not reported. Because of the size of their post cranial elements, they probably have been considered remains of moose, elk, or domestic animals (Hibbard and Hinds, 1960).

Genus BOOTHERIUM Leidy, 1852
BOOTHERIUM SARGENTI Gidley, 1908

Locality B—Muskegon County, 3 miles NE of Mooreland, NW¼ Sec. 16, T. 10 N, R. 14 W, 2–3 feet deep in a marsh on the farm of Charles McKay, upper portion of a skull with horn cores. The specimen was described by James W. Gidley (1908) and is preserved in the Museum of

Natural History at Grand Rapids, Michigan (text-fig. 1, loc. B).

The genus *Bootherium* has a long and turbulent history since the discovery of *Bootherium bombifrons* (Harland) at Big Bone Lick, Kentucky. No specimen, other than the type, was known until 1908 when *B. sargenti* was described from Michigan. Barbour (1931) recorded a (?) *Bootherium* from Douglas County, Nebraska, and Peterson (1926) discussed a *Bootherium* (very likely *Symbos*) from Frankstown Cave, Blair County, Pennsylvania. Since the discovery of *B. bombifrons*, there have been proposals that *Bootherium* was the female of *Symbos*. Osgood (1905) summed up the arguments and concluded that *Bootherium* could not be considered the female of *Symbos*. Allen (1913) agreed with Osgood. In 1960 Hibbard and Hinds again suggested that *Bootherium* was the female of *Symbos*.

After a review of the literature there can be little doubt that *Bootherium bombifrons* represents a genus distinct from *Symbos*. However, *B. sargenti*, the specimen examined by Hibbard and Hinds (1960), may be a female *Symbos*. The horn cores of *B. sargenti* overlap the frontals as in *Ovibos* and do not stand out on pedicels or have a burr on the core as in *B. bombifrons*. The skull of *B. sargenti* is elevated but appears intermediate between the *Bootherium* and *Symbos* condition. The horn cores do not drop abruptly downward as in *Ovibos*, but slope forward and downward as in *Symbos*. Unfortunately, the diagnostic basicranial region of *B. sargenti* is missing and therefore it is impossible to establish its generic relation. Allen (1913, p. 215) came to the same conclusion. Hay (1923, p. 251) objected to this after he examined more than 25 skulls of *S. cavifrons* and concluded that some of them must have been females.

Genus SYMBOS Osgood, 1906

SYMBOS CAVIFRONS (Leidy), 1852

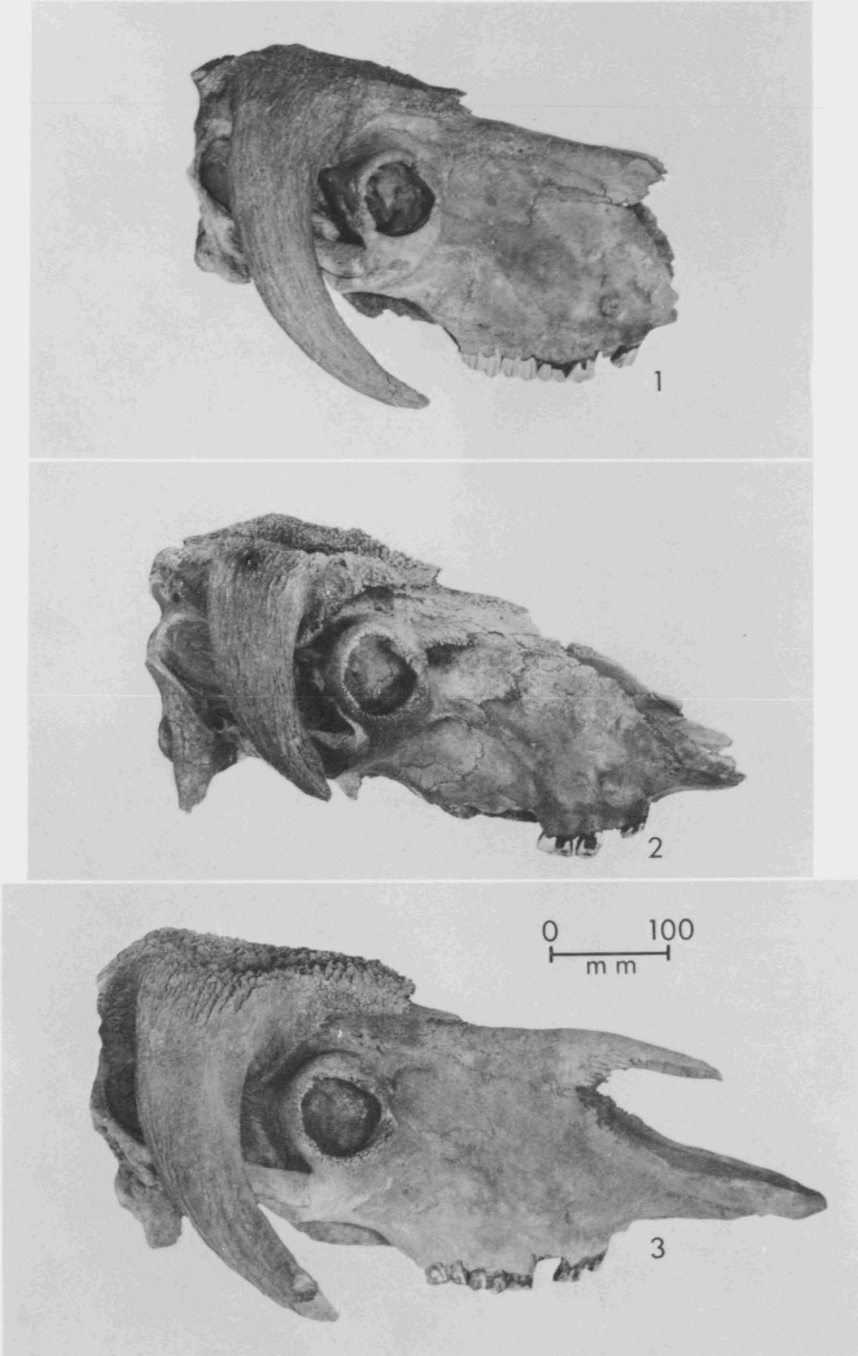
Specimens of the woodland musk ox from Michigan are listed in order of discovery.

Locality 1—Washtenaw County, ½ mile NW of Manchester, Sec. 1, T. 4 S, R. 3 E, recovered 4 feet below surface while excavating a drain through a bog in 1915 on the farm of Mr. William J. Schlicht. Skull with the region anterior to P^2 missing, University of Michigan Museum of Paleontology, hereafter UMMP 3450

EXPLANATION OF PLATE 129

Symbos cavifrons (Leidy)

FIG. *1*—Manchester specimen, UMMP 3450.
2—White Pigeon specimen.
3—Scotts specimen, KPM A2146 61: 379.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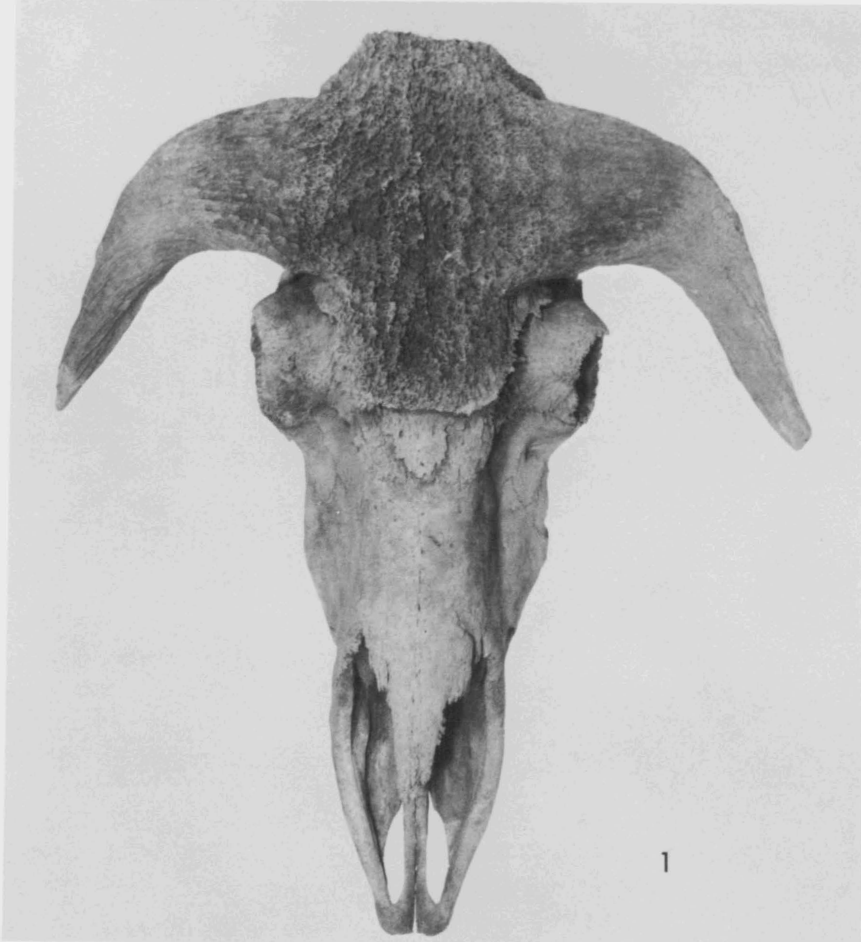
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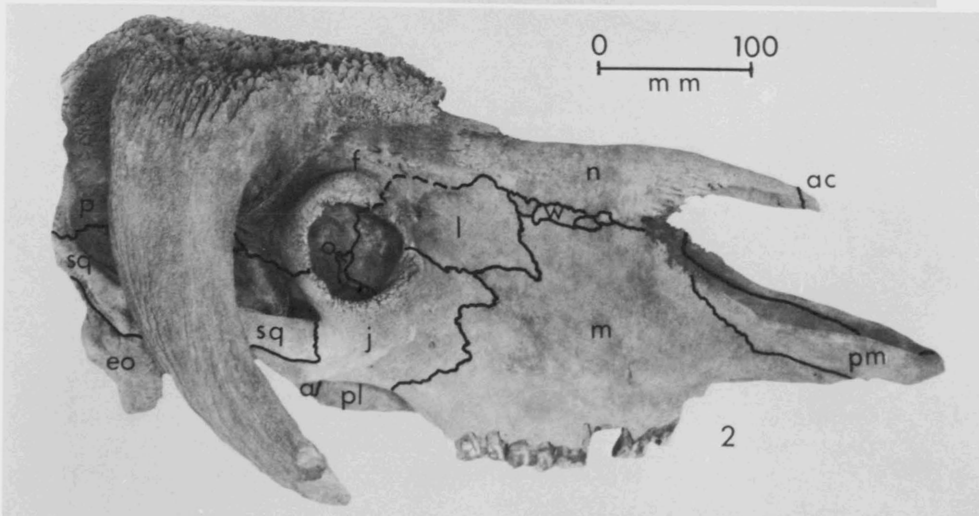


2

(Pl. 129, fig. 1). Reported by E. C. Case (1915, 1921) and by Hay (1923, p. 250), who corrected the location cited by Case (1915).

Locality 2—Hillsdale County, 2 miles S of Hillsdale, T. 7 S, R. 3 W, in a drainage ditch through a bog, collected in 1919. Complete set of horn cores, without frontals and parietals, UMMP 10567.

Locality 3—Van Buren County, ½ mile NE of Paw Paw, N½ NW¼ Antwerp Township, T. 3 S, R. 13 W, collected from a "marl" pit on the Max Schwanke farm in 1942. Posterior part of a weathered skull, UMMP 23113.

Locality 4—Kalamazoo County, 4 miles SE of Climax, 1 mile NE of Scotts, SE¼ Sec. 18, T. 3 S, R. 9 W, 4–6 feet below surface in a "marl" pit, collected in 1956. Atlas, axis, and third cervical vertebra, UMMP 34124. Reported by Hibbard and Hinds (1960), and Benninghoff and Hibbard (1961). The third cervical was dated by radio carbon at 13,200 ±600 BP by the University of Michigan Memorial Phoenix Project Laboratory. Gift of Ray Coville. This locality is approximately 1½ miles NE from the new locality immediately below.

Locality 5—New specimen, Kalamazoo County, ½ mile S of Scotts, Sec. 25, T. 3 S, R. 9 W, recovered by a dragline from a "marl" deposit in August 1961 by Ralph D. Stuble, Jr. and donated by him to the Kalamazoo Public Museum (KMP). Skull, scapula, 2 thoracic vertebrae, 2 lumbar vertebrae, 1 ulna-radius, 1 tibia, 1 right mandible fragment, 1 sternal rib and the epiphysis of a femur, KPM A 2146 61:379 (Pl. 129, fig. 3; Pl. 130, figs. 1,2). Fossil pollen and invertebrates associated. The fourth lumbar vertebra from this individual was submitted to the University of Michigan Memorial Phoenix Project Laboratory, was numbered M-1402, and dated at 11,100 ±400 BP.

Locality 6—New specimen, St. Joseph County, 3 miles SE of White Pigeon, Sec. 17, T. 8 S, R. 11 W. Recovered from beneath Marl Lake by a dragline on the property of Mr. Ray Yoder on August 2, 1962. Skull with premaxillaries missing, the left side of the face was damaged by the dragline (Pl. 129, fig. 2). Mr. Yoder had not donated this specimen to a museum at publication time, so no number is available. Fossil invertebrates and pollen associated.

Explanation of Plate 130

Scotts specimen, KMP A2146 61: 379

Fig. *1*—Dorsal view.

2—Lateral view. a, alisphenoid; ac, accessory; eo, exoccipital; f, frontal; j, jugal; l, lacrymal; m, maxillary; n, nasal; o, orbitosphenoid; p, parietal; pl. palatine; pm, premaxillary; sq, squamosal; w, wormian.

Literature on *Ovibos* is immense and anatomical comparisons of musk oxen, principally *Ovibos* with sheep, cattle, and to a lesser extent antelopes, are concerned with discussions of the affinities of musk oxen. However, *Symbos* is known from fewer than 50 localities (Kitts, 1953) and most of these specimens are fragmentary. Therefore, the woodland musk ox is not well described. Osgood (1905) gives a description of a fairly complete skull from the Yukon Territory of Canada and compares it with *Ovibos* in detail and with *Bison* in a lesser degree.

TEXT-FIG. *1*—Distribution of musk oxen in Michigan. *B*, *Bootherium*. *1–6*, *Symbos*.

TABLE *1*—MEASUREMENTS OF *Symbos Cavifrons* (mm.)

	Manchester UMMP 3450	Scotts, KPM A2146:369	White Pigeon No Number	Hillsdale UMMP 10567	Paw Paw UMMP 23113	Recent *Ovibos* UMMZ 102446
Maximum length	—	631	—	—	—	477
Mastoid width	190	192	201	—	183	163
Width across orbits	249	273	—	—	—	257
Zygomatic width	224	247	—	—	—	183
Basal length	—	581	—	—	—	444
Inferior lip foramen magnum to M^3 alveolus	252	251	—	—	—	203
Width of orbits	58	62	60	—	—	52
Basioccipital width	78	77	79	—	85	61
Exostosis length	273	295	277	269	255	189
Exostosis width anterior to horn core	124	127	118	120	132	—
Horn core diameter, horizontal	120	156	131	130	117	—
Horn core diameter, vertical	93	89	84	83	79	—
Width between horn core tips	600	590	560	—	—	—

Cranial elements—The Scotts specimen, Kalamazoo Public Museum no. A 2146:379 is shown in Plate 129, fig. 3; Plate 130, figs. 1,2; Plate 131, fig. 1; and in Plate 132, and is the basis of the following description.

The overall cranial aspect of *Ovibos* has been given by Lonnberg (1900), Osgood (1905), and Allen (1913). The following criteria, taken from these reports and available specimens, readily serve to distinguish *Ovibos* from *Symbos* on gross cranial anatomy: (1) orbits of *Symbos* do not extend laterally over the zygomatic arch, (2) skull of *Symbos* is deep, longer and narrower then *Ovibos*, (3) exostoses of *Symbos* meet across the top of the frontals, a narrow trough separates the exostoses in the midline of *Ovibos*, (4) horn cores of *Symbos* curve forward and downward at the base, the forward curve is much less developed in *Ovibos*, (5) basioccipital of *Symbos* is entirely divided by a deep median groove, the median groove of *Ovibos* contains a median ridge which obliterates the groove posterior to the anterior muscular fossae, and (6) bullae of *Symbos* form a sharp ridge and are not inflated, the bullae of *Ovibos* are inflated. Table 1 gives the cranial measurements taken on the Michigan specimens.

The purpose of the following description is to add to the data from a study of Michigan *Symbos* specimens in relation to *Ovis canadensis* (bighorn sheep), *Bison bison*, and *Ovibos moschatus* and to bring together some salient remarks from the literature on the comparative cranial osteology of musk oxen, sheep, and cattle.

The premaxillary borders the maxillary anteriorly and dorsally but does not come into contact with the nasal. The premaxillary comes relatively nearer the nasal in *Ovibos* than in *Symbos*. The gap is approximately 40 mm. in *Symbos* and 20 mm. in *Ovibos*. *Ovibos* resembles *Ovis* and *Symbos* resembles *Bison* in this respect. However, the maxillary—premaxillary suture of *Ovis* is directed more nearly vertically owing to a shorter predental portion of the maxillary. The maxillary process of the premaxillary gradually slopes up to the nasal region in *Ovibos* and *Bison*. In *Symbos* this process tends to parallel the palatine surface and then rises toward the nasals at a definite point of inflection. The palatine process of the premaxillary abuts the vomer and maxillary on the palate.

The maxillary borders the lateral portion of the nasals dorsally, the lacrymal and jugal posteriorly, and the palatines on the palate. Large wormian bones are present between the nasals and maxillaries on all specimens of *Symbos* examined. Small wormian bones were observed in all maxillary contacts. Wormian bones are common in *Symbos*, less common in *Ovibos*, and rare in *Ovis* and *Bison*.

The lacrymal occupies about $\frac{1}{4}$ of the orbit, is quadrate, contains a lacrymal fossa, and forms a large part of the facial region in both musk oxen. The lacrymal of *Ovis* and *Bison* is long, slender, forms a small segment of the orbit, and has no lacrymal fossa. The lacrymal fossa of *Symbos* is deep, occasionally paired, and has a strong, rugose dorsal shelf. The degree of rugosity is quite variable but always evident in relation to *Ovibos*. Osgood (1905, p. 175) stated "Lacrymal fossae about the same depth as in *Ovibos* but the shelves above them, instead of being at right angles to the axis of the skull run diagonally from the orbits to the frontals. . . ." The diagonal nature of the shelves is obvious in most specimens of *Symbos.* In the orbit the lacrymal joins the frontal dorso-posteriorly, the perpendicular part of the palatine and orbitosphenoid posteriorly, and the jugal ventrally. The large lacrymal bulla or protuberance of *Symbos* is angular in ventral aspect as in *Ovis.* This is opposed to a rounded lacrymal bulla in *Ovibos* and *Bison.* The jugal forms the lower half of the orbital tube, unites posteriorly and dorsally with the frontal, anteriorly and dorsally with the lacrymal, anteriorly with the maxillary and posteriorly with the zygomatic process of the squamosal. The squamosal-jugal suture forms a right angle on the zygomatic arch. In *Ovis* and *Bison* this suture is an inclined plane. Osgood (1905) mentioned a tendency for a secondary fossa just below the prominent lacrymal fossa and immediately in front of the rim of the orbit. The specimens observed have this slight secondary "lacrymal" fossa on the jugal and not on the lacrymal. The suture between the lacrymal and the jugal usually is fused and impossible to trace.

The jugal of *Ovibos* is swollen in the orbital region and is filled with sinus cavities. This condition does not exist in *Symbos.* The zygomatic process of the jugal lies below the glenoid fossa in both musk oxen and is level with the glenoid in *Ovis* and *Bison.*

Case (1915) mentioned a large cavity in the left cheek just below and anterior to the eye and concluded that the animal suffered a severe injury in combat. The Scotts specimen has a similar, but much smaller, injury in the same general position.

The squamosal is a large, heavy bone with a broad, flattened glenoid fossa and a prominent perpendicular post glenoid process. This arrangement is distinct from a more rounded glenoid of *Ovis* and *Bison.* The wings of the sphenoid rise abruptly from the glenoid region, separated from the glenoid by a small shallow groove. A deep broad groove divides these features in *Ovis* and *Bison. Symbos* has a much larger pterygoid crest than *Ovibos.* The squamosal extends posteriorly and forms, a heavy rugose ridge connecting the superior nucal line and the paramastoid process. The mastoid process is fused into the complex and therefore is not identifiable. Dorsally, the parietal-squamosal suture parallels the glenoid surface.

The petrosal of *Symbos* has a hook-like appearance, uninflated bulla, a blade-like muscular process, and a large external auditory meatus. *Ovibos* has an inflated bulla, a rod-like muscular process, and a more posteriorly deflected meatus. The muscular process of the sheep is blade-like, similar to *Symbos*, and rod-like in *Bison*, which is similar to *Ovibos.*

The petrosal of both musk oxen is more firmly anchored to the skull than in *Ovis* but is not completely fused to the squamosal as in *Bison.* The bulla of *Bison* is much larger and more inflated than in *Ovis* or *Ovibos.*

The exoccipitals of both musk oxen are massive and connected to the paramastoid process by a long shallow groove. The groove is much more pronounced in *Ovis* and very strong in *Bison.*

The basioccipital of both musk oxen resembles *Ovis* in its quadrate outline and in the presence of anterior muscular impressions. These impressions aremuch larger in the musk oxen and are not laterally placed or on ridges as in *Ovis.* This muscular area is represented by a tuberosity on the more conical basioccipital of *Bison.* The basioccipital of *Symbos* is divided by a deep median groove, is recilinear posteriorly and tapers medially in the muscular region. In *Ovibos*, the groove is shallow and contains a median ridge which frequently obliterates the groove posterior to the muscular impressions. Also, the *Ovibos* basioccipital is more quadrate than in *Symbos* and the median taper is more direct.

The basisphenoid is fused to the basioccipital and marked by a dorso-ventral angularity which declines from the basioccipital at approximately 33° in *Symbos*, 25° in *Ovibos*, 20° in *Ovis*, and 17° in *Bison.* The vomer overlaps the basisphenoid in *Symbos* and *Bison* but only reaches the presphenoid of *Ovibos* and *Ovis.*

The pterygoid of both musk oxen resembles a parallelogram with a hook, the hamular process, on that anterior-ventral border. The pterygoid of *Ovis* is archuate to hour glass-shaped. *Bison* has a large ventrally fan-shaped pterygoid.

The vomer of *Symbos* forms a broad shallow groove as opposed to a deep narrow groove in *Ovis* and *Bison.* The vomer of *Ovibos* is intermediate between *Symbos* and *Bison.*

The perpendicular portion of the *Symbos* palatine diverges from the palate forming a broad flaring choane, which converges again in the sphenoid region. In *Ovibos* the sphenoid and the palatines are in line and form a more rectilinear pattern. The perpendicular portion of the palatine is exposed in the orbit as a club-shaped bone in *Symbos.* In *Ovibos* and *Ovis* this projection reaches only the lower anterior portion of the orbit and is pointed, not club-shaped. The secondary palate posterior to M^3 is much longer in *Symbos* than in *Ovibos.* The anterior border of the internal choane is 40.0 mm. posterior to a point on the midline opposite the posterior border of the 3rd molars loop in *Symbos*, 15 mm. in *Ovibos*, and 20 mm. in *Bison*. The choane of *Ovis* is even with or anterior to the posterior loop of M^3.

The nasals, frontals, and parietals have been given attention by Lonnberg (1900), Osgood (1905), and Allen (1913). Most of their discussion has been devoted to the position, character, and development of the horns and horn cores. In review, the following points are characteristic of the skull roof: the nasals, frontals, and parietals are flat on the dorsal surface and are in the same plane, as in *Bison;* the frontals of *Ovis* are arched into a transverse ridge or "Knickung" which bears the horn cores; the horn cores of the musk oxen originate on the frontals and fan out over the frontals and parietals. *Ovibos* is easily distinguished from *Symbos* by the exposure of the frontals between the exostoses of the horn cores. The exostoses form a solid roof in *Symbos*. The horn cores of *Bison* are formed on a pedicel and are on the posterior corners of the skull.

The nasals of *Symbos* are strongly arched in the transverse plane and thus give a deep appearance to the facial region. *Ovibos*, *Ovis*, and *Bison*, have low, flat nasals. An accessory bone, anterior to the nasals, is common in *Symbos*, but usually is missing or fused in *Ovibos*.

The teeth of *Symbos* are larger, more quadrate, and have less developed labial costae than *Ovibos*. The labial costae of *Ovibos* are strongly developed and the posterior loop (costae) fits into a depression in the tooth directly to the rear. Frequently, the posterior loop of the *Ovibos* M^1 is not well developed and thus the depression is absent on M^2. The posterior loop of the premolars and molars of *Symbos* is very small and consequently there is no corresponding depression. The enamel, however, markedly thins where the teeth come into contact. Musk oxen dentition is similar to that of *Bison* except that the accessory cusp (lingual) is large in *Bison* and very small or absent in *Ovibos*. None of the *Symbos* specimens examined show any evidence of any accessory cusp. Depressions for posterior loops are not found in *Bison* or *Ovis*. Plate 131 illustrates the dentition of *Symbos;* measurements are in table 2.

Post-cranial elements—A number of post-cranial elements, listed with the locality data, were found associated with the Scotts specimen. Since post-cranial material of *Symbos* is not well known, the following descriptions and Plate 132 will aid in identification of isolated elements. Post-cranial elements of the musk ox from Frankstown Cave may belong to either *Bootherium* or, more likely, *Symbos* (Peterson, 1926).

TABLE 2—DENTAL MEASUREMENTS
Symbos cavifrons (mm)

		Manchester UMMP 3450	Scotts, KPM A2146:369	White Pigeon No number	Recent Ovibos 102446 UMMZ
Length upper tooth row		164	155	—	135
Length	PM^2	21	22	21	18
	PM^3	21	23	—	20
	PM^4	23	22	23	20
	M^1	28	26	32	23
	M^2	34	34	—	28
	M^3	41	40	—	33
Width	PM^2	19	20	22	16
	PM^3	24	26	—	17
	PM^4	26	26	28	22
	M^1	27	26	31	21
	M^2	28	28	—	20
	M^3	28	31	—	19

The tibia of *Symbos* (Pl. 132, fig. 1) is longer and more slender than *Bison*, and very similar in shape to *Ovibos* and *Ovis*. The medial malleolus usually terminates equal with or proximal to the lateral malleolus in *Bison* and terminates distal to the lateral malleolus in *Ovis*, *Ovibos*, and *Symbos*. The sulcus muscularis of *Symbos* is narrow and deep as in *Ovibos* and *Ovis* and not a broad shallow feature as in *Bison*. The tibia of *Symbos* is easily distinguished from *Ovis* and *Ovibos* in size. The tibia length of *Symbos* is 455 mm. (KPM A 2146 61:379); 307 mm. in *Ovibos* (UMMZ, 102448); 304 mm. in *Ovis* (UMMZ, 102446) and 411 mm. in a large *Bison bison* (UMMZ, 102162). The *Ovibos* tibia is much heavier than that of *Ovis*.

The *Symbos* ulna-radius (Pl. 132, fig. 3) also is longer and relatively more slender than in *Bison*. Maximum length of the Ulna-radius of the above are 510 mm. in *Symbos;* 363 mm. in *Ovibos;* 285 mm. in *Ovis*, and 451 mm. in *Bison*. Except for the olecranon process, the *Symbos* ulna-radius is very similar to *Ovis* and *Ovibos*. The olecranon process of *Symbos* is not as elongate or as slender as *Ovis*. Thus, in general proportions, the olecranon resembles *Bison*. The olecranon of the Scotts specimen, however, has been damaged by rodents. The distal surface of the *Bison* radius is distinct from *Symbos*. Size is the most important criterion for identifying the material.

The scapula of *Symbos* is similar to *Ovis* except that it is much larger and thicker around the neck. The distance from the glenoid fossa to the proximal edge of the blade is 464 mm. in *Symbos;* 215 mm. in *Ovis;* and 496 mm. in *Bison*. An *Ovibos* scapula was not available. The scapula of *Bison* is longer, the proximal border is more rounded, and the acromion process slopes toward the glenoid fossa. The acromian drops off at a right angle in *Ovis* and *Symbos*.

The thoracic vertebrae of *Symbos* (Pl. 132, fig. 2) and *Ovibos* are characterized by a small neural canal, a spool shaped, thin centrum, and a neural spine that is nearly parallel to the anterior face of the centrum in the first few thoracic vertebrae. The neural canal of *Ovis* and *Bison* is much larger, the centrum is more oval, and the first neural spines slope from 30°–40° posteriorly from the faces of the centra. These features readily separate both musk oxen from *Ovis* and *Bison*. *Symbos* is much larger than *Ovibos*. Comparative material is not complete enough to identify the exact position of the vertebra but the following measurements were taken from the largest thoracic vertebrae available. The maximum length was 421 mm. in *Symbos;* 323 mm. in *Ovibos;* and 520 mm. in *Bison*. *Ovis* was much smaller.

From the preceding discussion it is apparent that there are a number of differences between *Symbos* and *Ovibos*. Very often the differences are of the same magnitude as between *Ovis* or *Bison*. Frequently, one musk ox will have a feature in common with *Bison* while the same feature resembles *Ovis* in the other musk ox. For this reason *Symbos* and *Ovibos* must have had a long independent history and the musk oxen are properly set off from both sheep and cattle. However, the gross anatomy of the *Ovibovini* (musk oxen) suggests a closer relationship with the *Caprini* (sheep) than to the *Bovini* (cattle). Serological studies by Moody (1958) support this conclusion. Post cranial measurements indicate that *Symbos* was taller but more slender than *Bison bison*.

ASSOCIATED FOSSIL INVERTEBRATES

Interpretation of the mollusks (listed below) found associated with the Scotts and White Pigeon specimens is based on ecologic data published in Baker (1928) and Berry (1943). The ostracods are mounted on a single slide and catalogued under one University of Michigan Museum of Paleontology number (UMMP 47151). The number of specimens and University of Michigan Museum of Zoology catalogue number follows each species of mollusk.

	White Pigeon	Scotts
Class Ostracoda		
Candona elliptica ? Furtos	×	—
Candona ohioensis Furtos	×	—
Physocypria pustilosa (Sharpe)	×	—
Class Pelecypoda		
Sphaerium cf. *S. rhomboideum* (Say) 2/2 (215074)	×	—
Pisidium nitidum Jenyns 1/2 (215075)	—	×
Class Gastropoda		
Amnicola limosa (Say) 19 (215076)	×	—
Amnicola lustrica Pilsbry 7 (215077)	×	—
Valvata tricarinata (Say) 170 (215078)	×	—
1 (215079)	—	×
Fossaria obrussa (Baker) 7 (215080)	×	—
Gyraulus altissimus Baker 85 (215081)	×	—
1 (215082)	—	×
Gyraulus deflectus (Say) 4 (215083)	—	×
Helisoma anceps (Menke) 10 (215084)	×	—
Physa cf. *P. gyrina* (Say) 5 (215085)	×	—
Ferrissia parallela (Haldeman) 1 (215086)	×	—

The White Pigeon sample includes 9 species of mollusks, only one of which, *Gyraulus altissimus*, is not found living in the area today. All of the species represented are aquatic and together with the large number of prosobranch snails, *Valvata tricarinata*, *Amnicola limosa* and *Amnicola lustrica*, which require continuity of aquatic habitat, indicate a permanent body of ponded water at or near the site of deposition. The mollusks probably lived in a shallow, quiet embayment, with little or no current action in among dense beds of submerged aquatic vegetation which perhaps included such species as *Chara*, *Potomogton*, *Villisnaria*, and *Elodea*.

The reason for the total absence of terrestrial snails is not certain, but it is suggested that it might be related to the predominantly coniferous forest which did not support a large molluscan fauna and to the off shore location of the fossil locality. The mollusks as a group do not imply a climate different from that which presently prevails in the area.

The molluscan record from the Scotts locality is too meager to attempt any interpretation be-

TABLE 3—POLLEN SPECTRUM FOR THE SCOTTS MUSK OX SPECIMEN

Name	No. of Pollen Grains	% AP	% NAP	% Total Count
AP				
Picea	26	5.20	—	4.20
Abies	28	5.60	—	4.52
Pinus	343	68.60	—	55.41
Larix	24	4.80	—	3.88
Betula	15	3.00	—	2.42
Juglans cf. *cinerea*	2	0.40	—	0.32
Quercus	46	9.20	—	7.43
Ulmus	14	2.80	—	2.26
Acer	2	0.40	—	0.32
Totals for AP	500	100.00		80.76
NAP				
Nuphar	1	0.20	1.11	0.16
Potamogeton	6	1.20	6.67	0.97
Gramineae	1	0.20	1.11	0.16
cf. Iridaceae	1	0.20	1.11	0.16
Cyperaceae	22	4.40	24.44	3.55
Salix	3	0.60	3.33	0.49
Corylus	22	4.40	24.44	3.55
Alnus	5	1.00	5.56	0.81
Chenopodisceae/Amaranthaceae	1	0.20	1.11	0.16
Thalictrum	2	0.40	2.22	0.32
Compositae undifferentiated	2	0.40	2.22	0.32
Astereae		1.20	6.67	0.97
Ambrosia-type	2	0.40	2.22	0.32
Artemisia	14	2.80	15.56	2.26
cf. Dryopteris	2	0.40	2.22	0.32
Totals for NAP	90	17.00	99.99	17.52
Unidentified				
A	1	—	—	0.16
B	28	—	—	4.52
Totals for Unidentified	29			4.68
Total Pollen and Spores				
	619			100.01

yond stating that the four species present are aquatic and indicate the presence of a fresh-water habitat at or near the fossil locality.

ASSOCIATED FOSSIL POLLEN

Matrix contained in the skulls of the two most recent *Symbos* finds provided an opportunity for the application of palynology, similar to the pollen spectrum worked out by Benninghoff (Benninghoff and Hibbard, 1961). The pollen spectra for the two new musk ox finds, the Scotts, and White Pigeon specimens, when compared with each other, and with Benninghoff's (1961) spectrum for the Climax specimen, yield more knowledge of the environment of these animals.

A sample of calcareous peaty silt, recovered from the brain cavity, and sinuses of the Scotts musk ox specimen proved to be rich in pollen. The pollen was assumed to be contemporaneous, or nearly so, with the skull.

The pollen sample was treated with 10% hydrochloric acid, full strength hydrofluoric acid, and the pollen was concentrated by the use of saturated zinc chloride solution. Then the pollen was acetolysed and mounted in glycerine jelly, and 500 grains of tree pollen were counted. There was very little non-tree pollen (less than 15%) and about 5% of the grains have not been identified. The total count was 619 pollen grains and spores. Fungal spores were not included in the count. The precise results of the count are shown in table 3.

As shown in table 3, pine (*Pinus*) is the dominant pollen in the sample, with oak (*Quercus*) being the next most common. There are probably at least two species of pine represented in this sample, and the work of Cain and collaborators

(1948; Cain and Cain, 1948; Cain, Cain and Thompson, 1951), Deevey (1949), Dansereau (1953), suggests that the three most probable species are *Pinus strobus*, *P. resinosa* and *P. banksiana.* Size characteristics and the existence of a marginal flange on some gra ns support the possibility that *P. banksiana* and *P. resinosa*, respectively, may be present. The next most common pollen types after oak are spruce (*Picea*), balsam fir (*Abies*) and larch (*Larix*). The Betulaceae (Birch Family, *Betula*, *Corylus*, and *Alnus*, here), are present in significant numbers. The pollen grains of *Betula* were measured whenever they were sufficiently well oriented. Of the 15 grains of *Betula*, 14 could be measured, and of these, all had a diameter equal to or greater than 24 microns. Leopold (1956), has suggested that grains of *Betula* in this size range probably represent tree, and not shrub, birch.

The conditions of the grains is good to excellent, and it is believed that they are not redeposited. There is no evidence of prolonged water transport.

The existence of a late glacial "pine period" in the Great Lakes region is widely accepted. It has been noted by Potzger (1946), Deevey (1949), and Deevey and Flint (1957). These authors are in general agreement, and show a pine dominated period preceded by a spruce-fir forest and followed by a forest composed of hardwoods in Michigan (Potzger, 1946, p. 232) or pine-oak-elm-maple forest (Deevey, 1949, p. 1356, table 7), or oak-hemlock in New England (Deevey and Flint, 1957, p. 2, table 1). The pollen percentages from the Scotts musk ox specimen sample strongly resemble those of the lower, but not the lowest levels of the sediments in Third Sister Lake and the Birge and Gilbert Bogs in Michigan (Potzger, 1946, figs. 11,23,24). The first represents a typical bog deposit from Southern Michigan, and the other two, sandy soil areas in the Northern Peninsula of Michigan. The Scotts musk ox remains probably were deposited fairly early in the pine period.

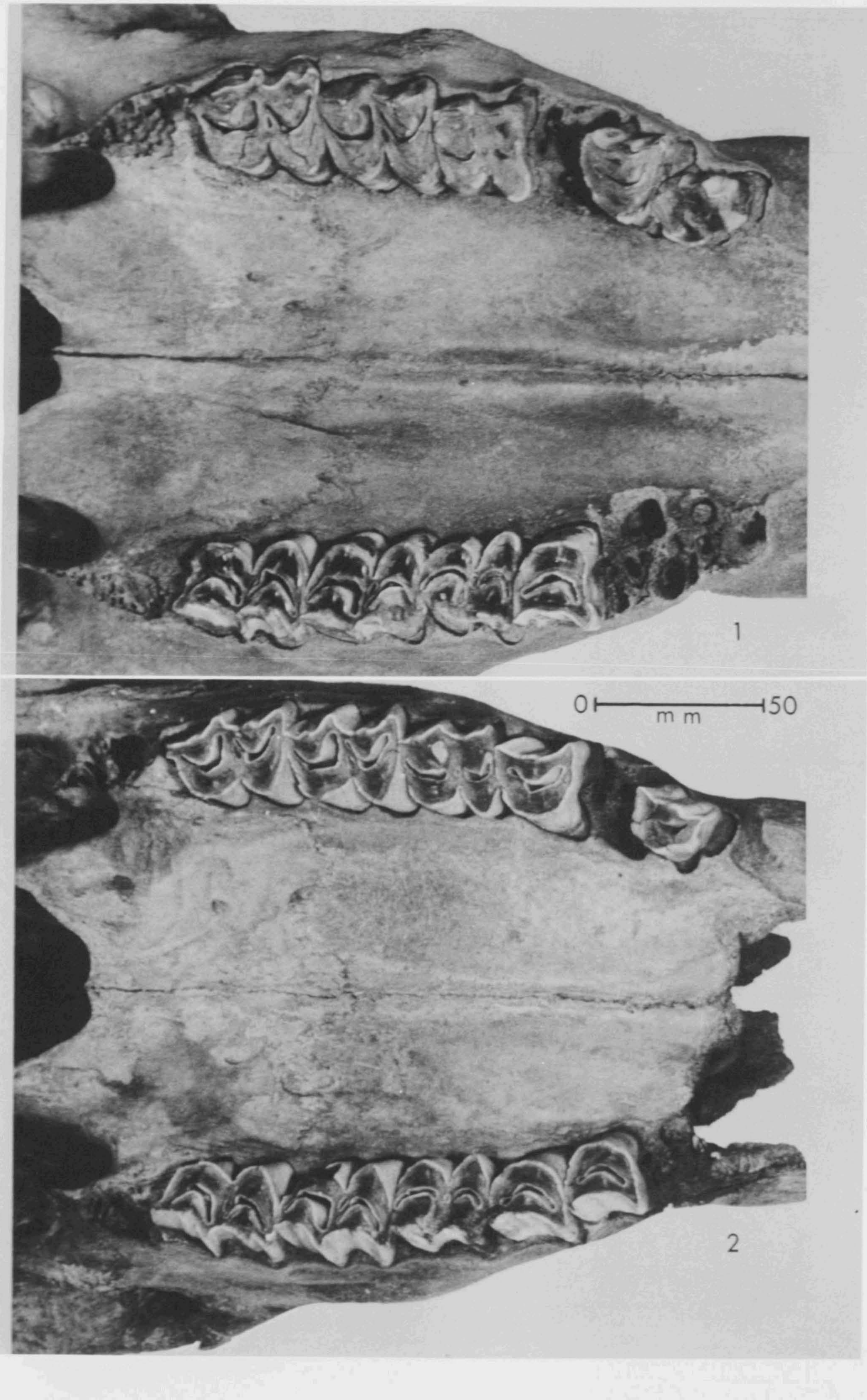
The pine period is assigned to the earlier Hypsithermal Interval (Deevey and Flint, 1957), and was thought to be "warmer and dryer than the present" by Deevey (1949). The sample under discussion is from a bog, and naturally, aquatic and bog species are represented. The *Salix*, *Alnus* and Betulaceae of the sample, as well as *Nuphar*, *Potomogeton*, *Cyperaceae*, and *Larix* pollen grains may be thought of as the portion of the sample indicating wet to moist conditions. *Ulmus* in greater quantities would also indicate wetter conditions. *Abies* and *Picea* may represent relics of an earlier, cooler climate forest, and may have occupied nearbog sites. The balance of the genera and the majority of the pollen in the sample are probably or possibly indicative of dryer conditions on nearby well drained uplands.

Dansereau (1953) discussed the pine period under two hypotheses and seven cases. His second hypothesis, in cases E, F, and G, proposes changed ecological requirements for pines (*Pinus strobus*, *P. banksiana*, and *P. resinosa*) in the past. This is a possibility that cannot be ignored. However, if it is accepted, then no firm interpretation of floristic evidence can be made. Thus, the interpretation can best be made on Dansereau's first hypothesis, that requirements are unchanged or nearly so. None of his cases (A–D) under this hypothesis exactly agree with the interpretations of other workers, except case A, in which the glacial fluctuations would result in a subclimax forest dominated by *Pinus strobus*. *Pinus strobus* is certainly a possibility in the flora associated with the Scotts musk ox. Case B, in which a climate dryer than the present, but approximately equivalent in temperature fluctuations leads to a climax forest of the pinesavanna type, in which *P. resinosa* and *P. banksiana* are dominant, is unlikely in the present instance. The low percentage of nontree pollen is not compatible with the savanna environment. However, if, as shown in Flint and Deevey (1957), the pine period coincides with the beginning of the Hypsithermal Interval, then the implication of temperature conditions would seem to agree. Case C of Dansereau, which postulates more illumination, and hence a *Pinus*

Explanation of Plate 131

Symbos cavifrons (Leidy) Dentition

Fig. *1*—Scotts specimen, KPM A2146 61: 379.
2—Manchester specimen, UMMP 3450.


1
0
mm
50
2

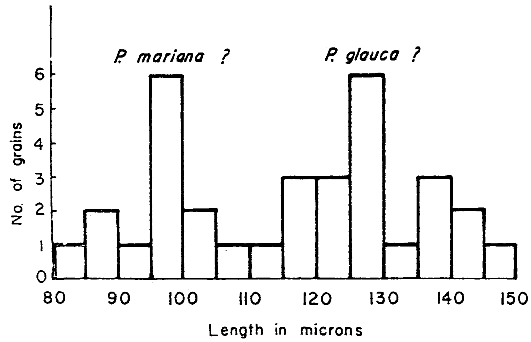

1
2
0
100
mm
3

strobus forest climax, cannot be proved or disproved. His case D supposes *Pinus strobus* to have been a climax in the Great Lakes region because of greater climatic anomalies at the time. However, evidence supporting greater anomalies is generally wanting. Thus, it is difficult on the basis of the pollen from the musk ox to draw definite conclusions. All that can be said is that the climate was probably warmer than, and not as wet, as maximum glacial times.

In 1960 a radio carbon date of 13,200 ±600 years BP was reported for the climax specimen (Hibbard and Hinds, 1960). Benninghof and Hibbard (1961) reported on the pollen associated with this musk ox. They said that the pollen recorded a spruce forest in the area of deposition. Thus, it can be stated with some certainty that the pollen from the Scotts musk ox would indicate a younger date, of perhaps 11,000 BP years or so. This figure is obtained by comparison with the temperature and dominant flora information provided by Flint and Deevey (1957) and Flint and Brandtner (1961). The radio carbon date obtained is 11,100 ±400 years BP.

Finally, the unidentified pollen grains should be mentioned. Type A are spherical, inaperturate, unornamented pollen grains or spores with a thin exine. Their affinities are not known. Type B is of greater interest and should eventually be identified. The grain is tricolpate, prolate, with a thick exine, that has a columellar structure. The surface of the exine shows a very faint sculpture pattern which is between a striate and an aligned reticulate condition. The grain is 66 microns long and has a diameter of 43 microns

Pollen and spores were recovered from calcareous gyttja found in the brain cavity and nasal sinuses of the White Pigeon specimen. The method of preparation was the same as that employed for the Scotts musk ox sample, except that the pollen was not concentrated by the zinc chloride method. The same counting procedure was followed. Five hundred grains of tree pollen, and a total of 625 grains of all types were counted.



TEXT-FIG. *2*—Histogram showing the size-frequency distribution of the 33 measurable *Picea* pollen grains.

Of the pollen and spores counted, 80% are tree pollen, approximately 13% are non-tree pollen, and 6% could not be identified (table 4). The predominant tree pollen is *Picea* (spruce) (73%). All grains of *Picea* that were sufficiently well preserved were measured, and the histogram of those measurements (fig. 2) suggests that two species of *Picea*, probably *P. glauca* and *P. mariana* are represented. *Quercus* (8.4%), *Pinus* (6.6%), and *Larix* (5%) are the next most common genera. Other trees make up 7% of the tree pollen.

Some of the tree genera, *Quercus*, *Carpinus/Ostrya*, *Juglans* cf. *nigra*, *Carya* and *Ulmus* may seem out of place in the presence of *Picea* and significant amounts of *Abies*. *Quercus* is present in significant amounts, and the pollen grains of all of these genera are well preserved, arguing against redeposition. In addition, it should be noted that these genera are persistent in the pre- and post-spruce maximum portions of the spruce dominant horizons of many bogs and lakes in

EXPLANATION OF PLATE 132

Scotts Specimen, KMP A2146 61: 379

FIG. *1*—Left tibia.
2—Thoracic vertebra.
3—Left ulna-radius.

TABLE 4—POLLEN SPECTRUM FOR THE WHITE PIGEON MUSK OX SPECIMEN.

Name	No. of Pollen Grains	%AP	%NAP	% Total
AP				
Picea	366	73.2	—	57.55
Abies	12	2.4	—	1.89
Pinus	33	6.6	—	5.9
Larix	25	5.0	—	3.93
Betula	1	0.2	—	0.15
Ostrya/Carpinus	6	1.2	—	0.94
Juglans cf. *niger*	2	0.4	—	0.31
Carya	1	0.2	—	0.16
Quercus	42	8.4	—	6.60
Ulmus	12	2.4	—	1.89
Totals for AP	500	100.0		78.62
NAP				
Typha latifolia	13	2.6	14.29	2.04
Potamogeton	24	4.8	26.37	3.77
Gramineae	7	1.4	7.69	1.10
Cyperaceae	11	2.2	12.09	1.73
Corylus	3	0.6	3.30	0.47
Chenopodiaceae/Amaranthaceae	3	0.6	3.30	0.47
Nuphar	1	0.2	1.10	0.16
Utricularia	5	1.0	5.49	0.79
Plantaginaceae	3	0.6	3.30	0.47
Compositae undifferentiated	2	0.4	2.20	0.31
Astereae	1	0.2	1.10	0.16
Ambrosia	7	1.4	7.69	1.10
Artemisia	8	1.6	8.79	1.26
Polypodiaceae	3	0.6	3.30	0.47
Totals	91	18.2	100.01	14.30
Unidentified				
A	2			0.31
B	1			0.16
C	42			6.60
Totals for unidentified	45			7.07
Totals for Pollen and Spores	636			99.99

Michigan, Indiana, and Minnesota (Potzger, 1946, figures 8, 9, 10: Engelhardt, 1960; Fries, 1961, 1962). Some of these genera also appear in the spruce maximum spectrum associated with the Climax musk ox (Benninghoff and Hibbard, 1961). These considerations tend to indicate that it may not be necessary to explain the presence of these hardwoods as either the result of extreme long distance transport or of redeposition. Benninghoff and Hibbard (1961) suggest that these genera may have followed closely the pioneer species invading the area shortly after deglaciation.

The low value for total non-tree pollen probably indicates a relatively unbroken forest cover, with such groups as the Gramineae and Compositae representing primarily openings adjacent to streams and lakes. The genera *Typha*, *Potamogeton*, and *Nuphar*, and the family Cyperaceae are aquatic or emergent plants, probably growing in or around the pond or small lake in which the musk ox skull was found. Nearly all of the unidentified entities are thin walled, psilate, and invariably crumpled spores that may be those of mosses, *Equisetum*, fungi, or *Juniperus*.

The age of the White Pigeon specimen cannot be fixed with any precision by one pollen sample. The relatively low value for *Picea* (73% as compared with 80–90% at localities cited above), make it unlikely that this spectrum represents the spruce maximum. The higher values for *Quercus* and *Pinus* ordinarily obtain either before or after the spruce maximum, although in general, the increase of *Pinus* is more rapid than that of *Quercus* as *Picea* declines. However, the values for the non-tree pollen are usually somewhat higher than here before the spruce maximum. Thus the only conclusion possible is that the White Pigeon specimen may be older or younger than the Climax specimen, but probably is not of the same age. It is older than the Scotts specimen.

CONCLUSIONS

The studies presented in this paper lead to the following conclusions:

(1) *Bootherium bombifrons* is not a female *Symbos*, but *B. sargenti* may be. It has been erroneously assigned to the genus *Bootherium*.
(2) The Ovibovini are properly set off from the Caprini and Bovini, but more closely resemble the Caprini in osteological characters.
(3) *Symbos* and *Ovibos* had long independent histories.
(4) *Symbos* was taller and more slender than *Bison bison*.
(5) The woodland situation of *Symbos cavifrons* is reaffirmed. This animal persisted in more than one type of forest.
(6) The evidence of the mollusks and pollen associated with the two new specimens of *Symbos* show that the late glacial and post glacial climates were different from the present, but that the difference was quantitatively small.
(7) The radio carbon date on the Scotts specimen (11,100 ±400 years BP) extends the known time range of *Symbos* in Michigan.

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