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AN EARLY QUATERNARY BISON POPULATION FROM UNTERMASSFELD: *BISON MENNERI* SP. NOV.

1. Introduction

During several years of excavation the new and very rich locality of Untermaßfeld near Meiningen in Southern Thuringia (Germany) has already yielded thousands of mammal fossils. Among them, the bones of a large bovid rank the highest (more than 1,000 specimens). To date, this is the largest collection of early Quaternary large bovids not only in Germany, but apparently in Europe. It deserves a comprehensive monograph. The present report can not cover all the skeletal elements in every detail. A peculiarity of the bovid collection from Untermaßfeld consists in an almost total lack of cranial material. Metapodials, and metacarpals in particular, turned out to be not only the best represented and preserved element, but at the same time one of the most informative.

The huge literature on large Quaternary bovids may create an impression of a well established taxonomy based on morphological features. In fact, many of these features are misleading due to the high morphological variability of the group. As a result, many controversies can be found in the literature, and even some generally accepted taxa need revision. This is especially true for the early Quaternary large bovids usually represented in collections by fragmentary fossils. For instance, the well-known task of discrimination between *Bison* and *Bos* postcranial elements, not so easy even for the late Quaternary fossils despite a dozen special research reports, is far more difficult for earlier bovids.

Large fossil samples of bovid bones all from the same locality are rather rare. When they are available and studied, we can often see that even a very important but single isolated fossil must mean almost nothing, as it may fall within the ranges of variation of two or even more different taxa which can be distinguished on population grounds only. In this respect, the importance of the Untermaßfeld sample can hardly be overestimated. It is a real fossil population, quite homogeneous and clearly falling into males and females. That is why the author believes that the measurements of individual elements of the Untermaßfeld collection have an independent importance, probably higher than the author's analysis or comments. They may serve for future students as a model of fossil population of large bovids.

To ascertain a systematic position for the Untermaßfeld bovid was a really hard task. The present taxonomy of large fossil bovids is based mainly on cranial characters, and basically on the horn core size and shape. Having no adult skulls or horn cores in the Untermaßfeld sample, the author had to concentrate on the limb bones. That is why he had to go deeper into the above mentioned problem of discrimination between *Bos* and *Bison* postcranium and to study as many collections of fossil bovid limb bones as possible. The examined material includes collections kept in Moscow, St. Petersburg and Kiev, Berlin, Weimar and Schwerin, London, Cambridge and Norwich, Heidelberg, and Fairbanks. Depending on opportunities, the author could study either all or some (metapodials in the first place) postcranial bovid material from such important Quaternary localities as Süßenborn, Taubach, Ehringsdorf, Mauer, Norfolk Coast, Tiraspol, Kairy and other Early Quaternary sites in Ukraine. With the kind help of Thomas Martin (Bonn) I was able to get very useful measurements of bison metapodials from Mosbach. Quite recently published bovid materials from such sites as Venta Micena in Spain, Casa Frata, Selvella, Pirro Nord and Isernia in Italy, Westbury-sub-Mendip in England and others cited below were very useful as well as the observations and comments included it these reports.

As a comparative material, the large sample of *Bison priscus* fossils collected by the writer in North-Eastern Siberia and some *Bison* samples from Alaska were used.

Results of this study have led the author to the conclusion that the Untermaßfeld bovid certainly belongs to *Bison* but at present can not be identified with any of the described species of the genus. The reason lies in some morphological features of the Untermaßfeld bovid (primarily limb bones proportions, metacarpals in particular) and in the fact that some early *Bison* species are inadequately known, being based on single isolated and sometimes incomplete specimens, and cannot be compared with the Untermaßfeld sample. At the same time, it would be a pity to introduce this excellent sample into the literature without a definite species name. That is why the author has come to a rather unexpected solution in describing the Untermaßfeld bovid as a new species basing himself mainly on postcranial characters contrary to the tradition of relying upon cranial characters in *Bison* taxonomy. He believes that at least some of the observed features permit to identify this very large and slender-legged bovid quite reliably. It evidently takes its place among the early representatives of the genus, being not so primitive as Villafranchian species like *B. palaeosinensis* but more archaic than most of the well-known Pleistocene species. Future finds and research will show whether this solution was correct.

1.1. Acknowledgments

The author wishes to extend his sincere gratitude to Prof. Dr. Dr. Hans-Dietrich Kahlke, former Director of the Institute of Quaternary Palaeontology in Weimar, for his invitation to process the interesting bovid collection from Untermaßfeld and for the facilities that he offered for this work. I am indebted also to mammalogists and collection curators who kindly offered me opportunity to study *Bison* and *Bos* material in several museums and institutes and to discuss important problems of bovid taxonomy: Natalya Belan (†) in Kiev, Ursula Lehmkul in Schwerin, Karl-Heinz Fischer in Berlin, Reinhart Kraatz in Heidelberg, Wighart von Koenigswald in Bonn, Adrian Lister in Cambridge, Antony Sutcliffe, Andrew Currant and Alan Gentry in London, Anthony Stuart in Norwich, Anatoliy David in Kishinev, Gennady Baryshnikov in St. Petersburg, Dale Guthrie and Roland Gangloff in Fairbanks. I express my special gratitude to Thomas Martin who made careful measurements of bison metapodials from Mosbach for my study. I would like to thank also Heinz Wöllner, Kurt Steiner and other colleagues in the Department of Quaternary Paleontology in Weimar for their friendly help in my work. This work would scarcely have been possible without the permanent assistance and patience of my wife, Anna Leirikh.

2. General characteristic of the collection

2.1. The sample

The list presented in Table 1 shows that skulls and horn cores are almost absent from the collection except for some badly preserved fragments of frontals belonging to very young individuals and some even smaller insignificant pieces. Much more numerous are maxilla and mandible remains, usually with some teeth or even complete tooth rows, but the number of intact specimens is very low. A rather peculiar feature of the sample is the very high percentage of juvenile and subadult individuals among mandible (42%) and especially maxilla remains (91%). The same is generally true for isolated teeth, though the share of adult individuals is higher among them. Vertebra and scapula remains are surprisingly few. The large limb bones are numerous, though the percentage of intact bones is low (29% for radius, 2 to 11% for the others). Very numerous and relatively well preserved are metapodials, especially metacarpals. Of 67 metacarpal bones 33 are almost complete. Smaller bones such as carpals, tarsals, and digital bones are even better preserved and rather numerous.

It is noteworthy that the share of the remains of young animals is very high among cranial and dental material but does not exceed 12-13% among postcranial elements (e.g. metapodials).

Skeleton element	Total number of specimens	Including:				Minimum number of individuals, ad+juv/sad
		intact bones	dex.	sin.	juv +sad.	
Cranium	5	0			3	
Maxilla, dentes (upper tooth rows)	23	2	14	4	21	6 + 10 (M^2, dP^3)
Dentes super. (isol.)	36	31	11	4	16	
Mandibula, dentes (lower tooth rows)	26	4	10	7	11	9 + 7 (M_2, dP_3)
Dentes infer. (isol.)	36	34			23	
Vertebrae	8	0				
Costae	2	0				
Scapula	9	0	4	3	1	
Humerus	49	1	26	22	1	23 + 1
Radius	51	15	32	14	4	19 + 3
Ulna	31	7	17	11	8	
Carpi radiale	24	21	16	8		16
Carpi intermedium	24	20	10	14	1	14 + 1
Carpi ulnare	25	20	13	12		13
Carpi accessorium	12	12	6	6		6
Carpale II+III	32	28	16	14		16
Carpale IV	31	26	19	12		19
Metacarpale III+IV	67	33	31	29	8	27 + 4
Pelvis	23	0				
Femur	20	1	12	8	1	
Patella	1	1				
Tibia	36	4	20	15	4	17 + 2
Astragalus	51	44	21	26		26
Calcaneus	58	27	27	26	4	27
Central tarsale	41	33	22	19		22
Tarsale II+III	37	34	17	20		20
Malleolare	18	18	10	8		10
Metatarsale III+IV	52	18	22	25	7	19 + 4
Metapodia indet.	12				3	
Phalanx I	71	51	33	27	6	
Phalanx II	56	46	25	21	2	
Phalanx III	34	21	18	14		
Total	1001					27 + 10

Tab. 1 Composition of the Untermaßfeld sample of *Bison*. Note: Ossa sesamoidea are not included.

2.2. Preservation and taphonomy

In general, bone preservation in the Untermaßfeld bovid sample is excellent. This is evidenced by the presence of such fragile specimens as lower jaws and undeveloped teeth of juvenile animals, or completely preserved ulnas separated from the radius. At the same time, more heavily built and larger sized bones are more rare in the sample. The most striking example is the complete lack of adult horn cores and skulls. It seems not possible to suppose that even the most solid parts of skulls (e.g., occipital regions) have been absolutely destroyed in the deposit. The only reasonable inference is that the heaviest parts of the skeleton have never been brought to the place of deposition.

However, the present material does not permit us to suggest any long transportation. This is evidenced not just by the preservation of fragile pieces and lack of bone rounding. More important is the rather large number of bones belonging together to the same individual. For instance, about 40% of carpal bones in the sample certainly belong with the other carpal bones, and sometimes to the radius or metacarpal, of the same individuals. The same is true for tarsals and some groups of digital bones. There are at least 8 more or less complete sets of carpal bones and 11 of tarsal bones in the collection. In fact, much higher number of bones in the sample belongs together, and they can be provisionally combined.

Consequently, we may suggest that bone accumulation was taking place very near to the place where animals died, but not exactly at that place. A transporting factor was powerful enough to bring in some parts of animal bodies butchered by large carnivores but it was not able to transport the whole carcasses of adult animals or even such parts as their heads.

2.3. Untermaßfeld population of *Bison*

Bison remains in the Untermaßfeld sample belong to at least 37 individuals including 27 adult (estimated on metacarpals) and 10 juvenile and subadult animals (estimated on upper teeth). Among adult metacarpals those belonging to female individuals make up 65%. That means that the sample represents at least 9 males, 18 females and 10 calves and youngsters. Evidently, these figures are very approximate but if we assume that they in any way reflect true ratios we would consider them as normal or at least possible for a natural bison population.

However, much more convincing is the morphological homogeneity of the sample. In the following sections we shall see that the ranges of variation in size and proportions of the most numerous skeletal elements in Untermaßfeld are not wider and are sometimes even more narrow than in other less rich localities. Various parameters of the Untermaßfeld bones are represented in compact clusters in the graphs below. Most of skeletal elements can be clearly divided into males and females. This distributional feature supports the suggestion that in Untermaßfeld we are dealing with a single fossil population of bison. This collection of large bovids bears no traces of the admixture of fossil remains of any other species either of the same geological age or redeposited from other horizons.

3. Description of fossil *Bison* remains from Untermaßfeld

3.1. Methods

Study of the large bovid collection from Untermaßfeld started with the general identification of bovid material and its separation from the fossils of large cervids. This was a special and sometimes uneasy job (especially as regards small carpal and tarsal bones and phalanges) with some interesting results, but these problems are beyond the scope of the present report.

Measurements of several hundreds of *Bison* bones constitute an essential part of this report which in my view has independent importance. I think that publishing not only statistical results but measurements of particular specimens makes the paper more useful for future students and more open for criticism and revision of the present author's conclusions. Besides, all the source data are kept as spreadsheets in PC memory and can be distributed if requested.

I tried to use standard ways of measuring as far as it was possible. Most of the measurements were taken in the same way as has been suggested by Stampfli (1963) and earlier authors and/or recently pictured with accuracy by Browne (1983), Brugal (1985), and Martin (1987). Special measurements are described in the text or tables.

Common abbreviations used in the tables for various bones are the following:

L - maximum length of the bone;
Wp - maximum proximal width;
Wd - maximum distal width;
Wm - width in the middle of the diaphysis;
Tp, Td, Tm - maximum transverse diameter (»depth«) of posterior end, distal end and the middle of the diaphysis;
H (min, max, ant, lat) - height (minimum, maximum, anterior, lateral).

Recognition of sex needs some comment. Most of skeletal elements in the Untermaßfeld bison population demonstrate a very wide range of sexual variation. Having started my study with metacarpals, I could see how easily they can be assigned to a certain sex if we use both size and relative massiveness at the same time (see below). The same principle – larger and more stout bones belong to males, and smaller and lighter and more gracile bones belong to females – proved to be applicable to the majority of bones with some rare exceptions. It is possible also to use extrapolations from some distinctly separated bones, e.g. metacarpals for carpal bones.

A very important source of information has been suggested by numerous records of some bones belonging to the same individual. For instance, a complete set of carpal bones has been found with the metacarpal of the same individual certainly belonging to a female. The other set of carpal bones – much larger in size – has been classified as male specimen by the contrast (cf. Fig. 9).

Similarly, some complete sets of tarsal bones have been found together with a metatarsal and/or tibia like the one pictured in Fig. 14. Numerous parts of toes have been also recognized as belonging to one individual, sometimes with at least partial metapodial elements. These examples served as important key points for sexual recognition. To provide additional checks, I used to classify samples of bones using their measurements, and then introduce key specimens with already determined sex affinity.

3.2. *Bison menneri* Sher, sp. nov.

Type Specimen. – IQW 1982/17 948 (Mei. 17 468), a right male metacarpal in the collection of the Department of Quaternary Palaeontology, Weimar. Fig. 1, Taf. 28, 1-3.

Type Locality and Geological Age. – Untermaßfeld near Meiningen in South Thuringia, Germany. Early Pleistocene.

Etymology. – The species is named in memory of Professor Vladimir Vasilyevich Menner (1905-1989), outstanding expert in stratigraphy and palaeontology.

Diagnosis. – Large and long-legged bison with relatively small skull and slender limbs. Metacarpal bones are the longest and at the same time the most gracile among all known large bovids. Their total length in male specimens is 275-297 mm, ratio of distal width to total length 27.5-31.3%, in females 262-283 mm, index 24.5-27.8%. The other long limb bones and metatarsals are the largest (males especially) or near the largest among the known bovids, being the most slender at the same time. Many limb bones demonstrate a mixture of characters peculiar to *Bison* and *Bos* with a prevalence of *Bison* features.

3.2.1. Neurocranium of young individual

Cranial fragment of a very young animal with almost complete frontals, slightly damaged right and broken away left horncore, and partially preserved parietals. IQW 1980/17 380 (Mei. 16 902), Taf. 22, 1-3; Fig. 2.

The following description is based mainly on this specimen. The second specimen, IQW 1986/21 665 (Mei. 21 184), is less well preserved, has approximately the same individual age and differs only in minor details.

The skull has a broad front and well developed posterior part (behind the horn cores). The neurocranium roof is made up of the frontal and parietal bones. The frontals between the horn cores are gently concave. From a small elevation along the medial suture they rise gently to the horns. The second specimen shows a pronounced elevation of the frontal surface just near the base of the horncore. In sagit-

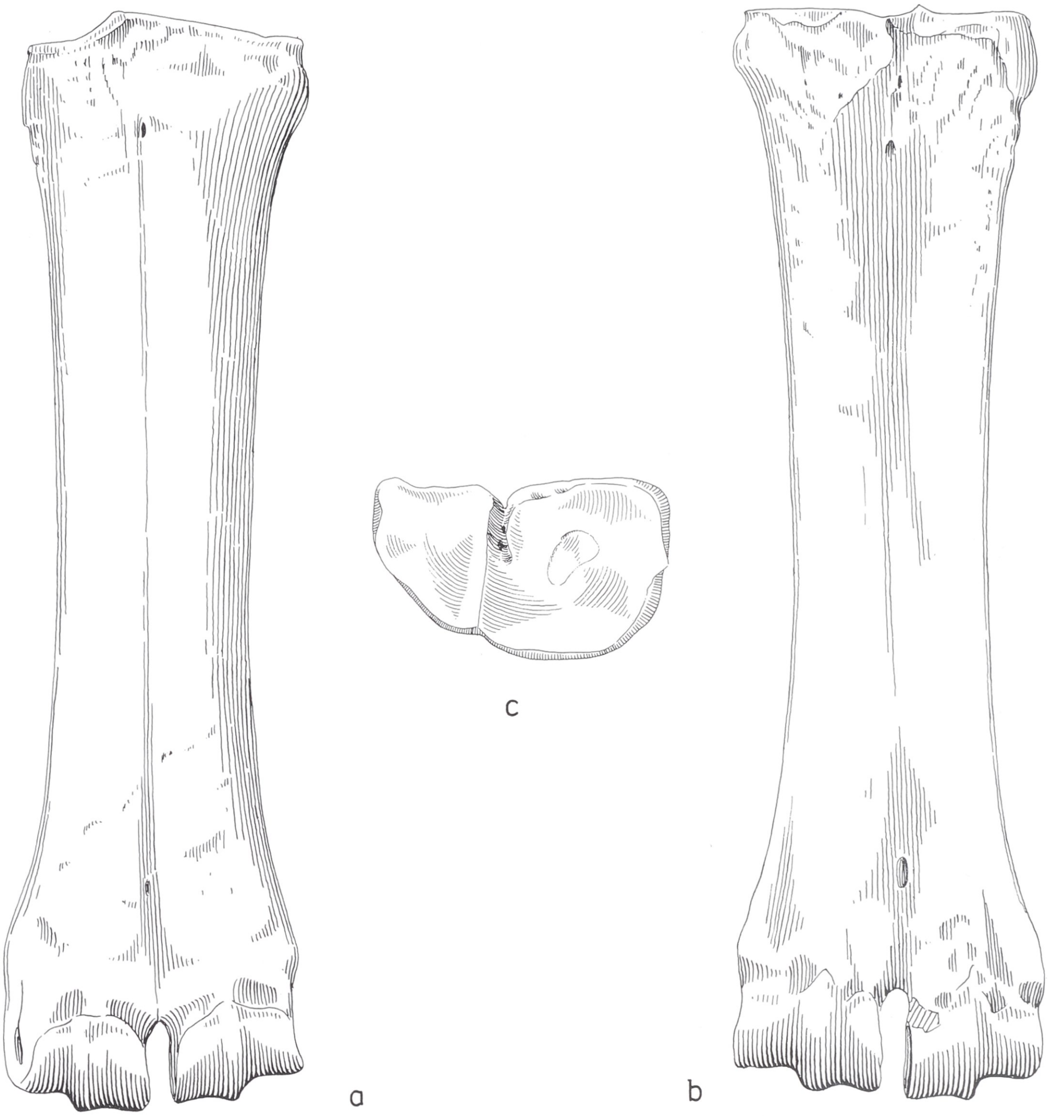

Fig. 1 *Bison menneri* sp. nov., Untermaßfeld. – a-c Metacarpal III+IV dex., IQW 1982/17 948 (Mei. 17 468), male; anterior, posterior and proximal views. Type specimen of *Bison menneri* sp. nov. – Scale = ca. 1:2.

tal section the skull roof is appreciably convex. The angle between frontal and parietal parts is about 138-140°, i.e. parietals and occiput take a lowered position. The parietal bones are rather long, being already fused with the interparietal.

The temporal fossae are broad, their dorsal edges completely lie lower than the horncore bases and are almost no depressed under the horn cores. Temporal fossae are essentially developed in caudal-dorsal direction. In occipital view, the minimum distance between their edges is no more than 51% of the minimum (postorbital) frontal width.

The horn cores are very short, directed backwards and upwards. The angle between the horncore axis and the sagittal line is about 60°. The apex of the horncore reaches the occipital plane. The horn cores have practically no pedicles but very massive bases that suggests that the pictured specimen belongs to a young male. Its oral-aboral diameter makes up 36-38% of postorbital width while even in adult females of *Bison* this ratio is not more than 32%. The horncore surface is highly porous, large cavities open at the distal end and seem to permeate the whole core. The cores are conic in shape, slightly

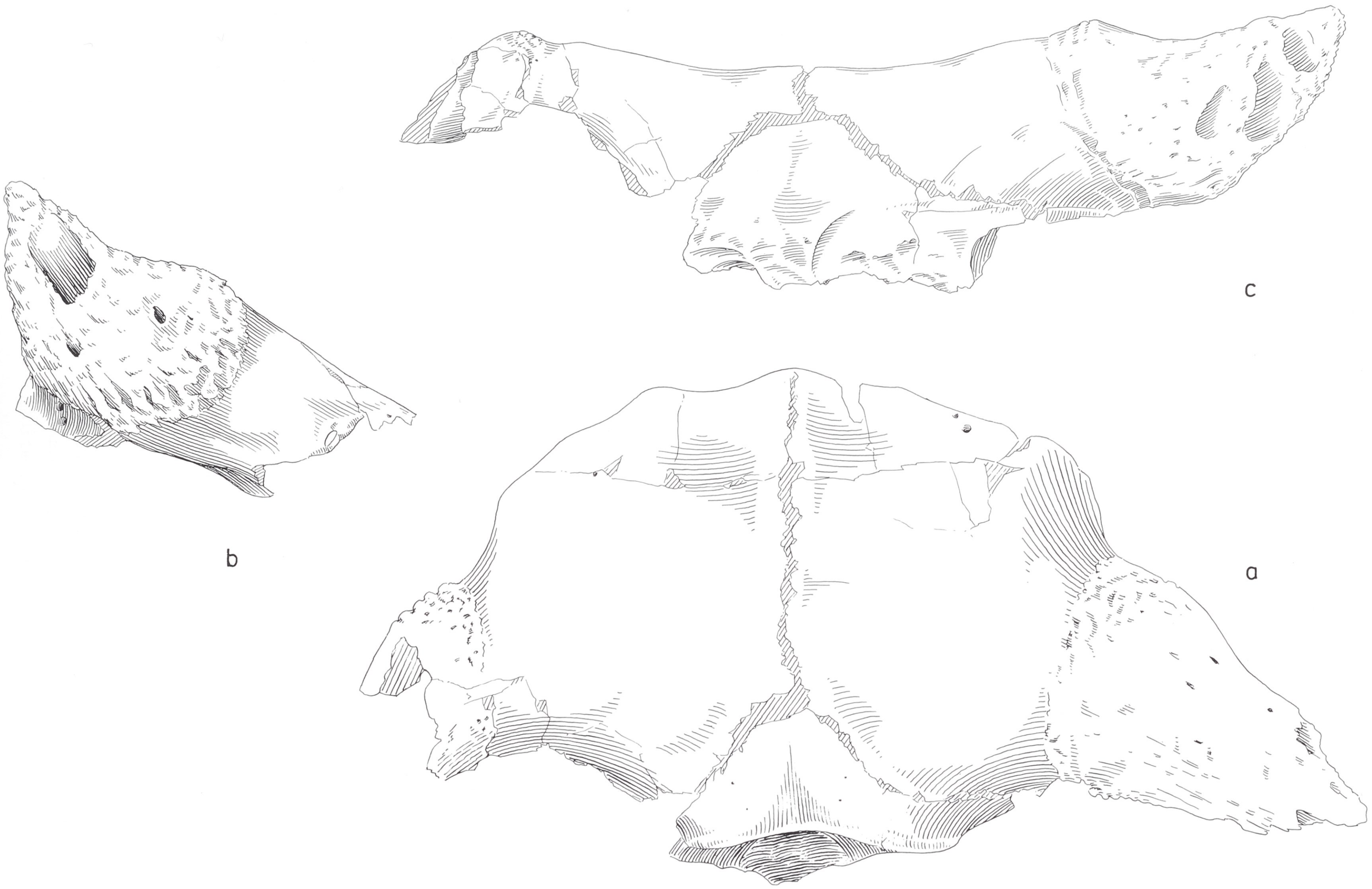

Fig. 2 *Bison menneri* sp. nov., Untermaßfeld. – a-c Cranial fragment of young individual IQW 1980/17 380 (Mei. 16 902); frontal, lateral and occipital views. – Scale = ca. 1:2.

curved upwards. They lie almost completely in the plane of frontal surface, only the tips rise somewhat above it.

Measurements. Postorbital width – 205 mm, minimum distance between the bases of horn cores (posteriorly) – 171 mm, estimated distance between the posterior edges of temporal fossae (minimum width of the occiput) – 104 mm, medial length of parietals (bregma - opisthion) – 70 mm, diameters of the horncore base: maximum, on the frontal plane – 74 mm, minimum, perpendicularly to it – 64 mm.

Comparison. The general appearance of the juvenile skull, and primarily, the position of the horn placed markedly further anteriorly than the posterior edge of the skull, clearly indicate its belonging to *Bison*, and not to *Bos*. But some features of the Untermaßfeld calf distinguish it from most of the Pleistocene and recent *Bison* species. However, we should be very cautious in our comparisons as we have juvenile specimens only. It is known that the peculiar appearance of the neurocranium of advanced Bovines that distinguishes them from more primitive forms with more developed parietal region, is strongly related to the development of heavy horns. That is why the neurocranium of young individuals of *Bison* looks more primitive as compared to adults. The same is true for females retaining juvenile features in their skull long into adult life (Flerov 1979).

Another point making our case more complicated is that some morphological features of early bison may be interpreted as retentions of juvenile characters in adulthood. For instance, such features of *Bison schoetensacki* (including *B. voigtstedtensis*) as relatively small horns on a large male skull, convex forehead, and slender limbs are interpreted by Sala (1986) as paedomorphic characters. That means that it is very difficult to decide whether any observed archaic features of a juvenile skull of early bison are actually archaic or juvenile only. In our case, we can adequately understand the evolutionary position of the Untermaßfeld skulls only if we compare them with the skulls of similar individual age. Unfortunately, we have no such opportunity for most of the described species of early bison. This lack can partially be compensated by comparing the Untermaßfeld neurocranium with the skulls of young individuals of *Bison priscus*. There are several neurocranium fragments of young females of this species in our collection from the Late Pleistocene of Northeastern Siberia. They have very weak horn cores and have been used for general comparison with the Untermaßfeld specimens.

Let us consider now those features of the Untermaßfeld juvenile skulls which may be important for understanding their evolutionary level and compare them with other bovids.

1. Elongated post-horn part of the skull in general and parietals in particular. The medial length of the parietals of the Untermaßfeld specimen makes up 34% of its postorbital width. About 90% of *Bison priscus* skulls (n = 45) and all male *Bison bonasus* skulls (n = 8) measured by Gromova (1955) have relatively shorter parietals. The same is true for 80% of young female skulls of *B. priscus* from our Siberian collection (n = 5). More frequently parietals of length similar to that of the Untermaßfeld specimen or slightly longer can be found among *B. bonasus* females (Gromova 1955).
2. Marked bending of the main cranium axis displayed by the angle between the sincipital and occipital surfaces of the frontal (138-140°). The skull roof of young females of Siberian bison is flatter and the angle is more obtuse – 143-148°. According to Sala (1986), in *B. priscus* this angle is between 160° and 165°, in *B. schoetensacki* – 140-155°. Sharper bending can be seen in primitive »*Eobison sp.*« from the Pirro Nord Fauna in Italy (De Giuli et al. 1986) – 140°, and in *Leptobos* – 135° (Dubrovo and Burchak-Abramovich 1986). Though this angle is difficult to measure, the general trend is evident. In this respect the Untermaßfeld skull holds an intermediate position between Villafranchian and truly Pleistocene species.
3. Width of temporal fossae and position of their caudal edges. In more primitive bovines the caudal parts of the temporal fossae stretch upward along the side walls of neurocranium. As a result, their nuchal edges come relatively close one to another, reducing the upper width of the occiput and making it trapezoidal in shape (Flerov 1979). In such archaic forms as *Leptobos, Adjiderebos, Probison* the distance between the nuchal edges of the temporal fossae is essentially less than 50% of the postorbital width of the skull (according to Dubrovo and Burchak-Abramovich 1986; Sahni and Khan

1968). A similar structure of the neurocranium is also found in such primitive bison as *B. palaeosinensis* (Flerov 1979). In the Pleistocene and Recent species of *Bison* temporal fossae intrude into the occiput far less, the latter then having an arched shape. The suggested index (minimum width of the occiput : postorbital width, %) is higher than 50%. The index is subjected to wide variation and changes much during the individual life. In *Bison priscus* it ranges between 56 and 77%, the lowest value measured by us in a young Siberian male is 52.4%. In the Untermaßfeld skull temporal fossae are well developed, the index being 50.7%.

4. Strong backward direction of the horn cores can be seen among some primitive bovines (*Leptobos, Probison*). Horn cores of advanced species of *Bison* are directed outwards more normally to the sagittal line. According to Gromova (1935), the angle between the horncore axis and sagittal line in *B. priscus* (n = 48) and *B. bonasus* (n = 15) is always more than 60° and reaches 80° (average about 72°). On the average, it is slightly more sharp in *B. bonasus* females (65.5°) and young females of *B. priscus* (our measurements) but never less than 60°. The horn cores of the Untermaßfeld specimen are directed notably backward: the angle is about 55°. The skull from Voigtstedt (Fischer 1965) also has the horn cores notably slanted backward (the angle is less than 60°). As a result, the horncore tips lie far behind the occiput. This was one of the reasons why Flerov (1979) separated *B. voigtstedtensis* from *B. schoetensacki* as independent species (the former had been originally described as a subspecies of the latter). However, this particular feature depends not only on the discussed angle but on the size and shape of the core (curving, twisting etc.). That is why the feature is highly variable both among *B. schoetensacki* (Sala 1986) and *B. priscus* (Flerov 1979).

Comments. Summarizing the characters of the juvenile skull of the Untermaßfeld bison, we can draw some conclusions despite the limitations of the material available. Though some peculiarities of the specimen are related to its individual age and weak development of horn cores, it still looks rather archaic even against juvenile female skulls of *B. priscus*. That gives us a basis for refering the Untermaßfeld form to a group of earlier European bison. Besides *B. schoetensacki* which is probably the most advanced species in this group, it includes *B. voigtstedtensis, B. tamanensis* and *»Eobison«* sp. from Pirro Nord. The features thought to be archaic in the Untermaßfeld form are peculiar to all or at least some of these forms. Unfortunately, they are represented by single fossils of adult age, some of them quite fragmented. For this reason the further and more detailed comparison of the Untermaßfeld skull with any of these forms seems impossible.

3.2.2. Maxilla of young individual

Fragment of left maxilla with dP^2-dP^4 and M^1, with a preserved part of intermaxillare. IQW 1980/15 358 (Mei. 14 870) – Taf. 22, 4-5; Fig. 4, a,b.

Individual age – juvenile, according to Skinner and Kaisen (1947 Plate 8, Figs. 2C and 3C). Anterior and posterior parts of dP^2 in the initial stage of merging by wear; lingual style of dP^4, as well as the corresponding structures on dP^3 are already involved in wear; M^1 is just at the beginning of wear. There are 5 more maxilla fragments with teeth of the same developmental age in the Untermaßfeld collection but their preservation is not so good.

Deciduous teeth are very rare in fossil collections, complete milk tooth rows even more so. There are 4 maxillas of almost the same individual age belonging to *B. priscus* from Northeastern Siberia in our collection. In size, general morphology, and detailed structure of teeth the Untermaßfeld specimen is very similar to them, especially to the maxilla PIN 3341-888 from the late Pleistocene of the Chukochya River. One of few distinctions is the number of vascular openings anterior to the foramen infraorbitale. In the Thuringian specimen there are two such small openings and one larger lying further anteriorly. Siberian bison have only one rather small opening at the level of the upper edge or the middle of f. infraorbitale. The Untermaßfeld maxilla has a straight contact with the intermaxillare. In *B. priscus* and *B. bonasus* this line is usually gently concave (Flerov 1979). The only juvenile specimen of Siberian bison where this region is preserved also shows a gently concave contact.

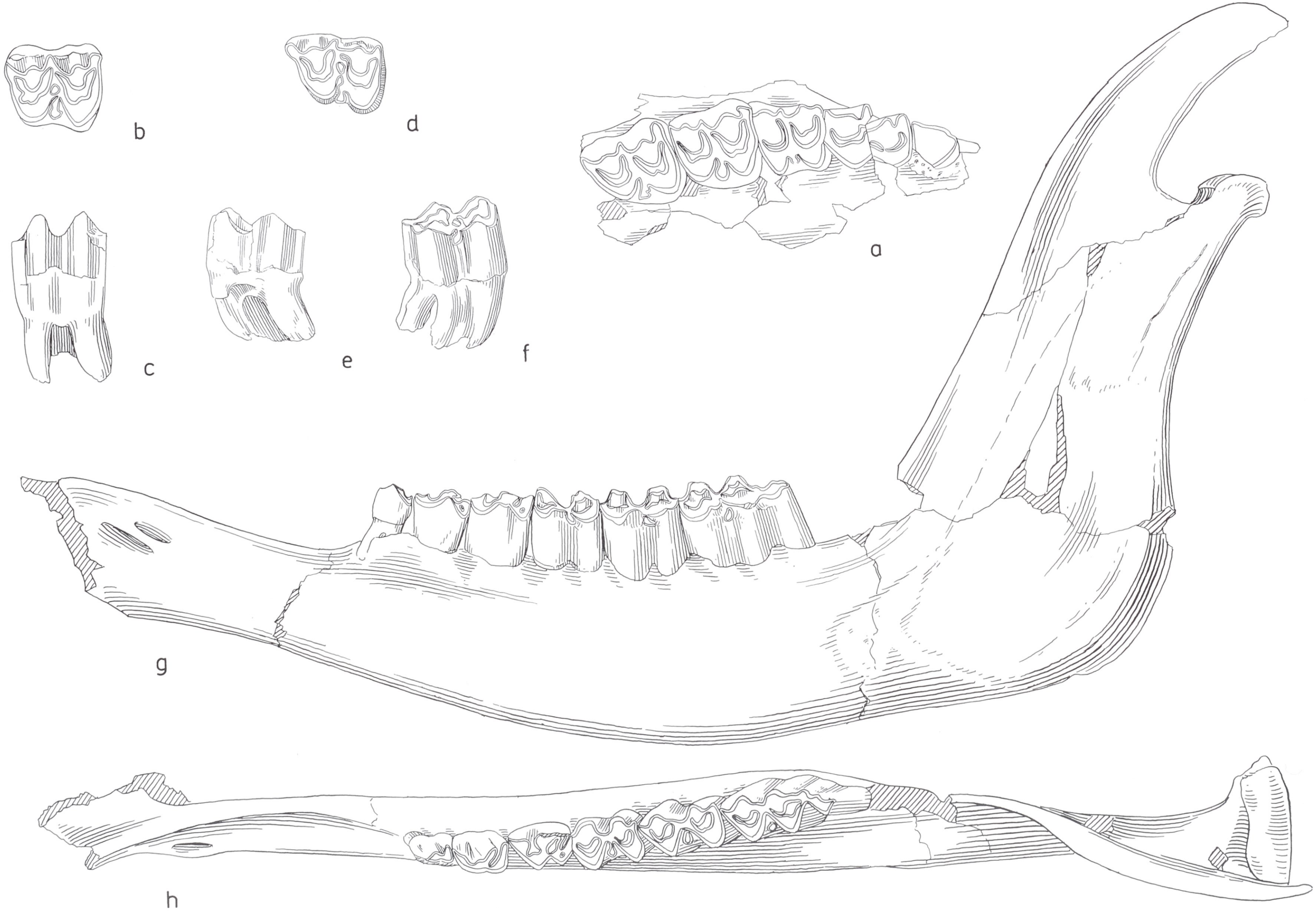

Fig. 3 *Bison menneri* sp. nov., Untermaßfeld. – a Complete upper tooth row of an old individual, dex., IQW 1980/15 231 (Mei. 14 713). – b, c M^2, dex., IQW 1980/15 901 (Mei. 15 412); occlusal and lateral views. – d-f M^3, dex., IQW 1980/17 501 (Mei. 17 023); medial, lateral and occlusal views. – g, h Mandible and tooth row, adult individual, ramus sin., IQW 1982/18 396 (Mei. 17 916); medial and occlusal views. – Scale = ca. 1:2.

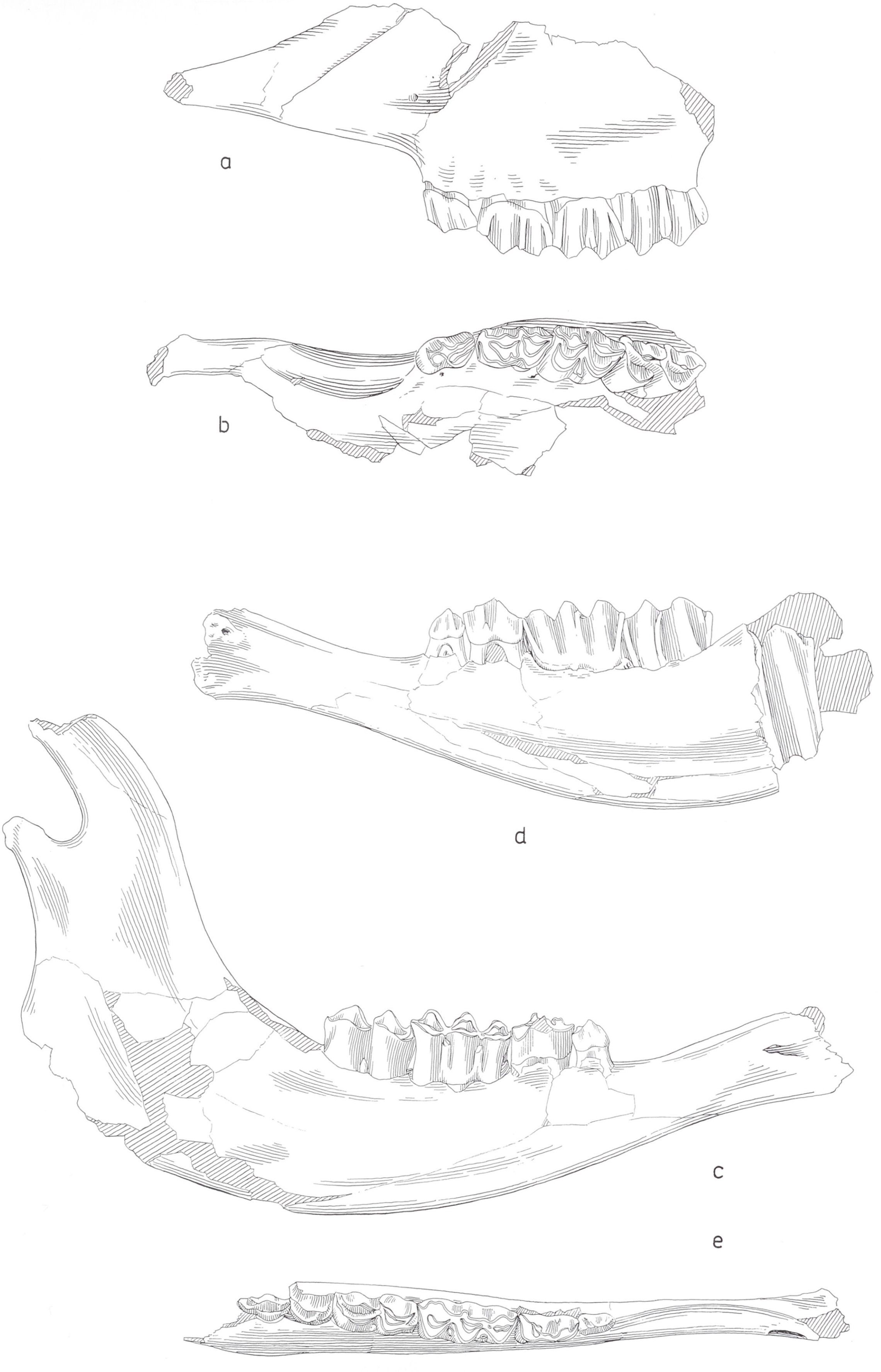

Fig. 4 *Bison menneri* sp. nov., Untermaßfeld. – a, b Fragment of maxilla of young individual with dP^2-dP^4 and M^1, sin., IQW 1980/15 358 (Mei. 14 870); lateral and palatine views. – c-e Mandible of young individual with dP_2-M_2, dex., IQW 1980/15 988 (Mei. 15 499); medial, lateral and occlusal views. – Scale = ca. 1:2.

Measurements. Alveolar length of dP^2-dP^4 – 64 mm, their length at the occlusal surface – 68 mm. In two Siberian maxillas the occlusal length of dP^2-dP^4 is 69-72 mm.

3.2.3. Upper dentition of adult individuals

Complete upper tooth row IQW 1980/15 231 (Mei. 14 713). Taf. 23, 16; Fig. 3, a.
Fragment of maxilla with P^4-M^1 IQW 1981/17 690 (Mei. 17 212). Taf. 23, 11,12.
Isolated teeth:
P^2 – IQW 1987/22 064 (Mei. 21 583);
P^3 – IQW 1987/21 964 (Mei. 21 483), IQW 1987/22 315 (Mei. 21 834);
M^2 – IQW 1980/15 901 (Mei. 15 412). Taf. 23, 9, 10; Fig. 3, b-c. IQW 1980/16 686 (Mei. 16 207), IQW 1980/16 952 (Mei. 16 473). Taf. 23, 13-15. IQW 1980/17 595 (Mei. 17 117), IQW 1986/21 154 (Mei. 20 673), IQW 1987/22 104 (Mei. 21 623), IQW 1987/22 108 (Mei. 21 627), IQW 1987/22 179 (Mei. 21 698).
M^3 – IQW 1980/17 501 (Mei. 17 023). Taf. 23, 17-19; Fig. 3, d-f. IQW 1987/21 962 (Mei. 21 481).

The only complete upper tooth row belongs to an old individual (stage S-4 according to Skinner and Kaisen 1947 Pl. 10 Fig.1 C). The fossette on P^2 is already worn out, that on P^3 is near this stage. The lingual style is near the final stage of wear and is well developed on M^{2-3}. The teeth are covered with a thick layer of enamel, M^2 and M^3 especially so. The posterior-lateral style of M^3 is moderately developed and insignificantly bent backward.

The alveolar length of the tooth row is noticeably less than in *B. priscus, B. bonasus* and *B. bison* (Table 2). The tooth row of the Untermaßfeld bison is slightly shorter even as compared with such primitive and not very large bovids as *Leptobos* (Saint Vallier – 135 mm, Seneze – 130 mm), *Adjiderebos* (138 mm), *B. palaeosinensis* (Nihowan – 131-144 mm) (Viret 1954; Merla 1949; Dubrovo and Burchak-Abramovich 1986; Teilhard and Pivetau 1930). Judging from the length of M^1-M^3 it is also shorter than in Voigtstedt, Süßenborn and Mauer bison (Table 2).

This distinction is not so sharp when isolated teeth are compared, M^2 and M^3 in particular. Teeth of the same size can be found, though not often, among Siberian *B. priscus* as well as in Voigtstedt and Süßenborn collections. It can be explained by a wide range of variation in tooth size in these localities and by tooth size also differing at various stages of wear. In general, the size of upper teeth of the Untermaßfeld bison seems to be most similar to the small bovine from Venta Micena (Moya-Sola 1987) (see Table 2) and more or less close to the teeth of the Pirro Nord bovid (De Giuli et al. 1986).

A low premolar/molar ratio in the Untermaßfeld specimen is also notable (Table 2). However, I incline to relate it to an old individual age of the specimen. In available series of *B. priscus* upper dentitions such a low ratio is found only in one senile specimen.

Comments. Numerous papers describing large bovid remains pay much attention to the structure and proportions of some tooth elements. Sometimes taxonomic importance is attached to these features. For instance, features are cited in *B. schoetensacki schoetensacki* and *B. schoetensacki lagenocornis* diagnoses such as ratio between the length of anterior and posterior main columns of M^2 and M^3, ratio between length and width of a tooth, shape of anterior and posterior walls of molars, development and direction of posterior-lateral style of M^3 (Flerov 1969; Flerov and David 1971). Observations on a large range material convinced the writer that all these features are subjected to a very wide variation and depend primarily on the stage of wear. For instance, crown width of upper molars notably increases to the base of the crown, while crown length slightly decreases. Due to that, the occlusal outline of the tooth changes in the course of wear from narrow and elongated to almost square at the crown base. Correspondingly, the index of tooth width to its length (on the occlusal surface) changes from 50% to almost 100% on the same tooth, and in M^1 even more than 100%. During wear, the posterior column of M^2 shortens faster than the anterior, and the ratio between their length changes.

Variability of proportions and minor details of structure of large bovine teeth are so wide that even the possibility of discrimination between *Bos primigenius*, *Bison priscus* and *B. bonasus* remains a matter of debate. Many students who dealt with very voluminous collections of bovines hold rather sceptical view

	Bison menneri Sp. n. Untermaßfeld		*B.voigtstedtensis* Voigtstedt (Fischer,1965)					*B.schoetensacki* Mauer,Süßenborn,Isernia				»*Bison*« sp. Venta Micena (Moya-Sola,1987)				*Bison priscus* Northeast Siberia			
	IQW 1980/ 15231 sen	isolated teeth*	Voi. 84	isolated teeth															
				N	MIN	MAX	AVG	N	MIN	MAX	AVG	N	MIN	MAX	AVG	N	MIN	MAX	AVG
Lp-m	126.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	138.0	159.0	150.6
Lp	46.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	54.0	65.0	59.0
Lm	81.0	-	86.2	-	-	-	-	2**	85.0	88.0	-	-	-	-	-	8	84.0	108.0	95.8
Lp:Lm,%	57.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	54.5	67.0	62.1
L P^2	17.0	-	-	2	18.0	19.0	-	-	-	-	-	3	13.5	21.2	17.4	2	18.0	19.0	-
L P^3	15.5	-	-	3	17.5	21.0	19.3	-	-	-	-	2	18.0	20.2	-	3	20.0	20.5	-
L P^4	16.5	16.5	-	-	-	-	-	-	-	-	-	4	15.5	19.5	17.5	4	17.0	21.0	19.1
L M^1	22.0	22.5;24.5	24.3	-	-	-	-	2**	23.0	24.0	-	11	22.8	27.2	25.9	6	22.5	30.0	25.4
L M^2	27.5	29.0	29.0	2	29.0	33.5	-	2**	30.0	31.0	-	9	26.2	30.9	28.7	10	26.5	36.5	32.3
L M^3	30.5	33.4	32.3	5	29.0	33.0	31.4	25	30.7	36.3	32.9	10	27.4	32.2	29.7	6	32.0	36.7	35.0

* P^4+M^1- IQW 1981/17690; M^1- IQW 1983/19907; M^2- IQW 1980/15901; M^3- IQW 1980/17501

** Cited values are for Mauer (Fischer,1965) and Süßenborn (Flerov,1969) respectively. These values for M^3 length are 31.3 and 31.0 respectively. Data for Isernia from Sala (1987).

Tab. 2 Measurements of upper dentition of *Bison menneri* sp. n. and various large bovids, mm, and indices, %.

on the subject, especially concerning isolated teeth (Lehman 1949; Stampfli 1963 etc.). At the same time, restricted samples of fossil bison often induced students to describe minor details of their structure. In order to avoid repeating this mistake, it seems reasonable to abstain from detailed description of teeth of the Untermaßfeld bison. This decision applies to the proportions and details of structure of lower dentition of the Untermaßfeld bison as well.

3.2.4. Mandible of young individual.

Incomplete right mandible with dP_2-M_2; angulus mandibulae is broken, incisive part is absent. IQW 1980/15 988 (Mei. 15 499). Taf. 23, 1-3; Fig. 4, c-e.

Individual age – juvenile, corresponding to the stage I of Skinner and Kaisen (1947 Pl. 12 Fig. 2-3). Milk premolars are in the stage of active work, M_1 is at the beginning of wear, M_2 has not yet erupted. Besides this most complete specimen there are 9 more mandible fragments of similar individual age.

The lower edge of the mandible is gently convex. Ascending ramus rises more vertically than in adults. Angulus mandibulae seems to project almost as far backward as processus condylaris. Dental part has high and narrow cross-section similar in proportion to adult mandibles. Diastema seems to be rather short – the distance between posterior point of foramen mentale and anterior point of the dP_2 alveole makes up 54% of length of dP_2-M_1 tooth row. In *B. priscus* and *B. bison* of similar individual age this ratio is between 57% and 63% (n=3).

Measurements. Anterior point of dP_2 alveolus (dP^2ant) – posterior point of foramen mentale – 53 mm; dP_2ant – proc. condilaris – 220 mm; dP_2ant – angulus mandibulae – ca 202 mm (reconstructed); height of pars dentalis at the anterior edge of M_1 – 49.5 mm; transverse width of pars dentalis at the same point – 25 mm; alveolar length of dP_2-M_1 – 98 mm, of dP_2-dP_4 – 68 mm.

3.2.5. Mandible of adult individuals

Four more or less complete mandibles of adult animals: IQW 1982/ 18 396 (Mei. 17 916) – Taf. 24, 4,5; Fig. 3, g, h. IQW 1980/ 21 5221 (Mei. 14 703) – Taf. 24, 1-3. IQW 1980/15 883 (Mei. 15 394), IQW 1984/ 20 081 (Mei. 19 601). Four damaged specimens (3 – senile, 1 – subadult) and five fragments with more or less complete tooth rows.

To represent the overall size of mandible, I used the length of pars dentalis measured from the anterior point of P_2 alveolus to the posterior point of angulus mandibulae (P_2 – a.m.). In this dimension the Untermaßfeld lower jaws are evidently smaller than those of the Holocene Bos primigenius (Degerbøl and Fredskild 1970) and of »*B. schoetensacki*« from Tiraspol. When compared with the not very large Late Pleistocene *B. priscus* from Northeast Siberia, the Untermaßfeld mandibles equals to the smallest specimens of this sample.

The length of the tooth row of normal adult specimens from Untermaßfeld is also smaller than of Tiraspol and Taubach *Bison, Bos primigenius*, and of most of Siberian *B. priscus*[1]. The Untermaßfeld tooth rows have approximately the same length as the single specimens from Voigtstedt and Süßenborn, but exceed the tooth row lengths of such primitive bovines as *Leptobos, B. palaeosinensis*, and *Ioribos* (Tables 3 and 4).

The ascending ramus of the mandible in *B. menneri* is noticeably deflected backwards similar to *B. priscus* and *Bos primigenius*. The dental part is high, and not inflated in cross-section. The height of pars dentalis at the level of M_3 measured on the inner side of ramus always exceeds the total length of M_1+M_2 (cf. Flerov 1979). Relative length and thickness of the toothless part of the mandible are the same as in *B. priscus*. Judging from single specimens preserved, the symphyseal part of *B. menneri* mandible is not so high as in *B. priscus*.

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[1] In subadult specimens the tooth row length is essentially longer due to elongated upper parts of the crowns while in senile specimens the tooth row became shortened.

		IQW 1980/ 15221 ad.	IQW 1982/ 18396 ad.	IQW 1984/ 20081 ad.	IQW 1980/ 15883 sen.	IQW 1980/ 17222 sen.	IQW 1983/ 19198 sen.	IQW 1985/ 20765 sen.	IQW 1981/ 17672 sad.	N	MIN	MAX	AVG	STD
1.	P_2 - a.m.	275.0	278.0	>258.0	c276.0	-	-	-	-	3	275.0	278.0	276.3	1.2
2.	P_2 - p.c.	316.0	325.0	314.0	312.0	-	-	-	-	4	312.0	325.0	316.8	5.0
	1:2, %	87.0	85.5	-	88.5	-	-	-	-	3	85.5	88.5	87.0	1.2
3.	W, M_3	32.0	35.0	32.5	30.7	c28.0	-	29.0	31.0	7	28.0	35.0	31.2	2.1
4.	H, M_3	c69.0	66.5	66.0	c67.0	c62.0	-	-	70.0	6	62.0	70.0	66.8	2.5
	3:4, %	46.4	52.6	49.2	45.8	45.2	-	-	44.3	6	44.3	52.6	47.3	2.9
5.	L: P_2-M_3	155.0	156.0	157.0	149.0	149.0	148.0	(142.0)	(169.0)	6	148.0	157.0	152.3	3.7
6.	L: P_2-P_4	54.0	54.0	58.0	55.0	52.5	56.0	(51.0)	(65.5)	6	52.5	58.0	54.9	1.7
7.	L: M_1-M_3	98.0	100.0	97.0	94.0	95.0	91.0	(91.0)	(101.5)	6	91.0	100.0	95.8	2.9
	6:7, %	55.1	54.0	59.8	58.5	55.3	61.5	(56.0)	(64.5)	6	54.0	61.5	57.4	2.8

P_2 - a.m. - distance from anterior point of P_2 alveole to the posterior point of angulus mandibulae
P_2 - p.c. - from the same point to the posterior point of processus condyloides
W, M_3 - transverse width of pars dentalis at the level of anterior end of M_3
H, M_3 - height of pars dentalis at the same point (measured on the interior side of mandible ramus)
( ) - measurements of too young or too old individuals not included in the statistics

Tab. 3 Measurements of mandibles and tooth rows of *Bison menneri* sp.n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n. Untermaßfeld					*Leptobos* S.Vallier, Seneze+)*)			*B.palaeosinensis* Nihowan*)	*B.schoetensacki*		*B.«schoetensacki«* Tiraspol			*Bison priscus* N.-E.Siberia, Late Pleist.					*Bos primigenius* Denmark, Neolithic Degerbøl & Fredskild, 1970				
	N	MIN	MAX	AVG	STD	N	MIN	MAX		Voigtstedt	Süßenborn	N	MIN	MAX	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
1. P_2 - a.m.	3	275.0	278.0	276.3	1.2										12	275.0	309.5	293.7	10.3	29	271.0	325.0	300.5	13.3
2. P_2 - p.c.	4	312.0	325.0	316.8	5.0										12	309.0	363.0	337.6	18.2	29	306.0	374.0	342.4	18.0
1:2, %	3	85.5	88.5	87.0	1.2	3	89.7	91.7	94.3						11	82.6	89.0	86.2	1.8	29	84.9	91.0	87.8	1.6
3. W, M_3	7	28.0	35.0	31.2	2.1										14	28.0	36.5	31.9	2.2					
4. H, M_3	6	62.0	70.0	66.8	2.5										14	62.0	71.0	65.8	2.5					
3:4, %	6	44.3	52.6	47.3	2.9										14	44.2	56.2	48.5	3.0					
5. L: P_2-M_3	6	148.0	157.0	152.3	3.7	2	140.0	143.0	148.0	156.5	156.5	3	170.0	175.0	14	148.0	173.0	160.0	6.8	29	158.0	194.0	172.3	7.1
6. L: P_2-P_4	6	52.5	58.0	54.9	1.7	2	51.0	52.0	58.5	60.5	58.5				14	49.0	62.0	55.7	3.6	25	56.0	65.0	60.5	2.7
7. L: M_1-M_3	6	91.0	100.0	95.8	2.9	2	89.0	91.0	88.5	96.5	98.0				14	94.5	114.0	104.0	5.3	27	100.0	124.0	110.6	5.1
6:7, %	6	54.0	61.5	57.4	2.8	2	57.3	57.1	66.1	62.7	59.7	3	55.0	58.0	14	45.4	58.5	53.7	4.2	25	50.0	60.0	54.9	2.8

+) Merla, 1949.
*) Teilhard & Pivetau, 1930.
See Table 3 for explanation of measurements.

Tab. 4 Measurements of mandibles and lower tooth rows of various bovids, mm, and indices, %.

3.2.6. Lower dentition of juvenile and subadult individuals

There are 10 mandible fragments with deciduous teeth, M_1 unworn or at the initial stage of wear, and with non-erupted M_2 (sometimes erupted but unworn). The best preserved specimen of this age, IQW 1980/15 988 (Mei. 15 499), is pictured on Taf. 23, 1-3, and Fig.4, c-e. Some isolated teeth belong to about the same ontogenetic stage: dP_3 – 3, dP_4 – 3, unworn M_1 – 7, unworn M_2 – 2. To a later stage belongs mandible IQW 1981/17 672 (Mei. 17 194) pictured on Taf. 23, 4-5, with P_2 and P_3 at the initial stage of wear; dP_4, M_1 and M_2 in the active wear, and unworn M_3. Isolated unworn P_2 (1) and M_3 (1) belong to approximately the same stage of individual development.

3.2.7. Lower dentition of adult individuals

There are 4 complete lower tooth rows: IQW 1982/18 396 (Mei. 17 916). Taf. 24, 4,5; Fig. 3, g, h.; IQW 1983/19 198 (Mei. 18 718). Taf. 23, 7,8; IQW 1985/20 765 (Mei. 20 284). Taf. 23, 6; IQW 1987/ 22 071 (Mei. 21 590). The other 6 specimens lack one or two premolars [e.g., IQW 1980/ 15 221 (Mei. 14 703) – Taf. 24, 1-3]; two more have only 2 or 3 teeth preserved. Among numerous isolated teeth only few belong to adult individuals: P_3 – 1, M_2 – 3, M_3 – 3, incisors – 4.

The total length of the tooth rows is commented on above (see Section 3.2.5 and Tables 3 and 4). Premolar/molar index of the Untermaßfeld lower tooth rows ranges within almost the same limits as in other bovines. On the average, it is slightly higher than in the latest bovines, *B. priscus* from Northeast Siberia and *Bos primigenius*, while in some earlier bovines the index seems to be more similar to the Untermaßfeld species. Though not very well pronounced, this feature is supported by the measurements of isolated lower teeth.

The length of the isolated lower teeth of *B. menneri* was compared with the large samples from Venta Micena (Moya-Sola 1987), Weimar-Ehringsdorf (Flerov 1975), and from the Late Pleistocene of Northeastern Siberia (the writer's collection), as well as with some other samples and some important specimens from the Early-Middle Pleistocene (Fig. 5).

P_2 and P_3 of all those bovines differ insignificantly in size, though there are some larger specimens in the Siberian sample. The P_4 length pattern is also more or less homogeneous. On the average, the Untermaßfeld P_4 are slightly longer than those from Venta Micena and shorter than the Siberian ones. The Ehringsdorf teeth are distinguished as the largest ones.

Being only slightly outlined on P_4, the same length differences become more and more pronounced on the molars. In spite of large overlapping of different samples, the general pattern is seen as the following: *B. menneri* teeth are only slightly larger than the corresponding ones from Venta Micena, and yield to all other samples in this respect. This is especially evident when the M_3 length is plotted. Even the largest of the Untermaßfeld M_3 are usually shorter than the average of the other samples excluding Venta Micena. It is important to note that in this feature the Voigtstedt sample is more similar to Isernia, Westbury, Süßenborn and Mauer samples than to the Untermaßfeld one. However, isolated small M_3 are reported from the lower bed of Westbury (Bishop 1982) and from Mauer (Freudenberg 1914).

The lower teeth of the Untermaßfeld bison retain the general morphological pattern peculiar to all bison and wisent species. Similarly to those species, they are widely variable in minor details. It is especially true for the depth of lingual reentrant valleys on premolars which determines their occlusal surface pattern at different stages of wear, height of labial accessory columns on molars, etc.

A common distinctive feature of adult molars from Untermaßfeld is a thick cement deposition. It starts as early as at the beginning of wear, and by senility the cement covers the whole tooth with a thick layer, making the tooth walls even. In Siberian bison, the cement layer is normally very thin and increases only in the valleys of the old individuals. I could not find any more or less thick cement cover on Taubach and Süßenborn teeth though in some cases it could have been not preserved. Cement deposition is more peculiar to the Voigtstedt teeth, though to a less degree than in Untermaßfeld.

Comments on mandible and **lower teeth**. Lower jaw and teeth of various species of large Quaternary bovines (and even of genera *Bison* and *Bos*) are essentially similar. However, some students tried to in-

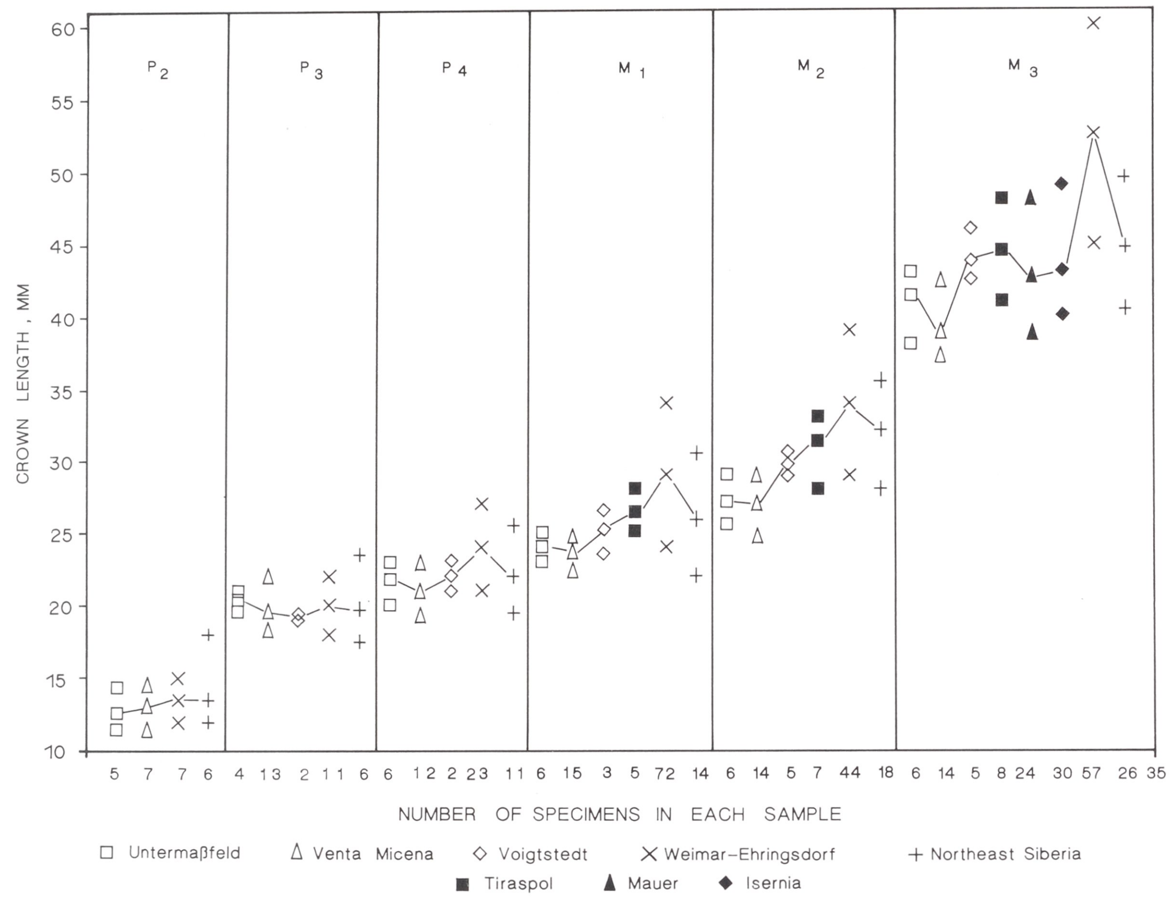

Fig. 5 Length of bovine lower teeth from various Quaternary localities, mm. – Untermaßfeld: *Bison menneri* sp. nov.; Venta Micena: *Bison* sp. (Moya-Sola 1987); Voigtstedt: *Bison schoetensacki voigtstedtensis* (Fischer 1965); Tiraspol: *Bison »schoetensacki«* (Flerov and David 1971); Mauer, Isernia: *Bison schoetensacki* (Sala 1986); Weimar-Ehringsdorf: *Bison priscus mediator* (Flerov 1975); Northeast Siberia: *Bison priscus*. – Each vertical column containing three similar symbols presents the minimum, average and maximum crown length in each sample. Values at the bottom of each column indicate the number of specimens in the sample. For instance, there are 6 specimens of M_2 in the Untermaßfeld varying in length from 25.5 to 29 mm (average 27.1 mm).

terpret some features of mandible morphology as indicating a certain degree of evolutionary development, or as demonstrating a certain ecological type of the species.

The features of the first kind are usually considered with respect to such primitive bovines as *Leptobos*, *B. palaeosinensis* and others. For instance, the *Leptobos* mandible has a more vertically positioned ascending ramus, with angulus mandibulae projecting almost as far backward as processus condyloides. The same feature has been reported for *B. palaeosinensis* (Teihard and Pivetau 1930). That probably induced Flerov (1979) to extrapolate this feature over all the members of newly proposed subgenus *Eobison*. According to Merla (1949), among Recent bovines *Bos* and *Bibos* look relatively primitive in this respect, while *Bison* is the most advanced and shows the strongest backward deviation of the ascending ramus.

To measure a degree of backward deviation of the mandible ascending ramus it is possible to use a ratio of two measurements: the first is the distance from anterior point of P_2 to the posterior point of angulus mandibulae (P_2 - a.m.), and the second is the distance from the same point to the posterior point of processus condyloides (P_2 - p.c.). The more vertical is the ramus position, the higher will be the index (P_2 - a.m.):(P_2 - p.c.), %. Estimation of this index for mandibles of the Untermaßfeld bison, Siberian *B. priscus* and *Bos primigenius* from the Danish Neolithic (Table 4) shows almost no difference between these forms. The suggested index confirms that *Leptobos* has a more vertically positioned ascending ramus as compared to *Bos* and *Bison*, but it is in *B. palaeosinensis* that this feature is the most pronounced

(Tab. 4). However, it should be noted that the only complete mandible from Nihowan belongs to a young individual with milk premolars still in use. A more vertical position of ascending ramus in young individuals is evidenced by the ontogenetic collection of American bison pictured by Skinner and Kaisen (1947) as well as by the juvenile mandible of the Untermaßfeld bison (Taf. 23, 2; Fig. 4, c). Hence, the question of manifestation of this feature in earliest *Bison* remains uncertain. In any case, *B. menneri* in this respect does not differ from more advanced bison.

Flerov (1979) suggested some features of the mandible indicating ecological variability of bison. He distinguished two main types: inhabitants of open steppe environments grazing on coarse grasses (he called them »true grassifages«), and forest inhabitants feeding on soft forest grasses, twigs, leaves and bark of trees and shrubs. Under the second heading Flerov (1979, 43) classified such species as *B. voigtstedtensis, B. schoetensacki, B. bonasus*, and *B. priscus athabascae*. Though certainly all bison were grazers with various degrees of selectivity (Guthrie 1990), for convenience I shall label these two Flerov types as »grazers« and »browsers«. In Flerov's opinion, a high and thin dental part (not inflated in cross-section) is characteristic for »grazers« while the »browsers« have a lower dental part of mandible, inflated at the level of the alveoli. In »grazers«, the height of pars dentalis at the level of M_3 considerably exceeds the total length of M_1+M_2, while in »grazers« these two measurements are roughly equal.

I tried to check this feature on the available material. In adult specimens from Untermaßfeld the medial height of the dental part at the anterior end of M_3 exceeds joint length of M_1+M_2 by 20-30%. Approximately the same ratio is observed in Siberian bison. Moreover, evaluation of this feature on 2 partially preserved mandibles from Voigtstedt shows that they also do not differ from *B. priscus*.

Another index – ratio of pars dentalis largest width (thickness) at the level of anterior end of M3 (W, 'M_3) to its medial height at the same place (H, 'M_3) – also shows similar values for *B. menneri* and Siberian *B. priscus* (Table 4). Indices of mandibles from Taubach, Ehringsdorf (according to Flerov's measurements) and from Tiraspol fall within the same range.

So, if I rely upon these features suggested by Flerov to distinguish between »grazing« and »browsing« bison, the similarity between the Untermaßfeld bison and such a typical grazer as Siberian *B. priscus* should cause me to interpret *B. menneri* also as a »grazer«. However, my observations failed to support the validity of the features, and we should abstain from using these criteria in any analysis of bison ecology for the present.

3.2.8. Vertebrae

The low number of bison vertebrae in the Untermaßfeld collection (up to 10 pieces) is surprising. Probably, not all of them have been identified. Most of them are fragmentary and show no peculiar features. The only more or less complete thoracic vertebra, IQW 1980/15 224 (Mei. 14 706) (Taf. 25, 1), has its neural spine longer than 380 mm. A complete neural spine of one of the anterior thoracic vertebrae (without vertebra itself), IQW 1985/20 723 (Mei. 20 242), is about 360 mm long.

According to Reshetov and Sukhanov (1979), spines of the vertebrae in the anterior third of the thoracic section of *Bison bonasus* and females of *Bison bison* have similar lengths on average. Approximately the same is the length of the spine of the first thoracic vertebra in Siberian *B. priscus* in our collection, though it may reach as much as 600 mm.

3.2.9. Scapula

There are 8 partially preserved scapulae, of which the best preserved one, IQW 1980/15 301 (Mei. 14 813), is pictured in Taf. 25, 2,3. Some measurements can be taken for 4 of them. One specimen, IQW 1980/15 627 (Mei. 15 139), is rather large, belonging probably to a male, the others are notably smaller. In greatest length of glenoid process the Untermaßfeld scapulae are on the average smaller than those of the Late Pleistocene *B. priscus* from Siberia (Table 5). The bladebones of *B. schoetensacki* from Mauer (Sala 1987) are essentially larger. The shape of the glenoid process in the Untermaßfeld specimens is typical for *Bison*. It has rather a strong tuber scapulae and oval glenoid cavity. In the largest specimen, IQW 1980/15 627 (Mei. 15 139), the cavity is more rounded.

	Bison menneri, sp. n. Untermaßfeld									*Bison priscus* Boj. North-East Siberia				
	IQW 1980/ 15301	IQW 1981/ 17653	IQW 1983/ 16964	IQW 1980/ 15627	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
1. L, p.g.	83.0	80.5	82.0	92.5	4	80.5	92.5	84.5	4.7	6	80.0	97.0	92.0	6.0
2. L, c.g.	67.5	70.0	68.0	77.0	4	67.5	77.0	70.6	3.8	5	65.0	81.0	75.4	6.1
3. W, c.g.	56.0	62.5	55.0	70.0	4	55.0	70.0	60.9	6.0	5	52.0	71.0	61.4	6.9
4. L, c.s.	71.0	67.0	-	82.0	3	67.0	82.0	73.3	6.3	5	69.0	91.0	81.0	8.9
2:1, %	81.3	87.0	82.9	83.2	4	81.3	87.0	83.6	2.1	5	80.0	88.0	82.8	2.8
3:2, %	83.0	89.3	80.9	90.9	4	80.9	90.9	86.0	4.2	5	77.1	87.7	81.3	3.5

1. L, p.g. - greatest length of glenoid process;
2. L, c.g. - length of the glenoid cavity;
3. W, c.g. - width of the glenoid cavity;
4. L, c.s. - length of collum scapulae.

Tab. 5 Measurements of scapula fragments of bisons, mm, and indices, %.

3.2.10. Humerus

Almost complete left humerus IQW 1982/18 398 (Mei. 17 918). Taf. 26, 1-3; Fig. 6, a-c. Two bones with damaged proximal end (tuberculum majus broken): IQW 1980/16 048 (Mei. 15 559) and IQW 1981/17 711 (Mei. 17 233). 45 distal fragments, about half of them with a part of diaphysis, and 1 fragment of proximal part.

Specimens with preserved proximal parts (caput humeri) seem to belong among the males, though not the largest in the Untermaßfeld sample (Table 6). They indicate a large-sized animal. In their length from the distal end to the proximal point of caput humeri (medial length) they approximate to the largest known bison, such as those from Burgtonna, Tiraspol (Table 7), Mosbach and Rhine Gravels (Martin 1987), as well as large *Bos primigenius*. They are noticeably longer than the bones of Siberian Late Quaternary *B. priscus*. However, in all available width measurements (of distal end and diaphysis) the Untermaßfeld bones appear to yield to almost all of the mentioned *Bison* populations. While male specimens from Untermaßfeld approximate in these measurements to rather small Siberian bison, most of females have no equivalents among the Siberian sample.

In total, this suggests that *B. menneri* humeri should have been rather gracile. However, it can be checked on the 3 more complete specimens alone. Comparison of ratios of diaphysis width and width of the distal articular surface to the medial length (Table 7) shows that these three male specimens are definitely more slender than humeri of *Bos primigenius* and Siberian *B. priscus*, not to mention such massive forms as Tiraspol and Burgtonna ones.

The distal end of the humerus in general has a structure typical for *Bison*. The trochlea has a rather developed lateral part. In 81% of the specimens its width measured from the lateral point of the trochlea to the middle of the guiding crest makes up more than 43% of the remaining (medial) part of the trochlea (Bibikova 1958). Relief of the trochlea is almost as smooth as in *B. priscus*. However, the shape of the guiding crest is more variable, on some specimens it is more sharp than it is usual for *Bison*. Up to 20% of specimens demonstrate a clearly asymmetric guiding crest (with a steeper lateral slope) that is thought to be characteristic of *Bos primigenius*. Another 25% have slightly pronounced asymmetry of the crest. Thus, about a half of the Untermaßfeld humerus sample shows smooth symmetrical guiding crest that is thought to be typical for *B. priscus*.

The fossa olecrani in the Untermaßfeld humeri is usually rather sharp-oval as in *B. priscus*. Some specimens have a more obtuse top of the fossa, but never reach such a shape as pictured by Martin (1987, Abb.7.10) for *Bos primigenius*.

Thus, the humerus of *B. menneri* is long, slender, and with a mosaic distribution of features ascribed to *Bos* and *Bison*, with the dominance of the latter.

Comments on humerus morphology. The distal end of the bison humerus is well studied as a result of numerous attempts to find discriminating features between *Bison* and *Bos*. On the large Untermaßfeld sample I examined many features suggested by Lehmann (1949), Bibikova (1958), Olsen (1960), Stampfli (1963). Recent work by Martin (1987) successfully demonstrates how variable are most of these features. According to Martin, three features of the humerus distal end are constant enough to discriminate between *Bos* and *Bison*. One is the position of guiding crest on the trochlea (relation between the lateral and medial parts of the trochlea). The second is the shape of this crest, and the third is the shape of olecranon fossa.

To value the first feature, I used the same index that Martin puts as Stampfli's Trochlea-Index (Tables 6,7, Wdal:Wda, %). Actually, this is only an arithmetic variation of the index suggested by Bibikova (1958). Of course, the boundary between *Bison* and *Bos* values is not so sharp as Bibikova believed, and the index can be used only on statistic grounds. The range of variation of the index for *B. menneri* is very similar to those of the Siberian and German samples of *B. priscus* (the latter two coincide almost exactly), and differs from *Bos primigenius* even more reliably than *B. priscus* does.

The shape of the guiding crest of the trochlea in *B. menneri* has been reported above. Sharp and asymmetric contours of the crest in *Bos* contrary to more flat and symmetric in *Bison* were noticed by Rüti-

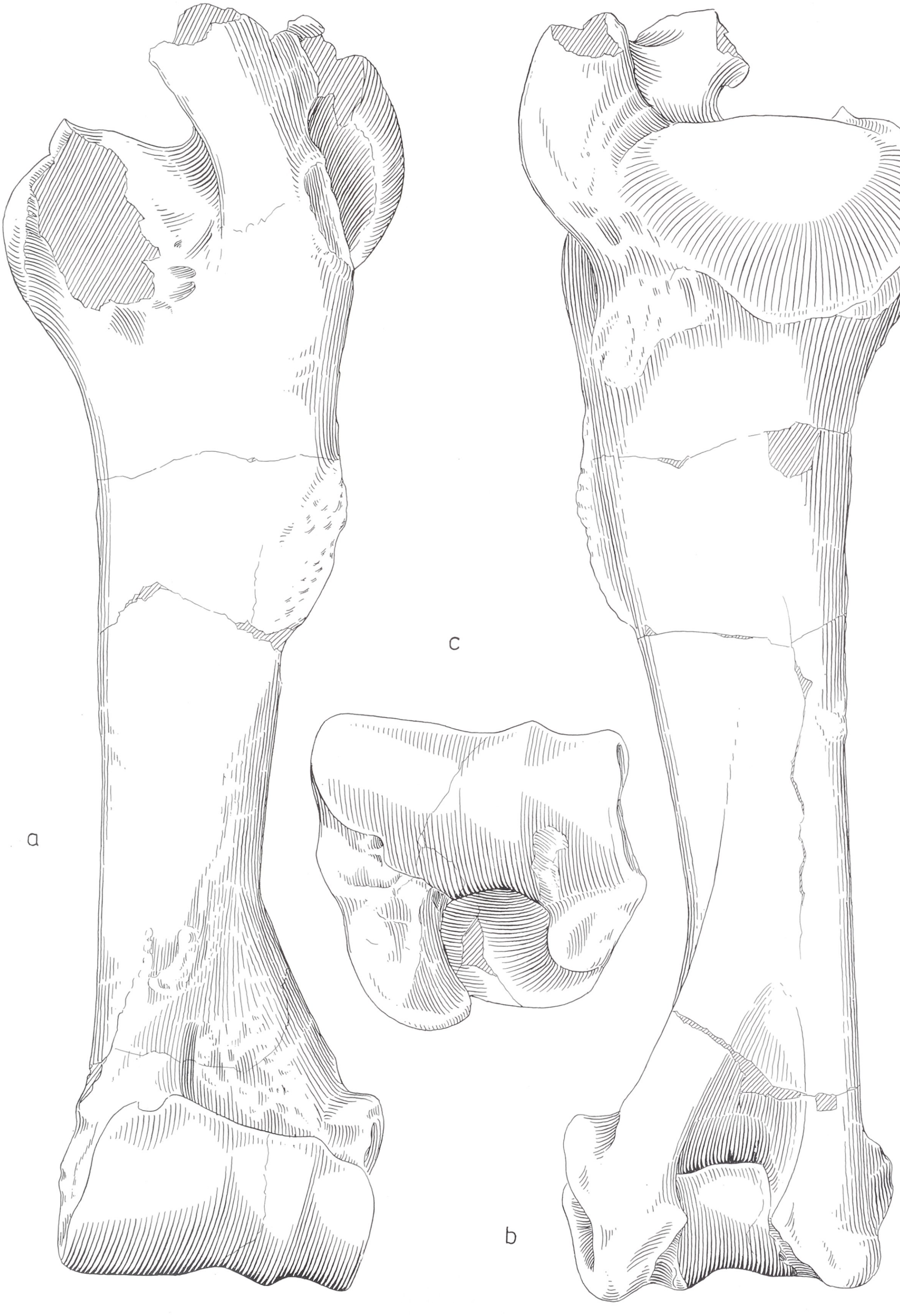

Fig. 6 *Bison menneri* sp. nov., Untermaßfeld. – a-c Humerus sin., IQW 1982/18 398 (Mei. 17 918), male; anterior, posterior and distal views. – Scale = ca. 1:2.

	IQW 1982/ 18398 m	IQW 1980/ 16048 m	IQW 1981/ 17711 m	IQW 1980/ 15361 m	IQW 1983/ 19156 m	IQW 1980/ 16166 m	IQW 1980/ 16114 m	IQW 1982/ 17881 m	IQW 1980/ 15212 m	IQW 1982/ 17836 m	IQW 1980/ 16345 m	IQW 1982/ 18347 m	IQW 1983/ 18908 m	IQW 1980/ 17332 m	IQW 1983/ 19187 ?	IQW 1980/ 17561 ?	IQW 1980/ 17422 f	IQW 1980/ 16124 f	IQW 1985/ 20426 f	IQW 1980/ 17361 f	IQW 1982/ 18529 f	IQW 1980/ 16112 f	IQW 1981/ 17680 f	IQW 1985/ 20900 f
L	434.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lc	385.0	389.0	370.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wp	137.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wm	54.5	56.0	55.0	59.0	-	55.0	56.0	c56.0	-	-	-	-	-	-	52.0	-	-	46.3	49.5	-	44.5	50.0	51.5	-
Wd	105.0	111.0	115.0	115.0	107.0	113.0	118.0	111.0	-	c120.0	c108.0	106.0	109.0	-	100.0	c102.0	-	101.0	-	-	101.0	100.0	-	c109.0
Wda	101.0	103.5	102.0	104.0	104.5	103.0	102.0	101.0	103.0	100.0	98.0	98.0	97.0	96.5	93.0	94.0	96.0	94.0	93.0	93.0	92.0	92.0	90.0	91.0
Wdal	-	33.5	31.0	32.0	c32.0	32.5	33.5	31.5	33.0	34.0	29.0	30.0	30.0	c31.0	-	27.0	32.5	30.0	29.0	28.0	29.0	29.0	30.0	27.0
Htm	-	66.0	63.0	67.5	62.5	65.5	67.5	63.5	-	63.5	64.0	68.0	61.0	-	58.5	59.0	c66.0	60.0	c57.0	55.0	58.0	c56.0	59.0	59.0
Hch	-	47.0	45.0	c50.0	43.5	-	46.5	46.0	-	47.5	46.0	45.0	46.5	-	44.5	43.5	48.0	43.0	46.0	44.0	41.5	41.0	-	>41.0
Wdal:Wda	-	32.4	30.4	30.8	30.6	31.6	32.8	31.2	32.0	34.0	29.6	30.6	30.9	32.1	-	28.7	33.9	31.9	31.2	30.1	31.5	31.5	33.3	29.7
Htm:Wda	-	63.8	61.8	64.9	59.8	63.6	66.2	62.9	-	63.5	65.3	69.4	62.9	-	62.9	62.8	68.8	63.8	61.3	59.1	63.0	60.9	65.6	64.8

	IQW 1980/ 16188 f	IQW 1980/ 17413 f	IQW 1981/ 17681 f	IQW 1985/ 20825 f	IQW 1983/ 19168 f	IQW 1983/ 19177 f	IQW 1987/ 21949 f	IQW 1980/ 16936 f	IQW 1980/ 17282 f	IQW 1983/ 18877 fj	N m	MIN m	MAX m	AVG m	STD m	N f	MIN f	MAX f	AVG f	STD f
L	-	-	-	-	-	-	-	-	-	-	1	434.0	434.0	434.0	0.0	-	-	-	-	-
Lc	-	-	-	-	-	-	-	-	-	-	3	370.0	389.0	381.3	8.2	-	-	-	-	-
Wp	-	-	-	-	-	-	-	-	-	-	1	137.0	137.0	137.0	0.0	-	-	-	-	-
Wm	-	48.0	c53.0	46.8	44.0	-	44.0	-	43.3	33.0	6	55.0	59.0	56.2	1.3	11	43.3	53.0	47.4	3.2
Wd	c96.0	c99.0	c96.0	96.0	90.0	95.0	94.0	c96.0	92.0	83.0	11	106.0	120.0	112.1	4.3	13	90.0	109.0	97.3	4.6
Wda	89.0	89.0	89.0	90.0	88.0	88.0	87.0	87.0	85.0	75.0	13	96.5	104.5	101.0	2.7	17	85.0	96.0	90.2	2.8
Wdal	26.0	27.5	26.0	31.0	30.0	27.0	25.0	29.5	26.0	24.0	13	29.0	34.0	31.8	1.5	17	25.0	32.5	28.4	2.0
Htm	54.0	58.0	57.0	57.0	57.0	53.5	55.0	52.0	56.3	49.5	11	61.0	68.0	64.7	2.2	17	52.0	66.0	57.0	3.0
Hch	41.5	40.0	41.0	c41.0	38.0	43.0	39.0	-	40.0	38.0	10	43.5	50.0	46.3	1.6	14	38.0	48.0	41.9	2.6
Wdal:Wda	29.2	30.9	29.2	34.4	34.1	30.7	28.7	33.9	30.6	32.0	13	29.6	34.0	31.5	1.1	17	28.7	34.4	31.5	1.8
Htm:Wda	60.7	65.2	64.0	63.3	64.8	60.8	63.2	59.8	66.2	66.0	11	59.8	69.4	64.0	2.4	17	59.1	68.8	63.3	2.5

Wda - width of distal articular surface (= BT in Martin,1987)
Wdal - width of lateral part of distal articular surface (= LAT)
Htm - height of trochlea (medial) (= MHT)
Hch - height of condylus humeri (= LHT)

Tab. 6 Measurements of humerus of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n.					*Bison priscus* Boj.					*Bison »schoetensacki«*				*Bos primigenius*							
	Untermaßfeld					North-East Siberia					Tiraspol				Ukraine, Germany				Rhine Gravels (Martin, 1987)			
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	N	MIN	MAX	AVG	N	MIN	MAX	AVG
L	1	434.0	434.0	434.0	0.0	4	353.0	418.0	370.3	27.6	1	-	-	435.0	2	401.0	450.0	425.5	6	409.0	455.0	439.3
Lc	3	370.0	389.0	381.3	8.2	6	316.0	360.0	336.5	18.5	1	-	-	387.0	3	334.0	385.0	356.3	9	372.5	397.5	388.6
Wp	1	137.0	137.0	137.0	0.0	6	104.0	123.0	109.8	6.9	1	-	-	150.0	3	119.0	149.0	137.7				
Wm	17	43.3	59.0	50.5	5.0	14	45.5	63.5	54.4	5.4	2	62.5	68.0	65.3	3	51.0	57.0	54.8	10	56	70	63.7
Wd	24	90.0	120.0	104.1	8.6	15	100.0	125.0	112.5	9.3	3	114.0	120.0	117.7	3	113.0	124.0	119.3				
Wda	30	85.0	104.5	94.8	6.0	15	90.0	111.0	100.4	7.2	3	111.5	118.0	115.7	3	94.0	105.5	99.5	10	102.0	121.0	109.7
Wdal	30	25.0	34.0	29.9	2.5	15	25.0	35.5	30.5	2.9	1	-	-	31.0	2	28.5	31.0	29.8	10	27	35.5	30.8
Htm	28	52.0	68.0	60.1	4.6	15	56.0	68.0	63.5	4.0					1	-	-	60.5	10	60.5	73	67.8
Wdal:Wda	30	28.7	34.4	31.5	1.6	15	27.8	34.0	30.4	1.7	1	-	-	27.8	2	30.3	31.3	30.8	10	26.5	29.4	28.0
Htm:Wda	28	59.1	69.4	63.5	2.5	15	59.6	67.7	63.3	2.3					1	-	-	64.4	10	65.6	73.1	69.2
Wda:Lc,%	3	26.2	27.6	26.8	0.6	6	28.1	30.1	29.9	0.8	1	-	-	30.5	3	27.4	28.3	27.9	9	27.5	30.6	28.5
Wm:Lc	3	14.2	14.9	14.5	0.3	6	14.4	17.4	15.7	1.1	1	-	-	17.6	3	14.6	16.9	15.4	9	15.0	17.7	16.6

Tab. 7 Measurements of humerus of various bovids, mm, and indices, %.

meyer (1862), neglected by Lehmann (1949) and reaffirmed by Bibikova (1958). Martin (1987) received 90% reliability of the feature. I have also never met in *B. priscus* such a sharply asymmetric crest as can be sometimes seen in *Bos primigenius*. However, a moderately asymmetric crest was observed in about 20% of *B. priscus* specimens examined, and vice versa, *Bos* can have quite symmetric outlines of the crest, as in the Friedland specimen of Lehmkuhl (1988, Taf.5). Anyhow, *B. menneri* is evidently intermediate in this feature between *Bos* and *Bison*.

I tried also to express with the help of some measurements the difference in relief of the trochlea, sharper in *Bos* and smoother in *Bison* (Stampfli 1963; Sala 1986). However, this feature appears to be too variable. I find it also very difficult to fix the shape of fossa olecrani as it cannot be measured.

Many students considered lateral tapering of the trochlea as a definite characteristic of *Bison* humeri contrary to *Bos*. According to Martin (1987), this feature expressed by Lehmann's trochlea index (ratio between heights of lateral and medial parts of trochlea) shows almost total overlapping in *Bos* and *Bison*. In *B. menneri* the range of variation of this index is still wider and almost completely overlaps both genera; however, it is notably shifted to the higher values. This shift is so large that we should rather interpret it as a result of different ways of measuring than as an evidence of a *Bos*-like feature.

Lehmann's trochlea index, %

Bison priscus (Martin 1987):	range 63.4-72.4, av.= 67.1, n=14
Bos primigenius (Martin 1987):	range 65.6-73.1, av.= 69.2, n=10
Bison menneri:	range 66.2-80.7, av.= 72.7, n=24.

In agreement with Martin, our estimations of the general proportions of the trochlea (medial height : width of trochlea, %) revealed no difference between *B. menneri*, Siberian *B. priscus*, and *Bos primigenius*. However, the resulting values are slightly higher than those cited by Martin, which also probably implies some differences in measuring.

Like Martin, I have failed to find any reliable features in morphology of the medial epicondyle.

3.2.11. Antebrachium and radius

5 complete antebrachii, 10 complete radii (some slightly damaged), 21 proximal and 15 distal fragments. Taf. 27, 1-8; Fig. 7, a-d, 8, a-e.

Radial bones of males and females of *B. menneri* are notably different in size (Table 8). Male specimens have the same overall length as a *Bos primigenius* sample from the Rhine Valley (Martin 1987), while female ones are more comparable with the much smaller form from the Danish Neolithic (Degerbøl and Fredskild 1970). The whole Untermaßfeld radius sample is equal in length to *B. priscus* from the Rhine Gravels, but on average exceeds the small Siberian Late Pleistocene form of the species (Table 9). Thus, judging from the size of radius, the Untermaßfeld bison does not differ essentially from the most common Quaternary bovids. However, it is strikingly larger than *Leptobos* and »*Bison* sp.« from Venta Micena.

In proportions, the Untermaßfeld radii seem to be more slender than most of the Quaternary bovids with the exception of the Venta Micena animal. This is especially evident in the index of the proximal width to the length of radius (Table 9), which is lower in *B. menneri* than in *Bos primigenius* and most *B. priscus* including few known complete specimens from such relatively early localities as Mosbach, Tiraspol, and Tologoy.

The lateral tuberosity of the proximal end is developed less than in *Bos*, and in this feature *B. menneri* cannot be distinguished from *B. priscus*. I could not find any difference in the proportions of the proximal articular surface between *B. menneri*, *B. priscus*, and *Bos primigenius*. However, the relief of this surface in *B. menneri* seems to suggest a wide variation between *Bison* and *Bos* features. The typical *Bos* condition is better pronounced relief of the proximal articular surface, with a deeper, sometimes asymmetric groove corresponding to the guiding crest of the humerus trochlea (see above), and deep V- or U-shaped notch for the lateral projection of the ulna. This surface in *Bison* has smoother relief, and a

Fig. 7 *Bison menneri* sp. nov., Untermaßfeld. Antebrachium sin., male (one individual). – a, b Radius sin., IQW 1982/18 360 (Mei. 17 880); anterior and proximal views. – c, d Ulna sin., IQW 1982/18 361 (Mei. 17 881); medial and anterior views. – Scale = ca. 1:2.

	IQW 1980/ 15213 m	IQW 1980/ 16938 m/sad	IQW 1980/ 16917 m	IQW 1982/ 18360 m	IQW 1980/ 16053 m	IQW 1980/ 17117 m	IQW 1982/ 18373 m	IQW 1980/ 16732 m	IQW 1982/ 18026 m	IQW 1987/ 22184 m	IQW 1980/ 17108 m	IQW 1983/ 19066 m	IQW m	IQW 1985/ 20384 ?	IQW 1982/ 18344 ?	IQW 1980/ 16646 f	IQW 1985/ 20824 f	IQW 1982/ 17797 f	IQW 1984/ 20088 f	IQW 1980/ 15271 f	IQW 1983/ 19179 f	IQW 1980/ 17358 f	IQW 1985/ 20901 f	IQW 1980/ 16990 f
Lant	-	-	-	528.0	-	518.0	-	500.0	-	-	-	-	-	-	-	-	-	470.0	-	451.0	-	-	-	-
L	418.0	c410.0	406.0	c404.0	c398.0	397.0	c385.0	375.0	-	-	-	-	-	-	-	370.0	367.0	363.0	355.0	350.0	-	-	-	-
Wp	-	110.0	115.0	110.0	-	111.0	110.0	-	118.0	117.0	112.0	111.0	110.0	-	106.0	99.0	100.0	104.0	98.6	97.0	103.5	101.5	101.3	101.0
Wpa	-	c101.0	105.0	99.0	-	-	98.0	-	106.5	105.0	106.0	99.0	101.0	96.5	97.5	91.5	91.0	93.7	90.0	89.6	93.5	93.5	93.0	92.3
Tpa	-	54.0	57.0	55.5	-	-	c48.5	-	54.0	53.0	55.0	52.0	50.0	48.0	51.0	47.2	45.5	47.2	43.0	47.4	46.5	47.0	48.0	46.0
Wm	65.5	59.0	63.0	61.0	64.0	60.0	65.0	63.0	-	-	-	-	56.0	-	57.0	55.5	52.0	54.0	55.0	52.0	-	-	53.0	-
Wd	98.0	102.0	c110.0	99.0	103.0	102.0	107.5	105.5	-	-	-	-	-	-	-	94.0	89.0	91.5	92.0	91.0	-	-	-	-
Wp:L,%	-	26.8	28.3	27.2	-	28.0	28.6	-	-	-	-	-	-	-	-	26.8	27.2	28.7	27.8	27.7	-	-	-	-
Tpa:Wpa,%	-	53.5	54.3	56.1	-	-	49.5	-	50.7	50.5	51.9	52.5	49.5	49.7	52.3	51.6	50.5	50.4	47.8	52.9	49.7	50.3	51.6	49.8
Wpa:Wp,%	-	91.8	91.3	90.0	-	-	89.1	-	90.3	89.7	94.6	89.2	91.8	-	92.0	92.4	91.0	90.1	91.3	92.4	90.3	92.1	91.8	91.4
Wm:L,%	-	14.4	15.5	15.1	16.1	15.1	16.9	16.8	-	-	-	-	-	-	-	15.0	14.2	14.9	15.5	14.9	-	-	-	-
Wd:L,%	-	24.9	27.1	24.5	25.9	25.7	27.9	28.1	-	-	-	-	-	-	-	25.4	>24.2	25.2	25.9	26.0	-	-	-	-

	IQW 1987/ 22117 f	IQW 1987/ 22173 f	IQW 1983/ 18891 f	IQW 1982/ 18393 f	IQW 1980/ 15461 f	mm					ff					mm + ff				
						N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
Lant	-	-	-	-	-	3	500.0	528.0	515.3	11.6	2	451.0	470.0	460.5	9.5	5	451.0	528.0	493.4	29.0
L	-	-	-	-	-	8	375.0	418.0	399.1	12.9	5	350.0	370.0	361.0	7.5	13	350.0	418.0	384.5	21.6
Wp	97.0	96.5	96.0	96.0	91.5	10	110.0	118.0	112.4	2.9	14	91.5	104.0	98.8	3.3	25	91.5	118.0	104.5	7.3
Wpa	89.0	87.0	89.5	87.3	83.0	9	98.0	106.5	102.3	3.2	14	83.0	93.7	90.3	2.9	25	83.0	106.5	95.1	6.3
Tpa	44.5	51.0	48.0	45.0	43.0	9	48.5	57.0	53.2	2.5	14	43.0	51.0	46.4	2.0	25	43.0	57.0	49.1	3.9
Wm	-	-	49.0	-	51.0	9	56.0	65.5	61.8	2.9	8	49.0	55.5	52.7	2.0	18	49.0	65.5	57.5	5.1
Wd	-	-	-	-	-	8	98.0	110.0	103.4	3.8	5	89.0	94.0	91.5	1.6	13	89.0	110.0	98.8	6.6
Wp:L,%	-	-	-	-	-	5	26.8	28.6	27.8	0.7	5	26.8	28.7	27.6	0.6	10	26.8	28.7	27.7	0.6
Tpa:Wpa,%	50.0	58.6	53.6	51.5	51.8	9	49.5	56.1	52.0	2.1	14	47.8	58.6	51.4	2.5	25	47.8	58.6	51.6	2.3
Wpa:Wp,%	91.8	90.2	93.2	90.9	90.7	9	89.1	94.6	90.9	1.7	14	90.1	93.2	91.4	0.9	24	89.1	94.6	91.29	1.3
Wm:L,%	-	-	-	-	-	7	14.4	16.9	15.7	0.9	5	14.2	15.5	14.9	0.4	12	14.2	16.9	15.4	0.8
Wd:L,%	-	-	-	-	-	7	24.5	28.1	26.3	1.3	5	24.3	26.0	25.4	0.6	12	24.3	28.1	25.9	1.2

Tab. 8 Measurements of radius of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n. Untermaßfeld - mm+ff					»*Bison*« sp. Venta Micena (Moya-Sola,1987)					*Bison priscus,* Rhine Gravels (Martin,1987)					*Bison priscus* Boj., North-East Siberia					*Bos primigenius* Rhine Gravels, Martin, 1987				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
Lant	5	451.0	528.0	493.4	29.0											5	423.0	483.0	444.6	22.4					
L	13	350.0	418.0	384.5	21.6	3	267.8	282.6	277.0	6.6	28	334.0	424.0	387.9	21.0	16	318.0	393.0	351.9	20.2	9	375.0	427.0	396.7	15.5
Wp	25	91.5	118.0	104.5.	7.3	3	70.0	76.3	73.5	2.6	24	95.0	125.0	113.0	8.6	16	97.0	120.5	106.1	6.8	9	113.0	129.0	122.1	4.5
Wpa	25	83.0	106.5	95.1	6.3						24	80.0	121.5	105.5	10.2	16	90.0	107.5	97.4	5.2	9	99.7	112.8	107.5	4.3
Tpa	25	43.0	57.0	49.1	3.9						25	47.5	77.0	64.7	7.1	16	43.5	58.5	50.1	4.0	9	49.2	60.0	55.5	3.2
Wm	18	49.0	65.5	57.5	5.1	3	42.0	42.4	42.2	0.2	24	89.5	114.0	104.4	6.8	16	46.0	63.5	54.4	5.0	9	58.8	74.0	70.0	4.5
Wd	13	89.0	110.0	98.8	6.6	2	65.0	69.2	67.1	2.1	26	42.0	57.5	51.6	3.8	15	86.5	111.0	97.9	8.7	9	95.5	119.0	111.1	6.3
Wp:L,%	10	26.8	28.7	27.7	0.6						24	26.1	32.2	29.2	1.6	16	28.1	32.4	30.2	1.6	9	28.8	33.3	30.8	1.2
Wpa:Wp,%	24	89.1	94.6	91.2	1.3	3	24.9	27.7	26.6	1.2	22	88.6	94.7	91.8	1.8	16	85.7	97.9	91.9	2.8	9	86.6	90.7	88.1	1.1
Wm:L,%	12	14.2	16.9	15.4	0.8	3	14.9	15.7	15.2	0.3	25	14.2	18.9	16.6	1.2	16	13.4	16.8	15.5	1.1	9	15.2	19.0	17.7	1.1
Wd:L,%	12	24.3	28.1	25.9	1.2	2	23.0	24.7	23.8	0.8	24	24.0	30.8	27.2	1.7	15	24.1	32.2	27.9	2.2	9	24.7	30.3	28.0	1.5
Budd:BI	6	68.8	81.3	74.4	4.0						20	52.6	78.9	66.8							7	69.8	81.0	75.2	
Bfdm:Bfdl	5	100.0	149.3	122.0	17.0						17	92.2	117.0	105.3							7	84.8	99.0	91.9	

Lant - greatest length of antebrachium ;
Wpa - greatest width of proximal articular surface;
Tpa - greatest transverse diameter of this surface
Budd:BI, Bfdm:Bfdl - indices of facets of the distal articular surface according to Martin, 1987.

Tab. 9 Measurements of antebrachium and radius of various bovids, mm, and indices, %.

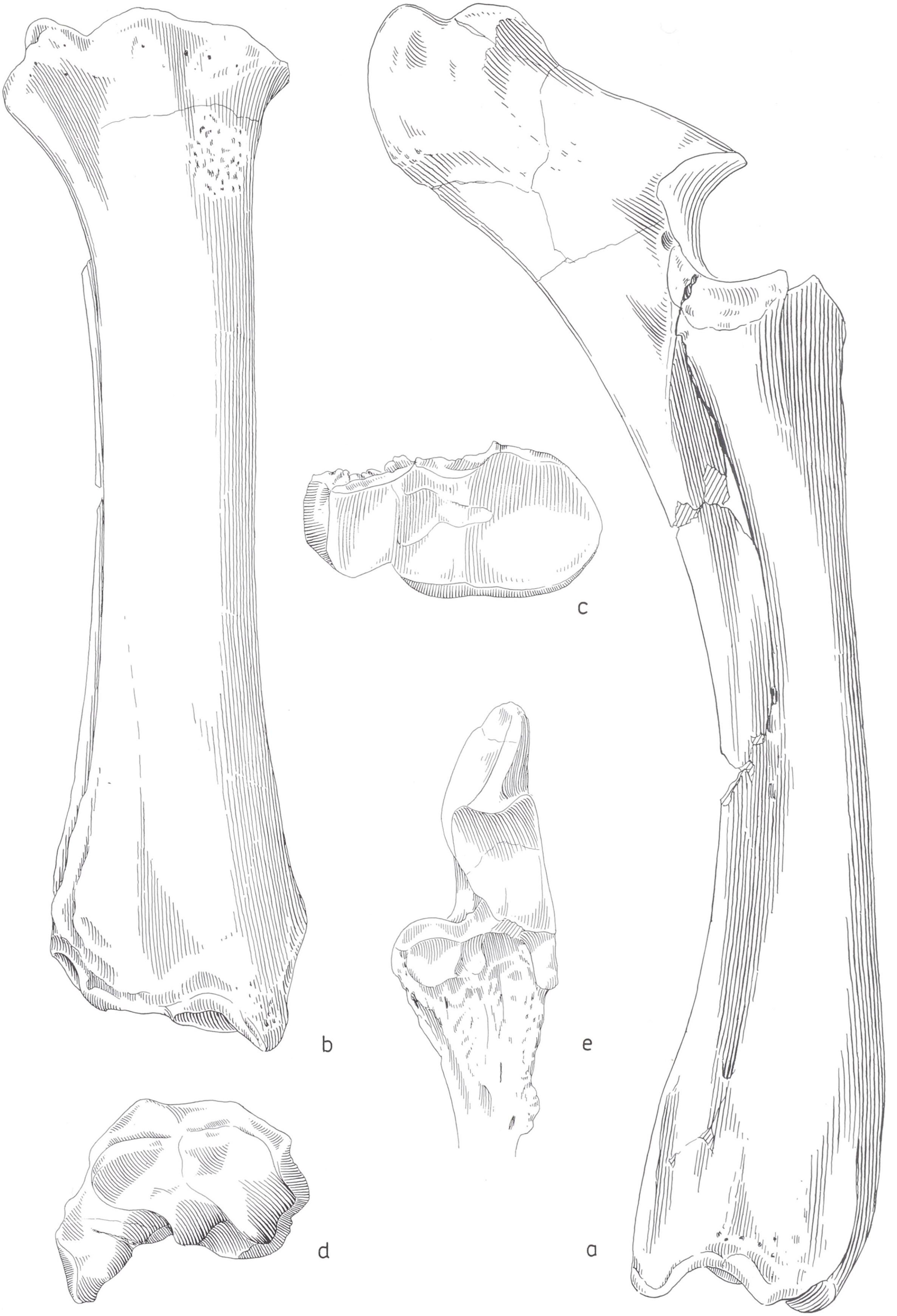

Fig. 8 *Bison menneri* sp. nov., Untermaßfeld. Antebrachium dex., IQW 1982/17 797 (Mei. 17 317), female. – a antebrachium, lateral view. – b-d radius: anterior, proximal and distal views. – e ulna: anterior view. – Scale = ca. 1:2.

wide and more obtuse notch. These are reliable discriminating features between the two genera. For instance, the *Bison* condition is well pronounced on more than 90% of bison bones studied by Martin (1987).

Some radius specimens in the Untermaßfeld population show an evident *Bison* condition like IQW 1982/17 797 (Mei. 17 317) (Taf. 27, 3; Fig. 8, c), or IQW 1980/15 271 (Mei. 14 783) (Taf. 27, 6). The other specimens show almost typical *Bos* condition, like IQW 1980/16 646 (Mei. 16 167) (Taf. 27, 7). There are many transitions between these two extreme types, e.g. IQW 1982/18 361 (Mei. 17 881), Fig. 7, b, so it is difficult to evaluate the share of each morphotype.

The distal end of the radius of *B. menneri* also demonstrates a mixture of *Bison* and *Bos* features. According to Martin (1987), the size relations between different facets of the distal articular surface suggested by Bibikova (1958) to discriminate between *Bos* and *Bison* are not so clear cut as Bibikova believed. For the Untermaßfeld sample I estimated two of Bibikova's indices in Martin's interpretation: ulnare/intermedium index (dorsal width) and index of distal articular surface (volar width, see Martin 1987). The first index shows that the facet for the intermedial carpal bone in *B. menneri* is relatively not so wide as in *B. priscus*, and more similar to *Bos primigenius*. However, the medial part of the distal articular surface in our sample is always larger than the lateral one (the second index), and that is typical for *Bison*.

In the presence of a fissure marking the contact of radius and ulna on the distal articular surface, *B. menneri* is more similar to *B. priscus*. Neither Martin, nor I could find a well pronounced fissure in *Bos primigenius*. Martin observed a well developed fissure on 16% of *B. priscus* radii from the Rhine Gravels, and a weakly developed one on 12%. In *B. menneri* the fissure is present on more than 30% of specimens.

Comments on radius. It is quite probable that many *Bos*-like features in *B. menneri* radii are related to the general slenderness of the bone, as if it is contracted in a transverse direction. This may be true for the deeper notch for the ulna on the upper surface, as well as for the narrower facet for the intermedial carpal bone.

3.2.12. Ulna

Five complete ulnae attached to the radius, two more or less complete isolated specimens, and 24 fragments at different state of damage. Male ulna IQW 1982/18 361 (Mei. 17 881), Taf. 27, 9, Fig. 7, c, d; female IQW 1982/17 797 (Mei. 17 317), Taf. 27, 1,5, Fig.8, a, e.

Like the radius, the ulna of *B. menneri* demonstrates high sexual dimorphism in size (Table 10). However, even male ulnae from Untermaßfeld are somewhat smaller in size than such large forms of *Bison* as those from Taubach and Tiraspol, or large *Bos primigenius*.

Unlike the radius, in the ulna sexual dimorphism is apparent in the morphology as well. In lateral view, the olecranon process of male ulnae is more rectangle-shaped, while in females it is more trapezoidal, narrowing more to the tuber (cf. Fig. 7, c, and Fig. 8, a). It is evidently demonstrated by the ratio between the smallest and largest transverse (dorsoventral) diameters of the olecranon process (Table 10, Tmin:Tmax). This feature was mentioned by Bibikova (1958) as one of the characteristics for discriminating *Bison*/*Bos*. She also indicated the different profile of the dorsal rib of the olecranon process as gently concave in *Bison* and convex in the lower part of the rib and concave in the upper in *Bos*. However, the concavity in the upper part of the olecranon dorsal rib is peculiar to females not only in *B. menneri*, but in *Bos primigenius* (Lehmkuhl 1988) and in *Bison bonasus* as well (Reshetov and Sukhanov 1979). The lower part of the rib in *Bos*, according to our observations, is usually straight or slightly convex. The same condition can be observed both on male and female ulnae of *B. menneri*, so in this respect they are more similar to *Bos*.

All the students agree that the best feature of the ulna to distinguish *Bos* from *Bison* is the structure of ulna/radius articulation. This feature corresponds to the arrangement of this articulation in the radius that has been considered above. Like the radius, the *B. menneri* ulna demonstrates the whole range of

	IQW 1980/ 18361 m!	IQW 1980/ 16544 m!	IQW 1980/ 17117 m!	IQW 1980/ 17481 m	IQW 1980/ 16937 m	IQW 1983/ 19066 m	IQW 1982/ 18372 ?	IQW 1982/ 17876 ?	IQW 1982/ 17797 f!	IQW 1980/ 15269 f!	IQW 1982/ 17798 f	IQW 1983/ 19179 f?	IQW 1982/ 18580 f	IQW 1985/ 20824 f	IQW 1980/ 15609 f/sad	IQW 1980/ 17139 f/sad	IQW 1980/ 15298 juv.	mm N	MIN	MAX	AVG	STD
L	509.0	c483.0	492.0	-	-	-	-	-	454.0	432.0	-	-	-	-	-	-	c420.0	3	483.0	509.0	494.7	10.8
Lpo	160.0	c159.0	165.0	>161.0	-	-	-	-	147.5	133.0	135.0	-	-	-	c133.0	-	142.0	4	159.0	165.0	161.3	2.3
Lant	149.0	c142.0	155.0	-	-	-	-	-	136.5	127.0	123.0	-	c120.0	-	c123.0	-	127.5	3	142.0	155.0	148.7	5.3
Tmax	105.0	98.0	97.0	-	c92.0	-	-	-	86.0	88.0	84.0	86.0	-	-	84.0	c84.0	88.0	4	92.0	105.0	98.0	4.6
Tmin	81.0	78.0	77.0	85.5	-	-	-	-	63.0	62.0	60.0	c65.0	-	-	60.0	-	65.0	4	77.0	85.5	80.4	3.3
Wmax	62.0	>52.0	61.0	-	-	66.0	59.0	56.0	60.0	c53.0	57.0	55.5	-	>54.0	53.0	55.0	57.0	3	61.0	66.0	63.0	2.2
Wsl	32.0	31.0	33.0	32.5	31.0	34.5	31.0	29.0	31.0	30.0	32.5	29.5	29.5	28.0	29.0	30.0	31.0	6	31.0	34.5	32.3	1.2
Tmin:Tmax	77.1	79.6	79.4						73.3	70.5	71.4	75.6			71.4		73.9	3	77.1	79.6	78.7	1.1
Wsl:Wmax	51.6	-	54.1	-	-	52.3	52.5	51.8	51.7	56.6	57.0	53.2	-	51.9	54.7	54.5	54.4	3	51.6	54.1	52.7	1.1

	Bison menneri sp.n. Untermaßfeld										*Bison priscus* Boj. Northeast Siberia					*Bison* sp.			*Bos primigenius*		
	ff					mm + ff										Taubach		Tiras-pol	Chau-sovo	Friedland m	f
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD						
L	3	420.0	454.0	435.3	14.1	6	420.0	509.0	465.0	32.2									515.0	447.0	372.0
Lpo	5	133.0	147.5	138.1	5.7	9	133.0	165.0	148.4	12.4	12	138.0	195.0	157.0	17.6	-	166.0	196.0	180.0	160.0	120.0
Lant	6	120.0	136.5	126.2	5.3	9	120.0	155.0	133.7	11.9	12	118.0	183.0	139.9	19.2	-	160.5	183.0	156.5	-	108.5
Tmax	7	84.0	88.0	85.7	1.7	11	84.0	105.0	90.2	6.7	13	80.5	128.5	100.5	14.0	124.0	114.3	126.0	102.0	92.0	74.5
Tmin	6	60.0	65.0	62.5	2.1	10	60.0	85.5	69.7	9.1	13	63.0	96.5	74.9	9.5	88.0	87.6	89.0	81.0	75.0	59.0
Wmax	8	53.0	60.0	55.6	2.2	13	53.0	66.0	57.6	3.7	13	55.5	75.0	62.3	5.9	>70.0	-	-	65.0	-	-
Wsl	9	28.0	32.5	30.1	1.2	17	28.0	34.5	30.9	1.6	13	26.0	37.0	30.5	3.2	-	-	39.5	35.0	31.5	27.0
Tmin:Tmax	6	70.5	75.6	72.7	1.7	9	70.5	79.6	74.7	3.2	13	71.5	78.3	74.7	2.1	71.0	76.6	70.6	79.4	81.5	79.2
Wsl:Wmax	8	51.7	57.0	54.2	1.8	13	51.6	57.0	53.6	1.8	13	44.1	54.2	49.0	3.2	-	-	-	53.8	-	-

Tab. 10 Measurements of ulna of *Bison menneri* sp. n., Untermaßfeld, and other bovids, mm, and indices, %.

conditions between the two genera. For instance, IQW 1982/17 797 (Mei. 17 317) (Fig.8, e) has a very wide lateral articulation with both radius and humerus, the lateral part of the ulna does not almost intrude into the proximal/posterior edge of the radius; this is a completely *Bison*-like condition. The opposite condition, typical for *Bos*, is observed on IQW 1983/19 179 (Mei. 18 699). Here the lateral part of the ulna articulation does not reach the lateral edge of the radius posterior articular surface. It forms a sharp triangular protuberance deeply intruded into radius. There are many transitional cases between these two extreme conditions.

3.2.13. Carpal bones

(Taf. 29, 7-12; Fig. 9). Carpal bones are very numerous in the Untermaßfeld sample. For instance, even the very rare pisiform (carpi accessorium) is represented by 12 specimens. Information on morphology of carpal bones is very scanty and sometimes contradictory (Bibikova 1958; Stampfli 1963; Sala 1986). That is why despite the richness of the sample, I can give only very short description accompanied by the measurements.

Carpi radiale (Table 11). 22 bones from Untermaßfeld have almost the same average height as 6 bones from Isernia, but at the same time they are not so wide as in Isernia. As a result, the index of width against the height is lower on the average in *B. menneri* than in *B. schoetensacki* from Isernia. According to Bibikova and Stampfli (but not to Sala !), a relatively narrow and high bone is more typical for *Bison* than for *Bos*. On the other hand, in *B. menneri* the carpi radiale is only slightly narrower than the carpi intermedium and sometimes almost equal to it in width, the condition assigned to *Bos* by Bibikova. I had a rare chance to check this on 6 pairs of bones each belonging to one individual. Bibikova's radiale/intermedium index is 86.1-101.9 in this sample, while this range for *Bos* is 95-105%, and for *Bison* – 80-85% (Bibikova) or 65.6-93.9% (Stampfli).

Carpi intermedium (Table 12). Attempts of previous authors to quantify proportions of this bone are hardly compatible in results, probably due to different ways of measuring (compare Bibikova and Stampfli, Stampfli and Sala). *B. menneri* bones are more or less equal in size with carpi radiale from Isernia, though on the average they have some higher values of width/height index.

Carpi ulnare (Table 13). It is still more difficult to compare measurements of this bone with the previous results due to its very complicated orientation. Moreover, the large Untermaßfeld sample shows how wide is its variation in one population.

Carpale II+III (Table 14). Bibikova (1958) suggested that this bone is relatively narrower in *Bison* than in *Bos* (though this statement contradicts her observations on the corresponding facet of metacarpal) and illustrated that by the ratio between transverse diameter and width. I have estimated the same ratio by the reversed index W:T1, where T1 is dorso-plantar diameter normal to the plantar edge of the bone. Calculations show, that *B. menneri* has the same ratio as Bibikova cites for *Bison*. In spite of this, many specimens of *B. menneri* carpale II+III look different from *B. priscus* which is in agreement with the character of the proximal surface of metacarpal (see below).

Carpale IV (Table 15). The Untermaßfeld sample of this bone (30 specimens) offers so wide a range of variation (e.g., the largest bone is 50% larger than the smallest!) that any comparison with the few published specimens of other bovines seems unreasonable.

Carpi accessorium (Table 16). This bone is represented in collections and described in the literature very poorly, so I have to confine myself to the measurements only. In one or two specimens the articulation is divided into two facets.

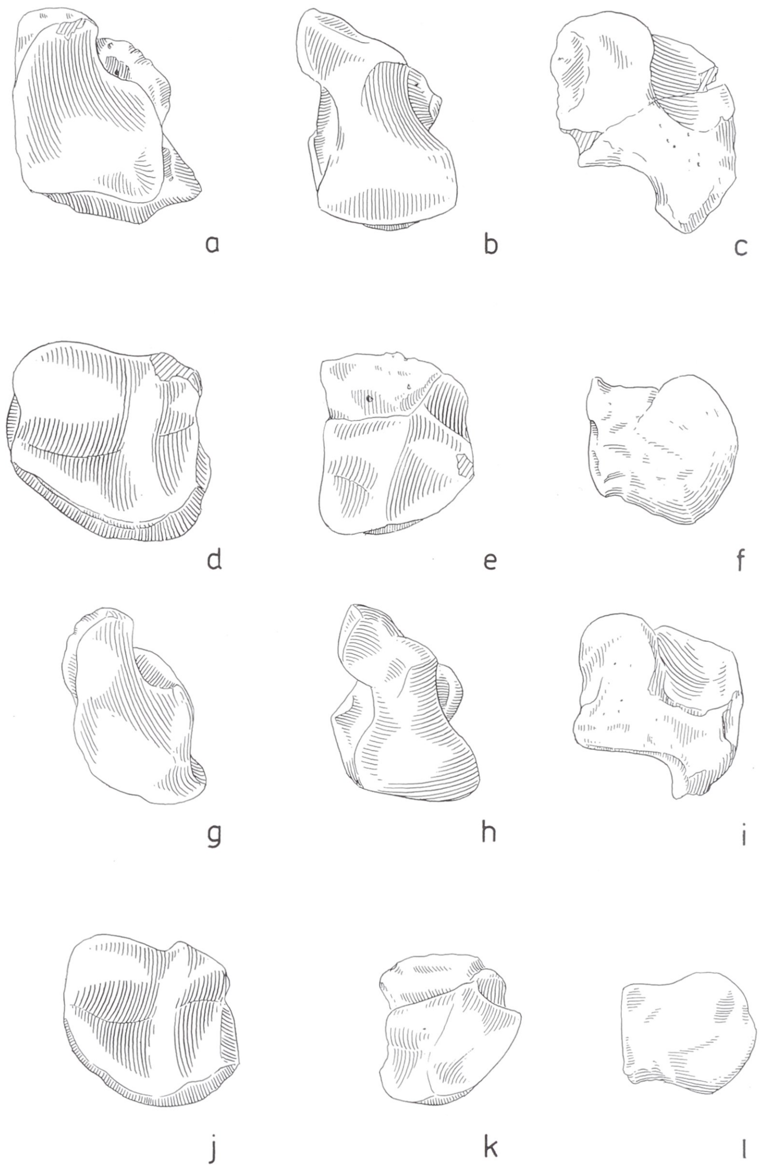

Fig. 9 *Bison menneri* sp. nov., Untermaßfeld. Carpal bones. – a-f Set of carpal bones of one male individual, sin. a-c. radiale, IQW 1981/17 718 (Mei. 17 240); b-c. intermedium, IQW 1981/17 721 (Mei. 17 243); c-c. ulnare, IQW 1981/17 720 (Mei. 17 242); d-c. II+III, IQW 1981/17 717 (Mei. 17 239); e- c. IV, IQW 1981/17 722 (Mei. 17 244); f-c. accessorium, IQW 1981/17 723 (Mei. 17 245). – g-l: Set of carpal bones of one female individual, sin. g-c. radiale, IQW 1980/16 714 (Mei. 16 235); h-c. intermedium, IQW 1980/16 712 (Mei. 16 233); i-c. ulnare, IQW 1980/16 710 (Mei. 16 231); j-c. II+III, IQW 1980/16 715 (Mei. 16 236); k-c. IV, IQW 1980/16 713 (Mei. 16 234); l-c. accessorium, IQW 1980/16 711 (Mei. 16 232). – Scale = ca. 1:2.

3.2.14. Metacarpal

There are 33 complete bison metacarpals in the Untermaßfeld collection, and 34 fragments. The metacarpal is one of the best represented and preserved bones in the sample. On the other hand, this is one of the bones which helps us to distinguish the Untermaßfeld bison from other large bison. One of the metacarpals, IQW 1982/17 948 (Mei. 17 468) (Fig. 1; Taf. 28, 1-3), has been chosen as the type specimen of a new species, *Bison menneri*. To give a better idea of this important skeletal element, I picture some well preserved male and female metacarpals (Taf. 28, 29, VIII, Fig. 10).

	IQW 1980/ 16982 m	IQW 1980/ 17516 m	IQW 1981/ 17718 m	IQW 1982/ 18339 m!	IQW N ? m	IQW N ? m	IQW 1980/ 15829 ?	IQW 1980/ 16955 ?	IQW 1984/ 19993 ?	IQW 1985/ 20878 ?	IQW 1986/ 21404 ?	IQW 1980/ 15296 f	IQW 1980/ 15806 f	IQW 1980/ 16714 f!	IQW 1980/ 16944 f	IQW 1980/ 17037 f	IQW 1980/ 17522 f	IQW 1980/ 17581 f	IQW 1980/ 17603 f	IQW 1982/ 18561 f	IQW 1983/ 19548 f	IQW 1985/ 20793 f	N	MIN	MAX	AVG	STD
Hant	40.0	40.5	42.0	44.0	44.5	43.5	40.0	41.0	39.0	37.5	37.0	39.5	39.0	39.0	41.5	37.0	38.0	38.0	38.5	36.5	36.0	38.3	22	36.0	44.5	39.6	2.3
Want	33.0	36.0	37.7	-	39.5	38.7	31.0	32.5	29.5	31.0	32.5	30.5	30.0	30.5	32.0	29.5	30.0	29.5	31.0	30.0	27.0	30.0	21	27.0	39.5	32.0	3.2
Tmax	53.5	59.0	62.0	-	62.5	62.0	57.0	54.0	54.5	51.5	-	53.0	52.0	52.0	54.5	54.0	52.0	49.5	49.5	49.0	49.0	-	19	49.0	62.5	54.2	4.3
Want:Hant,%	82.5	88.9	89.8	-	88.8	89.0	77.5	79.3	75.6	82.7	87.8	77.2	76.9	78.2	77.1	79.7	78.9	77.6	80.5	82.2	75.0	78.3	21	75.0	89.8	81.1	4.8
Tmax:Hant,%	133.8	145.7	147.6	-	140.4	142.5	142.5	131.7	139.7	137.3	-	134.2	133.3	133.3	131.3	145.9	136.8	130.3	128.6	134.2	136.1	-	19	128.6	147.6	137.1	5.5

Tab. 11 Measurements of carpi radiale of *Bison menneri* sp. n. Untermaßfeld, mm, and indices, %.

	IQW 1980/ 16768 m	IQW 1980/ 16923 m	IQW 1980/ 17497 m	IQW 1981/ 17721 m	IQW 1982/ 18340 m!	IQW 1986/ 21619 m	IQW 1986/ 21635 m	IQW 1980/ 15835 ?	IQW 1980/ 16970 ?	IQW 1985/ 20879 ?	IQW 1986/ 21134 ?	IQW 1986/ 21363 ?	IQW 1980/ 16516 juv!	IQW 1980/ 15893 f	IQW 1980/ 16644 f	IQW 1980/ 16712 f!	IQW 1980/ 17039 f	IQW 1980/ 17143 f	IQW 1980/ 17511 f	IQW 1981/ 17604 f	IQW 1984/ 19985 f	IQW 1985/ 20796 f	N	MIN	MAX	AVG	STD
Hant	40.5	37.0	35.0	37.5	39.3	37.0	38.5	34.5	34.5	32.0	33.5	29.0	32.5	32.0	35.0	34.7	35.0	34.5	35.5	36.0	35.0	32.5	22	29.0	40.5	35.0	2.6
Hmax	-	43.0	43.5	41.0	-	41.5	41.5	36.0	39.0	-	41.0	-	34.0	35.5	38.0	38.0	42.0	36.5	39.5	39.5	38.2	-	17	34.0	43.5	39.3	2.7
Want	41.8	39.5	37.0	37.0	40.5	39.0	38.8	36.5	35.5	34.0	34.0	30.5	30.5	32.0	34.0	34.0	32.5	34.5	35.5	36.0	34.0	33.0	22	30.5	41.8	35.5	3.0
Tmax	-	52.0	54.0	55.5	-	53.0	57.0	50.0	49.0	48.5	48.0	-	42.0	44.3	48.0	47.5	47.0	45.0	45.5	45.5	47.0	-	18	42.0	57.0	48.8	3.9
Want:Hant,%	103.2	106.8	105.7	98.7	103.1	105.4	100.8	105.8	102.9	106.3	101.5	105.2	93.8	100.0	97.1	98.0	92.9	100.0	100.0	100.0	97.1	101.5	22	92.9	106.8	101.2	3.8
Tmax:Hant,%	-	140.5	154.3	148.0	-	143.2	148.1	144.9	142.0	151.6	143.3	-	129.2	138.4	137.1	136.9	134.3	130.4	128.2	126.4	134.3	-	18	126.4	154.3	139.5	7.9

Tab. 12 Measurements of carpi intermedium of *Bison menneri* sp. n. Untermaßfeld, mm, and indices, %.

	IQW 1980/ 15386	IQW 1980/ 17001	IQW 1980/ 17496	IQW 1981/ 17720	IQW 1982/ 17914	IQW 1982/ 18341	IQW 1987/ 21959	IQW 1985/ 20666	IQW 1985/ 20789	IQW 1987/ 21952	IQW 1980/ 16522	IQW 1980/ 15754	IQW 1980/ 15805	IQW 1980/ 15941	IQW 1980/ 15964	IQW 1980/ 16645	IQW 1980/ 16710	IQW 1980/ 17096	IQW 1980/ 17523	IQW 1981/ 17601	IQW 1982/ 18395	IQW 1984/ 19997	IQW 1985/ 20661	N	MIN	MAX	AVG	STD
	m	m	m	m!	m	m!	m	?	?	?	juv!	f	f	f	f	f	f!	f!	f	f	f	f	f					
Hant	40.5	40.0	41.5	39.0	37.5	42.0	41.5	35.0	40.0	40.0	33.0	32.5	39.5	36.0	33.0	35.0	37.0	36.0	41.5	36.5	35.5	34.0	37.5	23	32.5	42.0	37.6	3.0
Hmax	54.5	58.5	52.0	58.0	49.0	56.0	54.0	47.0	49.0	51.5	43.0	40.0	53.5	-	40.0	46.5	45.0	51.5	48.5	49.0	47.5	45.0	46.0	22	40.0	58.5	49.3	5.1
Wmax	32.0	36.0	35.0	-	26.0	34.0	30.0	27.5	29.0	30.5	24.0	24.5	29.5	-	23.0	30.0	32.5	26.5	35.5	26.5	25.0	28.0	28.0	21	23.0	36.0	29.2	3.8
Tmax	50.0	49.0	53.0	48.0	49.5	51.5	52.0	50.0	48.0	48.0	36.5	42.5	45.0	-	40.5	43.5	44.5	42.0	47.5	39.5	40.5	43.0	42.0	22	36.5	53.0	45.7	4.5
Wmax:Hmax,%	58.7	61.5	67.3	-	53.1	60.7	55.6	58.5	59.2	59.2	55.8	61.3	55.1	-	57.5	64.5	72.2	51.5	73.2	54.1	52.6	62.2	60.9	21	51.5	73.2	59.7	5.7
Tmax:Hant,%	123.5	122.5	127.7	123.1	132.0	122.6	125.3	142.9	120.0	120.0	110.6	130.8	113.9	-	122.7	124.3	120.3	116.7	114.5	108.2	114.1	126.5	112.0	22	108.2	142.9	121.5	7.8
Tmax:Hmax,%	91.7	83.8	101.9	82.8	101.0	92.0	96.3	106.4	98.0	93.2	84.9	106.3	84.1	-	101.3	93.5	98.9	81.6	97.9	80.6	85.3	95.6	91.3	22	80.6	106.4	93.1	7.8

Tab. 13 Measurements of carpi ulnare of *Bison menneri* sp. n. Untermaßfeld, mm, and indices, %.

	IQW 1980/ 15392 m	IQW 1980/ 16818 m	IQW 1980/ 16945 m	IQW 1980/ 16956 m	IQW 1980/ 17471 m	IQW 1980/ 17494 m	IQW 1981/ 17717 m!	IQW 1982/ 18338 m!	IQW 1985/ 20601 m	IQW 1985/ 20662 m	IQW 1985/ 20839 m	IQW 1986/ 21276 m	IQW 1980/ 16974 ?	IQW 1980/ 17514 ?	IQW 1980/ 17529 ?	IQW 1987/ 21957 ?	IQW 1980/ 15274 f	IQW 1980/ 15297 f	IQW 1980/ 16715 f!	IQW 1980/ 17056 f	IQW 1980/ 17092 f!	IQW 1982/ 17912 f
W	49.5	48.0	48.5	47.0	47.5	52.5	52.0	47.5	48.0	47.0	52.0	47.5	46.5	46.0	45.5	45.0	41.0	44.0	43.0	39.3	-	-
T	53.0	52.0	47.0	47.5	49.0	50.0	51.7	54.0	45.0	49.0	52.0	49.0	45.0	52.0	44.5	45.0	42.0	48.5	46.5	42.5	44.0	40.0
T1	49.5	50.5	46.0	46.5	47.0	49.5	50.0	47.0	42.0	44.5	51.0	43.0	44.5	46.5	43.5	43.0	41.0	45.5	44.0	39.0	-	-
Hant	22.5	25.5	21.0	20.5	21.5	23.3	22.0	23.0	21.5	20.0	24.0	23.5	22.5	24.3	21.0	22.0	18.5	21.0	21.0	19.5	9.7	17.8
Wpmax	56.7	52.5	51.7	51.0	-	55.5	55.5	55.0	50.5	50.5	57.3	-	53.5	58.0	50.0	47.5	47.7	47.0	49.0	46.0	47.5	-
Wpmin	42.8	41.0	40.5	40.0	40.7	43.5	39.0	42.5	36.0	-	44.0	-	41.5	40.0	39.5	39.0	39.0	37.3	36.5	37.0	-	-
W:T,%	93.4	92.3	103.2	98.9	96.9	105.0	100.6	88.0	106.7	95.9	100.0	96.9	103.3	88.5	102.2	100.0	97.6	90.7	92.5	92.5	-	-
W:T1,%	100.0	95.0	105.4	101.1	101.1	106.1	104.0	101.1	114.3	105.6	102.0	110.5	104.5	98.9	104.6	104.7	100.0	96.7	97.7	100.8	-	-
Hant:W,%	45.5	53.1	43.3	43.6	45.3	44.4	42.3	48.4	44.8	42.6	46.2	49.5	48.4	52.8	46.2	48.9	45.1	47.7	48.8	49.6	-	-
Wpmin:Wpmax,%	75.5	78.1	78.3	78.4	-	78.4	70.3	77.3	71.3	-	76.8	-	77.6	69.0	79.0	82.1	81.8	79.4	74.5	80.4	-	-

	IQW 1982/ 17947 f	IQW 1982/ 18362 f	IQW 1985/ 20660 f	IQW 1985/ 20792 f	IQW 1985/ 20880 f	IQW 1986/ 21394 f	IQW 1980/ 16515 juv!	mm					ff					Total				
								N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
W	42.0	43.0	44.0	42.0	43.0	43.0	39.0	12	47.0	52.5	48.9	2.0	10	39.3	44.0	42.4	1.4	27	39.0	52.5	45.7	3.6
T	45.0	45.5	47.0	45.5	48.0	47.0	42.0	12	45.0	54.0	49.9	2.6	12	40.0	48.5	45.1	2.5	29	40.0	54.0	47.2	3.5
T1	42.5	40.5	41.0	41.0	42.0	43.0	39.3	12	42.0	51.0	47.2	2.9	10	39.0	45.5	42.0	1.8	27	39.0	51.0	44.5	3.5
Hant	19.5	18.7	21.0	20.9	19.0	19.5	19.5	12	20.0	25.5	22.4	1.5	12	17.8	21.0	19.7	1.0	29	17.8	25.5	21.2	1.9
Wpmax	47.0	47.5	52.0	45.0	49.5	51.0	48.0	10	50.5	57.3	53.6	2.5	11	45.0	52.0	48.1	2.0	26	45.0	58.0	50.9	3.6
Wpmin	38.0	34.0	37.0	33.0	37.8	-	34.7	10	36.0	44.0	41.0	2.3	9	33.0	39.0	36.6	1.8	24	33.0	44.0	38.9	2.9
W:T,%	93.3	94.5	93.6	92.3	89.6	91.5	92.9	12	88.0	106.7	98.2	5.2	10	89.6	97.6	92.8	2.1	27	88.0	106.7	96.0	5.1
W:T1,%	98.8	106.2	107.3	102.4	102.4	100.0	99.2	12	95.0	114.3	103.8	4.9	10	96.7	107.3	101.2	3.3	27	95.0	114.3	102.6	4.1
Hant:W,%	46.4	43.5	47.7	49.8	44.2	45.3	50.0	12	42.3	53.1	45.7	3.0	10	43.5	49.8	46.8	2.1	27	42.3	53.1	46.8	2.9
Wpmin:Wpmax,%	80.9	71.6	71.2	73.3	76.4	-	72.3	9	70.3	78.4	76.0	3.0	9	71.2	81.8	76.6	3.9	23	69.0	82.1	76.2	3.8

Tab. 14 Measurements of carpale II+III of *Bison menneri* sp. n. Untermaßfeld, mm, and indices, %.

	IQW 1985/ 20837 m!	IQW 1980/ 17191 m	IQW 1980/ 17508 m	IQW 1981/ 17722 m!	IQW 1980/ 16813 m	IQW 1980/ 15385 m	IQW 1982/ 18337 m!	IQW 1980/ 17526 m	IQW 1980/ 17349 m	IQW 1980/ 17057 ?	IQW 1980/ 15597 ?	IQW 1980/ 15940 ?	IQW 1980/ 16356 ?	IQW 1980/ 16713 f!	IQW 1985/ 20600 f	IQW 1980/ 16642 f!	IQW 1982/ 18306 f	IQW 1980/ 16966 f	IQW 1982/ 18127 f	IQW 1980/ 15353 f	IQW 1985/ 20881 f!	IQW 1982/ 18425 f
Wmax	45.0	43.0	42.0	c41.0	40.6	40.2	40.0	39.0	>35.0	38.5	38.0	37.5	37.5	37.5	36.5	36.0	36.0	35.5	34.5	c34.0	34.0	33.0
Tmax	-	46.0	44.5	46.5	45.5	44.0	46.0	46.0	c46.0	42.3	38.0	37.5	39.5	38.0	41.5	39.0	34.7	39.5	38.0	38.3	-	36.2
Hant	30.0	30.5	39.0	31.5	32.5	29.0	31.0	29.5	31.5	28.0	29.5	27.0	29.5	27.0	28.7	26.5	26.2	29.5	28.5	27.8	24.5	27.0
Wmax:Tmax,%	-	93.5	94.4	88.2	89.2	91.4	87.0	84.8	76.1	91.0	100.0	100.0	94.9	98.7	88.0	92.3	103.7	89.9	90.8	88.8	-	91.2

	IQW 1985/ 20663 f	IQW 1985/ 20665 f!	IQW 1985/ 21175 f	IQW 1980/ 17368 f	IQW 1980/ 16521 f	IQW 1980/ 16997 f	IQW 1980/ 17093 f!	IQW 1985/ 20794 f!	Total				
									N	MIN	MAX	AVG	STD
Wmax	c33.0	32.5	32.5	c32.0	30.5	-	>33.0	-	27	30.5	45.0	36.8	3.6
Tmax	41.0	c41.0	39.0	35.5	33.0	43.5	38.0	38.5	28	33.0	46.5	40.6	3.8
Hant	27.5	27.5	26.0	25.5	25.0	27.5	26.5	c22.0	30	22.0	39.0	28.4	3.0
Wmax:Tmax,%	80.5	79.3	83.3	90.1	92.4	-	-	-	25	76.1	103.7	90.4	6.4

Tab. 15 Measurements of carpale IV of *Bison menneri* sp. n., Unermaßfeld, mm, and indices, %.

	IQW 1980/ 15352	IQW 1980/ 15994	IQW 1980/ 16643	IQW 1980/ 16711	IQW 1980/ 16972	IQW 1980/ 17095	IQW 1980/ 17181	IQW 1981/ 17723	IQW 1984/ 19984	IQW 1986/ 20838	N	MIN	MAX	AVG	STD
Tmax	34.0	35.0	34.5	34.5	42.5	33.5	37.5	38.5	33.0	38.0	10	33.0	42.5	36.1	2.8
Hmax	32.0	32.0	32.5	32.0	41.5	30.5	36.0	40.0	32.5	39.0	10	30.5	41.5	34.8	3.8
Hfa	24.5	27.5	26.0	26.5	33.5	26.0	29.5	32.0	24.3	30.0	10	24.3	33.5	28.0	3.0
Wfa	15.5	17.0	15.0	14.5	19.5	15.5	18.5	17.0	15.5	19.5	10	14.5	19.5	16.8	1.8
Hmax:Tmax,%	94.1	91.4	94.2	92.8	97.6	91.0	96.0	103.9	98.5	102.6	10	91.0	103.9	96.2	4.2
Wfa:Hfa,%	63.3	61.8	57.7	54.7	58.2	59.6	62.7	53.1	63.8	65.0	10	53.1	65.0	60.0	3.8

Hfa - height of articular facet; Wfa - width of articular facet.

Tab. 16 Measurements of carpi accessorium of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

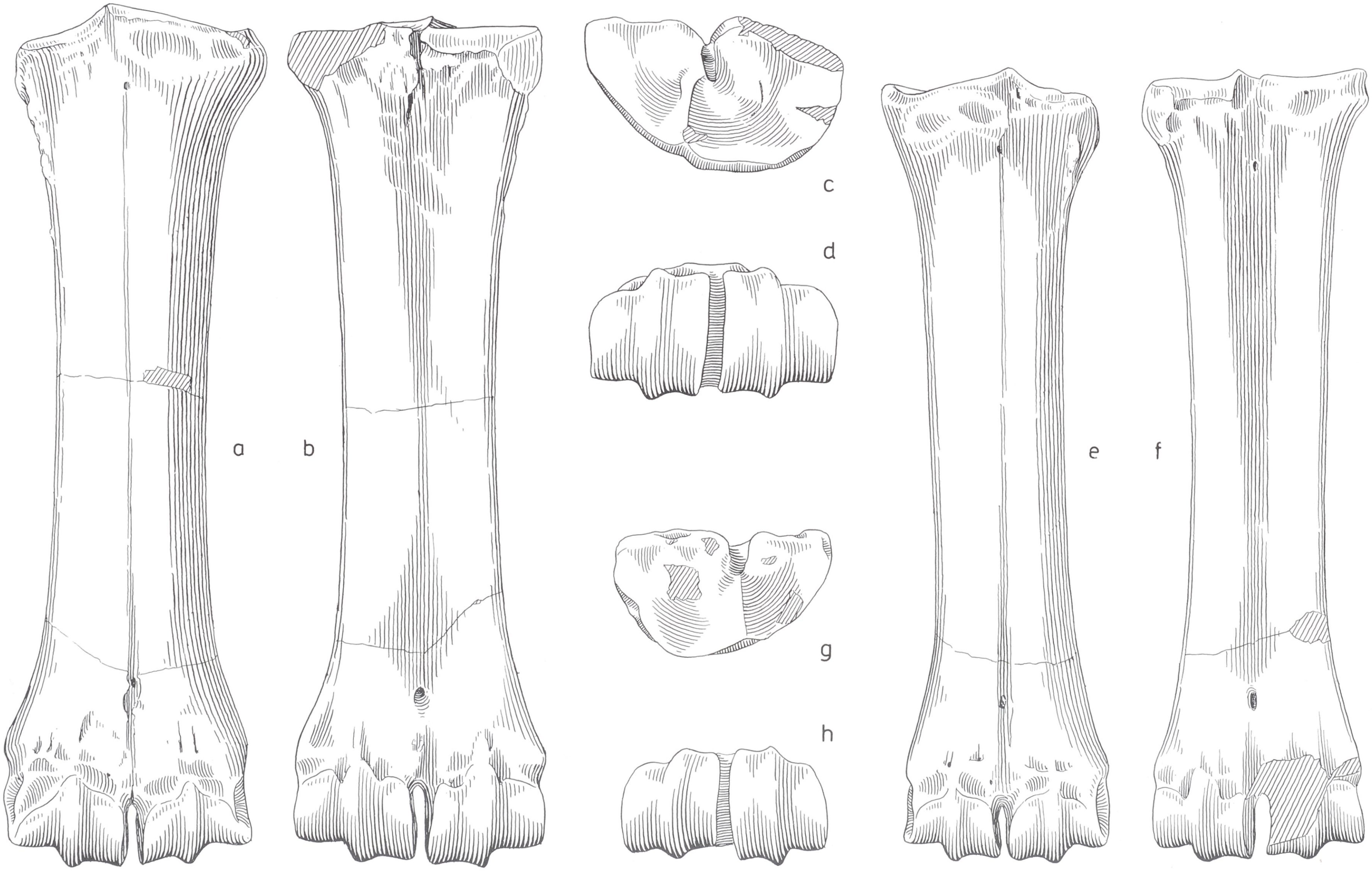

Fig. 10 *Bison menneri* sp. nov., Untermaßfeld. Metacarpal bones. a-d Metacarpal III+IV dex., IQW 1980/15 235 (Mei. 14 717), male; anterior, posterior, proximal and distal views. – e-h Metacarpal III+IV sin., IQW 1980/16 658 (Mei. 16 179), female; anterior, posterior, proximal and distal views. – Scale = ca. 1:2.

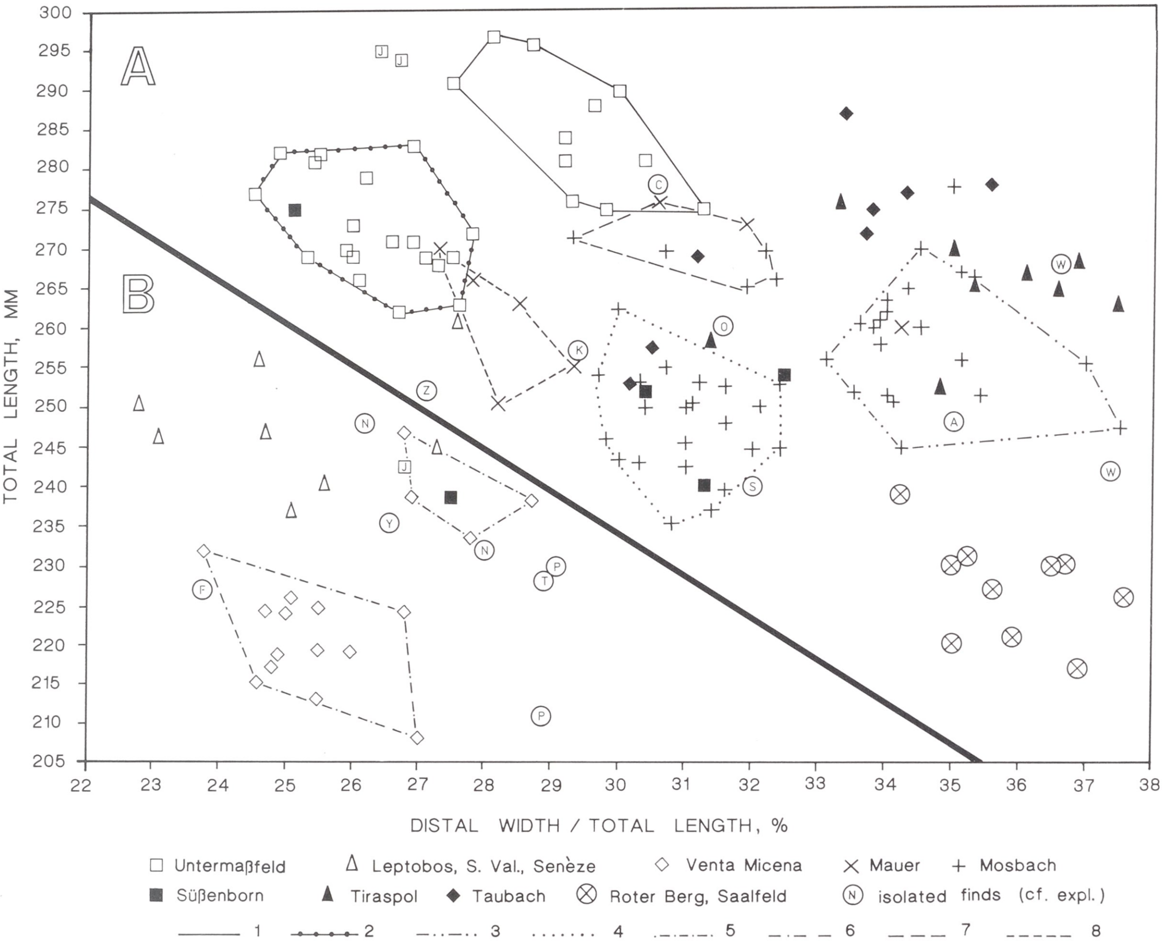

Fig. 11 Length and stoutness of fossil bovid metacarpals from various localities. Measurements of metacarpals of *Leptobos, Bison* sp. from Venta Micena, and of Chinese bovids are taken from the published sources (see references in the text). The remaining samples were measured by the writer. – Borders of male and female metacarpal distributions from certain sites. – 1, 2 Untermaßfeld. – 3, 4 Mosbach, *B. priscus*. – 5, 6 Venta Micena. – 7, 8 supposed distributions of male and female metacarpals of *B. schoetensacki* from Mauer and Mosbach. Isolated finds of metacarpals. Ukraine: C: Chertkovo, K: Kairy, Z: Cherevychniy. Italy: F: Casa Frata, P: Pirro Nord. China: N: Nihowan, Y: Yushe. England: T: Trimingham, S: Sidestrand, O: Ostend, A: Palling, W: Westbury-sub-Mendip. J: juvenile specimens of *Bison menneri*.

In total length, metacarpals of the Untermaßfeld bison are among the largest known for bovids (Fig. 11). On average, they exceed those of the large bison from Tiraspol, Mosbach, Mauer, and even such a huge form as the Taubach bison. They are also longer than the metacarpals of the large Quaternary *Bos primigenius*, e.g. from the British Ipswichian (cf. Browne 1983). The longest bovid metacarpal recorded previously in the literature or observed in collections was one from Taubach (IQW 1969/11 526 [Taub. 1131]), with a maximum length 287 mm. More than half the *B. menneri* male metacarpals are longer than that, the longest reaching 297 mm (Tables 17, 18).

On the other hand, *B. menneri* metacarpals are the most slender among the large bovids. Only *Leptobos* and a small bovid from Venta Micena have in general more slender metacarpals than *B. menneri*; however, they are also notably smaller in size.

Combination of these two features – size and slenderness – in one graph gives a good opportunity to observe this peculiarity of the Untermaßfeld metacarpals and to compare them with various other bo-

	IQW 1980/ 15234	IQW 1980/ 15235	IQW 1980/ 15331	IQW 1980/ 17359	IQW 1982/ 17928	IQW 1982/ 17948	IQW 1982/ 17973	IQW 1982/ 18269	IQW 1983/ 18503	IQW 1984/ 20071	IQW 1984/ 20084	IQW 1985/ 20844	IQW 1986/ 21747	IQW 1987/ 22214	IQW 1980/ 15236	IQW 1981/ 17620	mm					IQW 1980/ 15237	IQW 1980/ 15238	IQW 1980/ 15871	IQW 1980/ 16505
	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m/sad	m/juv	N	MIN	MAX	AVG	STD	f	f	f	f
L	276.0	297.0	296.0	-	284.0	291.0	275.0	281.0	-	290.0	281.0	294.0	288.0	275.0	295.0	294.0	12	275.0	297.0	285.7	7.8	283.0	282.0	-	-
Wp	84.7	86.8	88.0	88.0	81.0	79.0	c81.5	c82.0	84.0	>91.0	>83.0	88.0	87.4	84.0	78.0	78.7	12	79.0	88.0	84.5	3.0	78.4	76.4	76.2	c69.5
Tp	50.0	c53.0	52.0	51.7	50.0	47.0	c50.0	52.0	c49.0	-	50.0	c51.5	52.0	48.7	46.5	47.0	13	47.0	53.0	50.5	1.6	c45.0	49.5	45.0	40.5
Wd	81.0	83.5	85.0	86.0	83.0	80.0	82.0	82.0	85.0	87.0	85.5	>82.0	85.2	86.0	78.0	78.5	13	80.0	87.0	83.9	2.1	76.0	72.0	-	-
Wm	50.5	50.2	50.5	52.9	48.2	51.4	52.2	52.0	-	57.7	51.0	-	54.5	-	41.9	42.0	11	48.2	57.7	51.9	2.4	43.5	42.0	44.5	-
Tm	37.2	37.4	38.4	35.5	37.0	38.2	37.0	35.6	-	40.0	36.7	-	c40.0	-	33.0	33.6	11	35.5	40.0	37.5	1.4	33.6	34.7	31.4	-
Wp:L,%	30.7	29.2	29.7	-	28.5	27.1	c29.6	c29.2	-	>31.4	>29.5	29.9	30.3	30.5	26.4	26.8	10	27.1	30.7	29.5	1.0	27.7	27.1	-	-
Wd:L,%	29.3	28.1	28.7	-	29.2	27.5	29.8	29.2	-	30.0	30.4	>27.9	29.6	31.3	26.4	26.7	11	27.5	31.3	29.4	1.0	26.9	25.5	-	-
Wm:L,%	18.3	16.9	17.1	-	17.0	17.7	19.0	18.5	-	19.9	18.1	-	18.9	-	14.2	14.3	10	16.9	19.9	18.1	0.9	15.4	14.9	-	-

	IQW 1980/ 16658 f	IQW 1980/ 16918 f	IQW 1980/ 16935 f	IQW 1980/ 16978 f	IQW 1980/ 17005 f	IQW 1980/ 17034 f	IQW 1980/ 17038 f	IQW 1980/ 17051 f	IQW 1980/ 17090 f	IQW 1980/ 17115 f	IQW 1980/ 17197 f	IQW 1980/ 17383 f	IQW 1980/ 17469 f	IQW 1980/ 17599 f	IQW 1981/ 17622 f	IQW 1982/ 17904 f	IQW 1982/ 18305 f	IQW 1982/ 18330 f	IQW 1983/ 18906 f	IQW 1983/ 19055 f	IQW 1983/ 19056 f	IQW 1983/ 19114 f	IQW 1983/ 19125 f	IQW 1983/ 19133 f	IQW 1983/ 19155 f
L	270.0	266.0	-	277.0	-	271.0	272.0	269.0	-	269.0	269.0	282.0	-	279.0	269.0	271.0	-	-	-	-	-	262.0	268.0	-	-
Wp	74.5	68.0	c78.0	c71.2	76.0	74.5	c74.0	75.2	>72.0	74.5	71.6	73.5	74.0	74.5	71.5	73.5	71.5	73.0	77.8	-	72.0	-	72.8	77.8	c75.0
Tp	45.0	40.0	46.5	46.0	44.0	45.0	45.0	45.0	c44.0	45.0	c43.0	42.0	44.0	44.0	46.0	46.0	41.5	46.2	48.5	-	45.3	-	45.8	47.0	-
Wd	70.0	69.5	-	68.0	-	73.0	75.5	74.0	-	73.0	70.0	70.3	-	73.0	68.0	72.0	-	-	-	70.5	-	70.0	73.2	-	-
Wm	44.7	43.0	-	40.3	40.5	44.0	c45.0	44.5	c41.5	40.6	42.4	41.8	43.5	43.5	40.8	40.1	40.5	41.2	-	-	43.5	37.5	42.0	-	45.7
Tm	30.0	30.0	-	30.9	30.5	32.7	33.6	31.4	-	31.0	31.3	-	33.3	33.3	29.0	34.0	30.4	30.4	-	-	29.5	31.0	32.8	-	33.0
Wp:L,%	27.6	25.6	-	c25.7	-	27.5	c27.2	28.0	-	27.7	26.6	26.1	-	26.7	26.6	27.1	-	-	-	-	-	-	27.2	-	-
Wd:L,%	25.9	26.1	-	24.5	-	26.9	27.8	27.5	-	27.1	26.0	24.9	-	26.2	25.3	26.6	-	-	-	-	-	26.7	27.3	-	-
Wm:L,%	16.6	16.2	-	14.5	-	16.2	c16.5	16.5	-	15.1	15.8	14.8	-	15.6	15.2	14.8	-	-	-	-	-	14.3	15.7	-	-

	IQW 1984/ 20030	IQW 1985/ 20566	IQW 1985/ 20644	IQW 1985/ 20873	IQW 1985/ 21034	IQW 1986/ 21172	IQW 1980/ 16934	IQW 1980/ 16514	IQW 1983/ 19253	ff					Total				
	f	f	f	f	f	f	?	juv	pat	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	263.0	-	281.0	273.0	272.0	-	282.0	242.5	267.5	21	262.0	283.0	272.9	6.3	33	262.0	297.0	277.5	9.2
Wp	74.6	71.0	76.6	75.0	74.3	-	c77.0	67.3	80.0	32	68.0	78.4	74.2	2.5	44	68.0	88.0	77.0	5.3
Tp	44.0	-	45.0	43.5	46.0	-	47.0	40.7	47.8	31	40.0	49.5	44.8	2.0	44	40.0	53.0	46.5	3.2
Wd	72.5	-	71.5	c71.0	>67.5	75.6	>67.0	65.0	89.0	21	68.0	76.0	71.8	2.2	34	68.0	87.0	76.5	6.3
Wm	44.5	42.7	42.0	41.0	39.7	-	-	31.0	51.3	29	37.5	45.7	42.3	1.9	40	37.5	57.7	44.9	4.8
Tm	32.0	-	32.0	33.5	31.0	-	-	25.0	39.1	26	29.0	34.7	31.8	1.5	37	29.0	40.0	33.5	3.0
Wp:L,%	28.4	-	27.3	27.5	27.3	-	c27.3	27.8	29.9	20	25.6	28.4	27.1	0.7	30	25.6	30.7	27.9	1.4
Wd:L,%	27.6	-	25.4	c26.0	>24.8	-	>23.8	26.8	c33.0	19	24.5	27.8	26.3	0.9	30	24.5	31.3	27.5	1.7
Wm:L,%	16.9	-	14.9	15.0	14.6	-	-	12.8	19.2	20	14.3	16.9	15.5	0.8	30	14.3	19.9	16.4	1.5

Tab. 17 Measurements of metacarpals of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n. Untermaßfeld					»*Bison*« sp. Venta Micena (Moya-Sola,1987)					*Bison* spp. Mauer					*Bison* spp. Mosbach					*Bison* spp. Süßenborn			
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	MIN	MAX	AVG	STD
L	33	262.0	297.0	277.5	9.2	20	208.2	246.7	223.8	9.4	9	250.4	276.0	265.5	8.6	53	235.5	277.8	254.4	9.4	238.5	275.0	251.9	13.1
Wp	44	68.0	88.0	77.0	5.3	21	52.5	70.3	58.5	4.8	8	71.8	92.7	82.5	6.4	51	71.6	98.8	84.2	6.6	69.7	85.0	77.4	5.6
Tp	44	40.0	53.0	46.5	3.2	23	32.3	43.3	35.7	3.1	6	43.5	53.0	49.1	3.3	33	41.3	55.4	47.8	3.9	39.0	50.0	45.1	3.7
Wd	34	68.0	87.0	76.5	6.3	18	52.9	68.3	58.5	4.7	8	70.7	89.0	78.6	6.6	48	72.5	97.1	83.1	6.7	65.5	82.6	74.7	5.7
Td	33	38.0	48.5	43.7	2.7	21	30.6	37.0	33.2	1.7											37.0	45.0	40.8	3.4
Wm	40	37.5	57.7	44.9	4.8	20	31.3	42.0	34.2	3.2	9	41.6	56.6	50.0	5.1	51	40.7	62.5	51.5	5.4	40.5	54.3	46.5	3.6
Tm	37	29.0	40.0	33.5	3.0	20	24.3	32.8	27.1	2.1	7	29.6	37.7	33.8	2.9	19	29.0	40.7	34.2	2.7	28.1	37.5	33.3	2.7
Wp:L,%	30	25.6	30.7	27.9	1.4	16	24.6	28.5	25.9	1.1	8	28.7	34.0	31.1	1.9	51	29.6	37.3	33.0	1.9	26.9	33.3	29.9	2.0
Wd:L,%	30	24.5	31.3	27.5	1.7	17	23.8	28.7	25.8	1.3	8	27.3	34.2	29.7	2.2	48	29.3	37.5	32.6	2.0	25.1	32.5	29.3	2.7
Wm:L,%	30	14.3	19.9	16.4	1.5	20	14.3	17.6	15.3	0.9	9	15.4	21.5	18.8	1.7	51	17.3	23.6	20.2	1.8	16.2	19.7	18.0	1.3

	Bison sp. Tiraspol					*Bison priscus* Taubach					*Bison priscus* Northeast Siberia					*Bos primigenius* Ilford (Browne, 1983)				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	9	252.7	276.0	265.1	6.4	8	253.0	287.0	271.1	10.4	29	206.0	235.0	222.1	8.5	10	208.0	268.0	248.0	17.5
Wp	11	80.5	102.0	92.6	6.2	8	71.5	101.3	89.1	9.0	29	68.5	90.5	80.3	6.5	8	81.0	96.0	88.5	5.0
Tp	11	49.0	64.0	54.1	4.1	8	47.5	62.2	55.9	4.7	29	39.0	51.5	45.8	3.5					
Wd	10	81.0	99.0	93.9	5.3	8	76.5	99.0	89.2	7.9	29	71.0	95.0	82.8	6.8	10	79.0	95.0	88.7	5.0
Td	2	43.5	51.6	47.5	4.0	7	41.7	51.2	47.5	3.3										
Wm	11	46.6	67.6	58.2	5.7	8	41.0	61.5	54.1	6.9	29	38.7	62.0	49.1	6.2	9	47.0	58.0	53.6	3.1
Tm	4	33.7	38.7	36.7	1.9	8	32.5	42.0	37.4	3.2	29	28.0	37.0	32.5	2.7					
Wp:L,%	9	31.2	37.4	34.8	1.8	8	28.3	35.3	32.8	2.2	29	29.9	40.1	36.2	2.5	8	32.7	37.7	35.3	1.3
Wd:L,%	9	31.4	37.5	35.2	1.8	8	30.2	35.6	32.9	1.8	29	32.3	41.1	37.3	2.4	10	33.9	38.0	35.8	1.3
Wm:L,%	9	18.1	25.2	22.1	1.9	8	16.2	21.7	19.9	1.9	29	16.9	26.6	22.1	2.4	9	20.9	22.7	21.7	0.7

Tab. 18 Measurements of metacarpals of various fossil samples of large bovids, mm, and indices, %.

vids. After testing various graphs, I have decided in favour of the distal width index plotted against the greatest length (Fig. 11). Analysis of this graph allows the following inferences to be made.

1. The parameters of *B. menneri* metacarpals associate in compact clusters, and by analogy with homogeneous samples from other localities [2] clearly divide our sample into males and females. As in most samples of *Bison* and *Bos* metacarpals, sexual dimorphism is not so much manifested in the bone size (length) as in its proportions.
2. The compactness of the clusters corroborates the homogeneity of the Untermaßfeld population of bovids. It is highly unlikely that this sample includes remains of more than one species.
3. *B. menneri* has evidently larger and stouter metacarpals than all known species of *Leptobos* (including the largest and stoutest-legged *Leptobos etruscus*) and than »*Bison* sp.« from Venta Micena.
4. The combination of very large size and slenderness distinguishes *B. menneri* from all known *Bison* and *Bos* species. It has nothing in common with small Late Quaternary forms like the one from Roter Berg near Saalfeld in Thuringia, or Ukrainian or Siberian-Alaskan species. Being only slightly larger than the largest European forms like the one from Taubach, *B. menneri* metacarpals are impressively slender. The graph shows also a trustworthy distinction between the Untermaßfeld and Mosbach species, the latter being somewhat shorter and evidently more stout. If we plot on the same graph parameters of the metacarpals of the large Pleistocene *Bos primigenius*, most of them will fall within the clusters of the Mosbach bison.

Of all the studied samples, metacarpals from Mauer approach the Untermaßfeld sample most closely. Indeed, some of them fall within *B. menneri* clusters. However, if we consider Mauer male and female metacarpals separately, we can see that the most slender Mauer metacarpals correspond to the shortest and stoutest specimens from Untermaßfeld (cf. Fig. 11 and Table 18).

Besides some metacarpals from Mauer, I could find in numerous collections examined only two specimens that are within the limits of *B. menneri* clusters. One is from Süßenborn (IQW 1965/2333 (Süß. 9161)). It differs strikingly from the other Süßenborn metacarpals not only in larger size and slenderness, but in another kind of preservation. It is possible that this specimen is redeposited from earlier sediments, but it is very hard to prove that. The other one is from Chertkovo locality in Ukraine (see comments below).

The morphology of *B. menneri* metacarpals is strongly influenced by the general slenderness of the bone. The medial facet of the proximal articular surface is relatively narrow and rather often has a quadrangular shape. According to many authors (Schertz 1936a; 1936b; Bibikova 1958 and others), this condition is thought to be peculiar to *Bos* rather than to *Bison*. I tried to check it by measurements, estimating ratios between the width of lateral and medial facets (Wfl:Wfm, %) and between the transverse diameter and width of the medial facet (Tfm:Wfm, %) and found a very wide range of variation of these features (Table 19). Rather unexpectedly, I found no difference in the average values of either index between the studied samples of *Bos primigenius* and *Bison* priscus. However, *B. menneri* shows an appreciably more quadrangular medial facet than either of these species or the Mauer bison.

Correspondingly, the outlines of the proximal articular surface in many metacarpals of *B. menneri* are rather similar to the schematic *Bos* pattern suggested by Schertz (1936a) – with a quadrangular rather than a trapezoidal medial facet having roughly parallel sides and a more or less apparent dorso-medial angle (cf. Fig.1, c; Taf. 29, 4). But in the arrangement of the crista and sulcus, separating the two proximal facets, *B. menneri* metacarpals look more similar to *Bison* than to *Bos*. According to Bibikova (1958), this crista is better pronounced in *Bison*, being more sharp and longer than in *Bos*. Moreover, the

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[2] In course of my research I plotted in the same way the following samples of metacarpals: 1. Small *B. priscus* from Late Pleistocene locality Amvrosievka in Ukraine (n=59). 2. Small *B. priscus* from Late Pleistocene locality Lost Chicken in Alaska (n=26). 3. Small *B. priscus* from the Late Pleistocene of the Kolyma Lowland, N.-E. Siberia (n=32). 4. *Bos primigenius* from Neolithic of Denmark according to Degerbøl and Fredskild, 1970 (n=29). The volume of this comparative evidence is too large to be presented in this publication.

	Bison menneri sp. n. Untermaßfeld									*Bison priscus* Ukraine, Germany			*Bos primigenius* Ukraine, Germany		
	mm			ff			Total								
	N	AVG	STD	N	AVG	STD	N	AVG	STD	N	AVG	STD	N	AVG	STD
Wfl:Wfm	11	70.2	5.1	17	74.4	4.8	31	72.3	5.2	18	69.7	4.2	21	69.0	4.1
Tfm:Wfm	11	99.0	3.1	18	99.1	3.3	32	99.2	3.2	18	93.2	5.9	21	94.0	3.7
Wd1:Wd	12	98.3	2.4	16	97.7	1.8	28	98.0	2.1	27	96.9	2.2	27	92.6	3.1
Wd2:Wd	12	95.2	1.4	16	95.5	1.4	28	95.4	1.4	27	95.2	2.7	27	92.5	2.7

Wfl - greatest width of lateral part of posterior articular surface (facet for carpal 4);
Wfm - greatest width of medial part of this articulation (facet for carpal 2+3);
Tfm - greatest anterior-posterior diameter of proximal facet for carpal 2+3;
Measurements Wfl, Wfm and Tfm correspond to measurements 4, 2, and 1 indicated by Browne (1983), Fig. 21, respectively;
Wd1 - width of the distal end at the contact between the shaft and distal epiphysis;
Wd2 - width of the distal end just over the trochlea.

Tab. 19 Some indices of metacarpals of various bovids, %.

long crista is usually combined with a relatively short sulcus in *Bison* contrary to *Bos,* where in most cases the sulcus penetrates much deeper into the proximal articular surface while the crista is notably shorter.

Despite some individual variation, this seems to be a reliable distinction between *Bos* and *Bison*. It is difficult to take precise measurements of the length of crista and sulcus, and the ratio suggested in Table 19 should be considered as a crude estimation (cf. its very high standard deviation). Anyhow, this ratio demonstrates that the sulcus is almost always longer than the crista in *Bos*, and shorter in *Bison*. The Untermaßfeld bovid follows the *Bison* condition completely (Figs. 1, c; 10, c, g; Taf. 29, 4-6).

Among variable features suggested as discriminating between *Bos* and *Bison* metacarpals (Schertz 1936a; 1936b; Bibikova 1958; Olsen 1960; Stampfli 1963), I consider the shape of the distal end (contact of the shaft with the distal epiphysis) as the most reliable one. In *Bison*, the area of this contact is marked by well pronounced tubercles, the width of the bone in this area being roughly equal to the maximum distal width. Below these tubercles, a more or less pronounced constriction is usually observed. Most commonly, callipers placed in this constriction (just over the trochlea) cannot be moved upwards as they are restricted by the tubercles. Of course, there is some individual variation in *Bison* (cf. Browne 1983, Fig. 8), but this condition is practically absent in *Bos*. In the latter, the epitrochlear inflation is not pronounced and the distal end looks like a smooth prolongation of the side edges of the shaft. These features give quite a different shape to the distal ends of *Bos* and *Bison* metacarpals. I cannot agree with Sala (1986) that it is difficult to express this difference in the measurements suggested by Schertz (1936a). Certainly, it is more difficult to measure epitrochlear width in *Bos* than in *Bison*; however, the measurement at the corresponding place can be taken in *Bos* as well. The ratio of this width to the maximum distal width demonstrates a reliable statistical difference between *Bos* and *Bison* (Table 19). In most cases, the callipers cannot be fixed in the epitrochlear position in *Bos* metacarpals, as they lack the mentioned constriction.

In this respect, *B. menneri* has a full pronounced *Bison* condition. Despite the overall slenderness of its metacarpals, the epitrochlear tubercles are very well developed, as well as the constriction between them and the trochlea, both in males (Figs. 1; 10, a, b; Taf. 28, 1, 2; 29, 1-3) and females (Fig. 10, e, f; Pl. VII, 4,5). Only in some very slender female metacarpals are these features less pronounced (Taf. 28, 4,5) but even they still have rather a *Bison*-like than a *Bos*-like shape.

3.2.15. Pelvis

Bison pelves are represented in the Untermaßfeld collection by numerous (23) but badly preserved fragments. The best preserved specimens have the acetabulum with a part of the iliac bone, like IQW 1982/17 833 (Mei. 17 353), Taf. 25, 4. The structure of the acetabulum is usual for large bovids. Its width varies from 77 to 82 mm (n=4), its anteroposterior diameter from 65 to ca 87 mm (n=7).

3.2.16. Femur

One complete femur IQW 1982/17 796 (Mei. 17 316), Taf. 30, 1, 2, Fig. 12, and 19 fragments (12 of distal part, 3 of proximal part, and 4 of the shaft).

The only complete femur belongs to a female individual, being almost the smallest among the other fragments (Table 20). As compared to fossil *B. priscus* and *Bos primigenius*, this specimen is one of the smallest and the most gracile.

The proximal end has typical morphology for *Bison* in the position of trochanter major and the sharp angle of fossa trochanterica (cf. Martin 1987). Facies patellaris also has a *Bison*-like shape. However, its lateral edge has a slightly developed break in the caudal part (cf. Fig. 12, c) usually absent in *Bison* and more pronounced in *Bos primigenius*.

3.2.17. Tibia

Among 36 specimens of *Bison* tibia in the Untermaßfeld collection only four are more or less complete though slightly damaged: IQW 1980/ 15 372 (Mei. 14 884) (Taf. 30, 3, 4; Fig. 13) and IQW 1980/17 313 (Mei. 16 835), both belonging to males, IQW 1980/15 465 (Mei. 14 977) and IQW 1980/15 466 (Mei. 14 978) – females. The remaining specimens are almost exclusively represented by distal fragments. There is only one proximal fragment of tibia in the sample: IQW 1986/21 439 (Mei. 20 868) (Taf. 30, 5).

The tibia of *B. menneri*, like its radius, displays a notable size difference between males and females (Table 21). Male tibiae are as long as those of the largest *B. priscus* from Taubach and Tiraspol and close to the largest specimens of *Bos primigenius*, while females are more similar in size with the small Siberian *B. priscus* (Table 22). However, the *B. menneri* tibia is evidently larger than that of »*Bison* sp.« from Venta Micena.

At the same time, in transverse diameters the male tibiae from Untermaßfeld are somewhat smaller than those of the largest *B. priscus*, at least on the average, while females are notably smaller and can be compared only with the smallest *B. priscus* from Siberia. That means that the *B. menneri* tibia is relatively more slender than that of most known species of *Bison*. This seems to be confirmed by the indices of a few better preserved specimens of the Untermaßfeld bison; however, the difference is not very large.

Morphologically, the tibia of *B. menneri* shows features rather typical for *Bison*. The most remarkable is the structure of the articulation with the malleolus. In *B. menneri*, there are two facets separated by a deep groove, as in *B. priscus* (Taf. 30, 4, 6, 7; Fig. 13, c). In *Bos*, they are almost always confluent, the anterior one is essentially smaller than the posterior, flat, and facing distally (Bibikova 1958; Martin 1987). In *B. menneri*, the anterior facet for the malleolus always faces forward and can be seen in dorsal view entirely, or at least in part (Fig. 13, a). It depends on whether the whole facet has an oblique position, or whether it is convex and its anterior part bent upward. In more than 60% of the Untermaßfeld tibiae the anterior malleolus facet is rather wide (about 2/3 of the posterior), and projects more laterally than in *Bos*.

A groove for musculus flexor digitalis longus on the plantar-lateral side of the distal end (Martin 1987, Abb. 11.14) is shallow or sometimes even absent on the Untermaßfeld tibiae, as is thought to be typical for *Bison*. Only some specimens have a deeper groove accentuated by tubercles on both sides of its distal end.

The proximal part of the tibia is preserved on a few specimens only. A lateral outline of condylus lateralis is gently convex as Martin (1987) shows for *B. priscus*.

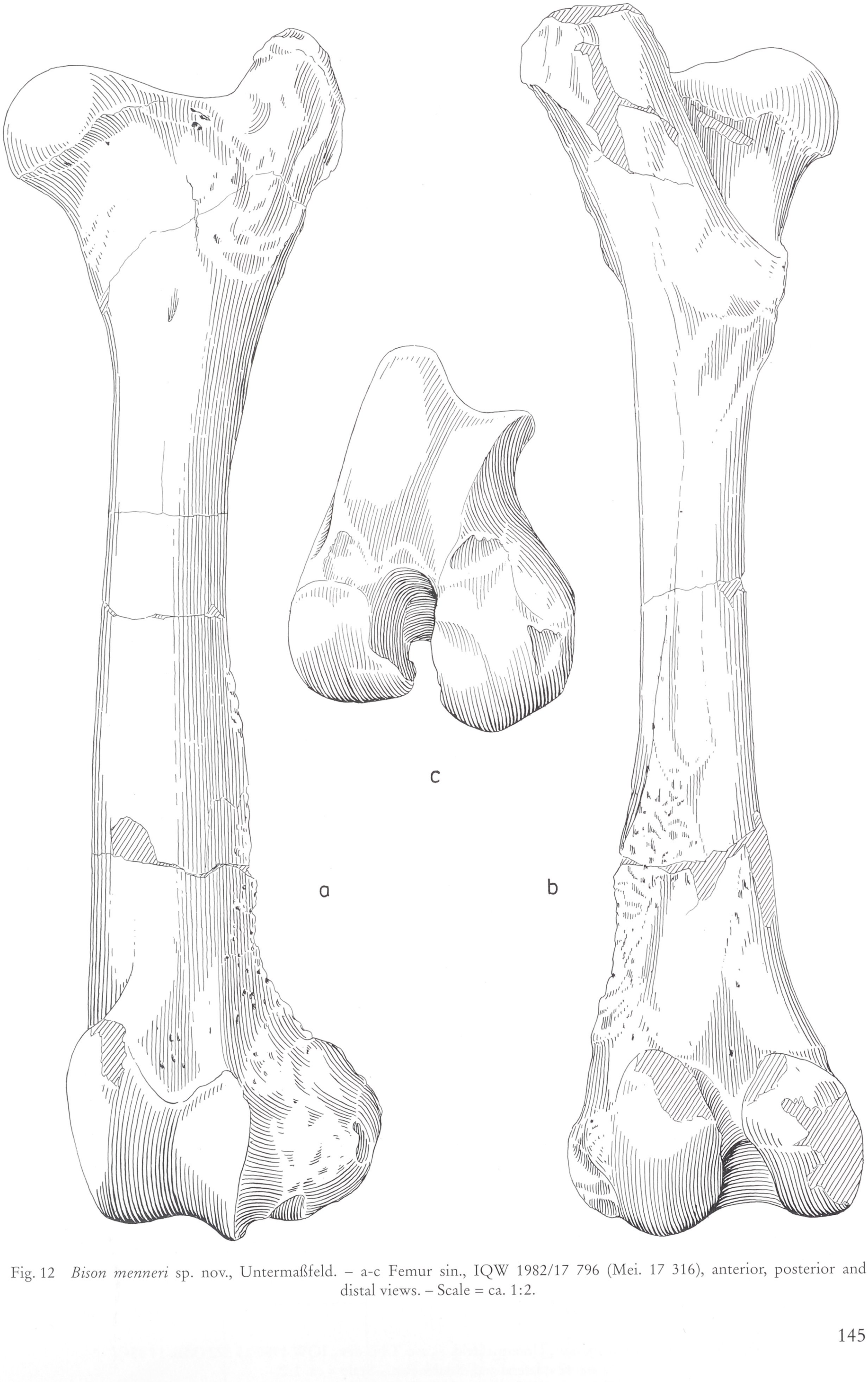

Fig. 12 *Bison menneri* sp. nov., Untermaßfeld. – a-c Femur sin., IQW 1982/17 796 (Mei. 17 316), anterior, posterior and distal views. – Scale = ca. 1:2.

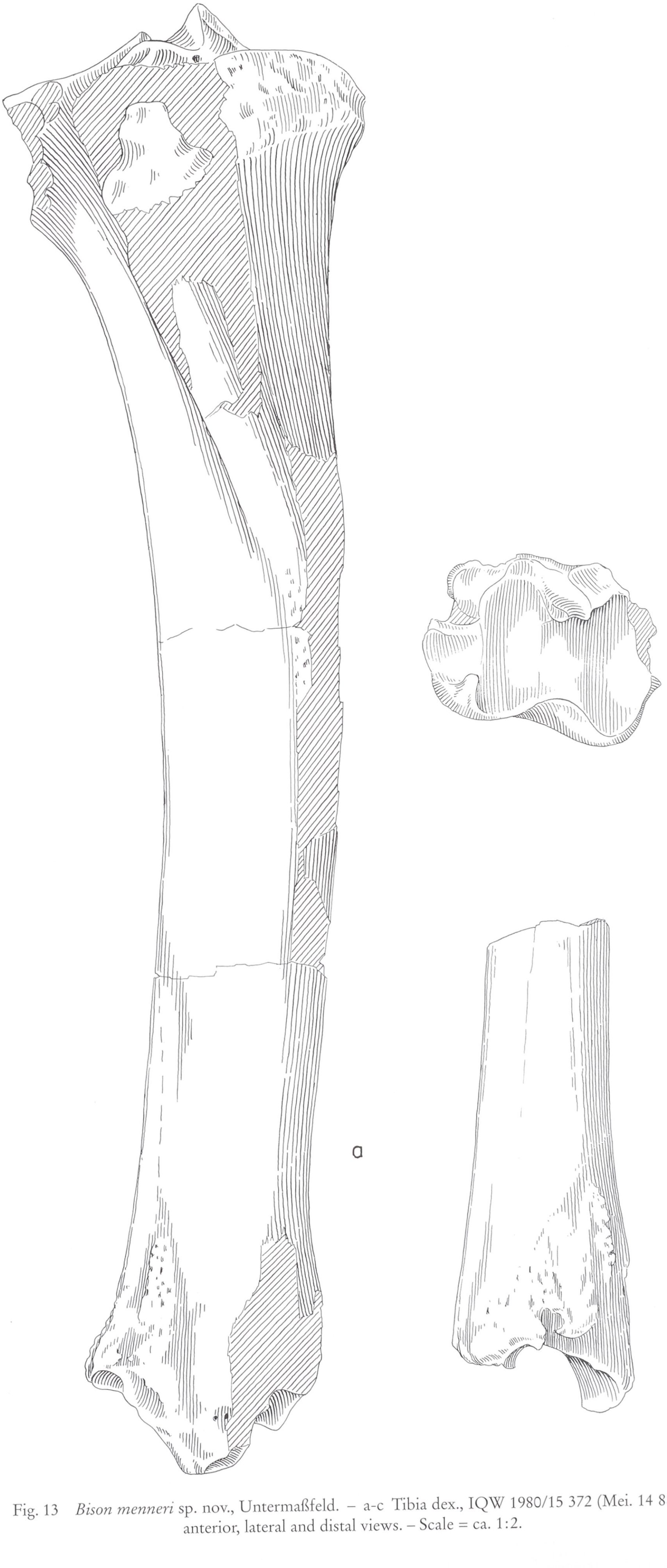

Fig. 13 *Bison menneri* sp. nov., Untermaßfeld. – a-c Tibia dex., IQW 1980/15 372 (Mei. 14 884), anterior, lateral and distal views. – Scale = ca. 1:2.

	Bison menneri sp.n., Untermaßfeld					*Bison priscus*												*Bos primigenius*				
	IQW 1982/ 17796	IQW 1980/ 16262	IQW 1986/ 21348	IQW 1980/ 17570	IQW 1980/ 15382	Rhine Gravels (Martin)					Mosbach,	Mauer	Northeast Siberia					Rhine Gravels (Martin)				
				juv.	juv.	N	MIN	MAX	AVG	STD			N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	c430.0	-	-	-	-	3	470.0	540.0	515.3	32.1	523.0	510.0	3	422.0	472.0	444.7	20.7	3	524.0	556.0	542.7	13.6
Lc	-	-	-	-	-	6	432.0	518.0	482.3	32.0	499.0	483.0	2	392.0	415.0	403.5	11.5	5	490.5	522.0	506.5	10.0
Wp	130.0	-	-	-	-	3	156.0	188.0	175.7	14.1	188.0	167.0	2	146.0	163.0	154.5	8.5	4	174.0	190.5	179.8	6.5
Wm	40.0	-	-	-	-	6	47.5	61.5	54.7	5.1	55.0	53.0	5	45.0	55.0	48.9	3.9	5	55.0	60.0	57.5	1.8
Wd	103.0	99.0	115.0	118.0	109.0	5	120.0	143.5	136.0	9.0	138.0		5	112.0	135.0	121.3	9.1	5	135.0	145.0	141.4	3.9
Td	136.0	135.0	154.0	c147.0	-								4	146.0	160.0	151.3	5.4					
Wp:L,%	30.2	-	-	-	-	3	33.2	35.1	34.1	0.8	35.9	32.7	2	34.5	34.6	34.6	0.0	3	32.7	34.3	33.5	0.7
Wm:L,%	9.3	-	-	-	-	3	9.4	10.1	9.8	0.3	10.5	10.4	3	10.2	11.1	10.8	0.4	3	10.0	10.8	10.5	0.3
Wd:L,%	24.0	-	-	-	-	3	25.5	26.6	26.2	0.5	26.4		3	25.9	27.6	26.9	0.7	3	25.0	26.5	25.7	0.6
Wm:Lc,%	-	-	-	-	-	6	10.2	12.7	11.3	0.9	11.0	11.0	2	10.8	12.0	11.4	0.6	5	10.5	11.9	11.4	0.4

Tab. 20 Measurements of femur of *Bison menneri* sp. n. and various bovids, mm, and indices, %.

	IQW 1980/ 15372 m	IQW 1980/ 17313 m	IQW 1980/ 16173 m	IQW 1980/ 17217 m	IQW 1980/ 17555 m	IQW 1981/ 17752 m	IQW 1982/ 17812 m	IQW 1982/ 17981 m	IQW 1982/ 18096 m	IQW 1983/ 19167 m	IQW 1985/ 20086 m	IQW 1986/ 21039 m	IQW 1986/ 21042 m	IQW 1986/ 21439 ?	IQW 1980/ 16666 ?	IQW 1985/ 20356 ?	mm				
																	N	MIN	MAX	AVG	STD
L	505.0	c490.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	490.0	505.0	497.5	–
Wp	>130.0	142.0	-	-	-	-	-	-	-	-	-	-	-	122.0	-	-	2	122.0	142.0	132.0	–
Wd	>82.0	-	90.0	88.0	89.0	90.5	86.5	89.0	89.0	90.0	>85.0	93.0	94.0	-	85.0	-	10	86.5	94.0	89.9	2.1
Td	>60.0	-	67.0	c63.0	66.0	c65.0	66.0	66.0	65.0	62.0	>60.0	65.0	-	-	66.5	-	9	62.0	67.0	65.0	1.5
Wm	58.5	61.0	62.0	60.0	60.0	59.0	57.0	c59.0	57.0	55.0	-	60.0	60.0	-	55.5	58.0	12	55.0	62.0	59.0	1.9
Wm:L,%	11.6	12.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	11.6	12.4	12.0	–

	IQW 1980/ 15466 f	IQW 1980/ 15465 f	IQW 1982/ 18119 f	IQW 1980/ 15207 f	IQW 1980/ 15295 f	IQW 1980/ 15401 f	IQW 1980/ 16073 f	IQW 1980/ 16157 f	IQW 1980/ 17483 f	IQW 1981/ 17651 f	IQW 1983/ 18893 f	IQW 1983/ 18933 f	IQW 1985/ 20563 f	IQW 1985/ 20867 f	IQW 1986/ 21371 f	ff				
																N	MIN	MAX	AVG	STD
L	441.0	439.0	>410.0	-	-	-	-	-	-	-	-	-	-	-	-	2	439.0	441.0	440.0	–
Wp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Wd	82.0	74.0	83.0	76.5	82.5	80.0	81.0	>70.0	80.0	80.0	79.0	76.0	80.0	81.0	80.5	14	74.0	83.0	79.7	2.5
Td	59.0	57.0	c64.0	61.0	57.3	64.0	>60.0	60.0	c55.0	58.0	59.5	59.0	59.0	c61.0	>59.0	13	55.0	64.0	59.5	2.5
Wm	54.0	51.5	52.5	-	53.6	c51.0	-	-	-	-	-	-	52.0	c49.0	50.0	8	49.0	54.0	51.7	1.6
Wm:L,%	12.2	11.7	<12.8	-	-	-	-	-	-	-	-	-	-	-	-	2	11.7	12.2	12.0	–
Wd:L,%	18.6	16.9	<20.2	-	-	-	-	-	-	-	-	-	-	-	-	2	16.9	18.6	17.7	–

Tab. 21 Measurements of tibia of *Bison menneri* sp.n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n.					»*Bison*« sp.			*Bison schoetensacki*					*Bison* »*schoetensacki*«				
	Untermaßfeld					Venta Micena			Mauer (Sala, 1987)					Tiraspol				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	4	439.0	505.0	468.8	29.2	2	366.0	404.0						4	485.0	513.0	497.0	10.1
Wp	3	122.0	142.0	129.7	8.8	2	93.6	106.0						3	132.0	154.0	145.3	9.6
Wd	25	74.0	94.0	84.0	5.4	4	60.0	62.2	7	77.0	91.0	85.1	4.4	4	89.0	94.0	92.8	2.2
Td	23	55.0	67.0	62.0	3.5	4	41.2	51.7	7	56.0	64.0	61.9	2.5	4	64.0	73.0	69.5	3.4
Wm	22	49.0	62.0	56.2	3.8	2	44.6	52.0	2	53.0	60.5	56.8	3.8	4	56.5	70.0	62.6	5.3
Wm:L,%	4	11.6	12.4	12.0	0.4	2	12.2	12.9						4	11.6	14.1	12.6	1.0
Wd:L,%	2	16.9	18.6	17.7	0.9	2	15.4	16.5						4	18.3	19.0	18.7	0.3

	Bison priscus Boj.											*Bos primigenius*				
	Rhine Gravels (Martin,1987)					Northeast Siberia					Taubach 1969/ 12321	Rhine Gravels (Martin,1987)				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD		N	MIN	MAX	AVG	STD
L	19	445.0	549.0	487.0	28.8	8	393.0	468.0	438.8	24.9	495.0	7	431.5	539.0	488.8	29.4
Wp	19	114.0	158.5	140.9	10.9	6	122.2	138.0	131.9	5.2	146.0	7	115.0	156.5	142.9	12.8
Wd	19	77.0	104.5	90.7	6.5	8	74.0	86.0	81.0	4.1	101.0	7	78.5	100.0	91.6	6.6
Td						8	51.0	65.5	58.8	5.3	76.0					
Wm	19	52.0	68.5	60.8	4.6	8	47.0	63.5	55.3	4.5	70.0	7	53.0	64.0	61.2	3.6
Wm:L,%	19	11.4	14.1	12.5	0.6	8	12.0	14.1	12.6	0.7	14.1	7	11.7	13.2	12.5	0.5
Wd:L,%	19	17.3	20.3	18.6	0.8	8	17.5	19.3	18.5	0.6	20.4	7	17.9	19.4	18.7	0.5

Tab. 22 Measurements of tibia of various bovids, mm, and indices, %.

3.2.18. Astragalus

The Untermaßfeld collection includes 51 astragali, most of them (44) intact or only slightly damaged. Male specimens (cf. IQW 1980/15 294 (Mei. 14 806), Taf. 31, 4-6, Fig. 14, e-g), are usually larger, especially in transverse dimensions, and correspondingly stouter, in particular at the distal end, than female (cf. IQW 1980/15 289 (Mei. 14 801), Taf. 31, 12, 13, Fig. 15, e-g). However, both measurements and indices of the two sexes overlap in part. A classification into males and females used the same technique as for metacarpals, taking into account both size and proportions (Table 23). For some specimens sex attribution should be considered as provisional only. Moreover, some specimens were excluded from the statistics as strongly deviating, like the extremely stout IQW 1980/15 299 (Mei. 14 811).

The astragalus is a very usual and well preserved bone in fossil bovid collections, so I could use a great number of bones for comparison studied by various students and myself (Table 24). It should be noted, however, that astragali of large Quaternary bovines (*Bison* and *Bos*) are much less differentiated in size and proportions than many other skeletal elements. Ranges of variation of most parameters of all the examined bovines are essentially transgressive, with the exception of only a small »*Bison*« sp. from Venta Micena which is markedly smaller than all the other asragali, including the Untermaßfeld and Siberian females. That is why in the further discussion of distinctions between the Untermaßfeld and other astragali I shall refer only to average values.

Unlike the long limb bones and metacarpal, the *B. menneri* astragali are not among the largest known for bovids. Even the largest Untermaßfeld specimens in length and distal width never reach the size of the largest among Taubach, Süßenborn and Tiraspol bisons and Lunel-Viel *Bos*. As a whole, *B. menneri* astragali are smaller than those of the above-mentioned forms as well as of the Mauer, Mosbach, and Isernia bison. They have the same width as astragali of the small bison from Northeast Siberia, being on the average slightly longer.

The general proportions of the astragalus are very similar in all examined bison (cf. index Wd/L in Table 24). Ranges of variation overlap completely, the mean values of the index changing from 67.1 in Taubach to 64.4 in Süßenborn[3]. Mean values of all the other examined *Bison* populations, including the whole Untermaßfeld sample (males + females) and Siberian sample, fall within this interval of less than 3% wide.

The comparative morphology of the *Bison* and *Bos* astragalus has been discussed by many authors (Schertz 1936a; Bibikova 1958; Stampfli 1963; Sala 1986). I agree with Sala that individual variation in most features suggested as diagnostic is too great to consider them as the reliable ones. For instance, the contact area between the plantar articulations with the calcaneus and central tarsal is thought to be important for that diagnosis. In *Bos*, these articular surfaces are usually more confluent, with a small insulated fossette between them only. In *Bison*, they are separated by a deep groove usually open on the lateral side (Schertz 1936a); the lower edge of the calcanear articulation sloping to this groove bears a special additional facet for the central tarsal bone (Bibikova 1958). Indeed, this additional facet is well marked in 97% of the astragali of Siberian *B. priscus* (less developed on 1 of 35 specimens). In 77% specimens of this sample the groove is open and can be seen as a notch in lateral view; in the rest of the sample the edges of the groove fuse together at the very lateral border, and the notch cannot be seen from lateral side. So, this condition seems to be rather constant in *Bison*. The opposite condition is usual in *Bos*; however, sometimes a narrow groove opening laterally can be seen in *Bos* as well.

In *B. menneri*, the variation in morphology of this area is evidently greater than in *B. priscus*. The well developed groove bearing an additional facet for the central tarsal is present in 66% of the sample (n=32), in 15% the facet is weakly developed, and it is absent in 19%. The groove is open laterally, and

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[3] The relative slenderness of Süßenborn astragali may be related to fluvial rounding of most specimens in the sample. I agree with Sala (1986) that this feature is more variable than Bibikova suggested. But I never observed in *B. priscus* such high values of the corresponding index as can be seen on some *Bos* astragali (higher than 58%). In *B. menneri*, about 30% of specimens has these values of index, that again evidences some shift towards the *Bos* pattern.

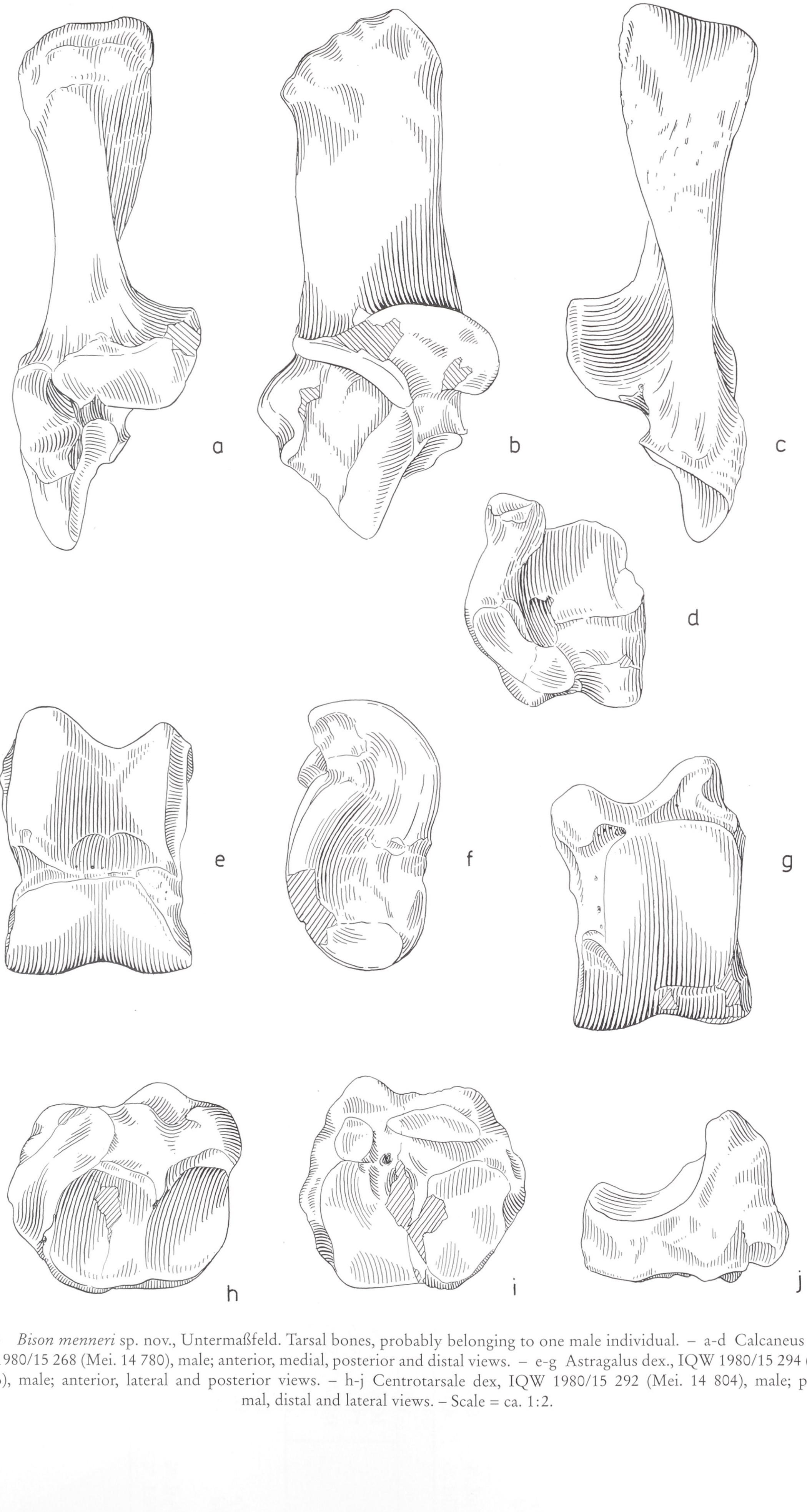

Fig. 14 *Bison menneri* sp. nov., Untermaßfeld. Tarsal bones, probably belonging to one male individual. – a-d Calcaneus dex., IQW 1980/15 268 (Mei. 14 780), male; anterior, medial, posterior and distal views. – e-g Astragalus dex., IQW 1980/15 294 (Mei. 14 806), male; anterior, lateral and posterior views. – h-j Centrotarsale dex, IQW 1980/15 292 (Mei. 14 804), male; proximal, distal and lateral views. – Scale = ca. 1:2.

	IQW 1980/ 15288 m	IQW 1980/ 15291 m	IQW 1980/ 15294 m	IQW 1980/ 17306 m	IQW 1980/ 17338 m	IQW 1980/ 17587 m	IQW 1981/ 17649 m	IQW 1981/ 17662 m	IQW 1982/ 18255 m	IQW 1983/ 19038 m	IQW 1983/ 19058 m	IQW 1985/ 20788 m	IQW 1986/ 21238 m	IQW 1986/ 21376 m	IQW 1986/ 21481 m	IQW 1980/ 15606 m?	IQW 1980/ 17018 m?	mm N	MIN	MAX	AVG	STD	IQW 1980/ 15299 m
L	87.5	90.0	94.0	95.5	c83.0	-	81.5	83.0	88.0	89.0	88.0	93.0	84.0	86.0	95.0	85.0	86.0	16	81.5	95.5	88.0	4.3	87.0
Wp	59.5	57.0	66.0	65.0	>56.0	63.0	57.5	58.0	59.5	59.0	-	62.3	59.0	60.0	63.7	56.5	57.5	15	56.5	66.0	60.2	2.9	63.0
Wd	57.0	57.0	62.8	64.5	56.5	61.5	55.5	56.8	58.0	57.0	57.6	59.0	58.6	60.5	63.0	56.3	56.0	17	55.5	64.5	58.7	2.7	64.4
Wp:L,%	68.0	63.3	70.2	68.1	-	-	70.6	69.9	67.6	66.3	-	67.0	70.2	69.8	67.1	66.5	66.9	14	63.3	70.6	68.0	2.0	72.4
Wd:L,%	65.1	63.3	66.8	67.5	68.1	-	68.1	68.4	65.9	64.0	65.5	63.4	69.8	70.3	66.3	66.2	65.1	16	63.3	70.3	66.5	2.0	74.0

	IQW 1980/ 15287 f	IQW 1980/ 15289 f	IQW 1980/ 15290 f	IQW 1980/ 16507 f	IQW 1980/ 16788 f	IQW 1980/ 16975 f	IQW 1980/ 17075 f	IQW 1980/ 17502 f	IQW 1980/ 17533 f	IQW 1982/ 18125 f	IQW 1983/ 18974 f	IQW 1984/ 19991 f	IQW 1985/ 20413 f	IQW 1985/ 20508 f	IQW 1985/ 20997 f	IQW 1985/ 21017 f	IQW 1986/ 21381 f	ff N	MIN	MAX	AVG	STD
L	84.7	85.0	82.5	c80.0	-	82.0	86.7	83.2	86.0	84.5	82.5	83.0	78.5	85.0	85.0	84.0	84.0	16	78.5	86.7	83.5	2.1
Wp	54.5	55.5	53.5	53.0	>52.0	>52.0	58.0	c53.0	57.5	53.5	57.0	55.4	56.2	57.0	>54.0	>56.0	57.0	13	53.0	58.0	55.5	1.6
Wd	54.0	55.0	53.0	52.0	>51.0	50.5	52.5	52.5	51.5	54.5	54.3	52.0	52.6	55.0	54.0	56.5	55.0	16	50.5	56.5	53.4	1.5
Wp:L,%	64.3	65.3	64.8	66.3	-	63.4	66.9	63.7	66.9	63.3	69.1	66.7	71.6	67.1	63.5	-	67.9	13	63.3	71.6	66.4	2.2
Wd:L,%	63.8	64.7	64.2	65.0	-	61.6	60.6	63.1	59.9	64.5	65.8	62.7	67.0	64.7	63.5	67.3	65.5	16	59.9	67.3	64.0	2.0

Tab. 23 Measurements of astragalus of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n. Untermaßfeld					»*Bison*« sp. Venta Micena (Moya-Sola,1987)					*Bison schoetensacki* Mauer (Sala,1987)					*Bison schoetensacki* Süßenborn				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	32	78.5	95.5	85.8	4.1	15	66.6	77.0	71.5	3.4	14	85.0	100.0	91.0	4.2	16	83.7	105.0	96.9	6.5
Wp	27	53.0	66.0	58.2	3.3											16	55.5	74.0	63.4	4.6
Wd	33	50.5	64.5	56.1	3.4	17	40.0	53.7	47.2	3.5	15	55.0	65.0	60.0	3.2	15	57.0	70.0	62.2	3.9
Wp:L,%	26	63.3	71.6	67.4	2.1											16	62.4	70.6	65.4	2.9
Wd:L,%	32	59.9	70.3	65.2	2.4	14	60.1	70.1	66.0	2.7	14	62.0	73.0	65.8	3.0	15	59.9	69.4	64.	3.1

	Bison schoetensacki Isernia (Sala,1987)					*Bison schoetensacki* Mosbach (Sala,1987)					*Bison* »*schoetensacki*« Tiraspol					*Bison priscus* Taubach				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	10	87.0	98.2	92.0	3.0	5	88.5	99.5	94.2	4.5	4	85.2	104.0	91.5	7.5	18	86.0	105.8	98.5	4.8
Wp											3	62.0	67.0	64.0	2.2					
Wd	11	55.0	65.6	60.9	3.2	4	55.0	66.0	61.8	4.1	4	55.0	65.5	61.0	3.8	18	53.5	74.5	66.1	4.7
Wp:L,%											3	64.4	72.1	68.6	3.2					
Wd:L,%	8	62.0	71.9	66.3	2.9	4	62.1	67.8	65.1	2.1	4	63.0	71.3	66.8	3.3	18	60.8	72.8	67.1	3.3

	Bison priscus Northeast Siberia					*Bos primigenius* Lunel-Viel (Brugal, 1985)									
	mm + ff					mm					ff				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	33	77.8	93.0	84.0	4.4	14	91.1	100.8	96.8	2.8	66	81.7	93.3	87.5	2.8
Wp	33	50.0	64.2	58.0	3.9	12	58.9	72.1	64.0	3.7	65	50.2	60.1	56.7	2.0
Wd	33	49.1	63.5	56.1	4.1	13	65.2	75.2	68.0	3.2	65	50.5	63.6	57.8	2.3
Wp:L,%	33	64.3	75.4	69.1	2.8				66.1					64.8	
Wd:L,%	33	62.5	73.9	66.8	2.7				70.2					66.1	

Tab. 24 Measurements of astragalus of various bovids, mm, and indices, %.

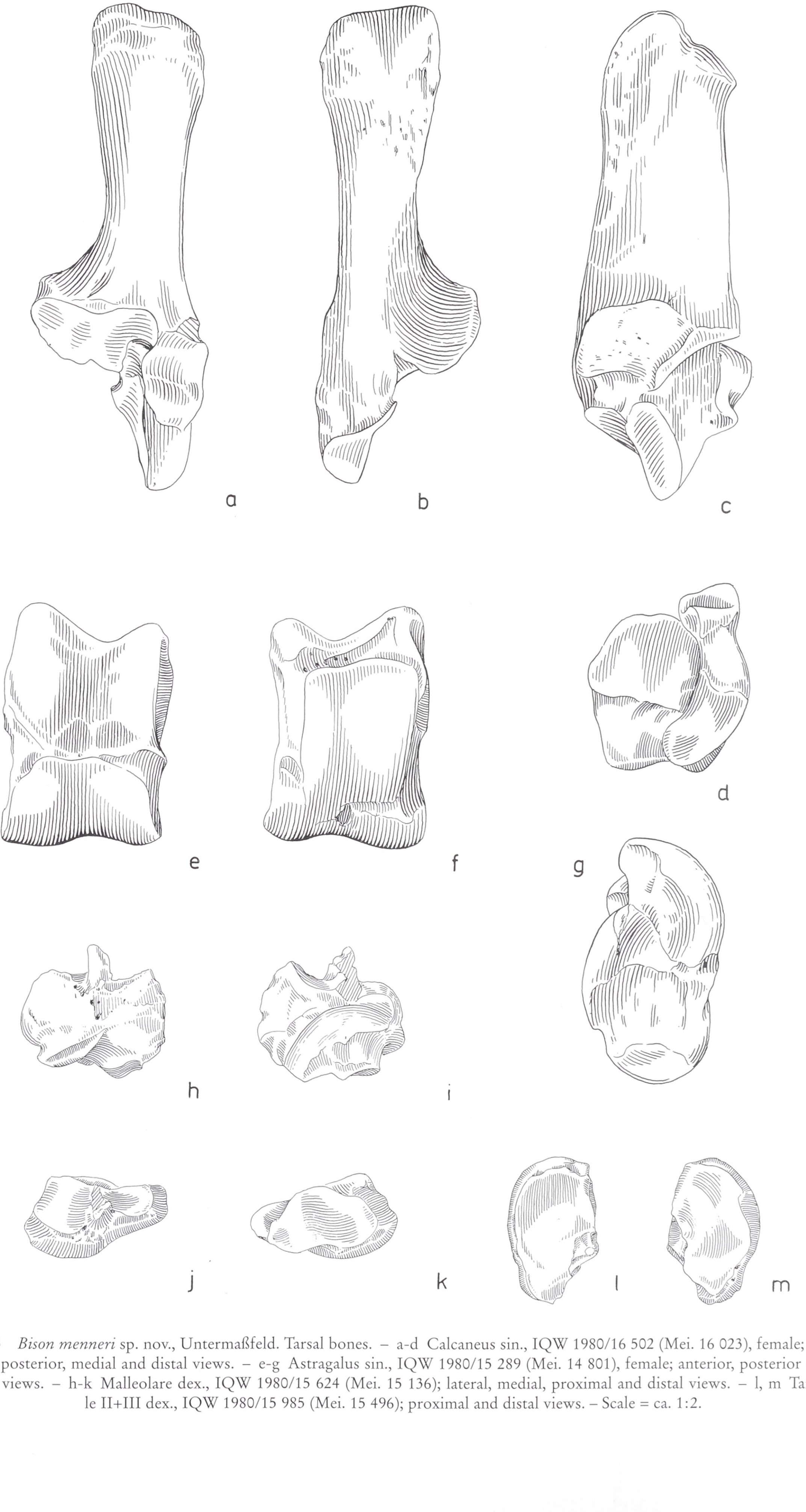

Fig. 15 *Bison menneri* sp. nov., Untermaßfeld. Tarsal bones. – a-d Calcaneus sin., IQW 1980/16 502 (Mei. 16 023), female; anterior, posterior, medial and distal views. – e-g Astragalus sin., IQW 1980/15 289 (Mei. 14 801), female; anterior, posterior and lateral views. – h-k Malleolare dex., IQW 1980/15 624 (Mei. 15 136); lateral, medial, proximal and distal views. – l, m Tarsale II+III dex., IQW 1980/15 985 (Mei. 15 496); proximal and distal views. – Scale = ca. 1:2.

the notch is deep and wide in 50% (cf. Fig. 15, f, g), weakly developed in 31% (cf. Fig. 14, f, g), and absent in 18% of specimens.

It can be concluded that in general *B. menneri* has a well pronounced *Bison*-like pattern in this area; however, the range of morphological variation is to some degree shifted towards a condition more usual for *Bos*.

A similar situation is observed with respect to the small facet for the calcaneus on the lateral side of the distal end of the astragalus. According to Bibikova (1958), it is more elongated and narrow in *Bison*, and its short diameter (height) never exceeds 54% of its length, while in *Bos* it has a more broadly elliptical shape, the same index being equal to or higher than 58%.

The lateral ridge of the proximal trochlea in *B. menneri* seems to be wide and more smoothly shaped than in *Bos*, and gives a *Bison*-like appearance to the intertrochlear fossa. As to other features of the astragalus mentioned by previous authors, I could not find in *B. menneri* any positive differences from *B. priscus*.

3.2.19. Calcaneus

The calcaneus is among the most numerous of skeletal parts in the Untermaßfeld bovid collection but of 58 specimens only 27 are more or less complete. Male specimens are larger in all linear dimensions than female ones, especially in maximum width and the width of tuber calcanei (Table 25). They are also relatively more stout, having higher indexes of width/length ratios. This is particularly evident in the index of the tuber calcanei width to the total length. The male calcaneus IQW 1980/15 268 (Mei. 14 780) pictured in Taf. 31, 1-3, and Fig. 14, a-d, is neither the largest nor the stoutest among the male specimens. The female calcaneus IQW 1980/16 502 (Mei. 16 023) has an especially narrow tuber calcanei (Taf. 31, 9-11; Fig. 15, a-d).

Like the astragalus, the calcaneus of *B. menneri* is far from being the largest among large Quaternary bovids (Table 26). They are shorter than the same bones of *B. priscus* from Taubach and *Bos primigenius* from Ilford. Only the Northeast Siberian *B. priscus* has some shorter bones. But in maximum width our sample has the lowest average values. Due to that, the *B. menneri* calcaneus is on the average the most slender among large bovids.

The shape, length and width of the two lower facets – for astragalus and central tarsale – are considered to be of great importance for *Bison*/*Bos* discriminating (Bibikova 1958; Stampfli 1963; Sala 1986). However, my measurements of various bison calcanei compared with the measurements of British *Bos primigenius* (Browne 1983) show extremely wide variation of these facets. Variation in the shape of facet for the central tarsale are the same as described below for that bone.

3.2.20. Central tarsal bone

Among 41 central tarsal bones of *Bison* in the collection 34 are practically intact, 14 of them being provisionally classified as male and 20 as female specimens. Male specimens are larger in all dimensions, especially in width (Table 27). Specimen IQW 1980/15 292 (Mei. 14 804) pictured in Taf. 31, 7, 8, and Fig. 14, h-j, is a middle-sized male bone belonging to the same individual as astragalus IQW 1980/15 294 (Mei. 14 806) and calcaneus IQW 1980/15 268 (Mei. 14 780) pictured in the same Tafel and Figure.

In size, the central tarsal bone of *B. menneri* is notably smaller than that of *Bos primigenius* from Lunel-Viel. The range of variation of its measurements overlaps with Taubach and Isernia bison (Table 28), but on average the Untermaßfeld bones are smaller. They have the same size as small Siberian *B. priscus*, considerably exceeding the Venta Micena form.

Morphological features of the proximal surface correlate well with those of the astragalus and calcaneus. Most *B. menneri* specimens demonstrate a pronounced additional facet for the astragalus (cf. Fig. 14, h). The calcanear articulation shape is quite variable. In some specimens this facet has the same width along the length (band-shaped) that is thought to be peculiar for *Bison* by Bibikova (1958) and for *Bos* by Sala (1986). In the other it narrows in the posterior (plantar) direction and has the maximum width in the middle of its anterior half (sole-shaped).

	IQW 1980/ 15229 m	IQW 1980/ 15292 m!	IQW 1980/ 15293 m	IQW 1980/ 15980 m!	IQW 1980/ 16577 m	IQW 1980/ 17308 m!	IQW 1980/ 17564 m!	IQW 1981/ 17659 m	IQW 1981/ 17725 m	IQW 1984/ 19931 m	IQW 1985/ 20812 m?	IQW 1986/ 21490 m	IQW 1987/ 22138 m	IQW 1987/ 22180 m	mm					IQW 1980/ 15209 f	IQW 1980/ 15230 f	IQW 1980/ 15232 f!
															N	MIN	MAX	AVG	STD			
Wmax	77.0	79.0	77.5	78.0	75.0	84.0	83.0	76.0	74.0	83.0	c73.0	77.5	83.0	82.0	14	73.0	84.0	78.7	3.5	70.0	70.5	71.0
Tmax	70.0	72.0	68.0	74.5	70.0	74.0	75.0	70.5	64.0	74.5	61.0	71.5	85.0	81.0	14	61.0	85.0	72.2	5.9	68.0	67.5	69.0
Hl	46.0	49.0	47.5	46.0	46.0	48.5	48.5	-	42.0	52.5	-	-	57.0	52.5	11	42.0	57.0	48.7	3.9	41.0	40.5	42.0
Hm	57.0	56.5	57.0	56.0	57.5	57.5	53.5	58.0	49.0	58.0	-	c58.0	60.0	59.0	13	49.0	60.0	56.7	2.7	53.0	53.0	52.5
Tmax:Wmax,%	90.9	91.1	87.7	95.5	93.3	88.1	90.4	92.8	86.5	89.8	83.6	92.3	102.4	98.8	14	83.6	102.4	91.7	4.7	97.1	95.7	97.2
Hl:Wmax,%	59.7	62.0	61.3	59.0	61.3	57.7	58.4	-	56.8	63.3	-	-	68.7	64.0	11	56.8	68.7	61.1	3.2	58.6	57.4	59.2

	IQW 1980/ 15262 f	IQW 1980/ 15467 f?	IQW 1980/ 15628 f	IQW 1980/ 16209 f	IQW 1980/ 16400 f	IQW 1980/ 16513 f	IQW 1980/ 17182 f	IQW 1980/ 17534 f!	IQW 1981/ 17633 f	IQW 1982/ 17865 f	IQW 1982/ 18152 f	IQW 1984/ 19992 f!	IQW 1985/ 20414 f	IQW 1985/ 20440 f?	IQW 1985/ 20529 f	IQW 1985/ 20923 f	IQW 1985/ 21014 f	IQW 1986/ 21382 f!	ff				
																			N	MIN	MAX	AVG	STD
Wmax	67.0	71.5	c68.0	66.0	67.0	68.0	70.0	69.0	71.0	68.5	65.5	67.0	68.5	71.5	70.0	-	66.5	69.0	20	65.5	71.5	68.8	1.8
Tmax	65.0	66.0	65.5	62.0	c58.5	62.0	64.5	67.0	64.0	62.0	61.5	63.5	64.0	65.5	61.5	66.0	c64.0	62.5	21	58.5	69.0	64.3	2.5
Hl	45.0	44.0	44.5	41.5	-	43.0	42.5	39.5	38.5	40.0	41.0	41.0	41.0	43.0	>38.0	44.0	41.0	42.0	19	38.5	45.0	41.8	1.7
Hm	50.0	c48.0	51.0	48.0	-	49.5	48.0	52.5	-	48.0	49.5	43.0	47.0	50.5	50.0	49.5	53.0	52.0	19	43.0	53.0	49.9	2.5
Tmax:Wmax,%	97.0	92.3	96.3	93.9	87.3	91.2	92.1	97.1	90.1	90.5	93.9	94.8	93.4	91.6	87.9	-	96.2	90.6	20	87.3	97.2	93.3	3.0
Hl:Wmax,%	67.2	61.5	65.4	62.9	-	63.2	60.7	57.2	54.2	58.4	62.6	61.2	59.9	60.1	-	-	61.7	60.9	18	54.2	67.2	60.7	3.0

Tab. 25 Measurements of central tarsal bone of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n. Untermassfeld					»*Bison*« sp. Venta Micena (Moya-Sola,1987)					*Bison schoetensacki* Isernia (Sala,1987)					*Bison priscus* Taubachh (Flerov,1977)				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
Wmax	34	65.5	84.0	72.9	5.6	5	52.6	65.1	58.4	4.6	8	75.4	84.0	79.3	2.8	14	67.0	92.0	83.9	6.0
Tmax	35	58.5	85.0	67.4	5.7	5	48.4	57.7	52.5	4.2	9	66.0	78.0	70.5	3.4	13	66.0	91.0	81.4	6.2
Tmax:Wmax,%	34	83.6	102.4	92.6	3.9	5	87.6	92.9	89.9	2.1	8	83.5	94.8	87.7	3.3	13	85.9	105.8	97.0	5.7

	Bison priscus Boj. Northeast Siberia					*Bos primigenius* Lunel-Viel (Brugal, 1985)									
	N	MIN	MAX	AVG mm + ff	STD	N	MIN	MAX	AVG mm	STD	N	MIN	MAX	AVG ff	STD
Wmax	11	64.5	83.7	72.2	4.9	12	86.3	94.0	89.8	2.8	51	69.6	80.5	73.7	2.6
Tmax	11	63.5	72.0	67.8	2.9	10	75.5	85.7	81.6	3.7	47	61.5	74.1	68.3	2.7
Tmax:Wmax,%	11	84.8	100.7	94.1	4.1				90.9					92.7	

Tab. 26 Measurements of central tarsal bone of various bovids, mm, and indices, %.

	IQW 1980/ 15267 m	IQW 1980/ 15268 m	IQW 1980/ 16598 m	IQW 1980/ 17014 m	IQW 1980/ 17221 m	IQW 1980/ 17304 m	IQW 1983/ 18999 m	IQW 1987/ 22062 m	IQW 1987/ 22074 m	IQW 1980/ 15273 m/sad			mm		
											N	MIN	MAX	AVG	STD
L	181.0	187.0	186.0	174.0	184.0	188.5	187.5	177.0	181.0	189.0	9	174.0	188.5	182.9	4.7
Wmax	63.6	62.6	63.0	57.6	59.2	68.3	64.0	59.0	66.0	c61.0	9	57.6	68.3	62.6	3.3
Tmax	69.6	69.6	68.1	71.1	78.6	77.6	74.6	71.0	72.5	63.6	9	68.1	78.6	72.5	3.5
Wtc	48.0	48.5	49.5	47.0	49.0	48.5	47.0	45.0	48.0	46.0	9	45.0	49.5	47.8	1.3
Ttc	59.3	56.0	55.5	50.5	58.4	56.0	53.5	53.5	53.0	c52.5	9	50.5	59.3	55.1	2.6
Wmax:L,%	35.1	33.5	33.9	33.1	32.2	36.2	34.1	33.3	36.5	32.3	9	32.2	36.5	34.2	1.4
Tmax:L,%	38.5	37.2	36.6	40.9	42.7	41.2	39.87	40.1	40.1	33.7	9	36.6	42.7	39.7	1.8
Wtc:L,%	26.5	25.9	26.6	27.0	26.6	25.7	25.1	25.4	26.5	24.3	9	25.1	27.0	26.2	0.6
Wtc:Ttc,%	80.9	86.6	89.2	93.1	83.9	86.6	87.9	84.1	90.6	87.6	9	80.9	93.1	87.0	3.5
Wfa:Wfc,%	90.3	100.0	78.9	103.4	-	83.3	90.0	87.5	78.9	96.8	8	78.9	103.4	89.1	8.4

	IQW 1984/ 20082 ?	IQW 1986/ 21375 ?	IQW 1980/ 15227 f	IQW 1980/ 16502 f	IQW 1980/ 17466 f	IQW 1980/ 17557 f	IQW 1981/ 17648 f	IQW 1982/ 18032 f	IQW 1983/ 19124 f	IQW 1985/ 20886 f	IQW 1987/ 22017 f			ff		
												N	MIN	MAX	AVG	STD
L	163.5	171.0	179.0	170.0	172.0	169.0	168.0	176.0	165.5	172.0	177.5	9	165.5	179.0	172.1	4.3
Wmax	58.0	58.0	56.4	56.4	55.6	56.9	56.0	53.4	54.0	56.0	56.0	9	53.4	56.9	55.6	1.1
Tmax	67.5	67.0	73.6	66.6	79.6	64.9	65.5	-	61.0	68.5	69.0	8	61.0	79.6	68.6	5.4
Wtc	45.0	43.0	42.0	39.5	42.7	40.0	c42.0	43.0	c37.0	42.0	43.0	8	39.5	43.0	41.8	1.2
Ttc	50.0	49.0	52.0	49.0	51.3	47.8	51.0	50.0	49.5	51.0	51.0	9	47.8	52.0	50.3	1.2
Wmax:L,%	35.5	33.9	31.5	33.2	32.3	33.7	33.3	30.3	32.6	32.6	31.5	9	30.3	33.7	32.3	1.0
Tmax:L,%	41.3	39.2	41.1	39.2	46.3	38.4	39.0	-	36.9	39.8	38.9	8	36.9	46.3	39.9	2.6
Wtc:L,%	27.5	25.1	23.5	23.2	24.8	23.7	25.0	24.4	-	24.4	24.2	8	23.2	25.0	24.2	0.6
Wtc:Ttc,%	90.0	87.8	80.8	80.6	83.2	83.7	82.4	86.0	-	82.4	84.3	8	80.6	86.0	82.9	1.7
Wfa:Wfc,%	96.8	70.0	86.7	93.3	107.4	103.7	89.3	64.7	96.6	-	75.0	8	64.7	107.4	89.6	13.3

Tab. 27 Measurements of calcaneum of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n. Untermaßfeld					*Bison priscus* Taubach					*Bison priscus* Northeast Siberia					*Bos primigenius* Ilford (Browne, 1983)				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	21	163.5	189.0	177.1	7.7	4	185.0	206.0	199.3	8.3	20	152.5	196.0	169.4	12.5	9	181.0	201.0	191.9	6.1
Wmax	21	53.4	68.3	59.1	4.0	4	69.9	77.1	74.0	3.0	20	50.0	77.0	62.5	6.8	9	63.0	78.0	71.4	4.2
Tmax	20	61.0	79.6	70.0	4.8	4	79.6	83.6	81.8	1.8	20	63.7	80.2	70.1	4.5					
Wtc	20	39.5	49.5	44.9	3.1	4	50.5	54.0	52.9	1.4	20	34.7	57.5	44.8	5.1					
Ttc	21	47.8	59.3	52.4	3.1	4	59.5	65.5	63.0	2.3	19	38.0	60.0	46.2	5.3					
Wmax:L,%	21	30.3	36.5	33.4	1.5	4	34.3	41.7	37.3	2.9	20	32.8	39.9	36.8	2.0	7	34.8	39.6	36.7	1.8
Tmax:L,%	20	33.7	46.3	39.5	2.5	4	38.6	43.6	41.1	1.7	19	38.6	43.6	41.4	1.3					
Wfa:Wfc,%	19	64.7	107.4	89.1	11.4	4	71.4	93.5	82.7	7.9	17	64.7	113.6	88.9	13.9	9	72.2	105.6	86.0	10.0

Tab. 28 Measurements of calcaneum of various bovids, mm, and indices, %.

3.2.21. Metatarsal

The Untermaßfeld collection includes in all 52 specimens of metatarsals, only 18 of them being more or less complete. Male specimens are notably larger and stouter. A representative specimen is IQW 1981/17 621 (Mei. 17 143), Taf. 32, 1-4, Fig. 16, a-d. Female specimens exemplified by IQW 1980/17 053 (Mei. 16 574) (Taf. 32, 5-8, Fig. 16, e-h) look very slender, especially in the shaft (Table 29).

B. menneri metatarsals are among the longest known for large bovids (Table 30). In total length, the Untermaßfeld male specimens have no equals in the collections except for two huge specimens from Tiraspol, but the latter are impressively stouter. *B. menneri* female bones are more similar in length to male metatarsals of *B. priscus* from such early localities as Mosbach, Mauer and Süßenborn but are notably more slender.

Considered as a whole sample, *B. menneri* metatarsals may be characterized as the longest and at the same time the most slender among the known samples of fossil *Bison* and *Bos*. They are much larger than those of *B. palaeosinensis* and »*Bison* sp.« from Venta Micena which have almost the same slenderness. As to late *B. priscus* and *Bos primigenius*, they have shorter and incomparably stouter metatarsals than *B. menneri*. Quite different from *B. menneri* are the metatarsals of *Leptobos* which are even more slender and very small.

The furrow on the dorsal surface of the shaft is rather well shaped. The plantar surface of the shaft is more or less flat, concave rather than convex, bearing the longitudinal furrow in the upper third. The plantar surface turns to the sides of the shaft rather abruptly. According to Bibikova (1958), these features are peculiar to *Bos* rather than to *Bison*. However, they are all subjected to variation and do not lend themselves to measuring.

The angle between the central tarsal and the tarsal II+III articulations on the proximal surface of the metatarsus is thought to be one of the most reliable distinctive features between *Bison* and *Bos* by many authors (Schertz 1936a; Bibikova 1958; Stampfli 1963; Sala 1986). Schertz has introduced values of this angle 13-22° for *Bos*, and 22-40° for *Bison*, and these values move on from one paper to another. Schertz published a misleading scheme of this angle (Abb. 1) at variance with his description of measuring (p. 52). But besides that, the measuring is very awkward due to the highly variable shape of the plantar/interior corners of both facets. My measurements support some trend to greater angle values in *Bison*, but the range of variation is much wider than Schertz's values. I could examine only 3 specimens of *Bos primigenius* (17°, 24° and 27°, av=22.7°). For Mauer bison the range is 30-35° (n=3, av=33°), for Tiraspol 26-32° (n=3, av=28.7°). Seven metatarsals from Untermaßfeld show a range of 19-29° (av=25.4°). It seems to indicate an intermediate position of *B. menneri* between *Bos* and *Bison* in this character, but I am not inclined to take these measurements too seriously. The fact is that it appears impossible to decide how to measure this angle on numerous specimens.

Meanwhile, there is one feature that demonstrates that the Untermaßfeld metatarsals belong to *Bison* without question. It is the shape of the distal end in the area of contact between the shaft and the distal epiphysis. As in metacarpals, the epitrochlear inflation typical for *Bison* is well pronounced in all *B. menneri* metatarsals. The distal width in this inflation (along the epiphyseal suture line) is roughly equal to the distal width in the trochlea or even greater than that. The ratio of epitrochlear to trochlear width ranges from 96% to 104.5% (av=99.2%, n=18). As this inflation is absent in *Bos* metatarsal, its width just above the trochlea is evidently less than the distal width. The same index for 14 metatarsals of *Bos primigenius* from England (Ilford), Germany and Ukraine ranges from 91% to 96% (av=94.0%).

A peculiar feature of the Untermaßfeld metatarsals is a well pronounced asymmetry of the distal end in most of specimens. The lateral trochlea protrudes distally notably more than the medial, and the whole distal end looks bent medially from the long axis of the bone (cf. Taf. 32, 1, 4). This feature can be observed in some metatarsals of both *B. priscus* and *Bos primigenius*, but it is usually much less pronounced than in *B. menneri*.

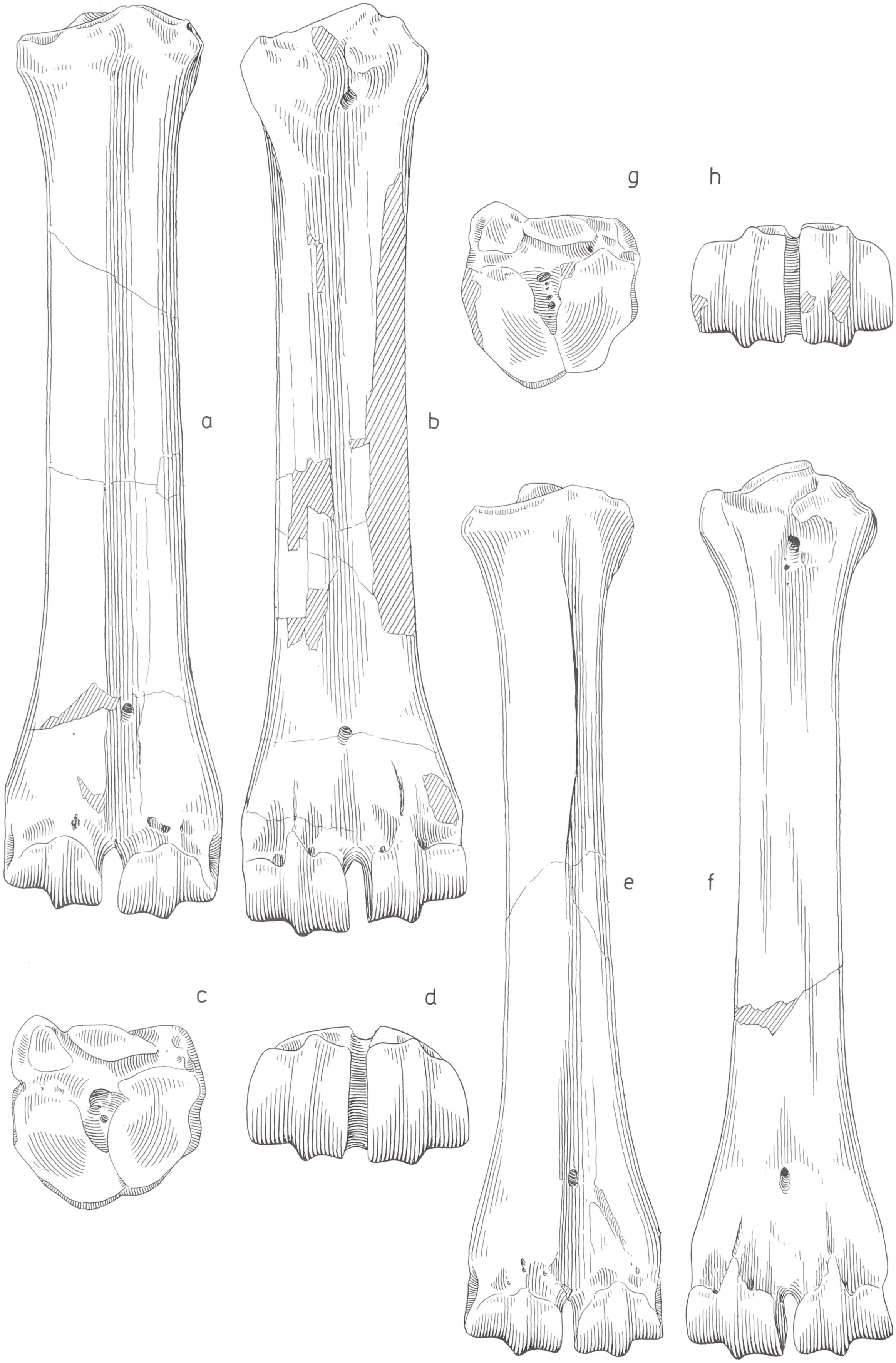

Fig. 16 *Bison menneri* sp. nov., Untermaßfeld. Metatarsal bones. – a-d Metatarsal III+IV sin., IQW 1981/17 621 (Mei. 17 143), male; anterior, posterior, proximal, and distal views. – e-h Metatarsal III+IV sin., IQW 1980/17 053 (Mei. 16 574), female; anterior, posterior, proximal, and distal views. – Scale = ca. 1:2.

	IQW 1980/ 15242 m	IQW 1980/ 15245 m	IQW 1980/ 15246 m	IQW 1980/ 16104 m	IQW 1980/ 17195 m	IQW 1980/ 17305 m	IQW 1980/ 17369 m	IQW 1981/ 17621 m	IQW 1981/ 17697 m	IQW 1983/ 19067 m	IQW 1985/ 20722 m	IQW 1988/ 22410 m	IQW 1980/ 15227 f/sad	IQW 1980/ 15239 f	IQW 1980/ 15241 f	IQW 1980/ 15243 f	IQW 1980/ 15244 f	IQW 1980/ 16679 f	IQW 1980/ 17012 f	IQW 1980/ 17053 f	IQW 1980/ 17137 f	IQW 1980/ 17179 f	IQW 1981/ 17654 f	IQW 1982/ 17801 f	IQW 1982/ 17835 f
L	-	320.0	324.0	-	329.0	-	-	326.0	-	-	325.0	c325.0	300.0	-	-	-	-	313.0	c299.0	314.0	-	-	-	301.5	-
Wp	65.0	c69.0	67.0	-	69.6	71.0	-	65.0	-	69.0	66.0	63.5	57.6	57.5	58.0	60.0	59.7	61.7	-	59.5	59.0	62.0	-	59.4	-
Tp	64.0	66.5	66.0	-	68.0	69.0	-	66.5	-	-	>61.0	c64.0	57.0	56.5	56.0	61.0	61.0	58.5	-	65.0	57.5	-	-	c55.0	-
Wd	-	75.0	77.0	75.5	79.0	-	81.5	77.0	77.0	-	72.7	75.7	67.0	-	-	-	-	71.0	67.0	68.0	-	-	68.0	67.0	70.5
Td	-	45.0	c46.0	47.0	46.3	-	51.0	46.0	46.0	-	45.0	47.0	40.0	-	-	-	-	c43.0	40.3	44.0	-	-	41.5	44.3	44.5
Wm	45.0	41.6	45.0	-	42.7	46.2	-	45.0	-	-	41.8	41.5	34.0	34.5	32.0	37.4	c37.5	36.0	36.5	34.0	37.5	-	-	37.5	41.3
Wp:L,%	-	c21.6	20.7	-	21.2	-	-	19.9	-	-	20.3	c19.5	19.2	-	-	-	-	19.7	-	18.9	-	-	-	19.7	-
Wd:L,%	-	23.4	23.8	-	24.0	-	-	23.6	-	-	22.4	c23.3	22.3	-	-	-	-	22.7	c22.4	21.7	-	-	-	22.2	-
Wm:L,%	-	13.0	13.9	-	13.0	-	-	13.8	-	-	12.9	c12.8	11.3	-	-	-	-	11.5	c12.2	10.8	-	-	-	12.4	-

	IQW 1983/ 18954 f	IQW 1983/ 19551 f	IQW 1984/ 19994 f	IQW 1984/ 20032 f	IQW 1984/ 20083 f	IQW 1985/ 20383 f/sad	IQW 1985/ 20636 f	IQW 1985/ 20648 f	IQW 1985/ 20653 f	IQW 1986/ 21156 f	IQW 1986/ 21370 f	mm					ff					mm + ff				
												N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	303.5	-	-	-	-	312.0	306.0	c295.0	c290.0	c317.0	312.0	6	320.0	329.0	324.8	2.7	12	290.0	317.0	305.3	8.1	18	290.0	329.0	311.8	11.5
Wp	56.9	61.5	-	c61.0	-	61.3	c64.0	>50.0	-	58.5	60.4	9	63.5	71.0	67.2	2.4	17	56.9	64.0	59.9	1.8	26	56.9	71.0	62.4	4.1
Tp	56.0	59.0	-	-	-	c58.5	63.3	56.0	-	c58.2	59.7	7	64.0	69.0	66.3	1.7	16	55.0	65.0	58.6	2.7	23	55.0	69.0	61.0	4.3
Wd	65.0	-	67.5	-	69.0	68.5	70.5	63.0	68.5	68.1	68.0	10	72.7	81.5	76.5	2.3	16	63.0	71.0	67.9	1.9	26	63.0	81.5	71.2	4.7
Td	40.0	-	42.5	-	41.0	44.0	43.5	>39.0	42.0	42.0	44.0	10	45.0	51.0	46.8	1.8	15	40.0	44.5	42.4	1.6	25	40.0	51.0	44.2	2.7
Wm	36.0	-	c39.0	38.5	-	c37.0	35.7	32.7	37.7	36.3	36.7	8	41.5	46.2	43.6	1.8	20	32.0	41.3	36.4	2.1	28	32.0	46.2	38.5	3.8
Wp:L,%	18.7	-	-	-	-	19.6	c20.9	>17.0	-	c18.5	19.4	6	19.5	21.6	20.5	0.7	9	18.5	20.9	19.4	0.7	15	18.5	21.6	19.9	0.9
Wd:L,%	21.4	-	-	-	-	22.0	23.0	21.4	c23.6	c21.5	21.8	6	22.4	24.0	23.4	0.5	12	21.4	23.6	22.2	0.7	18	21.4	24.0	22.6	0.9
Wm:L,%	11.9	-	-	-	-	c11.9	11.7	11.1	c13.0	c11.5	11.8	6	12.8	13.9	13.2	0.5	12	10.8	13.0	11.7	0.6	18	10.8	13.9	12.2	0.9

Tab. 29 Measurements of metatarsals of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	Bison menneri sp. n.					»*Bison*« sp.					*Bison schoetensacki*									
	Untermaßfeld					Venta Micena (Moya-Sola,1987)					Mauer					Süßenborn				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	18	290.0	329.0	311.8	11.5	8	248.5	271.5	262.4	6.5	5	280.0	315.0	298.3	11.9	5	277.0	316.0	301.4	13.8
Wp	26	56.9	71.0	62.4	4.1	20	43.5	75.4	52.0	6.6	8	53.6	66.0	59.4	4.0	5	53.0	67.3	63.1	5.3
Tp	23	55.0	69.0	61.0	4.3	19	43.7	54.6	48.9	3.4	6	55.5	61.5	59.4	2.2	5	48.0	68.0	62.1	7.3
Wd	26	63.0	81.5	71.2	4.7	14	55.3	63.5	59.4	2.2	5	65.5	76.0	68.0	4.0	5	62.0	80.7	74.4	6.5
Td	25	40.0	51.0	44.2	2.7	14	31.9	38.3	35.1	1.8						5	38.0	47.4	43.4	3.1
Wm	28	32.0	46.2	38.5	3.8	8	30.0	37.0	33.2	2.3	10	36.0	44.5	38.7	2.9	5	32.5	41.0	37.9	3.2
Wp:L,%	15	18.5	21.6	19.9	0.9	8	18.5	28.7	20.9	3.3	4	17.8	20.4	19.3	0.9	5	19.1	22.1	20.9	1.2
Wd:L,%	18	21.4	24.0	22.6	0.9	8	21.4	24.1	22.7	1.1	4	22.3	24.1	23.1	0.7	5	22.4	25.6	24.7	1.2
Wm:L,%	18	10.8	13.9	12.2	0.9	8	11.5	14.1	12.7	0.8	5	12.1	14.1	12.9	0.9	5	11.7	13.1	12.6	0.5

	Bison priscus					*Bison* »*schoetensacki*«					*Bison priscus*					*Bos primigenius*				
	Mosbach					Tiraspol					Northeast Siberia					Ilford (Browne,1983)				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	22	270.5	314.0	300.3	12.2	6	297.3	340.0	313.9	15.0	25	254.0	283.0	266.4	7.2	12	282.0	307.0	292.8	6.3
Wp	22	56.4	81.0	66.5	5.9	6	61.0	76.5	66.9	5.9	25	51.5	69.5	58.5	4.7	12	70.0	79.0	74.3	3.2
Tp	22	56.5	73.5	63.1	4.7	6	62.5	78.5	66.8	5.6	24	52.5	66.0	58.0	3.8					
Wd	22	66.2	88.0	77.2	6.3	6	70.5	93.0	79.7	7.2	25	62.0	81.7	69.8	4.9	10	78.0	87.0	81.9	2.7
Td																				
Wm	22	34.0	52.3	42.7	5.0	6	40.0	50.5	45.5	4.1	25	29.5	48.0	36.6	4.5	12	44.0	50.0	46.9	1.8
Wp:L,%	22	19.7	26.0	22.1	1.5	6	20.2	22.5	21.3	1.0	25	19.9	25.6	21.9	1.5	12	23.9	26.7	25.4	0.9
Wd:L,%	22	21.8	28.3	25.7	1.6	6	23.7	27.4	25.3	1.3	25	24.1	29.5	26.2	1.5	10	26.6	30.2	27.9	0.9
Wm:L,%	22	11.8	16.8	14.2	1.3	6	13.4	16.2	14.5	1.0	25	11.4	17.7	13.7	1.4	12	15.1	17.1	16.0	0.6

Tab. 30 Measurements of metatarsals of various large bovids, mm, and indices, %.

3.2.22. Phalanges

The large collection of *Bison* phalanges from Untermaßfeld (161 specimen) presents a hard task for research. Wide sexual variation in *B. menneri* hampers discrimination of anterior and posterior phalanges that is not always easy to begin with. Moreover, even two phalanges of one foot are sometimes slightly different. Due to all these kinds of variation, any species characteristic of phalanges without their correct classification by the limb and sex is rather senseless. That is why I tried to classify the Untermaßfeld phalanges in four groups based on some specimens found together in the excavation (and in very few occasions together with cannon bones) and on previous works. However, some confusions in my classification are quite possible.

Phalanx I (Taf. 33, 1-8; Fig. 17, a-h; Table 31). Anterior phalanges are shorter but wider than posterior, so all the indexes of their transverse measurements to the length are the highest in the sample. Male phalanges (both anterior and posterior) are in general larger and stouter. The most remarkable are the male anterior phalanges – the most heavily built. Male posterior phalanges were identified as the longest in the sample but more slender than anterior ones. Relatively stout phalanges having the shortest length were considered as anterior female. The smallest (but not the shortest) and most slender phalanges are interpreted as posterior female ones.

However, the statistics resulting from my classification show that female anterior and posterior phalanges are not very different in linear measurements, while posterior male and female phalanges have almost the same slenderness.

There is not too much published material with phalanges measurements. A sample of 13 first phalanges of *B. priscus* from Taubach has been classified into all 4 categories (Flerov 1977). Results of Flerov's classification are not in a good agreement with my attempts. However, if we compare the whole samples, it is clear that *B. menneri* phalanges, being almost equal in length to the Taubach ones or even slightly shorter, are smaller in all width measurements and certainly more slender. This inference agrees quite well with the previous comparison of *B. menneri* bones with the Taubach bison, one of the largest and stoutest known.

It is not unexpected that *B. menneri* first phalanges are notably longer and more slender than those of Northeast Siberian *B. priscus*.

Phalanx II (Taf. 33, 9-16; Fig. 17, i-p; Table 32). According to my classification of 38 second phalanges of the Untermaßfeld sample, fore limb phalanges are on the average only slightly longer than hind limb ones, but at the same time somewhat wider, and consequently more massive in width/length index. This difference is less pronounced in females, which are generally smaller and more slender. Posterior phalanges narrow more obviously toward the distal end than do the anterior ones. This can be demonstrated by the ratio between distal and proximal width, the index having much lower values in hind limb phalanges. This is in agreement with my observations on some more or less complete sets of limb bones from one bovid individual.

As a whole sample, *B. menneri* second phalanges are on the average longer than those from Isernia (Sala 1986) and Siberia, and slightly longer than those from Taubach (Flerov 1977). At the same time they are on the average considerably more slender than the second phalanges of these three bison populations.

Phalanx III (Taf. 33, 17-24; Fig. 17, q-x; Table 33). Classifying 26 hoof phalanges of the Untermaßfeld bovid I proceeded from the following basic points:

1. Anterior phalanges are considerably longer and slightly wider than the posterior. This is based on Reshetov and Sukhanov (1979) and supported by my observations on complete fossil skeletons of the Alyoshka *B. priscus* (Northeast Siberia) and Chausovo *Bos primigenius* (Ukraine). This statement disagrees with Sala (1986) that the forelimb phalanx is shorter than the hind limb one.
2. The largest in all linear dimensions and the most powerfully built are male anterior phalanges as is shown by paired specimens IQW 1982/18 065 (Mei. 17 585), IQW 1982/18 069 (Mei. 17 589) belonging to a complete manus.

	IQW 1980/ 17073 ant m	IQW 1982/ 18067 ant m	IQW 1985/ 20869 ant m	IQW 1985/ 20870 ant m	IQW 1980/ 16586 post m	IQW 1980/ 17229 post m	IQW 1980/ 17370 post m	IQW 1980/ 17371 post m	IQW 1982/ 17908 post m	IQW 1980/ 15261 ant f	IQW 1980/ 16905 ant f	IQW 1980/ 17568 ant f	IQW 1982/ 18408 ant f	IQW 1982/ 18409 ant f	IQW 1983/ 19090 ant f	IQW 1983/ 19091 ant f	IQW 1984/ 20003 ant f	IQW 1985/ 20346 ant f	IQW 1985/ 20602 ant f	IQW 1985/ 20605 ant f	IQW 1985/ 20639 ant f	IQW 1985/ 20725 ant f	IQW 1985/ 20913 ant f
L	90.0	89.5	91.0	90.0	95.0	95.0	92.6	91.8	94.3	85.0	81.3	84.5	84.0	82.5	79.0	81.0	81.6	82.0	80.0	81.0	81.0	79.0	81.5
Wp	45.5	c43.0	44.7	45.5	40.6	c39.0	c41.0	40.8	42.0	38.0	33.5	40.2	43.5	43.3	37.0	36.0	38.0	38.0	37.3	38.0	36.5	37.0	38.0
Tmax	50.0	c47.0	47.7	52.0	47.7	47.7	47.7	48.1	46.5	43.5	39.2	45.0	46.0	45.5	40.5	40.0	43.0	40.0	41.5	41.0	c41.5	43.0	43.5
Wm	41.5	41.5	-	41.0	37.0	35.0	36.5	35.9	36.5	35.2	29.5	34.0	38.5	37.2	31.5	33.0	35.0	36.5	31.0	34.2	33.0	32.2	35.0
Wp:L,%	50.6	48.0	49.1	50.6	42.7	41.	44.3	44.4	44.5	44.7	41.2	47.6	51.8	52.5	46.8	44.4	46.6	46.3	46.6	46.9	45.1	46.8	46.6
Wm:L,%	46.1	46.4	-	45.6	38.9	36.8	39.4	39.1	38.7	41.4	36.3	40.2	45.8	45.1	39.9	40.7	42.9	44.5	38.8	42.2	40.7	40.8	42.9

	IQW 1980/ 15265 post f	IQW 1980/ 16197 post f	IQW 1980/ 16709 post f	IQW 1980/ 16949 post f	IQW 1980/ 17074 post f	IQW 1980/ 17275 post f	IQW 1980/ 17579 post f	IQW 1981/ 17623 post f	IQW 1984/ 19989 post f	IQW 1984/ 20001 post f	IQW 1985/ 20428 post f	IQW 1985/ 20429 post f	IQW 1985/ 20716 post f	IQW 1985/ 20717 post f	IQW 1985/ 21233 post f	IQW 1985/ 21377 post f	IQW 1985/ 21378 post f	IQW 1985/ 21383 post f	IQW 1985/ 21384 post f	IQW 1980/ 16314 juv.	IQW 1980/ 16530 juv.	IQW 1985/ 20619 ?
L	85.5	84.7	85.5	85.4	83.9	83.5	87.4	82.6	85.0	85.0	85.3	83.5	84.5	86.5	83.0	88.7	88.0	84.5	83.0	76.4	-	83.3
Wp	32.5	37.4	38.8	33.4	33.0	36.5	39.0	35.0	36.5	35.7	35.6	35.5	35.0	36.0	36.2	38.6	38.0	34.6	34.7	32.0	31.3	-
Tmax	41.0	43.4	43.0	40.0	39.0	42.9	43.9	41.5	44.0	41.5	42.0	42.7	c44.0	42.5	c41.0	47.5	46.0	44.0	43.8	37.4	37.2	-
Wm	29.0	32.0	34.5	30.5	28.8	31.0	35.2	30.3	32.0	31.6	31.5	32.0	32.0	33.7	31.7	35.0	34.0	31.0	30.5	27.4	28.5	-
Wp:L,%	38.0	44.2	45.4	39.1	39.3	43.7	44.6	42.4	42.9	42.0	41.7	42.5	41.4	41.6	43.6	43.5	43.2	40.9	41.8	41.9	-	-
Wm:L,%	33.9	37.8	40.4	35.7	34.3	37.1	40.3	36.7	37.6	37.2	36.9	38.3	37.9	39.0	38.2	39.5	38.6	36.7	36.7	35.9	-	-

	mm ant					mm post					ff ant					ff post					Total				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	4	89.5	91.0	90.1	0.5	5	91.8	95.0	93.7	1.3	14	79.0	85.0	81.7	1.8	19	82.6	88.7	85.0	1.6	42	79.0	95.0	85.4	4.2
Wp	4	43.0	45.5	44.7	1.0	5	39.0	42.0	40.7	1.0	14	33.5	43.5	38.2	2.6	19	32.5	39.0	35.9	1.8	42	32.5	45.5	38.1	3.3
Tmax	4	47.0	52.0	49.2	2.0	5	46.5	48.1	47.5	0.5	14	39.2	46.0	42.4	2.1	19	39.0	47.5	42.8	1.9	42	39.0	52.0	43.8	3.0
Wm	3	41.0	41.5	41.3	0.2	5	35.0	37.0	36.2	0.7	14	29.5	38.5	34.0	2.4	19	28.8	35.2	31.9	1.8	41	28.8	41.5	33.8	3.2
Wp:L,%	4	48.0	50.6	49.6.	1.1	5	41.1	44.5	43.4	1.3	14	41.2	52.5	46.7	2.7	19	38.0	45.4	42.2	1.9	42	38.0	52.5	44.6	3.3
Wm:L,%	3	45.6	46.4	46.0	0.3	5	36.8	39.4	38.6	0.9	14	36.3	45.8	41.6	2.5	19	33.9	40.4	37.5	1.7	41	33.9	46.4	39.7	3.2

Tab. 31 Measurements of phalanx 1 of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	IQW 1980/ 16919 ant m	IQW 1980/ 17233 ant? m?	IQW 1980/ 17578 ant m	IQW 1982/ 18063 ant m	IQW 1985/ 20871 ant m	IQW 1986/ 21457 ant m	IQW 1980/ 17220 post m	IQW 1980/ 17360 post m	IQW 1982/ 18089 post m	IQW 1980/ 15260 ant f	IQW 1980/ 17363 ant f	IQW 1983/ 19092 ant f	IQW 1985/ 20603 ant f	IQW 1985/ 20606 ant f	IQW 1985/ 20726 ant f	IQW 1985/ 20756 ant f	QW 1985/ 20914 ant? f?	IQW 1985/ 20915 ant? f?	IQW 1980/ 15266 post f	IQW 1980/ 17540 post f	IQW 1983/ 19002 post f	IQW 1984/ 19986 post f	IQW 1984/ 19990 post f	IQW 1984/ 20227 post f	IQW 1985/ 20443 post f	IQW 1985/ 20613 post? f?	IQW 1985/ 20711 post f	IQW 1985/ 20718 post f	IQW 1985/ 20719 post f	IQW 1986/ 21048 post f	IQW 1986/ 21141 post f
L	66.5	65.4	69.0	>57.0	67.5	62.3	67.2	63.0	67.0	64.5	>50.0	57.0	56.4	57.2	59.0	57.3	57.0	55.5	c55.0	63.0	c55.0	57.0	56.5	55.7	55.5	-	c54.0	56.5	58.0	56.0	53.5
Wp	42.7	40.0	43.8	42.5	45.0	41.0	41.3	42.0	42.5	37.2	c31.0	36.0	c36.5	36.6	35.5	37.8	37.0	37.5	34.0	37.5	36.0	35.3	36.0	37.0	34.5	38.5	c39.0	37.0	38.5	36.0	38.0
Wm	34.0	33.0	34.5	36.0	35.3	30.2	31.0	33.8	31.0	28.5	28.8	c29.0	27.2	27.3	27.0	27.0	27.0	28.0	25.0	27.8	26.4	27.0	26.2	27.3	26.0	27.0	28.5	28.0	27.5	25.8	27.7
Wd	36.0	34.1	38.7	39.0	37.6	c35.0	c31.0	33.7	33.3	31.0	31.5	32.7	30.0	32.7	30.0	31.0	29.0	28.5	c27.0	28.8	c27.5	27.2	27.2	29.0	c26.2	30.5	29.0	29.0	28.0	28.0	30.0
Tm	35.0	32.8	34.5	36.8	37.2	30.3	32.0	33.2	31.0	30.9	30.0	31.0	29.0	28.8	29.0	32.0	31.0	31.0	27.8	29.0	28.5	28.0	27.0	29.5	27.7	29.6	-	30.0	29.0	26.5	31.5
Wp:L,%	64.2	61.2	63.5	-	66.7	65.8	61.5	66.7	63.4	57.7	-	63.2	64.7	64.0	60.2	66.0	64.9	67.6	61.8	59.5	65.5	61.9	63.7	66.4	62.2	-	72.2	65.5	66.4	64.3	71.0
Wd:L,%	54.1	52.1	56.1	-	55.7	56.2	46.1	53.5	49.7	48.1	-	57.4	53.2	57.2	50.8	54.1	50.9	51.4	49.1	45.7	50.0	47.7	48.1	52.1	47.2	-	53.7	51.3	48.3	50.0	56.1
Wd:Wp,%	84.3	85.3	88.4	91.8	83.6	85.4	75.1	80.2	78.4	83.3	-	90.8	82.2	89.3	84.5	82.0	78.4	76.0	79.4	76.8	76.4	77.1	75.6	78.4	75.9	79.2	74.4	78.4	72.7	77.8	78.9

	IQW 1986/ 21242 post f	IQW 1986/ 21263 post f	IQW 1986/ 21379 post f	IQW 1986/ 21380 post f	IQW 1986/ 21385 post f	IQW 1986/ 21410 post f	mm ant					mm post					ff ant					ff post					Total				
							N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	59.0	60.0	61.0	60.5	58.0	60.0	5	62.3	69.0	66.1	2.3	3	63.0	67.2	65.7	1.9	8	55.5	64.5	58.0	2.6	18	53.5	63.0	57.5	2.6	34	53.5	69.0	59.6	4.3
Wp	38.6	33.3	38.2	40.0	35.6	37.0	6	40.0	45.0	42.5	1.7	3	41.3	42.5	41.9	0.5	9	31.0	37.8	36.1	1.9	19	33.3	40.0	36.8	1.8	37	31.0	45.0	38.0	3.0
Wm	29.0	27.0	30.0	28.0	28.4	28.0	6	30.2	36.0	33.8	1.9	3	31.0	33.8	31.9	1.3	9	27.0	29.0	27.8	0.8	19	25.0	30.0	27.4	1.2	38	25.0	36.0	28.9	2.7
Wd	29.0	-	29.2	28.6	28.5	28.3	6	34.1	39.0	36.7	1.8	3	31.0	33.7	32.7	1.2	9	28.5	32.7	30.7	1.4	18	26.2	30.5	28.4	1.1	37	26.2	39.0	30.7	3.2
Tm	30.5	30.0	29.5	29.0	28.5	28.0	6	30.3	37.2	34.4	2.4	3	31.0	33.2	32.1	0.9	9	28.8	32.0	30.3	1.1	18	26.5	31.5	28.9	1.2	37	26.5	37.2	30.4	2.5
Wp:L,%	65.4	55.5	62.6	66.1	61.4	61.7	5	61.2	66.7	64.3	1.9	3	61.5	66.7	63.9	2.1	8	57.7	67.6	63.5	3.0	18	55.5	72.2	64.1	3.8	34	55.5	72.2	63.9	3.3
Wd:L,%	49.2	-	47.9	47.3	49.1	47.2	5	52.1	56.2	54.8	1.5	3	46.1	53.5	49.8	3.0	8	48.1	57.4	52.9	3.0	17	45.7	56.1	49.4	2.6	33	45.7	57.4	51.1	3.4
Wd:Wp,%	75.1	-	76.4	71.5	80.1	76.5	6	83.6	91.8	86.4	2.8	3	75.1	80.2	77.9	2.1	8	76.0	90.8	83.3	4.7	18	71.5	80.1	76.7	2.2	35	71.5	91.8	80.0	5.0

Tab. 32 Measurements of phalanx 2 of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

	IQW 1980/ 17180 ant m	IQW 1982/ 18031 ant m	IQW 1982/ 18065 ant m	IQW 1982/ 18069 ant m	IQW 1980/ 15257 post m	IQW 1980/ 17183 post m	IQW 1980/ 17218 post m	IQW 1980/ 17230 post m	IQW 1983/ 19100 post m	IQW 1982/ 18308 ? m	IQW 1980/ 15258 ant f	IQW 1980/ 15259 ant f	IQW 1983/ 19053 ant f	IQW 1983/ 19094 ant f	IQW 1984/ 20004 ant f	IQW 1984/ 20059 ant f	IQW 1984/ 20267 ant f	IQW 1985/ 20604 ant f	IQW 1985/ 20607 ant f	IQW 1985/ 20729 ant f	IQW 1986/ 21387 ant? f?	IQW 1986/ 21442 ant f	IQW 1986/ 21455 ant f	IQW 1980/ 17367 post f	IQW 1980/ 17544 post f	IQW 1985/ 20439 post f	IQW 1985/ 21019 post f
L	107.8	104.0	-	-	97.7	100.0	84.5	87.0	>82.0	-	87.8	89.0	86.0	91.3	>77.0	86.0	c88.0	-	-	-	-	>79.0	82.0	-	72.5	c73.0	79.0
W	36.8	34.5	36.0	36.0	33.5	35.9	30.5	31.0	33.0	-	30.5	28.0	30.0	30.0	29.5	32.0	c29.0	28.0	30.5	31.5	30.0	29.0	29.5	27.7	27.8	26.5	28.0
H	61.0	60.5	58.8	57.0	58.8	63.5	50.3	53.0	c49.0	56.6	53.3	51.5	46.0	51.5	c44.0	>44.0	>43.0	c47.5	-	-	>46.0	>43.0	c46.5	47.7	48.4	c43.0	-
W/L,%	34.1	33.2	-	-	34.3	35.9	36.1	35.6	<40.2	-	34.7	31.5	34.9	32.9	<38.3	37.2	c33.0	-	-	-	-	<36.7	36.0	-	38.3	c36.3	35.4
H/L,%	56.6	58.2	-	-	60.2	63.5	59.5	60.9	<59.8	-	60.7	57.9	53.5	56.4	<57.1	>51.2	>48.9	-	-	-	-	-	c56.7	-	66.8	c58.9	-
W:H,%	60.3	57.0	61.2	63.2	57.0	56.5	60.6	58.5	-	-	57.2	54.4	65.2	58.3	67.0	<72.7	<67.4	c58.9	-	-	<65.2	<67.4	c63.4	58.1	57.4	c61.6	-

	mm ant					mm post					ff ant					ff post					Total				
	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD	N	MIN	MAX	AVG	STD
L	2	104.0	107.8	105.9	1.9	4	84.5	100.0	92.3	6.7	7	82.0	91.3	87.2	2.7	3	72.5	79.0	74.8	3.0	16	72.5	107.8	88.5	9.7
W	4	34.5	36.8	35.8	0.8	5	30.5	35.9	32.8	1.9	13	28.0	32.0	29.8	1.1	4	26.5	28.0	27.5	0.6	26	26.5	36.8	30.9	2.9
H	4	57.0	61.0	59.3	1.6	4	50.3	63.5	56.4	5.1	7	44.0	53.3	48.6	3.2	3	43.0	48.4	46.4	2.4	19	44.0	63.5	52.9	5.6
W/L,%	2	33.2	34.1	33.7	0.5	4	34.3	36.1	35.5	0.7	7	31.5	37.2	34.3	1.8	3	35.4	38.3	36.7	1.2	16	31.5	38.3	35.0	1.7
H/L,%	2	56.5	58.2	57.4	0.8	4	59.5	63.5	61.0	1.5	5	53.5	60.7	57.0	2.3	2	58.9	66.8	62.8	3.9	12	53.5	66.8	59.2	3.4
W:H,%	4	57.0	63.2	60.4	2.2	4	56.5	60.6	58.2	1.6	7	54.4	67.0	60.6	4.3	3	57.4	61.6	59.0	1.8	18	54.4	67.3	60.1	3.7

Tab. 33 Measurements of phalanx 3 of *Bison menneri* sp. n., Untermaßfeld, mm, and indices, %.

3. There are two types of middle-sized hoof phalanges in the sample. One has the same shape and proportions as the male anterior phalanges. The other is relatively shorter and higher, with a steeper slope of the dorsal rib (cf. Fig. 17, s). I interpret the first type as female anterior phalanges, and the second as male posterior ones. Due to their relatively great height, the latter have the lowest values for width/height ratio.
4. The specimens which are the smallest in length and width have the same proportions as the second type (male posterior) that suggests their belonging to female posterior phalanges.

Comments on phalanges. The resulting statistics on phalanx morphometry (Tables 31-33) support the suggested logic of their classification in general. However, some particular specimens do not quite fit the pattern in some of their parameters. For instance, one of the most important specimens is a set of all three phalanges belonging to the same toe IQW 1980/15 261 (Mei. 14 773), ph.1; IQW 1980/15 260 (Mei. 14 772), ph.2; IQW 1980/15 258 (Mei. 14 770), ph.3 (Fig. 17, e-f, m-n, and u-v resp.). Correct attribution of this set is very important. According to several lines of evidence, it has been interpreted as female forelimb toe. However, both first and second phalanges are marginal in the corresponding series for their great length, and the second phalanx distinguishes itself from the other anterior ones in its slenderness, though in the index of distal narrowing it fits this group quite well.
The other confusing case is phalanx IQW 1980/17 544 (Mei. 17 066) chosen as a typical female hind limb phalanx for illustration (Taf. 33, 23, 24; Fig. 17, w, x). It is marginal in the whole third phalanx sample for its shortest length and correspondingly the highest indexes of massiveness. However, a phalanx very similar in size and proportions is pictured by Flerov (1977, Abb. 16, 2) from Taubach and interpreted as female hind limb one. The above implies that we should consider the suggested classification only as a provisional one.

4. Systematic position of the Untermaßfeld bison among the other early Quaternary bovines

The above description of particular skeletal elements indicates that *B. menneri* was a very large, long-legged animal. The body height in males evidently reached the size of the largest of known bovids, like the Taubach bison, but the Untermaßfeld animal was more lightly built. Judging by the size of mandible and tooth rows, its head was relatively small, noticeably inferior to the large and heavy head of *B. priscus*. It seems likely that the horn cores of *B. menneri* were relatively small in size too.
Larger body size strikingly distinguishes the Untermaßfeld bison from the majority of primitive Pliocene and Villafranchian bovines such as *Leptobos*, *Ioribos*, *Adjiderebos*, *»Bison« palaeosinensis*. Besides, *B. menneri* probably had a different build, much more similar to true *Bison*. In fact, along with a considerably smaller size, the majority of *Leptobos* species had a more gracile appearance, approaching that of antelopes. Most of the known Pliocene/Villafranchian genera demonstrate many features considered to be primitive with respect to modern Bovini, in cranial morphology especially. Though the adult skull of *B. menneri* remains unknown, it seems that the new species was markedly more advanced than those earlier forms. This manifests itself in a larger backward deflection of the mandible ascending ramus in *B. menneri*. Its dentition looks more specialized and in practice cannot be distinguished from the large Pleistocene *Bison* and *Bos*.

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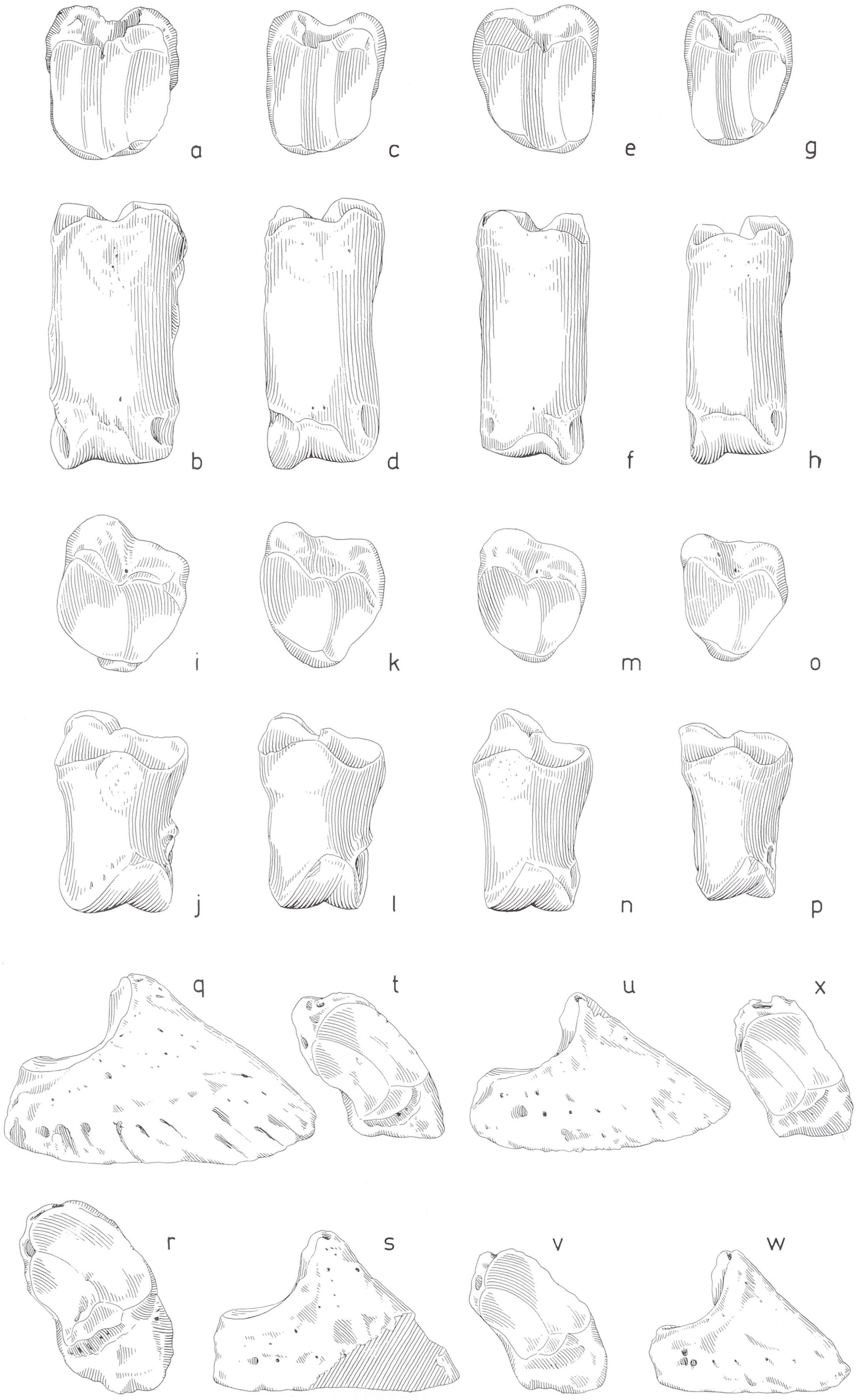
Fig. 17 *Bison menneri* sp. nov., Untermaßfeld. Phalangs. – a, b Phalanx I sin., IQW 1980/17 073 (Mei. 16 594), ant., male; proximal and anterior views. – c, d Phalanx I sin., IQW 1980/17 371 (Mei. 16 893), post., male; proximal and anterior views. – e, f Phalanx I dex., IQW 1980/15 261 (Mei. 14 773), ant., female proximal and anterior views. – g, h Phalanx I sin., IQW 1985/20 428 (Mei. 19 948), post., female; proximal and anterior views. – i, j Phalanx II dex., IQW 1980/16 919 (Mei. 16 440), ant., male; proximal and anterior views. – k, l Phalanx II dex., IQW 1980/17 360 (Mei. 16 882), post., male; proximal and anterior views. – m, n Phalanx II dex., IQW 1980/15 260 (Mei. 14 772), ant., female; proximal and anterior views. – o, p Phalanx II dex., IQW 1985/20 443 (Mei. 19 263), post., female; proximal and anterior views. – q, r Phalanx III dex., IQW 1982/18 031 (Mei. 17 551), ant., male; lateral and proximal views. – s, t Phalanx III dex., IQW 1980/17 230 (Mei. 16 752), post., male; lateral and proximal views. – u, v Phalanx III dex., IQW 1980/15 258 (Mei. 14 770), ant., female; lateral and proximal views. – w, x Phalanx III dex., IQW 1980/17 544 (Mei. 17 066), post., female; lateral and proximal views. – Scale = ca. 1:2.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Describing particular skeletal elements of *B. menneri*, I had to linger on the correlation of features characteristic of *Bison* and *Bos*. It has been shown that on the whole the new species demonstrates a more pronounced mixture of characters of these two genera than can be usually observed in a population of *Bison* or *Bos*. However, among the most reliable diagnostic features those typical for *Bison* are more constant. Attribution of the new species to the latter genus is strongly supported by the presence of fragments of juvenile skulls which certainly belong to *Bison*, and by the homogeneity of metapodial and other large bone samples. A strong admixture of some *Bos*-like postcranial characters may represent a peculiarity of this relatively early form. Some of these features, however, can be related to the greater slenderness of *B. menneri* limb bones as compared with most other *Bison* species.

To define the relationship of the new species with the numerous described forms of *Bison* is a more difficult task due to the peculiar composition of the fossil sample from Untermaßfeld. The species taxonomy of the genus is based almost completely on the structure of adult skull and horn cores which are absent from our collection. The inclusion of dentition characters in descriptions and even diagnoses of species and subspecies is hardly expedient. As well as showing a morphology characteristic of *Bison* (which is actually little different from *Bos*), the teeth of bison display considerable variability in minor details and in proportions. This variability is of individual character but greatly depends on the degree of wear (cf. section 3.2.3).

This being the case, I was obliged to compare various Quaternary *Bison* species in terms of their limb bone characters, especially those of metapodials. It must be noted that I do not consider such a comparison as something defective. Both habitus and constitution type of animal should be taken into account in determining its taxonomic position, provided they have been revealed on the basis of a large sample as is actually so in our case. At any rate, those are no less essential characters than the shape and size of horn cores, which are known to be highly variable. In turn, the structure of the *Bison* neurocranium, which is usually thought to be taxonomically important, is greatly affected by the size of the horn cores. Certainly, I am not going to reject cranial taxonomy of *Bison* completely, but in the course of this research I have become convinced that well established limb bone characters too can be very useful for taxonomic analysis. At least several cases have been revealed during this research, where the limb bone analysis suggests the inadequacy of taxonomic conclusions made on the basis of *Bison* horn cores and skulls. In the following consideration of *B. menneri* relationships with other bovine taxa we turn again to the diagram of metacarpal size and slenderness, which is one of the most representative and informative sources.

The general view of this graph (Fig. 11) comprising several hundred metacarpals (the large samples of late *B. priscus* and *Bos primigenius* are not plotted) reveals two megafields. Clusters of all Quaternary species of *Bison* locate within one of them (A), being arranged more or less parallel in one layer having a *B. menneri* cluster at one end, and small and stout *B. priscus* from the European Weichselian at the other. Though widely varying in size and slenderness, the metacarpal samples of all these species (including unplotted Siberian and Alaskan *B. priscus* and European *Bos primigenius*) have something in common and the transitions between samples are often gradual.

Another megafield (B) occupies the bottom left corner of the graph and comprises more primitive Pliocene and Villafranchian bovids like *Leptobos*, *B. palaeosinensis*, *Ioribos*, *Bison* sp. from Venta Micena and elsewhere. Metacarpals of all these bovids correspond in size to small and middle-sized bovids of the first group, but are markedly more slender as compared with advanced bovines of the same size. For instance, the bones of the Venta Micena animal have on average the same length as those of Siberian *B. priscus*, but their distal and proximal widths are about 30% less (cf. Table 18). Actually, those were quite different animals in their constitution!

Analysis of *B. menneri* relations based on metacarpals is restricted to those taxa, for which these bones are well known or at least available. We start it with the field B.

***Bison* sp. from Venta Micena.** As I have already noted, metacarpals of this animal are radically different from *B. menneri* and most of other *Bison* and *Bos*. The same is true for the most of the other examined limb bones of the Spanish bovid. As in Untermaßfeld, the Venta Micena sample gives the impression of a homogeneous population, easily separated into males and females. The corresponding clusters on the graph adjoin the *Leptobos* area. In general, some limb bones from Venta Micena are very similar in size and proportions to *Leptobos etruscus* (Moya-Sola 1987). Assignment of the Spanish bovid to *Bison* rather than to *Leptobos* is based mainly on the dentition, as cranial material is not available in this locality. If this conclusion is correct, we should expect that it would not be easy to discriminate separate limb bones of this *Bison* from *Leptobos*. This might be true for other small and primitive bovines. In this respect, bovine fossils from some recently described Italian localities of the Late Villafranchian age are very important.

Bovines from Casa Frata and Pirro Nord. Though rather scanty, the Pirro Nord record (De Giuli et al. 1986) is extremely important. For the first time it gives a clear idea on what kind of metacarpal corresponds to the earliest type of *Bison* in Europe. I agree with my Italian colleagues that the Pirro Nord specimen »shows more *Bison*-like skull features than *Leptobos* and conforms well with the definition of *Eobison* given by Flerov«. It looks rather similar to *B. palaeosinensis* and has common features with the fragment of skull described as *B. tamanensis*. The Pirro Nord metacarpals also have a *Bison*-like appearance. They are stouter than metacarpals of *Leptobos* and of the Venta Micena bovid, and in general the stoutest among the metacarpals of the field B. At the same time they are incomparably more slender than the metacarpals of *B. priscus* of the same length.
The metacarpal from Casa Frata (De Giuli and Masini 1986) is not only much more slender than the Pirro Nord metacarpals, but has a more *Bos*-like appearance, and I agree with the authors that it could very likely belong to *Leptobos*.

***Bison palaeosinensis*.** The available information on metacarpals of this species is rather scanty. Two metacarpals from Nihowan (Teilhard and Pivetau 1930) are rather similar to male metacarpals from Venta Micena. Later Teilhard and Trassaert (1938) described some bovine material from Yushe deposits (Zone III, »Villafranchian«). Some fossils, including two metacarpals and two metatarsals were referred to *B. palaeosinensis*, others to a larger form, *Bison* sp. The cannon bones assigned to *B. palaeosinensis* (Fig. 65) are too small to be comparable with any Bovini (unless there is an erroneous indication of the scale for the picture). The metacarpal of a larger form, according to the cited measurements, fits Nihowan (and Venta Micena) material quite well. It is noteworthy that both types of metacarpals have been found in the same locality (Loc. 6, Haiyen).
Thus, the field B of the graph under consideration includes, besides *Leptobos*, metacarpals of *Bison palaeosinensis*, and *Bison* sp. from Venta Micena and Pirro Nord. There are also some isolated *Bison* fossils found within the same field, such as a metacarpal from the Norfolk Coast of England (Trimingham) and one from Süßenborn (see below). It should be also noted that some of the smallest *Bos* metacarpals intrude upon the field B, such as females of the Neolithic aurochs (Degerbøl and Fredskild 1970) and small aurochs from Venosa (Caloi and Palombo 1980).

B. *schoetensacki*. Coming to the field A, first of all we face the problem of *B. schoetensacki* which is usually thought to have the most slender limb bones among Quaternary *Bison*. Its case seems to be the most confused, in part due to the fact that this species is listed together with *B. priscus* in such important European localities as Mosbach and Mauer. This is reasonable, as, for instance, plotting all *Bison* metacarpals from Mauer shows that the sample dispersion is too large to represent a single species. Five complete metacarpals from Süßenborn are dispersed still more widely. The Mosbach sample from the Mainz and Darmstadt collections measured by Martin looks more homogeneous, especially the female cluster. As to the males, there are several specimens deviating from the remaining rather compact cluster. Judging from their position on the graph, these compact Mosbach clusters must belong to a stout animal of *B. priscus* type rather than to *B. schoetensacki*. How, in this case should *B. schoetensacki* metacarpals look? To understand the problem, we should consider the original idea and definition of this species.

Freudenberg (1914) described *B. schoetensacki* metapodials as lightly built and gracile in contrast to the heavily built and clumsy metacarpals of *B. priscus*. To illustrate his idea, Freudenberg compared photos of two metacarpals (op. cit., 96, Fig. 45-46): *B. priscus* from Hundsheim and *B. schoetensacki* from Mosbach. Despite the printing error (the pictures should be switched), the idea itself is quite clear and corresponds to Freudenberg's primary diagnosis of *B. schoetensacki*: »...The transverse measurements of the limbs are smaller than in young-Diluvial forms. The metapodials are in particular striking due to their slenderness reminding of *Bos primigenius*« (Freudenberg 1910, 133).

Schertz (1936a, 61) determined that Freudenberg (1914, Fig.45) had pictured the Mosbach metacarpal No. M.1807 from the Senckenberg collection (Frankfurt) as *B. schoetensacki*. However, Schertz held another concept of this species, going back to Schoetensack (1908), Hilzheimer (1909) and Soergel (1914), namely that *B. schoetensacki* was an early small form of forest bison ancestral to *Bison bonasus*. While Freudenberg emphasized its smaller horns and more slender legs versus *B. priscus*, Schertz believed that Mauer bison (*B. schoetensacki*) was the smallest form among all the fossil *Bison* species. The latter has given rise to a long-living myth that *B. schoetensacki* was not only short-horned, but small-sized in general, which is evidently not true. Quite the contrary, Mauer metapodials are among the largest known, with the exception of *B. menneri*. Schertz was amazed by the large size of metacarpal of *B. schoetensacki* pictured by Freudenberg (M.1807), and being influenced by the above-mentioned concept, interpreted this specimen as female of *B. priscus*.

After plotting large samples of metacarpals from such fossil populations as Untermaßfeld, Venta Micena, Amvrosievka, and other places, where the sexual distribution is very clear, I realized that Schertz's idea on the sexual dimorphism of metapodials from Mauer and Mosbach was very far from being adequate. The metacarpal in question (M.1807) cannot be referred to a female, any more than can at least 4 other metacarpals of Schertz's (1936b) sample from Mosbach and Mauer (Ffm. 1808, Dmstdt. A, Hdlbg. 4601 and 4603). The metacarpal M.1807 certainly belongs to a male individual, but it is one of the most slender male metacarpals in Mosbach or Mauer, and clearly represents Freudenberg's image of metacarpals of *B. schoetensacki*.

Another basic point in Freudenberg's description is the metacarpal from Hessler near Wiesbaden which he marked as *B. schoetensacki* (1914, 93). Its measurements given by Freudenberg place this specimen exactly in the same area of the graph as the previous one, i.e. between the distributions of Mosbach *B. priscus* and *B. menneri*.

These two basic points suggest an exact notion of how Freudenberg, formal author of the species *B. schoetensacki*, conceived the morphological type of limb bones of this animal. Subsequent publications distorted this idea. In particular, Schertz (1936a; 1936b) replaced Freudenberg's typical large male metacarpal of B. schoetensacki by a small female bone (M.1803, 58, Fig. 14b) which he presented as *B. schoetensacki*. However, essentially larger female metacarpals known from Mauer make it much more likely that M.1803 from Mosbach belongs to a *B. priscus* female. Schertz's substitution misled the later researchers. It seems remarkable that Shertz's concept left no place for the pattern of the male metacarpal of *B. schoetensacki*, so he did not separate sexes in this species at all.

This analysis has led me to the following conclusions: 1. Both Mauer and Mosbach samples of metacarpals are heterogeneous. 2. According to the original indication by Freudenberg (1914) and to my observations on various bovines, relatively longer and more slender metacarpals of these samples should be interpreted as *B. schoetensacki* Freud., while shorter and stouter ones as *B. priscus* Boj. (with the account of sexual dimorphism).

In view of this concept, the following metacarpals can be referred to *B. schoetensacki*:

Mauer:	HDLBG M.291, M.319, M.1472 – males; HDLBG M.1474, M.1481, 4605[4], HLMD 401[4], HLMD 25[4] – females.
Mosbach:	NHMM 1958/90 1962/720 1932/842 (?), SMF 4105[4], SMF 1807[4] – males; NHMM 1926/17[5], 1959/764 (?).

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[4] Schertz 1936b.

[5] Sala 1986.

Thus, most of metacarpals collected in Mauer seem to belong to *B. schoetensacki* (8 of 9), while in Mosbach only about 10% do so (5 or 7 of 53). The rest belongs to *B. priscus*. As the total number of metacarpals assigned to *B. schoetensacki* in Mauer and Mosbach is not very large, I could only provisionally outline possible male and female clusters on the graph (Fig. 11). They hold an intermediate position between the *B. priscus* and *B. menneri* distributions, overlapping partially with both of them. That means that it can be rather hard to distinguish some single metacarpals of *B. schoetensacki* from *B. menneri* or *B. priscus*.

Metatarsal plotting gives a similar though not so distinctive pattern. The typical *B. schoetensacki* metatarsal from Mauer in the Darmstadt collection cited by Freudenberg (1914, 93) belongs to a female individual. Like the metacarpal, it lies on the graph between *B. menneri* and most of *B. priscus* from Mosbach. Two more complete metatarsals from Mauer and about 4 from Mosbach can be provisionally referred to *B. schoetensacki*, 2-3 of them (plus one metatarsal from Hochheim indicated by Freudenberg as *B.* cf. *schoetensacki*) being found within the area of *B. menneri*. The majority of Mosbach metatarsals (more than 20 specimens) are located in the *B. priscus* zone.

***Bison* sp. from Süßenborn.** Flerov (1969) described three forms of bison from Süßenborn: *B. schoetensacki lagenocornis*, *B. schoetensacki schoetensacki*, and *B. priscus priscus*. All three were based on cranial and dental material. Postcranial material was not classified (*Bison* sp.). Flerov suggested that these three forms came from horizons of different age and formed a chronological succession. He related the first subspecies to the latest Cromerian – earliest Elsterian, the second – to the late Elsterian, and the third – to the Holsteinian. None of the existing age interpretations of this locality, however, imply the presence of late Elsterian and Holsteinian horizons in the section. The particles of large-sized gravel found inside the *B. priscus* skull suggest that it comes from the main gravel thickness, and not from the uppermost horizons (H.-D. Kahlke, pers. comm.).

My study of postcranial material from Süßenborn showed a striking heterogeneity of the sample. Among 5 complete metacarpals available, three fall within the range of *B. priscus* from Mosbach. One, IQW 1965/2331 (Süß. 5876), lies in the middle of the male distribution of *Bison* sp. from Venta Micena and very close to *Leptobos* area. The last one, IQW 1965/2333 (Süß. 9161), has a notably different type of preservation from most Süßenborn fossils. Its large size and very pronounced slenderness suggest only one possible identification: female of *B. menneri* (cf. Fig. 11). In view of these two specimens Wüst's remark on the presence of *Leptobos* in Süßenborn looks not so strange. I suppose that at least a *B. menneri*-like metacarpal is redeposited into the Süßenborn gravel from earlier deposits. As far as I know, the possibility of admixture of older material in Süßenborn has never been considered seriously, but bovine metacarpals make us do that.

More important in our case, however, is the conclusion that *B. priscus* was certainly present in the main Süßenborn fauna which is supported by the above comment on the skull of this species.

Bison metatarsals from Süßenborn look more homogeneous. Four complete specimens are rather similar and lie on the graph between the scatters of *B. priscus* (Mosbach) and *B. schoetensacki*. At least one of them could belong to *B. schoetensacki* but the presence of *B. priscus* is very likely. The fifth one, worse preserved, is again very near *Leptobos* and the Venta Micena zone. However, Flerov (1969, Fig. 14) interpreted it as juvenile female individual.

***Bison* sp. from Tiraspol (Moldavia).** Flerov and David (1971) studied a large collection of *Bison* fossils from this key locality. Basing themselves on cranial and horn core fragments, they affirmed the presence of the same two subspecies of *B. schoetensacki* as described from Süßenborn, with a similar stratigraphic position. The rich postcranial material from Tiraspol was referred to *B. schoetensacki*, though the authors mention that the Tiraspol bison had massive limb bones not different from *B. priscus*.

My study of Tiraspol material in Moscow, Kiev and Kishinev has shown that metacarpals from this locality are much more massive than those referred to *B. schoetensacki* in the type localities (Mauer and Mosbach). Moreover, on the average they are even more massive than *B. priscus* samples from these localities. Though I cannot completely exclude the presence of *B. schoetensacki* in Tiraspol (some metatarsals, for instance, are very similar to those known from Süßenborn), it is clear that the majority of postcranial elements in Tiraspol belongs to a much more heavily built animal than *B. schoetensacki*. That animal had an even heavier build than early priscoid bison in Europe.

V. Gromova (1965) believed that not only the more massive limb bones but also the horn core characters of the Tiraspol bison do not allow us to refer it to typical *B. schoetensacki*. This opinion was ignored during 20 years, but finds new support in my research. It is necessary to revise our view of the Tiraspol collection of bison, and admit that it was probably more similar to priscoid forms inhabiting open spaces than to *B. schoetensacki*.

Bison voigtstedtensis. This form from Voigtstedt was originally described as a subspecies of *B. schoetensacki* (Fischer 1965). Later Flerov (1975) raised its status to a species rank. This was not generally accepted. Studying the large sample of *B. schoetensacki* skulls from Isernia in Italy, Sala (1986) concludes that the range of skull variation found in this fossil population covers morphotypes of *B. voigtstedtensis*, *B. schoetensacki lagenocornis* and *B. schoetensacki schoetensacki*. Sala assumes that Fischer could be more right regarding the Voigtstedt bison as a primitive form of *B. schoetensacki*. As to *B. schoetensacki lagenocornis*, Sala suggests that its features reflect a male secondary sexual character.

Unfortunately, it is not possible to compare *B. menneri* with *B. voigtstedtensis*, as no postcranial material is known from Voigtstedt. Dental characters are more or less similar in early bison (see above).

Bison suchovi. This species has been described by Alekseeva (1967) on scanty fossils from the Dolinskoye locality in the Odessa Region. Alekseeva (1977) supposed that some scattered fossils of small bovines from the Eopleistocene (Villafranchian) deposits could belong to *B. suchovi*. In my opinion, she repeated the common delusion of identifying small size of skull (horn core, mandible) with small body size. The bison from Dolinskoye was not a small animal. Its metatarsal corresponds in size and proportions to those from Süßenborn, Mauer and Mosbach. The same is true for the size of humerus (fragment) and molar row.

Most students (Flerov 1975; Gromov and Baranova 1981) believe that this is only a junior synonym of *Bison tamanensis* Vereshchagin.

Bison tamanensis. It would be very important to compare *B. menneri* with this species which is thought to be the earliest *Bison* in Europe and till recent times the only one referred to subgenus *Eobison*. However, no material is known as positively belonging to this species with the exception of the fragmentary type skull.

Some isolated postcranial remains from three Ukrainian localities including three complete *Bison* metacarpals are assigned to *Bison tamanensis* (David and Svistun 1981). One of them is accompanied by a fragment of a horn core, but the main argument for species determination is that the localities are thought to have rather an early geological age (pre-Tiraspolian). The parameters of a metacarpal from Kairy correspond quite well with those from Mauer and Mosbach thereby placing it on the graph (Fig. 11) near the suggested boundary between *B. schoetensacki* and *B. priscus* females. The largest of the Ukrainian metacarpals, one from Chertkovo, is found within the area of overlap of male *B. schoetensacki* and *B. menneri* dots. Only the smallest metacarpal from Cherevychniy deviates in the direction of the field B and could be comparable with the Venta Micena form.

All the three metacarpals are clearly different from the Tiraspol bison (which, as we saw above, cannot be assigned to *B. schoetensacki*) and belong to more slender-legged bovines. However, it is not possible to decide definitely whether they (or some of them) could belong to *Bison tamanensis*. If we assume that some of them do, there are two choices. If *Bison tamanensis* had metacarpals like those from Chertkovo or Kairy, that means that this species should be classified within the same group of early bison as *B. schoetensacki* and *B. menneri*. If the Cherevychniy specimen can be related with *Bison tamanensis*, this will support the affinity of this species with more primitive bovines like those from Venta Micena, Pirro Nord and Nihowan, and essentially contribute to the concept of *Eobison*. However, we need a more representative record for a more adequate understanding of this problem.

5. Comments on early evolution of *Bison*

Until very recent years the earliest and most primitive bison were known only from southeast Asia (*Probison dehmi*, *Bison sivalensis*, *Bison palaeosinensis*). They had some features in common with *Leptobos* and were quite different from other bison. Flerov (1972) united them into the subgenus *Eobison*. He believed that in southeastern Europe bison first appeared in the Tamanian time (i.e. at the very end of Villafranchian) at the stage of *Bison tamanensis* which he assigned to the same subgenus. According to Flerov (1975, 1979), bison reached Central Europe and England later in the Cromerian at the stage of *B. voigtstedtensis*, which he attributed to an independent species in the subgenus *Bison*.

The very last few years have provided us with a much earlier and very important record of bovines in Europe (Pirro Nord, Venta Micena, Untermaßfeld). The analysis of postcranial skeletal elements made in this paper has shown that the early European bovines can be classified into two distinct groups, which reflect quite different types of bodily constitution. One of them includes small and lightly built animals similar to *Leptobos* in their constitution. This group comprises the Pirro Nord and Venta Micena bovines, as well as *B. palaeosinensis*. The other group includes very large but slender-legged bovines like *B. menneri* from Untermaßfeld and *B. schoetensacki* from Mauer. There are reasons to suppose that these species, despite their large body size, had not yet acquired those heavy heads carrying large horns typical for *B. priscus* sensu lato.

Comparison of large samples of metacarpals shows the difference between the two groups especially impressively. If the assumption that the species of the first group are still more *Bison*-like than *Leptobos*-like is correct, I would support the opinion of my Italian colleagues (De Giuli et al. 1986) that these groups deserve separate generic status. I find their proposal to place these small species into the genus *Eobison* quite reasonable though I agree that a revision of *Leptobos*/*Eobison* relationships is vital.

Bison menneri sp. nov., being the largest of known bison, belongs to genus *Bison* together with *B. schoetensacki* and *B. priscus* sensu lato. It was probably the earliest and most primitive member of the genus *Bison* in the above suggested sense. The striking size difference makes its direct descent from European *Eobison* rather unlikely. That is why it cannot give us now any direct evidence for the geological age of the Untermaßfeld fauna.

The age of the Pirro Nord and Venta Micena faunas with *Eobison* is estimated as latest Villafranchian, between 1.4 and 0.97 M*a* (De Giuli et al. 1986; Agusti et al. 1987). Spanish colleagues place Venta Micena in the middle of the *Allophaiomys pliocaenicus* biozone. In Eastern Europe, this time corresponds to the Odessan faunal complex[6]. Such above mentioned localities with bovine fossils as Kairy and Dolinskoye are referred to this stage. If these correlations are correct (and we have no reasons to call this in question now), that means that large *Bison* species existed in Eastern Europe at the same time as small *Eobison* inhabited southwest Europe.

There are some other indirect indications that two lineages of bison (*Bison* and *Eobison*) could have existed simultaneously in West and East Eurasia in the late Villafranchian. Teilhard and Trassaert (1938) noted the presence of a large *Bison* (»of a typical *Bison* appearance«, and I would add – of priscoid type) in the same Yushe Villafranchian localities, which yielded small *B. palaeosinensis*. The second important area of bovine speciation was the Caucasus, where several quite peculiar bovines are known from the Villafranchian, such as *Protobison, Adjiderebos*, *Ioribos* and some other without special names (Burchak-Abramovich and Vekua 1980; Dubrovo and Burchak-Abramovich 1986). In theory, some of them could produce large *Bison* offshoots into the Black Sea area rather early in Villafranchian. At the moment the Chinese stock seems a more reasonable source, but of course we need to get acquainted with more recently collected Chinese material.

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[6] Corresponds to the Early Tamanian of David and Svistun (1981) and some other authors, and to the Late Khaprovian of Alekseeva (1967).

Azzaroli (1983) considers the appearance of large and heavy bovines in West Europe as one of the major elements of the »end-Villafranchian dispersal event« marking the beginning of the Galerian. In typical Galerian faunas (late Cromerian and Elsterian) at least two forms of *Bison* existed: short-horned, large and slender-legged (*B. schoetensacki*), and long-horned and more stocky (*B. priscus* of Mosbach type). To the east, an even heavier and larger form is known (*Bison* sp. from Tiraspol). As shown above, *B. menneri* from Untermaßfeld differs from all these forms of the typical Galerian, and could be more ancient than the late Cromerian. However, we have insufficient grounds for shifting it back to the Villafranchian. In general terms, we can only say that this new form of *Bison* could be evidence in favour of transitional position of the Untermaßfeld fauna between Villafranchian and Galerian, i.e. the early Cromerian in a broad sense.

Flerov (1979) believed that long-legged bison of relatively light constitution were forest dwellers. This conclusion is attributable to the new form from Thuringia which was the tallest and the most slender-legged form among the bovines of the genus *Bison* (sensu stricto).

Summary

Intensive excavations of the recently discovered locality of Untermaßfeld in South Thuringia (Germany) have provided one of the richest and most interesting of Early Pleistocene faunas in Central Europe. One of its most representative parts is a sample of large bovid fossils including more than 1,000 specimens. The sample has a peculiar composition: among postcranial bones adult animals prevail, while cranial material is scanty and belongs to juvenile individuals only. The proportion of young animals among dentitions is also high. The preservation of bones is excellent.

This report on the Untermaßfeld large bovid sample includes a detailed description of most of the skeletal elements accompanied by measurements and its comparison with various Quaternary bovids from German, British and Former USSR (Moscow, St. Petersburg, Kiev, Kishinev) collections. A peculiar feature of the Untermaßfeld large bovid bone sample is its homogeneity. That permits us to consider this sample as a fossil population of one species. The sample includes fossils of a minimum of 27 adult and 10 juvenile individuals. Most of adult bones can be easily classified into male and female according to their size and massiveness.

The lack of adult skulls and horn cores and the wide variation in dental characters caused us to pay most attention to features of the limb bones. The study of metapodials, and especially metacarpals, turned out to be the most fruitful. The sample of 33 intact metacarpals from Untermaßfeld was compared with the samples of those bones of large bovids from the most important Early Pleistocene faunas in Europe (Mauer, Mosbach, Süßenborn, Tiraspol, Venta Micena, etc.) and with those from younger faunas in Europe, Siberia, and Alaska.

Juvenile cranial fragments from Untermaßfeld certainly belong to *Bison*. Postcranial bones demonstrate a mixture of *Bos* and *Bison* features, with the clear prevalence of the latter. At the same time, the limb bone character does not allow us to assign the Untermaßfeld bison to any of the known species of *Bison*. It was a very large animal, one of the tallest bison ever existed, with the most gracile constitution amongst all the known large Quaternary bovids. This led us to consider the Untermaßfeld bison as a new species, *Bison menneri*.

Problems of bovine morphology, taxonomy, and evolution, mostly of early bison, are discussed. The most confused issue is that of the morphological type of *Bison schoetensacki*. It seems necessary to reestablish Freudenberg's original definition of this species as a very large bison with slender legs, as evidenced by the metapodials from Mauer. It cannot be excluded that the Voigtstedt bison should be considered as the same species. The bison from Tiraspol cannot be assigned to *Bison schoetensacki*, as it was a very heavily built animal of priscoid type.

A review of postcranial features of various bovines suggests that the early European bison (Late Villafranchian – Cromerian) can be classified into two groups by their type of bodily constitution. The first one includes relatively small and lightly built forms, more or less similar to *Leptobos* in their constitution and displaying some archaic cranial features. This group includes *Bison palaeosinensis*, as well as the

bovines from such localities as Venta Micena (Spain) and Pirro Nord (Italy). It seems reasonable to join these forms under the genus *Eobison,* though a comprehensive revision of their morphological distinctions from *Leptobos* is necessary.

The second group embraces the true bison (*Bison*), where *B. menneri*, *B. schoetensacki*, and B. *priscus* sensu lato belong. *B. menneri* was probably the earliest representative of this group in Europe, followed some time later by *B. schoetensacki*. Those were very large animals with long and slender limbs, but they probably had not yet acquired very large horns similar to *B. priscus*, so they had a relatively smaller head size. *B. schoetensacki*, however, shared its range with the heavily built *B. priscus* of earlier type in the same faunas (Mosbach, etc.). Priscoid bison could immigrate from Asia, which is indirectly supported by some evidence from Moldavia, Ukraine, and China. Co-existence of those two bison lineages in Europe at the end of the early and beginning of the middle Pleistocene could be evidence in favour of the hypotheses of forest adaptations of *B. menneri* and *B. schoetensacki*, although we could not find any direct morphological indications of that in the Untermaßfeld bison, besides its long and slender limbs.

The appearance of the large *B. menneri* in Europe, replacing smaller and gracile Villafranchian bovids, represented probably the earliest stage of the flourishing of large bovids, so characteristic for the Pleistocene as a whole. Thus, this new species can be referred to the early Cromerian sensu lato.

Zusammenfassung

Intensive Ausgrabungen im Gebiet der neuentdeckten Fundstelle Untermaßfeld in Südthüringen (Deutschland) haben in den letzten Jahren eine der reichsten und zugleich interessantesten frühpleistozänen Faunen Mitteleuropas erbracht. Dabei gehören die fossilen Boviden-Reste, die mehr als 1000 Einzelfunde umfassen, zu den repräsentativsten Teilen dieser großen Sammlung. Die *Bison*-Funde von Untermaßfeld zeigen eine sonderbare Zusammensetzung: die postkranialen Skelettreste gehören hauptsächlich zu adulten Individuen, während Schädelreste relativ selten sind und nur von jugendlichen Individuen stammen. Auch bei den Zahnfunden überwiegen solche jugendlicher Tiere. Die allgemeine Erhaltung der Skelettreste ist außergewöhnlich gut.

Die vorliegende Arbeit über den großen Boviden von Untermaßfeld umfaßt eine eingehende Beschreibung der meisten Skelettelemente, eine Vorlage der Maßtabellen sowie Vergleiche mit anderen quartären Boviden aus deutschen und britischen Sammlungen sowie Museen der ehemaligen UdSSR (Moskau, St. Petersburg, Kiev, Kishinev). Eine Besonderheit der fossilen Boviden-Reste von Untermaßfeld ist ihre Homogenität, die es erlaubt, von der Fossilpopulation nur einer Art zu sprechen. Das Material fossiler Boviden von Untermaßfeld umfaßt Skelettreste von zumindest 27 adulten und von 10 juvenilen Individuen. Dabei lassen die meisten der vorliegenden Skelettreste adulter Individuen nach Größe und Robustheit eine Unterscheidung von männlichen und weiblichen Individuen zu.

Das Fehlen von Schädeln oder Hornzapfen adulter Individuen und die große Variationsbreite in der Ausbildung der Zähne bewogen uns, den postkranialen Skelettelementen, und unter diesen besonders den Extremitätenknochen, größere Aufmerksamkeit zu widmen. Dabei zeigte es sich, daß die Untersuchung der Metapodien, und hier wiederum der Metacarpi, besonders erfolgreich war. Bei diesen Untersuchungen war es möglich, 33 vollständig erhaltene Metacarpi von Untermaßfeld mit solchen der wichtigsten frühpleistozänen Faunen Europas (Mauer, Mosbach, Süßenborn, Tiraspol, Venta Micena, etc.) sowie mit solchen jüngerer pleistozäner Fundstellen Europas, Sibiriens und Alaskas zu vergleichen.

Die juvenilen Schädelreste von Untermaßfeld gehören fraglos zur Gattung *Bison.* Die postkranialen Skelettelemente aber zeigen eine Mischung von *Bos*- und *Bison*-Eigenschaften, mit einem Überwiegen der *Bison*-Charakteristika. Gleichzeitig erlaubt es die Form der Extremitätenknochen der Untermaßfeld-Population nicht, diese einer bisher schon beschriebenen Bison-Spezies zuzuordnen. Der Bison von Untermaßfeld war sehr groß, er gehörte einer der größten *Bison*-Arten an, die je existierte, verbunden mit einer außergewöhnlichen Grazilität, die ihn von allen bekannten großen quartären Bisons trennt. Diese Unterschiede ermöglichten die Aufstellung einer neuen Spezies, *Bison menneri* n. sp.

Probleme der Morphologie, der Taxonomie und Evolution der Bovini, hauptsächlich der frühen Vertreter der Gattung Bison, werden diskutiert. Dabei stellt sich heraus, daß die meiste Verwirrung durch die Interpretation des Typus *Bison schoetensacki* ausgelöst wurde. Es erscheint uns daher notwendig, zur ursprünglichen Definition durch Freudenberg zurückzukehren, der diese Species als einen sehr großen Bison mit schlanken Extremitäten – nach den Metapodien von Mauer zu urteilen – charakterisierte. Es erscheint uns nicht ausgeschlossen, daß der Bison von Voigtstedt dieser Spezies zugehört. Der Bison von Tiraspol indessen kann nicht zu *Bison schoetensacki* gestellt werden, da er ein sehr massig gebautes Tier des *priscus*-Typs war.

Ein Überblick über die Eigenschaften der postkranialen Skelettelemente verschiedener Bovinen führte zu der Überzeugung, daß die frühen europäischen Bisons (spätes Villafranchium bis Cromerium) nach ihrem Körperbau auf zwei Gruppen verteilt werden können. Die erste Gruppe umfaßt relativ kleine und leicht gebaute Formen, die in ihrer Konstitution mehr oder weniger *Leptobos* entsprachen und archaische Merkmale im Schädelbau aufweisen. Zu dieser Gruppe gehören *Bison palaeosinensis* wie auch die Bovinen von Venta Micena (Spanien) und Pirro Nord (Italien). Es erscheint begründet, diese Formen in die Gattung *Eobison* zu stellen, obgleich eine umfassende Revision ihrer morphologischen Unterschiede gegenüber *Leptobos* notwendig ist.

Die zweite Gruppe umfaßt die Bisons im engeren Sinne (Gattung *Bison*), zu der *Bison menneri* n. sp., *Bison schoetensacki* und *Bison priscus* s. l. gehören. *Bison menneri* n. sp. war wahrscheinlich der früheste Vertreter dieser Gruppe in Europa, gefolgt von *Bison schoetensacki*, der erst etwas später auftrat. Dieses waren sehr große Bisons mit langen und schlanken Extremitäten, aber wahrscheinlich besaßen sie noch nicht die großen Hörner, wie sie von *Bison priscus* bekannt sind, und es ist anzunehmen, daß die Schädel relativ kleiner waren. *Bison schoetensacki* trat aber schon zusammen mit einem schweren *Bison priscus* frühen Typus (Mosbach etc.) auf. Der priscoide Bison ist wahrscheinlich von Asien eingewandert, was indirekt durch einige sehr frühe Nachweise in Moldavien, der Ukraine und China angezeigt wird. Eine Koexistenz dieser beiden Bison-Linien in Europa am Ende des frühen und zu Beginn des mittleren Pleistozäns könnte die Hypothese einer Wald-Anpassung von *Bison menneri* n. sp. und *Bison schoetensacki* unterstützen, obgleich wir keine direkten morphologischen Hinweise für diese Behauptung beim frühen *Bison* von Untermaßfeld anführen können, abgesehen von den langen und schlanken Extremitäten.

Das Erscheinen des großen *Bison menneri* n. sp. in Europa, der die kleineren und grazileren villafrankischen Boviden ablöste, ist wahrscheinlich als frühestes Stadium des Aufblühens der großen Boviden anzusehen, das so charakteristisch für das gesamte Pleistozän werden sollte. In diesem Sinne kann die neue Spezies dem frühen Cromerium s. l. zugewiesen werden.

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