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THE WÜRMIAN FOXES OF BOHEMIAN AND MORAVIAN KARST

INTRODUCTION

Foxes are not a frequent object of interest of palaeontologists. There are of course many reasons for this, and they may be summarized as follows:

1. The recent fox is a solitary animal; fossil foxes evidently had the same mode of life. Thus, finds are rare. The fossil remains usually belong to one or a few individuals, but they are almost always incomplete. Finds of masses of bones belonging to a great number of individuals, as is the case with bears, horses etc., have not yet been made in a natural environment or in human settlements.

2. The great uniformity of canids leads either to underestimation or overestimation of morphological or metrical differences. This results either in the endeavour to concentrate all Pleistocene foxes into one or two recent species, or the creation of a great number of new species based on subordinate features only.

3. The stratigraphic data on foxes have so far been very little utilized, partly because of the foxes' rare occurrence and the vagueness of nomenclature, partly because of the frequently indefinite stratigraphic assignment of the find — foxes often hollowed out and still do hollow out their lairs in the entrance of a cavern, at the margin of a shelter cave, so that bones of geologically younger animals may become part of older sediments.

4. The body sizes of foxes are relatively small, so that they escape attention (they are too small for macropalaeontological and too large for micropalaeontological investigation).

Originally, all fossil foxes were assigned to recent genera and species, later they were described under separate names as species and subspecies (see e.g. NORDMANN 1858, SCHMERLING 1834, BOURGUIGNAT 1875, NEHRING 1878 and others). J. N. WOLDŘICH (1878) was the first – and up to the present time the sole author — to try to revise the systematic classification of foxes. This author „solved" the problem abolishing all genera and species reported up to his time, and introducing his own new ones often based on insufficient material or contradicting nomenclatorical rules, even those which at his time were generally accepted. Many authors did not approve of Woldřich's genera and species or acknowledged them partly only; others advocated them, so that the revision, instead of removing the existing confusion, augmented it further, as very often it is not clear what some authors understand as a synonym and what as a separate species.

The first half of the twentieth century has brought many findings, especially as far as Early Pleistocene foxes are concerned. However, the individual finds are described in reports on finds only or they are given in lists of species without any further data; an elaboration and evaluation is therefore lacking. Late Pleistocene foxes remained in the background of interest in the literature of the first half of this century. Only in the fifties were they the subject of a study, by R. MUSIL (see the references), who was elaborating the osteological material from the Moravian Palaeolithic stations.

I wish to thank the directorate of the Moravian Museum, Brno, especially the head of the Department of Palaeontology, Dr. R. Musil, DrSc., for the kind loan of the substantial part of the material elaborated in this paper, Prof. Dr. Z. Špinar of the Department of Palaeontology of the Faculty of Science, Charles University, Prague, for his instructions on the formal layout of the paper, Mr. J. Chlumský for taking the photographs and my wife A. Benešová for making all the diagrams, drawings and annexes.

METHOD OF WORK

In this paper I have elaborated the foxes from the Würmian cave sediments of the Bohemian and Moravian karst. The localities are described in detail in a separate chapter.

The material studied is derived partly from the collections of the National Museum, Prague, partly from those of the Moravian Museum, Brno.

For measuring the material I used mostly Duerst's metod (DUERST - BERN 1926) and partly — for the sake of instructiveness — Hue's method (HUE 1907). Details are given in descriptions of the individual bones. The dimensions shown in the appended tables are given throughout in mm. Both dated and undated specimens were measured. Among older fossil bones especially those from Woldřich's and Mašek's collections, I dealt in greater detail with the material labelled as Woldřich's „species" *Vulpes meridionalis, Vulpes moravica, Vulpes minor, Vulpes vulgaris fossilis* and *Leucocyon lagopus fossilis*. The work was very time-consuming, but was not in vain — as will be shown in the conclusion.

In addition to the metrics, I devoted attention to the morphological distinction of bones of the individual species or bones of other species and genera readily mistakable for bones of foxes (especially those of the genus *Lepus*). For details see the description of the individual bones.

A great problem was attaining uniform stratigraphic dating. The earlier collections were dated throughout as „Pleistocene" only, without any further data, the later collections (from the thirties to fifties) were dated according to Soergel's stratigraphy. Only R. Musil's latest collections were dated in accordance with current stratigraphic usage. For the sake of simplificacion, I use Soergel's symbols which, however, should be understood in a broader sense. „W_1" indicates the whole Early Würm up to „$W_{1/2}$". „$W_{1/2}$" is a warm interval, earlier designated as „Göttweig interstadial" and in the latest papers on stratigraphy as „Pod hradem" interstadial (MUSIL and VALOCH, 1966) or „Hengelo" (HAMMEN et al., 1967). „W_2" indicates the Middle (Main) Würm in the concept of K. VALOCH (1968) irrespective of its internal division (the correlation of cave sediments is therefore fairly difficult). „$W_{2/3}$" denotes the „Stillfried interstadial" („Stillfried B interstadial") earlier designated as „Paudorf interstadial"; „W_3" is the interval from the Stillfried interstadial to the close of the Würm.

REVIEW OF LOCALITIES

The localities of the Bohemian karst (see Fig. 1) did not yield much material suitable for study. The available fossils derive mostly from old collections without stratigraphic data. I was obliged to set aside the material containing evidently mixed finds of different geological ages, such as the large collection from the Kalvarie cave near Řeporyje, as I had not enough time at my disposal to reconstruct the locality and revise the material. Furthermore I could neither elaborate the foxes from Liebus's collection from Dobrkovice near Český Krumlov nor those from Želízko's collection from the Volyně localities (specimens deposited in Volyně), as both these collections are practically inaccessible. I hope to be able to elaborate these materials in the future although I do not suppose that they could substantially influence the results already obtained. For each locality is presented the name of the town or village, to whose cadastre the locality belongs.

The T u r s k á M a š t a l cave (near Tetín) was for the greater part destroyed by a quarry at the close of the past century. Today, a small remnant only is preserved, designated as „Poslední síň". In 1890, before quarrying, the cave was investigated by J. Kafka and L. Píč. J. KAFKA (1892, 1893, 1900) has published a monograph dealing with the profile of the cave, reported according to the possibility of that time, and containing a list of fauna. The fauna of the cave was elaborated in greater detail by J. N. WOLDŘICH (1893). According to J. Kafka and J. N. Woldřich the list of fauna is as follows: *Panthera pardus* (determined by J. Kafka as *„Felis lynx"*), *Felis catus* (or possibly *Felis silvestris* — note by J. Beneš), *Crocuta spelaea, Canis lupus, Ursus spelaeus, Vulpes vulpes, Meles taxus, Coelodonta antiquitatis* (determined by J. Kafka as *„Atelodus*

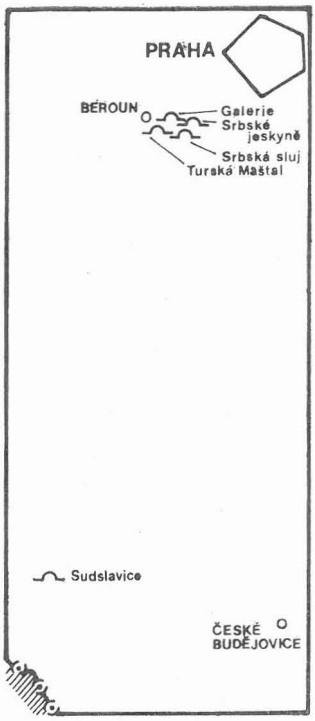


Fig. 1 The caves of Bohemian karst.

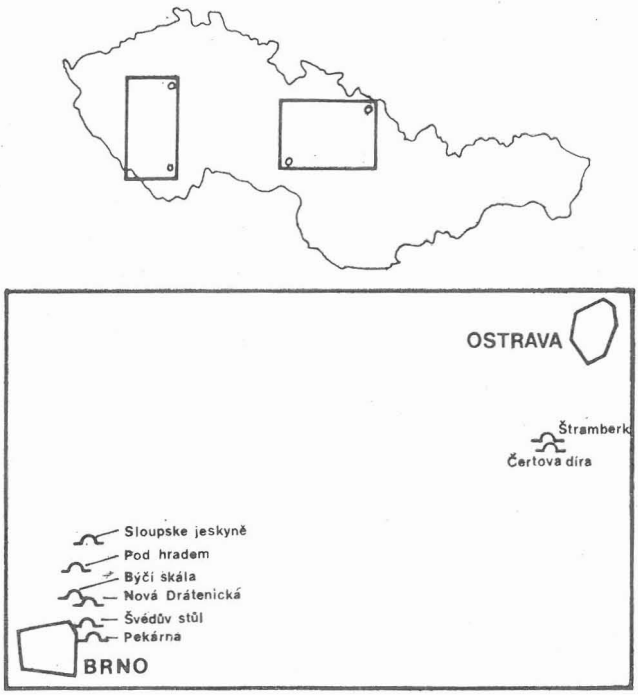


Fig. 2 The caves of Moravian karst.

Merckii"), *Sus scrofa, Mammuthus primigenius, „Bos brachyceros", Ibex sp., Capra sp., Rangifer tarandus, Cervus elaphus* aff. *maral, Capreolus capreolus, „Equus cabalus fossilis* RÜTIMEYER", *„Equus caballus fossilis minor* WOLDŘICH". This list of fauna surprisingly agrees with the faunal association of the Early Würm as it was defined by R. MUSIL (Musil, Valoch, 1966). It permits the subsequent dating of this fauna, i. e. its assignment to the interstadial $W_{1/2}$. Of the material deposited in the National Museum, Prague, I had at my disposal two mandibles of the arctic fox *Alopex lagopus* which was given neither by J. Kafka nor J. N. Woldřich in their lists. This material is designated in the old catalogue as No ČN 106 *„Vulpes vulgaris fossilis"*. There is no reason to assume that it derives from layers stratigraphically higher than $W_{1/2}$, because for instance in the well stratified material from the „Pod hradem" cave (see below), the presence of the arctic fox in the interstadial „$W_{1/2}$" has been proved.

The remnant of the locality Turská Maštal, „Poslední síň", was investigated in the thirties by J. PETRBOK (1932a, b, 1955) who has established the existence of several layers there ranging in age „from the Lartetian through the Magdalénian, the Neolithic and the Bronze Age to the Middle Ages". This author has reported the following mammal fauna: *Crocuta spelaea, Ursus spelaeus, Alopex lagopus, Bos primigenius, „Cervus* cf. *primigenius", Arctomys bobac.* He refers these finds to the Palaeolithic

without any more detailed stratigraphic assignment. They correspond mainly to the fauna of the Main Würm (probably „W_3"). This material is for the greater part deposited in the collections of the National Museum, Prague. However, I did not find the above-mentioned fox among these fossils.

The S r b s k á s l u j cave (near Korno) locality was destroyed by a quarry as early as at the close of the past century. J. N. WOLDŘICH (1890) reported it as the „Saint Ivan Cave (St. Ivan Höhle)". This cave should not be confused with the „Nad Ivankou" cave sometimes designated as „jeskyně sv. Ivana" cave lying in the area of the church and monastery of the village Svatý Jan pod Skalou. The Srbská sluj cave was discovered by chance; it is especially the railway station master J. Neuman who has to be credited for the preservation of the material found there. J. N. WOLDŘICH (1890) gives the following species in his list: *Lynx lynx*, *„Felis magna"*, *Vulpes vulpes*, *Alopex lagopus* (in J. N. WOLDŘICH *„Vulpes (corsac ?)"*), *Canis lupus* (*„Lupus Suessii"*), *Lutra lutra*, *Mustela foina*, *Ursus spelaeus*, *Ursus arctos*, *Talpa europea*, *Sorex vulgaris*, *Arvicola terrestris* (= *A. amphibius*), *Arvicola agrestis*, *Sciurus vulgaris*, *Arctomys bobac*, *Coleodonta antiquitatis*, *„Equus cabalus fossilis* RTM.", *„Equus caballus fossilis minor* WOLDŘ.", *Equus hydruntinus*, *Bos primigenius*, *„Bos brachyceros fossilis"*, *Rupicapra rupicapra*, *Capra ibex*, *Capreolus capreolus*, *Cervus elaphus*, *Rangifer tarandus*. This „association" is for the greather part an Early Würmian fauna with admixed younger fauna (probably an up to the Holocene). No profile or ground plan of the cave has been preserved. I had at my disposal only an ulna of *Vulpes vulpes* and a femur of *Alopex lagopus* (denoted by J. N. Woldřich as *„Vulpes (corsac ?)"*).

The S r b s k é j e s k y n ě caves (near Srbsko) consist of galleries and domes about 350 m in length (SKŘIVÁNEK 1954). The „Poslední dóm" dome ends on the surface by a broad chimney with a fill containing osteological material. From 1938 to 1943 J. Petrbok assembled the material here (his collection was later elaborated by V. MOSTECKÝ 1964, and after him O. FEJFAR 1956).Recently, the author of this paper works at this locality. The following fauna was found: *Panthera spelaea*, *Crocuta spelaea*, *Canis lupus*, *Vulpes vulpes*, *Alopex lagopus*, *Gulo gulo*, *Coelodonta antiquitatis*, *Equus germanicus*, *Bos primigenius* (or more probably *Bison priscus* — note by J. BENEŠ), *Rangifer tarandus*, *Rupicapra rupicapra*, *Lepus timidus*, *Marmota bobac*, *Microtus nivalis*, *Microtus agrestis*, *Arvicola terrestris*, *Sorex sp.* and undetermined birds and reptiles. This fauna is typical of the Middle Würm. A detailed stratigraphy has not yet been determined, as the sediments are disturbed by later landslides. Some of Mostecký's conclusions and my new finds testify most probably to „W_2". For my study some bones of *Vulpes vulpes* were available (my own collections from 1966 and 1969).

The G a l e r i e cave (Srbsko) was excavated in the years 1939—1941 by J. Petrbok. His collections have not yet been elaborated. J. PETRBOK (1955) has assigned the cave sediments to the „Pleistocene and the Neolithic". Of this material I have described one ulna of the *Vulpes vulpes*,

assigned by Petrbok to the Riss-Würm (=Eem), but in my opinion it belongs rather to some of the Würmian interstadials ($W_{1/2}$?).

The Svatoprokopská jeskyně cave (in Prague-Hlubočepy) was quarried in 1887—1888. Under the cave itself, fissures with fossiliferous sediments were discovered. These finds were reported by J. KOŘENSKÝ (1883, 1888). Material was deposited in the National Museum, Prague. But part of the material was deposited in the museum in Ohrada near Hluboká, and was elaborated by J. N. WOLDŘICH (1889). A revision of the material derived from this cave was carried out by E. VLČEK (1952) on the occasion of a revision of the human osteological material. According to E. VLČEK,the cave contained two layers or formations with two faunal groups; the first layer is of Holocene, the second of Pleistocene age. Among the Pleistocene fauna the following species were represented: *Crocuta spelaea, Ursus spelaeus, Mammuthus primigenius, Coleodonta antiquitatis, „Equus caballus fossilis* RTM", *„Equus caballus fossilis minor* WOLDŘ.", *Bos sp., Rangifer tarandus, Capra ibex.* The composition of the fauna is fairly vague bearing witness to the Main Würm. E. VLČEK dates the finds as most probably of „W_2" age. In my study I had at my disposal *Vulpes vulpes* teeth which are not given in any report on the finds, but belong to the Würmian fauna according to their colour and fossilization mode.

The Sudslavice locality (in Sudslavice) no longer belongs to the Bohemian karst; it arose in the crystalline limestones of the Moldaunubicum. The finds occurred in two fissures filled with fossiliferous sediments. In 1879 they were discovered during stone quarrying. The mammalian fauna from Sudslavice was elaborated by J. N. WOLDŘICH (1880a, b, 1881a, b, 1883a, b — also see J. KAFKA 1892). In his final survey J. N. Woldřich gives more than 100 different species; however, the existence of some Woldřich's „species" is debatable. From fissure I, J. N. Woldřich reports: *„Vulpes vulgaris fossilis", Vulpes meridionalis", Vulpes moravica", „Leucocyon lagopus fossilis", „Spermophilus (rufescens)", Dicrostonyx torquatus, Lemnus lemnus, Arvicolidae* (several species), *Alactaga jaculus, Rangifer tarandus, Capra ibex, Rupicapra rupicapra* (in the concept of J. N. Woldřich *„Antilope sp."*), *„Equus caballus fossilis minor* WOLDŘ.", *Equus hydruntinus* (in Woldřich,*„Asinus sp."*) and numerous species of birds and amphibians. The stratigraphic assignment of this „assemblage" is very problematic. Arvicolids, the mole and wild ass etc. would point to the Early Würm., *Allactaga, Lemnus,* ibex and chamois would suggest the Middle Würm (up to „W_3"). It is clear that a mixed material of different ages is involved; differentiation according to stratigraphic position has either not been performed or was not possible. From fissure II, J. N. Woldřich reports the following species: *Talpa europaea, Sorex alpinus, Sorex araneus, „Felis minuta", „Felis fera", „Felis magna", „Felis catus", Panthera spelaea, „Vulpes vulgaris fossilis", Canis* (several species), *Gulo borealis?, Ursus arctos, Sciurus vulgaris, Glis glis, Cleithrionomys glareolus, Apodemus silvaticus, Lepus timidus, Sus scrofa, Bison priscus, Bos sp., Capra sp., (small form), Alces alces, Ovis (cf. aries), Rangifer tarandus, Cervus elaphus, „Equus caballus fossilis* RTM", *„Equus caballus fossiis minor* WOLDŘ.", *Coelodonta antiquitatis,* a number of birds mostly

of forest and aquatic species, and bones of frogs. In this case too, faunas of several time intervals are mixed. The lion, rhinoceros, reindeer and wolverine still belong to the fauna of cold steppe and tundra; most of the rodents, the elk, the red deer and the bear point to a vast area of forest. Stratigraphically, the end of the Middle Würm may be involved here, but certainly the Late Würm and probably also Holocene (*Capra, Ovis, Canis, Gallus domesticus).* The foxes referred to in this paper derive from fissure I. I had at my disposal Woldřich's originals which he used for his papers of 1881 and 1883, and some not reported materials determined by Woldřich as *„Vulpes meridionalis"*, deposited in the National Museum, Prague, inventory number 12 204.

From the Moravian karst localities (see Fig. 2) a great quantity of material was available for my study. These fossils are deposited mainly in the collections of the Moravian Museum, Brno. The material derives partly from old collections devoid of stratigraphic data, partly from recent collections using the modern stratigraphic classification.

The P o d h r a d e m cave (near Těchov) is known from earlier excavations undertaken by J. KNIES (1901) and R. TRAMPLER (1897). From 1956 to 1958, K. Valoch and R. Musil made excavations showing a profile about thirty metres long where layers of „$W_{1/2}$" to „W_3" are observable. R. MUSIL (1965) distinguishes four faunal associations, of which Fauna IV is of little interest. Only cave bears are represented, finds are scanty and their preservation is poor. Stratigraphically, this fauna may fall within the close of „W_1". Fauna III belongs to „$W_{1/2}$", comprising the following species: *Lepus sp., Crocuta spelaea, Vulpes vulpes, Canis lupus, Ursus spelaeus, Mammuthus primigenius, Sus scrofa, Rangifer tarandus, Bos* seu *Bison, Rupicapra rupicapra, Capra ibex.* Fauna II embraces a fairly large number of bears and in addition to *Vulpes vulpes, Alopex lagopus* also appears. Certain changes also occur in rodents. The composition of fauna points to a deterioration of the climate at the end of the interstadial. Fauna I is that of extremely cold steppe. *Vulpes vulpes* disappears being replaced by *Alopex lagopus,* the number of cave bears diminishes and, in contrast, the number of reindeer and snow grouse increases. By its stratigraphic position this fauna corresponds to the Main Würm, predominantly „W_3". I had at my disposal a large set of fox bones from the collections of K. Valoch and R. Musil from the years 1956—1958.

The P e k á r n a cave (near Mokrá) locality was also designated, in the earlier literature, as „Kostelík". Excavations of larger extent were made there by M. Kříž in 1884 and 1885. After him, many scientific specialists (K. J. Maška, J. Knies, A. Makowsky, R. Czižek) and amateurs dug in the cave. In 1925 K. Absolon and R. Czižek undertook an extensive investigation there. Recently B. Klíma made excavations in the cave. As far as I know, no revision of the fauna found was made. In their report K. ABSOLON and R. CZIŽEK (1926) give the stratigraphy of the cave, indicating the fossiliferous layers, but as to fauna they declare that it „has not yet been elaborated". For my study, I had at my disposal a large set of fox bones (Coll. Absolon et Czižek 1925—1930) labelled mostly as „layer g to h" (i.e. the Magdalénian); part of the material had no indication of layer. Furthermore, Absolon's collection was available to

me, but it was not dated and the stratigraphic indications were vague; I also could study Kříž's collection, devoid of indication of year and stratigraphy. Some bones were labelled as Woldřich's „species" *Vulpes meridionalis* and *Leucocyon lagopus fossilis.* Klíma's most recent collection (from 1963) bears the designation „loess around a Magdalénian hearth". All this material is deposited in the collection of the Moravian Museum, Brno.

The Nová drátenická jeskyně cave (near Křtiny) was discovered after the Second World War. Conservation work was conducted by B. Klíma and J. Pelíšek; the mammal fauna found was elaborated by Z. Hokr (in Klíma, 1949). Hokr divides the mammal fauna into two groups: the older one, established in the lowermost beds is represented by the cave bear. The younger group from the Magdalénian cultural waste layer comprises the species *Talpa europaea, Canis lupus, Vulpes vulpes, Alopex lagopus, Mustela erminea, Felis* cf. *silvestris, Ursus spelaeus, Coelodonta antiquitatis, Bos* seu *Bison, Equus sp., Cervus elaphus* (the index species, most numerous), *Capra ibex, Lepus sp., Arvicola terrestris* and *Discrostonyx torquatus.* According to the remains of the reindeer, ibex, the arctic fox and the arctic lemming, Z. Hokr assigned the fauna found into „W_3". The presence of forest species (mole, red deer, cat) points to the outset of the Late Würm. A mandible of *Vulpes vulpes,* and a maxilla and two mandibles of *Alopex lagopus* (collected by B. Kíma in 1948) were available for my study.

The Švédův stůl cave (near Ochoz) became known by the find of the „Ochoz mandible" made in 1905. It was for the first time systematically investigated by M. Kříž in the years 1886 and 1887. It was also M. KŘÍŽ (1903) who presented the first list of fauna. In later publications this list was adapted and supplemented (for details see R. Musil, 1961). On the basis of new investigations in 1953-1955 carried out by the Archeological Institute of the Czechoslovak Academy of Sciences, Brno, R. MUSIL (1961) performed a new analysis of the mammal fauna of the cave. This author distinguishes four faunal associations. The „$W_{1/2}$" fauna comprises the species *Lepus sp., Castor fiber, Panthera pardus, Felis silvestris, Crocuta spelaea, Canis lupus, Vulpes vulpes, Alopex lagopus* or *Vulpes corsac, Gulo, gulo, Lutra lutra, Meles meles, Martes martes, Ursus spelaeus, Mammuthus primigenius, Coleodonta antiquitatis, Sus scrofa, Cervus elaphus, Alces alces, Megaloceros sp., Rangifer tarandus, Bos primigenius, Bison priscus, Rupicapra rupicapra, Ovis* seu *Capra sp., Marmota sp., Equus mosbachensis-abeli, Equus germanicus, Equus hydruntinus, Equus* cf. *gmelini.* The „W_2" fauna includes the species *Lepus sp., Crocuta spelaea, Canis lupus, Vulpes vulpes Ursus spelaeus, Coelodonta antiquitatis, Rangifer tarandus, ?Equus mosbachensis-abeli, Equus germanicus, Equus* cf. *gmelini.* The „$W_{2/3}$" fauna is composed of the species *Crocuta spelaea, Ursus spelaeus, Ursus arctos, Coelodonta antiquitatis Rangifer tarandus* and *Equus germanicus.* The „W_3" fauna embraces the species *Crocuta spelaea, Ursus spelaeus, Ursus arctos, Coleodonta antiquitatis, Rangifer tarandus, Equus* cf. *gmelini* and *Equus sp.* In addition, the following are usually reported from earlier collections without stratigraphic assignment: *Lepus timidus, Panthera spelaea, Ovi-*

bos moschatus, Capra ibex and some rodents. Of the fossil bones from the Švédův stůl cave I could study the fox bones from Kříž's collection (1886—1887 without stratigraphy) and Klíma's collection (1935—1955 — „$W_{1/2}$" and „W_2"), all deposited in the Moravian Museum in Brno.

B a l c a r k a cave (near Ostrov). Arctic fox bones from this cave were available mostly from J. Knies's collection, not dated stratigraphically. A similar minor collection from the S l o u p s k é j e s k y n ě cave (near Soup) also was at my disposal. Arctic fox bones from the B ý č í s k á l a cave (near Habrůvka) I had from Kříž's collection (undated), Absoon's collection (1936), Valoch's collection (undated) and Musil's collection, several specimens from each. The material evidently belongs to the main and possibly also the Late Würm. Of the localities already elaborated, the following two — the Šipka cave and the Čertova díra cave lie in northern Moravia on Kotouč Hill near Štramberk.

The Š i p k a cave is known in the literature by the find of a human mandible in 1880. K. J. MAŠKA (1884a, b, 1886) undertook excavations in this cave. This author divides the cave sediments into four groups: I=Magdalénian, II=Gravettian, III+IV=Mousterian. Groups III and IV are probably derived from the underlying beds. The faunal associations from Maška's collection were revised by R. Musil (VALOCH, MUSIL, JELÍNEK 1965). The material designated as „Šipka I" contains the species *Lepus sp., Felis silvestris, Bos* seu *Bison, Rangifer tarandus, Ursus spelaeus, Panthera spelaea* and *Equus germanicus.* This material may be assigned to the outset of „W_2" and up to the close of „W_3". In addition it also includes some subfossil or recent species *(Felis silvestris).* The „Šipka II" material is evidently derived from several layers (some specimens are labelled „Šipka I—II"). The following species have been recorded: *Bos primigenius, Bison priscus, Ursus spelaeus, Rangifier tarandus, Mammuthus primigenius*; to a lesser extent are represented: *Ursus arctos priscus, Equus germanicus, Vulpes vulpes, Alopex lagopus, Meles meles, Gulo gulo, Alces alces, Cervus elaphus, Coelodonta antiquitatis, Panthera spelaea, Panthera pardus, Crocuta spelaea* and *Saiga tatarica.* R. Musil has referred this material to „$W_{2/3}$", „W_2" and possibly also „$W_{1/2}$". The „Šipka III" material belongs predominantly to „$W_{1/2}$", the material from the overlying layer is also present sporadically. The following species occur here: *Cervus elaphus, Bison priscus, Coelodonta antiquitatis, Equus mosbachensis-abeli, Equus hydruntinus, Crocuta spelaea, Ursus spelaeus, Panthera spelaea, Panthera pardus, Canis lupus, Vulpes vulpes* and *Gulo gulo.* In the „Šipka IV" material mostly „$W_{1/2}$" sediments are included. The following species are represented: *Panthera spelaea* (frequently), *Panthera pardus* (very often), *Ursus spelaeus, Canis lupus, Cuon alpinus, Vulpes vulpes, Mammuthus primigenius, Sus scrofa, Cervus elaphus* aff. *maral, Capreolus capreolus, Saiga tatarica, Ovibos moschatus, Rupicapra rupicapra, Bos primigenius, Bison priscus, Coelodonta antiquitatis, Equus mosbachensis-abeli, Equus hydruntinus, Castor fiber* and a solitary jaw of *Dicrostonyx torquatus.* The remains of horses described by J. N. WOLDŘICH (1882) as belonging to *„Equus* aff. *stenonis"* have been determined by R. Musil as milk teeth belonging to *Equus mosbachensis-abeli.*

From Maška's collection I had at my disposal the fox bones from layers II to IV and some specimens without stratigraphic dating.

The Čertova díra cave was investigated by K. J. Maška (in the eighteen-eighties) (MAŠKA 1884a, b, 1886). After him J. N. WOLDŘICH (1886) made excavation at Štramberk. The material obtained has been deposited mostly in the collections of the Moravian Museum, some specimens from Woldřich's collection in the National Museum, Prague. On Woldřich's material the stratigraphic position is not indicated at all, on Maška's material rarely only (designations „Č. d. II" and „Č. d. III"). This material was important for my study, as it was determined by Maška or by Woldřich himself as Woldřich's „species" *Vulpes vulgaris fossilis, Vulpes meridionalis, Vulpes minor* and *Leucocyon lagopus fossilis.* In two cases *„Canis Mikii"* is given.

SYSTEMATIC PART

Order	*Carnivora* BOWDICH, 1821
Family	*Canidae* GRAY, 1821
Subfamily	*Caninae* GILL, 1872
Genus	*Vulpes* OKEN, 1816

1816 *Vulpes* OKEN, Lehrbuch Naturgesch. Zoologie, 3, p. 1033.
1830 *Cynalopex* SMITH, Nat. Libr. Mamm. p. 222.
1931 *Vulpes* OGNEV, Zvery vost. Evr. i sev. Azii 2, p. 266.
1951 *Vulpes* ELLERMAN et MORRISON-SCOTT, Checklist, p. 223.
1956 *Vulpes* NOVIKOV, Chiščnye mlek. fauny SSSR, p. 56.

Diagnosis: G. A. NOVIKOV, 1956: Medium size, body elongated on not very long slender feet. Skull with a narrow facial part, supraorbital area slightly raised above the nasal part of the skull. Snout elongated, narrow, pointed.

Dental formula: $\frac{3.1.4.2}{3.1.4.3} = 42$

Type species: *Vulpes vulpes* (LINNÉ, 1785).

Stratigraphic range: At the present time, many species of *Vulpes* are spread throughout Europe, North Asia, India, China, Africa and North America to New Mexico and California.

It seems that earlier the distribution of *Vulpes* did not considerably differ from that of today, although the geographic distribution of the individual species varied.

Vulpes vulpes (LINNÉ, 1758) — common fox
(figs 3—6 and fig. 21; Tab. I, fig. 1; Tab. II, fig, 1)

1758 *Canis vulpes* LINNAEUS, Syst. nat., ed. 10, 1, p. 40.
1811 *Canis vulpes* PALLAS, Zoogeogr. Rosso-Asiatica, I, p. 45—51.
1816 *Vulpes vulgaris* OKEN, Lehrb. d. Naturgesch., III, 2, p. 1034.
1834 *Vulpes maior* SCHMERLING, Rech. oss. foss. de Liège, p. 39.
1838 *Canis vulpes spelaeus* CUVIER, Ossem. foss., 4 od., p.
1854 *Canis vulpes fossilis* POMMEL, Cat. meth. vertébr. foss., p. 69.
1875 *Vulpes vulgaris* BOURGUIGNAT, Rech. ossem. foss. de Canidae, p. 52.
1878 Vulpes *vulgaris fossilis* WOLDŘICH, Denkschr. Ak. Wiss., 39, p. 46.
1882 *Canis Mikii* VOLDŘICH, Mit. Anthrop. Ges., p. 14—16.

1890 *Vulpes vulpes* MIVART, Monogr. Canidae, p. 92.
1906 *Vulpes spelaeus* MAKOWSKY, Verh. Naturf. Ver. Brünn, 44, p. 39.
1912 *Vulpes vulpes* MILLER, Catal. Mamm. West. Europe, p. 326—330
1941 *Vulpes vulpes* POCOCK, Fauna Brit. India, Mann., II, p. 110.
1951 *Vulpes vulpes* ELLERMAN et MORRISON-SCOTT, Checklist of Palaearct. and Ind. Mamm., p. 223.
1956 *Vulpes vulpes* NOVIKOV, Chiščnye mlekop. fauny SSSR, p. 60.
1975 *Vulpes vulpes* HANÁK et HERÁŇ, Lynx IV, p. 45.

Holotype: Not determined (the species has been described according to the specimen from the environs of Uppsala, Sweden).

Stratum typicum: Holocene (Recent, 18th century).

Locus typicus: Uppsala, Sweden.

Diagnosis of the species (NOVIKOV, 1956): Skull slender, not very high, braincase somewhat raised above the face; length of braincase approximately equalling that of the face. Crista sagittalis weakly developed, crista occipitalis being very marked. Cristae frontales externae extending backward from the processi zygomatici of the frontal bone, describing an acute angle with it and bounding a narrow and short triangular facet (see fig. 3). Canine teeth long; lower canines — in frontal view — reaching behind the upper margin of the alveoles of the upper canines, the ends of upper canines reaching as low as below the lower margin of the jaw (fig. 4).

Diagnosis extended according to further authors: Hypocone of M^1 always developed (J. BENEŠ — see fig. 5). Protocone and hypocone of M^1 connected by a ridge but not fusing. Talon of M^1 massive, its breadth equalling that of the protocone and hypocone (J. N. WOLDŘICH, 1880a, b). The presence of a protoconulus between paracone and protocone reported by J. N. WOLDŘICH (1880a, b) as a diagnostic feature important for the distinction between *Vulpes vulpes* and *Alopex lagopus* is rather debatable. In younger specimens, on the ridge linking paracone with protocone, a sign of a further protoconulus is observable (sometimes may be double); however, on teeth of older specimens this sign of a secondary protoconulus is absent due to abrasion. This can also be observed on the M^1 of arctic fox (*Alopex lagopus*) and therefore the author of this paper does not regard this features as reliable. The lower carnassial (M_1) on the lingual side of the crown, between metaconide and entoconide has yet an additional protoconulus (WOLDŘICH, 1880a, b) — see fig. 6. The protoconide of M_2 compared with the paraconide is somewhat shifted backward, also being more massive, so as to give the tooth a „big-bellied" shape. The talon of M_2 is slightly narrower than the frontal part of the tooth (Hagmann 1899). Between the entoconide and metaconide there lies a crest-shaped ridge disappearing by abrasion (Hagmann 1899; Zittel 1911). The skull of the male differs from that of the female in larger size and the following features: broader nasal region and hard palate, larger canines, longer row of upper teeth; the relative length of the braincase strongly diminishes with the individual's age, the facial part becoming larger, this being connected with the transition to a flesh-eating diet and with the strengthening of the masticatory muscles (OGNEV 1931).

A diagnosis of the postcranial skeleton has not been given; V. GROMOVA (1950) describes the postcranial skeleton of the common fox (*Vulpes vulpes*) together with that of the arctic fox (*Alopex lagopus*) pointing out that a „distinction is possible on the basis of measurement only, the possibility of confusion of extreme values being considerable".

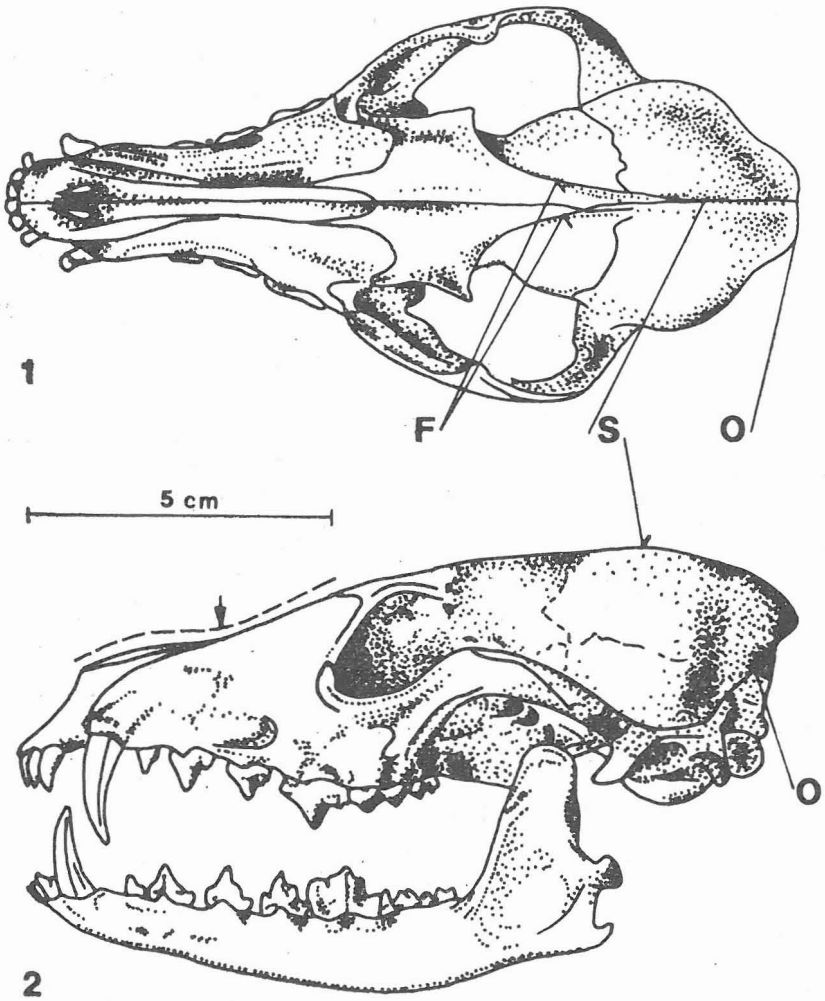


Fig. 3 Skull of the common fox (*Vulpes vulpes*).
(According to G. A. NOVIKOV, 1956 — adapted)

1 — norma verticalis;
2 — norma lateralis;
F — cristae frontales externae;
S — crista sagittalis;
O — crista occipitalis

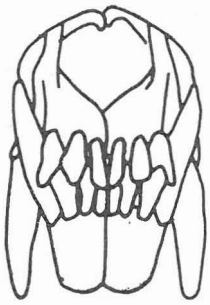


Fig. 4 Canine teeth of the common fox (*Vulpes vulpes*) in anterior view (norma oralis).
(According to G. A. NOVIKOV, 1956)

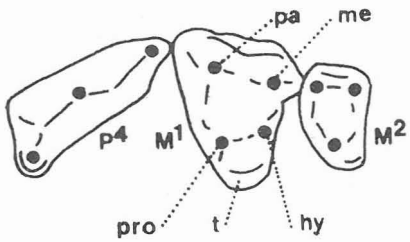


Fig. 5 Scheme of the structure of upper teeth (P^4 — M^2) of the common fox (*Vulpes vulpes*). — (Orig.)
pa = paracone; hy = hypocone;
me = metacone; t = talon;
pro = protocone;

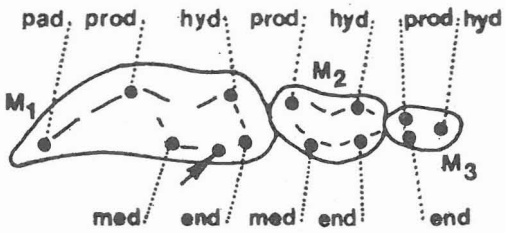


Fig. 6 Scheme of the structure of lower teeth (M_1—M_3) of the common fox (*Vulpes vulpes*). — (Orig.)
pad = paraconide; med = metaconide;
prod = protoconide; end = entoconide;
hyd = hypoconide; the additional cusp on M_1 is indicated by an arrow.

Material studied: Of the bones of the Würmian common fox the following were available: 4 fragments of cranium and 17 fragments of maxillae of various grades of preservation, with or without teeth, 86 mandibles of equal character, 37 isolated upper teeth and 10 isolated lower teeth, mostly canines, 3 fragments of shoulder blades, 33 shoulder bones, entire or fragments, 34 spindle bones, 30 elbow bones, 18 fragments of pelvic bones, 7 thigh bones, 27 shin bones, 8 tals (talus bones) and 18 heel bones.

The Moravian material derives from the earlier collections assembled by M. Kříž, J. N. Woldřich, K. J. Maška and K. Absolon (det. J. N. Woldřich, K. J. Maška and A. Stehlík) and from the recent collections of B. Klíma, K. Valoch and R. Musil (det. mostly R. Musil). The earlier Bohemian material has been assembled mostly by J. Petrbok nad J. Beneš. The bones collected earlier have been determined as belonging to *„Canis vulpes"* or *„Vulpes vulgaris fossilis"*, sometimes also *„Vulpes maior"*, and in some few cases as *„Canis Mikii"* (already K. J. Maška was in doubt about this

determination). In the recent collections, the bones of common foxes have been designated as those of „*Vulpes vulpes*". For more detailed data on the collections see the chapter „Survey of localities".

For comparative study, I used skulls and skeletons of the common foxes from the collections of the Department of Palaeontology of the Moravian Museum, Brno (a material of local origin without detailed indications) and the skull and bones of the common fox from the environs of Banská Bystrica deposited in the collections of the Department of Zoology in the National Museum, Prague (4 complete skulls, 1 shoulder blade, 3 arm bones, 3 spindle bones, 1 elbow bone, 1 complete pelvis, 3 thigh bones, 3 shin bones, 3 tals (talus bones) and 1 heel bone.

Description of the material studied

Skull. In morphological and metrical evaluations the skull is very often given as a decisive indicator of the distinctive diagnostic features. As the material at my disposal was very fragmentary, the only features which could be followed up were breadth of half palate (measured mostly only on one half of the palate). The results obtained are given in greater detail below, in the chapter on the arctic fox.

Upper teeth. In the material studied the upper teeth were represented in relatively few specimens; particularly lacking was material stratigraphically dated with sufficient accuracy.

Upper incisors (dentes incisivi superiores). Upper incisors were mostly absent. According to V. Gromova (GROMOVA, DUROVO, JANOVSKAJA, 1962) the posterior talons of the incisors of the common fox *Vulpes vulpes* are less developed than those of the arctic fox *Alopex lagopus;* I agree with this opinion. The metrical data cannot be evaluated due to the insufficient representation of incisors in the material studied.

Upper canine teeth (dentes canini superiores). The upper canines are longer and more slender than the lower ones. The ratio length of canines: height of jaws is an important diagnostic feature (see the diagnosis of the species according to G. A. NOVIKOV.

In the fossil material the upper canines were mostly isolated so I cannot judge their value as a distinctive feature. A great number of the canines are damaged on the cusps of the crown, either mechanically or due to abrasion, so that it was necessary to reconstruct the height of the crown. A survey of the measurements obtained is given in text-table 1. The measurement did not yield utilizable results. It would be possible to compare the results obtained by measuring the upper canines of the common fox *Vulpes vulpes* with the metrical data of the upper canines of the arctic fox *Alopex lagopus* shown in texttable 12. The upper canines of the common fox are substantially larger than those of the arctic fox.

Upper premolars (dentes premolares superiores). The upper premolars display the morphology usual in all canids. In isolated teeth, the P^2 and P^3 may be confused. The P^3 usually has a larger talon and a sign of an additional protoconulus behind the principal one. In the common fox the morphological difference between P^2 and P^3 is much greater than that in the arctic fox where P^2 and P^3 resemble each other very much. The P^4 of the common fox is relatively more massive than that of

Text-table 1 **Metrical data on the upper canine teeth of the common fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown			Height of crown		
			variation range	number of specimens	average	variation range	number of specimens	average	variation range	number of specimens	average
Vulpes vulpes	Morava	Recent	6.6—7.4	3	7.1	4.2—5.0	3	4.6	12.8—18.5	3	15.6
Vulpes vulpes	B. Bystrica	Recent	7.0	1	7.0	4.7	1	4.7	17.7	1	17.7
Vulpes vulpes	Pekárna	W_3 ?	7.0	1	7.0	4.8	1	4.8	19.5	1	19.5
„Vulpes vulgaris fossilis"	Šipka III	$W_{2/3}$	7.0	1	7.0	5.0	1	5.0	—	—	—
Vulpes vulpes	Švédův stůl	W_2	7.0	1	7.0	4.6	1	4.6	17.2	1	17.2
„Vulpes vulgaris fossilis"	Šipka III	$W_{1/2}$	7.5	1	7.5	5.0	1	5.0	—	—	—
„Vulpes vulgaris fossilis"	Čertova díra	not determined	6.3—7.7	12	6.9	4.2—5.3	12	4.5	16.2—20.0	6	17.9

Text-table 2 **Metrical data on P^4 of the common fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Vulpes vulpes ♂	Morava	Recent	12.3—13.2	2	12.8	5.5—6.0	2	5.8
Vulpes vulpes ♀	Morava	Recent	12.8	1	12.8	5.8	1	5.8
Vulpes vulpes ♂	B. Bystrica	Recent	14.5	1	14.5	5.9	1	5.9
Vulpes vulpes	Pekárna	W_3 ?	14.4	1	14.4	6.0	1	6.0
—	—	$W_{2/3}$	—	—	—	—	—	—
Vulpes vulpes	Sv. Prokop	W_2 ?	14.6	1	14.6	7.7	1	7.7
Vulpes vulpes	Pod hradem	$W_{1/2}$	14.8	1	14.8	6.2	1	6.2
„Vulpes vulgaris fossilis"	Čertova díra	Not determined	12.6—15.8	3	14.3	5.5—7.2	3	7.0
„Canis Mikii"	Čertova díra	Not determined	14.2	1	14.2	5.7	1	5.7

the arctic fox, the protoconal excrescence on the lingual side of the crown being relatively more massive, standing out strikingly from the anterior margin of the tooth (fig. 5). On its margin a conspicuous ridge is developed, which in the arctic fox is lacking throughout or is developed slightly only (J. BENEŠ). In text-table 2 I give the metrical data made on the P^4 of common fox *Vulpes vulpes* the values are listed in stratigraphic order, and also the metrical values of the P^4 in Woldřich's species *„Vulpes vulgaris fossilis"* and *„Canis Mikii"* are given. The relatively small number of measurements does not permit further conclusions to be drawn. But from the above data it follows that the Würmian foxes were larger in size than the recent ones. Woldřich's species *„Vulpes vulgaris fossilis"* falls within the metrical breadth range of the common fox of the Main Würm („W_2" to „W_3") while *„Canis Mikii"* in this respect approaches the recent common foxes.

Upper molars (dentes molares superiores). The upper molars are described from the morphological point of view in the extended diagnosis of the species. Here I can point out only that the first milk molar resembles rather the permanent M^1 of the arctic fox *Alopex lagopus* than that of the common fox *Vulpes vulpes.* The paracone and metacone only are developed on the bucal side, while on the lingual side a narrow triangular talon is located, displaying a sign of protoconulus in the places where in a permanent tooth a hypocone is developed. Unfortunately, it was not possible for me to compare the milk dentition of the common fox with that of the arctic fox, as I found no skull of an arctic fox cub in the collections accessible to me. The complete metrical data obtained from the measurement of M^1 are presented in stratigraphic order supplemented by data on Woldřich's species *„Vulpes vulgaris fossilis"* and *„Canis Mikii"* in text-table 3. However, from the not very large quantity of data obtained no generally valid conclusions can be drawn. But from these data it follows that Woldřich's species do not deviate from the variability range of *Vulpes vulpes.*

Lower teeth. The lower teeth yielded substantially more data for elaboration than did the upper ones.

Lower incisors (dentes incisivi inferiores). The lower incisors as well as the upper ones were absent in the material studied.

Lower canine teeth (dentes canini inferiores). Compared with the upper canine teeth, the lower canines are bent not only anterio-posteriorly but also on the bucal side. The base of the crown is relatively longer than that of the crown of the upper canines. In older specimens it extends into a kind of talon (J. BENEŠ). The relative length of the canine teeth in relation to that of the jaws is regarded by G. A. NOVIKOV (1956) as a diagnostic feature of species (see the diagnosis of the species). I could not verify the validity of this feature in fossil material because of the absence of complete skulls and mandibles. Data obtained by measuring fossil and recent speciments are given in text-table 4. It is impossible to draw satisfactory stratigraphic conclusions because of the small number of measurements. But it is interesting to compare Woldřich's species *„Vulpes vulgaris fossilis"* with the other data. Woldřich's species does not deviate from the breadth variation range of *Vul-*

Text-table 3 **Metrical data on M^1 of the common fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Vulpes vulpes ♂	Morava	Recent	8.9—9.0	2	9.0	10.7—13.4	2	12.0
Vulpes vulpes ♀	Morava	Recent	8.9	1	8.9	11.2	1	11.2
Vulpes vulpes ♂	B. Bystrica	Recent	7.8	1	7.8	11.5	1	11.5
Vulpes vulpes	Pekárna	W_3 ?	8.6	1	8.6	11.9	1	11.9
—	—	$W_{2/3}$	—	—	—	—	—	—
Vulpes vulpes	Sv. Prokop	W_2 ?	7.8—8.5	2	8.1	11.8—12.3	2	12.0
Vulpes vulpes	Pod hradem	$W_{1/2}$	7.9	1	7.9	11.2	1	11.2
„Vulpes vulgaris fossilis"	Čertova díra	Not determined	7.0—7.8	2	7.4	10.3—11.5	2	10.9
„Canis Mikii"	Čertova díra	Not determined	8.5	1	8.5	11.7	1	11.7

Text-table 4 **Metrical data on the lower canine teeth of the common fox**

Species	Locality	Age	Length of crown			Breadth of crown			Height of crown		
			variation range	number of specimens	average	variation range	number of specimens	average	variation range	number of specimens	average
Vulpes vulpes ♂	Morava	Recent	8.7—9.6	2	9.1	5.0	2	5.0	15.4—15.9	2	15.7
Vulpes vulpes ♀	Morava	Recent	8.0	1	8.0	4.6	1	4.6	14.8	1	14.8
Vulpes vulpes ♂	B. Bystrica	Recent	7.0	1	7.0	4.3	1	4.3	16.2	1	16.2
Vulpes vulpes	Pod hradem	W_3	7.6	1	7.6	4.4	1	4.4	14.0	1	14.0
Vulpes vulpes	Pekárna	W_3 ?	6.9	1	6.9	4.1	1	4.1	19.5	1	19.5
—	—	$W_{2/3}$	—	—	—	—	—	—	—	—	—
Vulpes vulpes	Švédův stůl	W_2	8.3	1	8.3	5.0	1	5.0	—	—	—
Vulpes vulpes	Pod hradem	$W_{1/2}$	7.3—8.6	2	7.9	4.4—4.8	2	4.6	—	—	—
Vulpes vulpes	Šipka III	$W_{1/2}$	7.1	1	7.1	4.9	1	4.9	11.4	1	11.4
„Vulpes vulgaris fossilis"	Čertova díra	Not determined	6.8—8.8	15	7.8	4.9—5.5	15	4.6	13.0—17.8	9	15.1

pes vulpes; it is possible to observe only a shift toward the upper limit of the breadth variations which means that *Vulpes vulpes* is involved, having dimensions approaching rather those of the North European subspecies *Vulpes vulpes vulpes* than the Central European subspecies *Vulpes vulpes crucigera.*

Lower premolars (dentes premolares inferiores). J. N. WOLDŘICH (1880a, b) tried to elaborate premolars from the morphological point of view, endeavouring to find features distinguishing the common fox from the arctic fox. His conclusions are given in detail in this paper in the paragraph dealing with the lower premolars of the arctic fox. The distinctive features given by J. N. Woldřich are based on the configuration of the main and secondary protoconuli; however, Woldřich's criteria are rather doubtful. From my observations I may report that P_2 differs from P_3 and P_4 in not having a secondary protoconulus. Differentiation of the P_2 in the common fox and in the arctic fox is possible in a metrical way only. P_3 and P_4 of the common fox differ very little from each other; in isolated teeth it is rather difficult to decide whether a P_3 or P_4 is involved. For the differentiation between the last premolar of the common fox and that of the arctic fox, J. N. WOLDŘICH (1880a, b) sees a diagnostic feature in the fact that „both secondary protoconuli (i.e. the protoconulus and the talonide — note by J. BENEŠ) are inexpressive in *Vulpes vulpes,* being more marked in *Alopex lagopus.* To this I remark that P_4 of the arctic fox is relatively shorter than that of the common fox. Accordingly, the prtotoconuli of the arctic fox are so to speak „pressed against each other" so that they stand out more strikingly than the relative long P^4 of the common fox. In the jaw of common fox the premolars are aligned relatively loosely, with small interstices, the anterio-posterior axis of the tooth crown being parallel to the axis of the jaw — this is the difference from the arctic foxes in which premolars are more pressed against each other, the axis of the tooth crown not coinciding with that of the jaw (coulisse arrangement of teeth) (J. BENEŠ). Dimensions of P^4 are given in stratigraphic order in text-table 5. This table is supplemented by an instructive diagram in fig. 7. From the table and the diagram it may be seen that P_4 of the common fox *Vulpes vulpes* of an Early Würmian age (interstadial „$W_{1/2}$") are smaller than those of common foxes from the Main Würmian. The size maximum falls into the interstadial „$W_{2/3}$". Recent common foxes are smaller.

Lower molars (dentes molares inferiores). A description of lower molars from a morphological point of view is given in the extended diagnosis of the species. It should be added that on the first molar of the milk dentition no protoconulus is developed between the metaconide and entoconide so that it approaches the shape of M_1 in the arctic fox. Some selected data obtained by measuring M_1 and their stratigraphic comparison are shown in text-table 6. From the table follows the same as I have said of P_4 (compare with text-table 5!). Only the M_1 of recent foxes are not so strikingly smaller than the P_4 of the same species at the same time span. The metrical relations are shown in fig. 8.

Lower jaws. The same features as ascertained in lower teeth I have also found on mandibles. I measured the height of the lower

Text-table 5 **Metrical data on P_4 of the common fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Vulpes vulpes ♂	Morava	Recent	9.4—10.0	2	9.7	4.1—4.3	2	4.2
Vulpes vulpes ♀	Morava	Recent	8.4	1	8.4	4.3	1	4.3
Vulpes vulpes ♂	B. Bystrica	Recent	9.2	1	9.2	3.4	1	3.4
Vulpes vulpes	Pekárna	W_3 ?	8.2—9.1	2	8.7	3.5—3.6	2	3.6
Vulpes vulpes	Šipka II	$W_{2/3}$	10.2—11.6	3	10.7	3.7—4.8	3	4.3
Vulpes vulpes	Švédův stůl	W_2	10.2	1	10.2	3.5	1	3.5
Vulpes vulpes	N. drátenická	W_2 ?	9.0	1	9.0	3.4	1	3.4
Vulpes vulpes	Pod hradem	$W_{1/2}$	9.1—9.3	3	9.2	3.0—3.8	3	3.5
„Vulpes vulgaris fossilis"	Čertova díra	Not determined	9.0—11.0	17	9.9	3.0—4.6	17	3.7
„Canis Mikii"	Čertova díra	Not determined	9.4—11.0	2	10.2	3.7—4.0	2	3.8

Text-table 6 **Metrical data on M_1 of the common fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Vulpes vulpes ♂	Morava	Recent	13.2—15.0	2	14.1	5.7—6.7	2	6.2
Vulpes vulpes ♀	Morava	Recent	15.2	1	15.2	5.9	1	5.9
Vulpes vulpes ♂	B. Bystrica	Recent	15.9	1	15.9	5.4	1	5.4
Vulpes vulpes	Pekárna	W_3 ?	14.3—16.4	2	15.8	5.5—5.8	2	5.7
Vulpes vulpes	Šipka II	$W_{2/3}$	16.2—17.8	3	16.8	5.6—6.8	3	6.2
Vulpes vulpes	N. drátenická	W_2 ?	17.2	1	17.2	5.0	1	5.0
Vulpes vulpes	Pod hradem	$W_{1/2}$	14.8—15.9	3	15.3	4.2—5.5	3	5.3
„Vulpes vulgaris fossilis"	Čertova díra	Not determined	14.9—16.8	15	15.7	4.3—6.4	15	5.3
„Canis Mikii"	Čertova díra	Not determined	16.0—16.2	2	16.1	5.3—5.9	2	5.6

jaw in front of P_1, between P_3 and P_4, below M_1 and, where it was possible, also behind M_3. It was impossible to measure and investigate the angular part, because the facial angle has been practically unpreserved in any case. The measurement of the height of the mandible has yielded very interesting results. In *Vulpes vulpes* (see fig. 9) measurement confirmed the differences between the foxes of the Early Würm, which are smaller, and those of the Main Würm which are larger in size. Recent foxes occupy the whole field randomly.

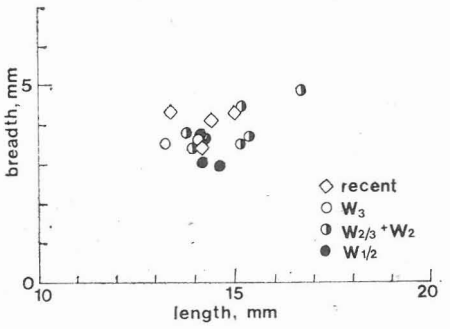


Fig. 7 Length breadth ratio of the crown of P_4 of the comon fox (*Vulpes vulpes*).

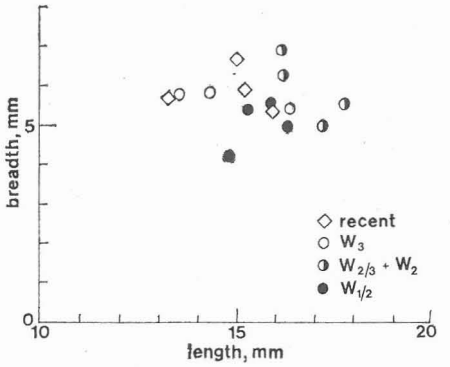


Fig. 8 Length breadth ratio of the crown of M_1 of the common fox (*Vulpes vulpes*).

Postcranial skeleton. The postcranial skeleton was represented in the material investigated by a large number of specimens but these were fragments only of long bones not determined stratigraphically.

Shoulder blade (scapula). Of shoulder blades mostly only basal parts, i. e. the cavitas glenoidalis with part of the column, have been preserved, often being damaged mechanically. Only two fragments were available, one from the Pekárna cave and one from the Srbské jeskyně caves. It was not possible to derive from such a small number of specimens morphological features suitable for determination.

Arm bone (humerus). Of arm bones of the common fox several pieces were represented in the material investigated. They were partly stratigraphically dated, but the specimens were mostly distal heads, for a greater or minor part diaphyses. The metrical data are shown in text-table 7. From the small number of dated specimens it may be concluded that the transverse breadth of the distal head of the humerus of Early Würmian foxes is somewhat less than that of foxes stratigraphically younger. The humeri of the foxes from the Main Würm do not differ very much metrically from those of recent foxes. The metrics of the humeri

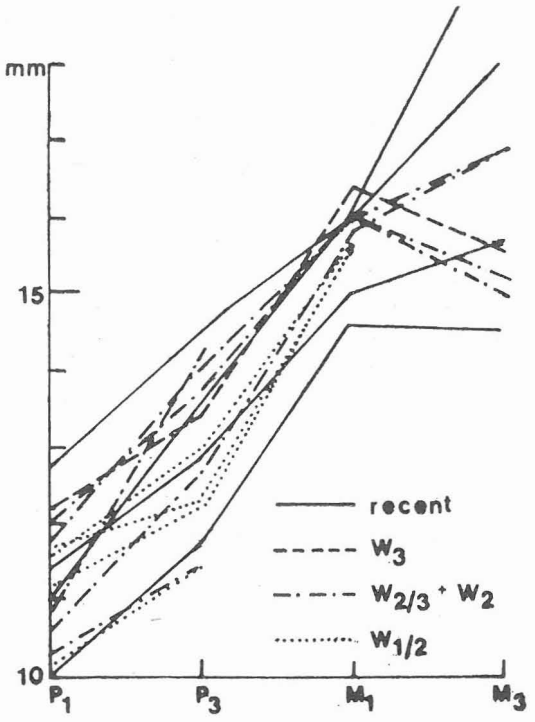


Fig. 9 Height variations of mandible of the common fox (*Vulpes vulpes*).

of the foxes from the Čertova díra cave determined as *Vulpes vulgaris fossilis* correspond, in general, to the measurements of the humeri of common foxes from the Main Würm. The variation range corresponds on the whole to the data given by V. GROMOVA (1950). It is easy to distinguish between the humeri of the common fox *Vulpes vulpes* and the arctic fox *Alopex lagopus* on a metrical basis, as the humerus of the arctic fox is noticeably smaller. The morphological differences are much less prononuced. It may be pointed out that with the common fox the tuberculus maius of the proximal head of the humerus is larger and more massive in relation to the surface of the proximal head than with the arctic fox. It should be noted that all edges of the humerus of the arctic fox are more sharply developed and more marked than those of the common fox. Both the above features, however, can be traced only with difficulty. With regard to the metrical differences, confusion of the humerus of the common fox with that of the arctic fox is hardly probable.

S p i n d l e b o n e (radius). The radius of the common fox was represented in the material studied by a major number of fragments (34 specimens) without any stratigraphic assignment.

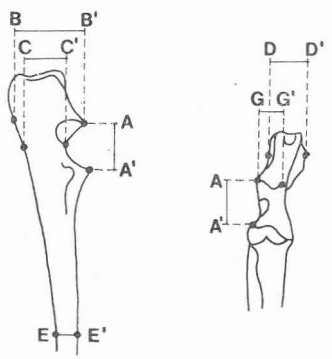
E l b o w b o n e (ulna). The material studied yielded few specimens only of this bone. Metrical data are given in text-table 8. Some morphological comparisons are given in the paragraph on the elbow bone of the arctic fox.

Text-table 7 Metrical data on the arm bone (humerus) of the common fox (in mm)

Locality	Age	Total length	Transverse breadth of diaphyse	Transverse breadth of distal head
Morava ♂	Recent	135.8	8.6	22.0
Morava ♀	Recent	129.6	8.4	20.8
Pod hradem	W_3	—	8.7	19.4
Šipka	$W_{2/3}$	—	8.1	22.4
Srbské jeskyně	W_2	—	8.7	19.4
Pod hradem	$W_{1/2}$	—	—	18.5

Text-table 8 Metrical data of the elbow bone (ulna) of the common fox (in mm)

Locality	Age	A—A'	B—B'	C—C'	D—D'	E—E'	G—G'
Morava ♂	Recent	13.4	17.5	10.2	6.0	6.7	5.8
—	W_3	—	—	—	—	—	—
Šipka	$W_{2/3}$	12.2	16.3	9.0	7.4	6.0	5.8
Srbské jeskyně	W_2	12.0	16.8	9.7	6.9	6.0	5.8
Srbské jeskyně	W_2	11.1	16.2	9.5	6.2	—	5.4
Šipka	$W_{1/2}$	14.2	17.3	9.8	7.3	6.8	6.9



Carpal bones (ossa carpi, carpalia, ossa metacarpalia) and phalanges are omitted in this elaboration as in the material studied they were represented only to a negligible extent. For the same reason I was obliged to omit elaboration of the axial skeleton (vertebrae and sacrum) although this would be a wery attractive subject, this topic not having been mentioned at all so far in the literature.

Pelvic bone. Of pelvic bones fragments only occurred in the material studied. Some measurable data were sometimes yielded only by acetabulum; the dimensions of other parts of the pelvis could be recognized only sporadically. No stratigraphically dated material was available.

Thigh bone (femur). Of thigh bones a small number of specimens was available, again, mostly without stratigraphic assignment. The metrical data fall within the breadth ranges established by V. GROMOVA (1950). In other respects the material is too poor to serve as a basis for more important conclusions.

Shin bone (tibia). The tibia specimens were very numerous in the material studied but complete pieces were rare. Mostly isolated proximal or distal heads were available. The metrical data obtained are given in text-table 9.

Outer postaxial bone of the hind limb (fibula). Some fragments of fibula were present in the material studied; these could not be used as basis for metrical or morphological elaboration.

Sole bones. Of sole bones the tals and the heel bone (calcaneus) yielded metrical data. The results of measurement are shown in text-table 10. They correspond to those given by V. GROMOVA (1950) as well as to the conclusions drawn from the measurements of other parts of the skeleton. The remaining parts of the sole were either lacking in the material studied or were represented by one specimen only.

Text-table 9 Metrical data of the shin bone (tibia) of the common fox (in mm)

Locality	Age	Total length	Anterioposterior breadth of proximal head	Transverse breadth of proximal head	Transverse breadth of diaphyse	Anterioposterior breadth of distal head	Transverse breadth of distal head
Morava ♂	Recent	159.0	25.1	26.4	9.6	11.4	18.8
Morava ♀	Recent	151.0	25.5	23.0	8.9	11.3	16.0
Pekárna	W_3	—	—	—	—	11.0	15.8
Šipka	$W_{2/3}$	—	—	—	8.2	11.0	16.5
Srbské jeskyně	W_2	141.6	25.6	22.9	9.5	10.2	15.0
Pod hradem	$W_{1/2}$	—	—	—	—	11.1	14.1
Šipka	$W_{1/2}$	—	—	—	9.2	11.7	16.4
Šipka	$W_{1/2}$	—	—	—	9.0	11.7	16.7

Text-table 10 Metrical data on the tals and heel bones of common fox (in mm)

Locality	Age	Tal		Heel bone	
		Total length	Transverse breadth	Total length	Transverse breadth
Morava ♂	Recent	20.8	10.2	34.2	13.0
Morava ♀	Recent	20.0	10.0	33.0	12.5
Šipka	$W_{2/3}$	21.4	11.2	—	—
Šipka	$W_{2/3}$	22.4	11.6	—	—
Šipka	$W_{1/2}$	—	—	—	11.0
Šipka	$W_{1/2}$	—	—	—	11.4

Ecology

Biotope. The biotope of the recent common fox *Vulpes vulpes* is considerably heterogeneous. Nevertheless it may be stated that this fox avoids flat, plain, heavily forested or swampy regions, preferring woods alternating with fields and meadows, river valleys, steppes (or cultural steppe) and the surroundings of human settlements. In mountains the common fox occurs even above the forest line (in the Caucasus up to altitudes of 2700 m — NOVIKOV, 1956).

It seems that the biotope of the fossil common fox did not considerably differ from that of the recent representatives of the species. In the Early Würm in a broad sense the common fox lived in areas of mixed forests and warm steppe with minor outcrops or trees and bushes. With progressing cooling of the climate during the Main Würm the common fox became adapted to a cold steppe. However, a specialization to a pronounced cold climate, such as was attained e. g. by the arctic fox *Alopex lagopus,* never developed in the common fox. The extensive quantitative distribution of the common fox, at least in our countries, must always have taken place during a warm interval (J. BENEŠ). In the stratigraphically dated material studied the common fox from the interstadial „$W_{1/2}$" is represented by 18 specimens, that from the beginning of the Main Würm („W_2") by 7 specimens, that from the inersadial „$W_{2/3}$" by 11 specimens and that from the last stadials („W_3") by 7 pieces. These numbers are of course distorted by the quantity of the material from different localities. Nevertheless, I regard these numbers as fairly instructive (compare with the results of the quantitative representation of the arctic fox *Alopex lagopus* in various time-spans of the Würm — J. BENEŠ).

Geographic distribution. At the present time common fox is very widespread. In the north, the common fox occurs even on the coast of the Northern Ice Sea, in minor numbers also on Kolguev Island and, though very rarely, also in the southern part of the Novaya Zemlya Island. In Siberia, the northern boundary of the common fox's distribution practically coincides with the northern forest line. In Western and Central Europe, the common fox *Vulpes vulpes* is a true common animal. In the south its occurrence reaches North Africa, Palestine and Arabia (NOVIKOV, 1956).

During the Late Pleistocene, the common fox was in the whole Europe an animal as common as at the present time. But its occurrence has to be ruled out in glaciated regions perhaps together with the immediate neighbourhood of such areas (tundra and the periglacial area) which results in considerable distribution variations during individual climatic oscillations. For the present it remains difficult to determine the boundaries of the occurrence of the common fox in the Late Pleistocene outside Europe, as various problems of stratigraphic correlation of various areas appear (especially in Asia) and there is the problem of insufficient finds, particularly in North Africa (J. BENEŠ).

Stratigraphic range: Late Pleistocene (?) — Recent.

Final notes

1. The stratigraphic range of the species *Vulpes vulpes* is not yet clear.

No evidence of the existence of this species in the Early Pleistocene has not so far been furnished. From the English localities Red crag and Forest Bed, remains of fox skulls have been described (NEWTON, 1880, 1894; LYDEKKER, 1884) which may have been somewhat larger in size than the recent *Vulpes vulpes*; from the Forest Bed locality even a part of humerus is known. However it cannot be excluded that a younger material is involved which became associated secondarily with the Pleistocene sediments. Most scientists (e. g. HAUPT, 1935; KRETZOI, 1938; THENIUS, 1954) do not regard the presence of *Vulpes vulpes* in the Early Pleistocene as real. This problem cannot yet be definitively solved, as the characteristic localities of the Early Pleistocene in Central Europe, e. g. Mauer, Mosbach and Süssenborn are devoid of foxes. The remains of a fox of Early Pleistocene age, derived from the Stránská skála (Leitener Berg) crag near Brno, described by K. SCHIRMEISEN (1927) as *Vulpes vulpes* belong to *Vulpes angustidens* THENIUS (J. BENEŠ).

The existence of *Vulpes vulpes* in the Middle Pleistocene is doubtful. Only D. JÁNOSSY (1962) has reported *Vulpes* cf. *vulpes* without a detailed description and evaluation, from the locality Tarkö in the Bükk Mountains in Hungary, where the Middle Pleistocene age of the locality (the Mindel-Riss) has been proved by the presence of bear, *Ursus deningeri,* and Middle Pleistocene rodents.

In the Late Pleistocene, *Vulpes vulpes* was represented very abundantly. K. KOWALSKI (1959) reported the age of the finds to have been proved as of Würm glacial. R. MUSIL (1960) has shifted this boundary to the Riss-Würm (Eemian) interglacial.

2. As it follows from the metrical results obtained on the material studied the common foxes of Early Würm (in a broad sense — interstadial „$W_{1/2}$") are smaller in size than those from the Main Würm. This fact strikingly appeared not anly during the measurement of teeth, especially lower premolars and molars but also in the data obtained by measurements of the postcranial skeleton. However, the latter resuls are not so pronounced, as parts of the postcranial skeleton were represented by a much smaller number of specimens in the material studied.

The increasing size of foxes of the Main Würm may be explained partly by the general trend of the development directed to an increase of size, partly by Bergmann's rule on the increase of bodily dimensions during passing from a warmer to a cooler climate. A certain influence may also be attributed to biological-ecological dependence. The boundary between the Early Würm in a broad sense and the Main Würm (at the close of the interstadial „$W_{1/2}$") also represents an important faunal boundary. Natural conditions and the specific and quantitative representations animals change. The changes in the representation of species and the quantitative representation of smaller mammals and birds must have necessarilly also become manifest in foxes, in their mode of life and acquisition of food; these changes then also affected the trend of their general bodily development. It was and could not be the aim of this paper to ascertain to what extent these factors participated in the build of the foxes' body at the Early Würm (in a broad sense) / Main Würm boun-

dary, as this would require a special investigation of the changes in the composition of small-size vertebrate fauna and of the variations of further natural factors.

3. The representatives of the nominate species *Vulpes vulpes* (LINNÉ, 1785) of the Main Würm are metrically similar rather to the recent North-European subspecies *Vulpes vulpes vulpes* (LINNÉ, 1785) than to the recent Central European subspecies *Vulpes vulpes crucigera* (BECHSTEIN, 1789) which is of smaller size. This may be readily intepreted by the analogy of the natural conditions of present-day Northern Europe and those of Central Europe during the Middle Pleistocene (TOEPFER, 1963). But it may also be assumed that the large Würmian foxes of Central Europe who to a certain extent became adapted to life in a cold steppe, retreated at the close of the Würm, together with other representatives of cool fauna, to Northern Europe where they gave rise to the recent subspecies *Vulpes vulpes vulpes* (LINNÉ) (J. BENEŠ). The recent subspecies *Vulpes vulpes crucigera* probably appeared in Central Europe as late as in the Holocene (having migrated from Southern Europe — note by J. BENEŠ). According to J. BOESSNECK (1963), neolithic common foxes are smaller and slimmer than those of the Late Pleistocene. This statement also confirms my measurement of Early Holocene common foxes from the Žitného jeskyně cave in the Moravian karst, which are strikingly smaller than the Würmian foxes (the results of this measurement are not included in this paper).

4. Late Pleistocene representatives of *Vulpes vulpes* are usually designated — in earlier collections — as a separate subspecies *Vulpes vulpes fossilis* WOLDŘICH, 1878 or even as separate species *Vulpes spelaeus* MAKOWSKY, 1906 and *„Canis Mikii* WOLDŘICH, 1882". The taxnomic assignment is simplest in *Vulpes spelaeus* MAKOWSKY which is an evident synonym of the fossil representatives of *Vulpes vulpes* (LINNÉ, 1758).

However the assignment is a more complicated problem in Woldřich's „species". J. N. WOLDŘICH (1878) considered the trinomic designation *„Vulpes vulgaris fossilis"* to be the name of a species and not of a subspecies. But he himself is aware that „because of insufficient quantity of fossil material this species cannot be determined in detail", and — „for the sake of conformity of nomenclature" he sets in apart (WOLDŘICH ibid.). Several of Woldřich's contemporaries themselves did not acknowledge this Woldřich's „species" A. NEHRING (1880) reports a find of fossil foxes from Sudslavice, using Woldřich's designation, but does not give his opinion as to the justified use of the term „species" (this author saw only part of the Sudslavice material which, however, did not include foxes). F. BAYER (1905) gives Woldřich's „species" as a synonym for *„Vulpes vulpes"*, and so also does V. TEPPNER (1914). It follows from my measurements (see the metrical tables in the text) that Woldřich's „species" *„Vulpes vulgaris fossilis"* does not deviate from the breadth variations range of the species *Vulpes vulpes,* but it may be identified as the common fox of the Main Würm. J. N. Woldřich evidently discovered metrical differences, but did not know their stratigraphic dependence and, at his time, could not know them. He therefore overestimated the

recognized differences, using them as the basis for his determination of a new species.

The case of the „species" „*Canis Mikii* WOLDŘICH, 1882" is still more complicated. J. N. Woldřich has identified this „species" on the material from the Čertova díra cave as a species (or rather subspecies) of dog „*Canis familiaris Mikii,* pointing out that the „designation *»familiaris«* in diluvial dogs is ungrounded while in the domesticated prehistoric dog it is justified" (WOLDŘICH, 1882b). This new „species" of his is regarded by him as an ancestor of *Canis palustris* RÜTIMEYER. The donator of the specific name was Woldřich's friend, entomologist Prof. J. Mik, so that the name of species should be in the present-day transcription „*Canis miki*". J. N. Woldřich has determined the new species on the basis of a fragment of the uper jaw with P^4, M^1 and M^2 (in the material studied this fragment was designated by number 470/8). The jaw belongs to an old individual; the crowns were abraded by mastication almost to their roots, so that the structure of the crown and the distribution of cusps is discernible with difficulty only. Together with this maxilla, J. N. Woldřich also reports a fragment of the left lower jaw with M_1 and M_2 (No 470/6) as a type material, and he himself admits that the dimensions of this jaw „approach the size of a very old fox *Vulpes vulgaris* GRAY" (WOLDŘICH 1882b). Already J. Maška who to a certain extent acknowledged this Woldřich „species", left with Woldřich's type material a label with the inscription: „Woldřich's famous Canis Mikii, but in my opinion a large *fox* only (underlined by K. J. Maška himself) Vulpes vulgaris — 5. 6. 1887 Maška". On the basis of my measurement and study of the morphology of Woldřich's type material I drew the same conclusion as K. J. Maška did; I regard Woldřich's „species" as a more robust individual, probably a male of the common fox of the Main Würm. The name *„Canis Mikii"* itself should be regarded as an invalid synonym of *Vulpes vulpes* (LINNÉ, 1758).

Genus *Alopex* KAUP 1829

1829 *Alopex* KAUP, Skizz. Entwicklungsgesch. i. nat. Syst. europ. Thierwelt, I. p. 38.
1869 *Leucocyon* GRAY, Proc. Zool. Soc. London, p. 521.
1912 *Alopex* MILLER, Cat. Mammals of west. Europe, p. 352.
1931 *Alopex* OGNEV, Zveri vost. Evropy i sev. Azii, II, p. 239.
1956 *Alopex* NOVIKOV, Chiščnye mlek. fauny, p. 73.

Diagnosis (G. A. NOVIKOV, 1956): Stouter than *Vulpes,* legs shorter, muzzle shorter and blunter. Skull strikingly less constricted behind the orbits. Other features congruent with those of the type species.

Dental formula: $\frac{3.1.4.2}{3.1.4.3} = 42$

Type species: *Alopex lagopus* (LINNÉ, 1758)

Stratigraphic range: Late Pleistocene to Recent

Geographic distribution: The recent representatives of the genus live in northernmost Europe, North Asia, Canada and Greenland. The geographic distribution of the fossil representatives was considerably wider; it will be dealt with in greater detail in the description of the species *Alopex lagopus.*

Alopex lagopus (LINNÉ, 1858) — arctic fox

(figs. 10—13 and 20—22; pl. I, fig. 2; pl. II, fig. 2)

1758 *Canis lagopus* LINNAEUS, Syst. nat., ed. X, p. 4.
1811 *Canis lagopus* PALLAS, Zoograph. Rosso-Asiat., I, p. 51—57.
1816 *Vulpes arctica* OKEN, Lehrb. d. Naturgesch., III, 2, P. 1033.
1834 *Vulpes minor* SCHMERLING, Rech. ossem. de Liège, T. VII. f. 7; T VIII, f. 11.
1868 *Leucocyon lagopus* GRAY, Proc. Zoolog. Soc., London, p. 521.
1875 *Vulpes minor* BOURGUIGNAT, Rech. sur les ossem. de Canidae.
1878 *Vulpes minor* WOLDŘICH, Denkschr.Ak. Wiss., 39, Bd, p. 144.
1878 *Vulpes meridionalis* WOLDŘICH (nec NORDMANN, 1858), Denkschr. Ak. Wiss., 39 Bd., p. 143.
1878 *Leucocyon lagopus fossilis* WOLDŘICH, Denksch. Ak. Wiss., 39 Bd., p. 144.
1912 *Alopex lagopus* MILLER, Cat. Mamm. of west. Eur., p. 319—324.
1951 *Alopex lagopus* ELLERMAN et MORRISON-SCOTT, Checklist of Palaearctic and Indian Mamm., p. 222—223.
1956 *Alopex lagopus* NOVIKOV, Chiščnye mlek. fauny, p. 74.
1975 *Alopex lagopus* HANÁK et HERÁŇ, Lynx IV, p. 45.

Holotype: Not determined. The species has been described according to the species from Lapland.
Stratum typicum: Holocene (Recent, 18th century)
Locus typicus: Not determined.

Diagnosis of species (NOVIKOV 1956): Medium size, body less elongated and lower than that of *Vulpes vulpes*. Skull massive, less elongated and less flat than in *Vulpes vulpes*. Braincase distinctly projects above the facial part, being usually longer than the face. Crista sagittalis and crista occipitalis are weakly developed. Outer cristae frontales externae extend from processi zygomatici of frontal bones at an acute angle, bounding a long and narrow triangular platform (see fig. 10). Canine teeth relatively slender and short; jaw being closed, the ends of lower canines insensibly overlap the margin of alveoles of upper canines, and the ends of upper canines are far from reach the lower margin of the lower jaw (fig. 11).

Extended diagnosis (according to further authors): Hypocone of M^1 slender, often lacking throughout (J. BENEŠ). Talon of M^1 substantially shorter and more slender than that of *Vulpes vulpes* (J. N. WOLDŘICH 1880a, b). Tooth crown strongly narrowing at an acute angle on lingual side — see fig.12. M^2 similar in structure to M^1, hypocone practically always reduced (J. BENEŠ). Secondary cusp on lingual side of M_1 between metaconide and entoconide (fig. 13) occurs very rarely only Woldřich, 1880a, b — adapted by J. BENEŠ). The outer and inner cusps of M_2 are arranged in one row, the crown is longitudinal in its ground plan, being more slender than in *Vulpes vulpes* (HAGMANN 1889 — adapted by J. BENEŠ). Postcranial skeleton distinguishable metrically only from postcranial skeleton of the common fox (*Vulpes vulpes*) only on the basis of measuring (GROMOVA, 1950).

Material studied. Of the bones of fossil arctic foxes the following were available: 23 maxillae — mostly fragments of different preservation grades, with or without teeth, 75 mandibles of the same character, 35 isolated upper teeth and 62 isolated lower teeth, mostly canines, 14 fragments of shoulder blades, 49 arm bones, 29 spindle bones, 12 elbow

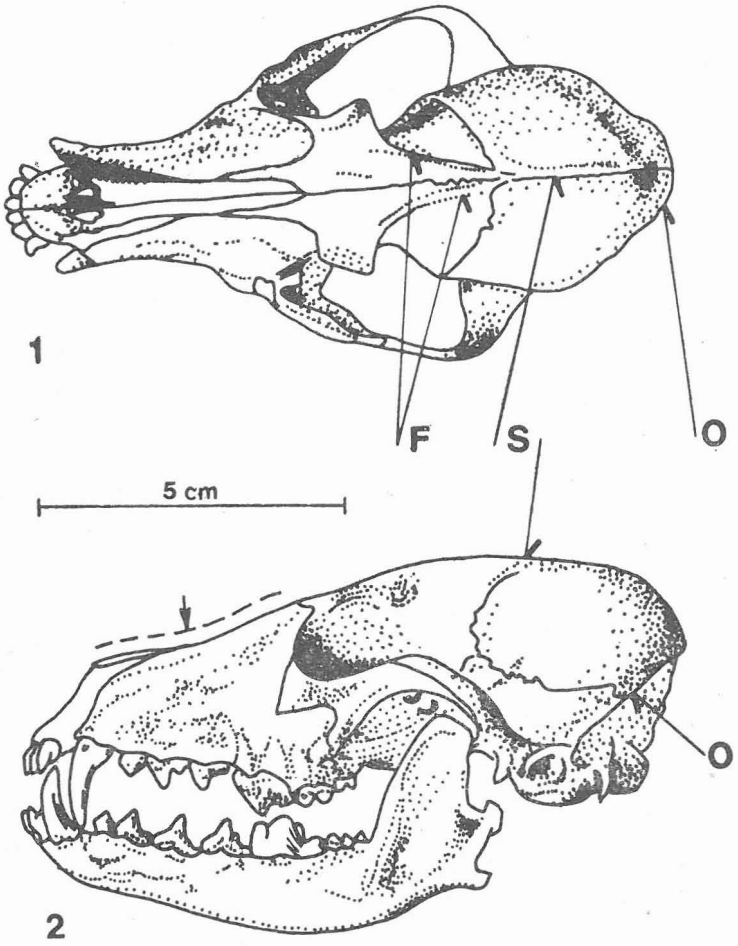


Fig. 10 Skull of the arctic fox (*Alopex lagopus*).
(According to G. A. NOVIKOV, 1956 — adapted)
1 = norma verticalis; F = cristae frontales externae;
2 = norma lateralis; S = crista sagittalis;
O = crista occipitalis.

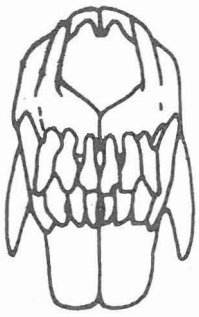


Fig. 11 Canine teeth of the arctic fox (*Alopex lagopus*) in anterior view (norma oralis).
(According to G. A. NOVIKOV, 1956).

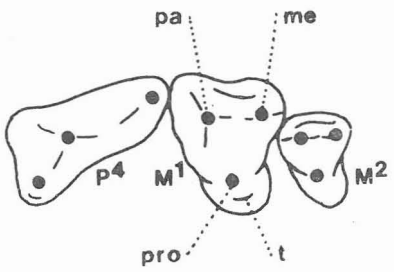


Fig. 12 Scheme of the structure of upper teeth (P^4—M^2) of the arctic fox (*Alopex lagopus*). — (Orig.)
pa = paracone; pro = protocone;
me = metacone; t = talon.

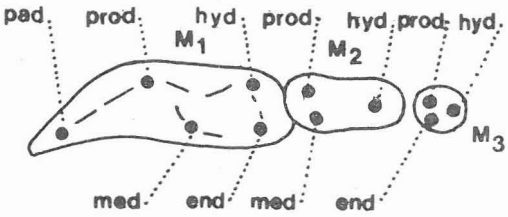


Fig. 13 Scheme of the structure of lower teeth (M_1—M_3) of the arctic fox (*Alopex lagopus*). (Orig)
pad = paraconide;
prod = protoconide;
hyd = hypoconide;
med = metaconide;
end = entoconide.

bones, 16 fragments of pelvis, 10 thigh bones, 109 shin bones, 6 tals and 20 heel bones.

The material derives from earlier collections made by M. Kříž, J. Knies, J. N. Woldřich, K. J. Maška, K. Absolon (det. J. N. Woldřich, K. J. Maška and A. Stehlík) and from the recent ones made by J. Klíma, K. Valoch and R. Musil (det. R. Musil). In the earlier collections arctic foxes were designated „*Canis lagopus*" (Kříž's and Knies's collections) or *Leucocyon lagopus fossilis, Vulpes meridionalis, Vulpes moravica, Vulpes minor* and *Vulpes minor* (Woldřich's and Maška's collections), in the recent collections they were mostly labelled *Alopex lagopus.* For more detailed data on these collections see the chapter „Review of localities". For comparison, I used the skulls and skeletons of arctic foxes from Tromsö, from the comparative collection of the Department of Palaentology of the Moravian Museum, Brno (3 complete skulls, 1 shoulder blade, 3 arm bones, 3 spindle bones, 1 elbow bone, 1 complete pelvis, 3 thigh bones, 3 shin bones, 1 tals (talus bone) and 1 heel bone).

Description of the material studied

Skull. The skull is a frequent object of osteological investigation and measurement. Unfortunately, among all specimens only one almost complete skull of arctic fox was available. In other cases the remains were fragments only, of various degrees of preservation. The sole part of the skull suitable for study is the breadth of hard plate between P^4 and M^1. According to J. N. Woldřich, the breadth of the palate represents a distinctive feature for *Vulpes meridionalis* (sensu Woldřich nec Nordmann — note by J. BENEŠ); in the latter species it exceeds the corresponding dimension in *Vulpes vulpes* (Woldřich 1878). I measured the

breadth of palate of eight arctic *Alopex lagopus,* Woldřich's originals *Leucocyon lagopus fossilis, Vulpes moravica* and *Vulpes meridionalis* from Sudslavice and — for comparison — the palate breadth of eight common foxes *Vulpes vulpes* and one *Alopex corsac.* The results are given in text-table 11. (The vaules indicated by a cross were obtained by measuring only one half the palate.) From these results it follows that the palate breadth of Woldřich's species *„Vulpes moravica"* moderately exceeds that of the recent and fossil arctic foxes *Alopex lagopus* but does not attain the breadth of the palate in recent and fossil common foxes *Vulpes vulpes,* although — according to J. N. Woldřich — it should exceed the palate breadth of common fox. As the maxilla is broken immediately behind M^2, the fragment optically suggests a massive character and considerable breadth; this may have led J. N. Woldřich to his diagnosis of this species.

U p p e r t e e t h. A smal number only of stratigraphically dated upper teeth were available.

Text-table 11
Comparison between palate breadths of various species of fossil and recent foxes

Species	Locality	Age	Breadth of palate in mm
Vulpes vulpes ♂	Morava	Recent	38.0
Vulpes vulpes ♀	Morava	Recent	38.0
Vulpes vulpes ♂	B. Bystrica	Recent	35.1
Vulpes vulpes	Pekárna	W_3	35.8
Vulpes vulpes	Pod hradem	$W_{1/2}$	36.0 *
Vulpes vulpes	Pekárna	Not determined	28.2 *
„Vulpes vulgaris fossilis"	Čertova díra	Not determined	28.0 *
Alopex lagopus	Tromsö	Recent	32.0
Alopex lagopus	N. drátenická	W_2	25.8 *
Alopex lagopus	Sloupské jeskyně	Not determined	32.4 *
Alopex lagopus	Sloupské jeskyně	Not determined	25.8 *
Alopex lagopus	Pekárna	Not determined	30.0 *
„Leucocyon lagopus fossilis"	Sudslavice	Not determined	32.5
„Vulpes moravica"	Sudslavice	Not determined	32.8
„Vulpes meridionalis"	Sudslavice	Not determined	32.5
Alopex corsac	Not given	Recent	29.5

* Measured on one half of the palate

Upper incisors (dentes incisivi superiores). The upper incisors were mostly lacking. According to V. GROMOVA (GROMOVA, DUBROVO, JANOVSKAJA, 1962) the posterior talons of the incisors of the arctic fox are more massive than those of the common fox. I agree with this statement. The metrical data cannot be evaluated because of the small number of specimens investigated.

Upper canine teeth (dentes canini superiores). The upper canines differ morphologically from the lower ones by a bend in an anterio-posterior direction, being more slender than the lower canines. The height of the upper canines in relation to that of the jaws is usually given as a diagnostic and distinctive feature (see the diagnosis of *Alopex lagopus* and *Vulpes vulpes*). In the fossil material upper canines occurred mostly as isolated pieces, so that their value as a diagnostic feature strongly diminished. This disadvantage is further increased by the fact that a number of canines have the cusp of the crown either mechanically damaged, or, in older specimens, strongly abraded, so that the real height of the crown sometimes has to be reconstructed, naturally without expecting accuracy. The results of measurements are given in text-table 12.

Upper premolars (dentes praemolares superiores). The morphological structure of the upper premolars of this species do not deviate from the normal shape range of the teeth of canids. In isolated teeth, P^2 and P^3 may be confused. P^3 usually has a longer talon with a sign of an additional cusp which may be absent or disappear due to strong abrasion. P^4 is narrower and sharper than that of *Vulpes vulpes,* the protocone excrescence on the lingual side of the crown is slimmer not projecting so strongly from the anterior margin of the tooth than in *Vulpes vulpes.* The metrical data obtained on P^4 are summarized in text-table 13. I give a survey of the measurements of the dated material and of Woldřich's species *„Leucocyon lagopus fossilis“*, *„Vulpes moravica“* and *„Vulpes meridionalis“*. The small number of stratigraphically dated specimens renders difficult the establishment of metrical differences in finds of different geological ages. But the table shows that Woldřich's species do not deviate markedly from the variation range of *Alopex lagopus.*

Upper molars (dentes molares superiores). The morphology of upper molars has been given in the extended diagnosis of the species. A survey of the geologically dated material and the emasurements of Woldřich's „species“ are shown in text-table 14. Neither premolars nor molars give an instructive conclusion.

Lower teeth. In the material studied, lower teeth were more numerous than upper teeth.

Lower incisors (dentes incisivi inferiores). Like the upper incisors, the lower ones were mostly absent, so that they could not be evaluated metrically. From a morphological point of view, both lower and upper incisors equally can be evaluated.

Lower canine teeth (dentes canini inferiores). Morphologically, the lower canines give on the whole a similar picture as the upper ones. Compared with the upper canines, the lower canine teeth are bent not only anterio-posteriorly but also bucally. In younger specimens the

Text-table 12 **Metrical data on the upper canine teeth of the arctic fox**

Species	Locality	Age	Length of crown			Breadth of crown			Height of crown		
			variation range	number of specimens	average	variation range	number of specimens	average	variation range	number of specimens	average
Alopex lagopus	Tromsö	Recent	6.2—7.2	3	6.7	3.8—4.2	3	4.0	11.0—14.3	3	12.2
Alopex lagopus	Pekárna	W^3 ?	5.8—7.0	14	6.5	3.1—4.6	14	3.9	13.2—17.0	13	15.4
Alopex lagopus	Pod hradem	W_3	6.6	1	6.6	4.1	1	4.1	14.5	1	14.5
—	—	$W_{2/3}$	—	—	—	—	—	—	—	—	—
—	—	W_2	—	—	—	—	—	—	—	—	—
Alopex lagopus	Pod hradem	$W_{1/2}$	6.8	1	6.8	4.0	1	4.0	15.0	1	15.0
„Leucocyon lagopus fossilis“	Čertova díra	Not determined	5.9—7.9	8	6.6	3.5—4.7	8	3.9	13.3—15.4	7	14.4
„Leucocyon lagopus fossilis“	Sudslavice	Not determined	6.8	1	6.8	3.9	1	3.9	14.0	1	14.0
„Vulpes moravica“	Sudslavice	Not determined	6.4	1	6.4	3.9	1	3.9	14.8	1	14.8
„Vulpes meridionalis“	Sudslavice	Not determined	6.4	1	6.4	4.0	1	4.0	15.0	1	15.0

Text- table 13 **Metrical data on P^4 of the arctic fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Alopex lagopus	Tromsö	Recent	11.0—12.0	3	11.5	4.6—5.0	3	4.8
Alopex lagopus	Pod hradem	W_3	11.3	1	11.3	6.0	1	6.0
Alopex lagopus	Pekárna	W_3 ?	12.1—13.5	6	12.9	5.5—6.3	6	5.9
—	—	$W_{2/3}$	—	—	—	—	—	—
Alopex lagopus	N. drátenická	W_2	11.3	1	11.3	5.2	1	5.2
—	—	$W_{1/2}$	—	—	—	—	—	—
„Leucocyon lagopus fossilis"	Sudslavice	Not determined	12.3	1	12.3	5.8	1	5.8
„Vulpes moravica"	Sudslavice	Not determined	13.1	1	13.1	5.9	1	5.9
„Vulpes meridionalis"	Sudslavice	Not determined	12.9	1	12.9	5.7	1	5.7

Text-table 14 **Metrical data on M^1 of the arctic fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Alopex lagopus	Tromsö	Recent	7.0—7.5	3	7.3	9.6—10.0	3	9.8
—	—	W_3	—	—	—	—	—	—
—	—	$W_{2/3}$	—	—	—	—	—	—
Alopex lagopus	N. drátenická	W_2	6.5	1	6.5	9.9	1	9.9
—	—	$W_{1/2}$	—	—	—	—	—	—
„Leucocyon lagopus fossilis"	Sudslavice	Not determined	6.2	1	6.2	8.9	1	8.9
„Vulpes moravica"	Sudslavice	Not determined	6.7	1	6.7	9.7	1	9.7
„Vulpes meridionalis"	Sudslavice	Not determined	6.5	1	6.5	9.1	1	9.1

base of the crown is short in the anterio-posterior direction, in the older ones it becomes progressively longer, giving rise to a kind of talon on its posterior part. That teeth of old individuals are really involved, is evidenced by the fact that the canine teeth of a great anterio-posterior length have abraded cusps throughout. The metrical data on the lower canine teeth of arctic foxes obtained on a recent and a fossil material are summarized in text-table 15. It shows a survey of the measurements in stratigraphic order and a review of the metrical values of Woldřich's species. Stratigraphic conclusions could not be drawn, as the number of measurements on the specimens dated in greater detail was relatively too small. Interesting is the comparison of the metrical data on Woldřich's species *„Leucocyon lagopus fossilis"*, *„Vulpes meridionalis"* and *„Vulpes minor"* with those obtained on the other material — it becomes clear that the data obtained on Woldřich's species not only do not deviate from the variation ranges of *Alopex lagopus* but even do not markedly differ from each other.

Lower premolars (dentes praemolares inferiores). Already J. N. Woldřich tried to elaborate their morphology; he tried to discover on them some distinctive features between *Vulpes vulpes* and *Alopex lagopus.* This author indicates as important features

1. the main cusp P_3 which in *Alopex lagopus* stands directly in the centre of the crown; on the crown's anterior margin a further faint cusp is visible;

2. both secondary cusps of the posterior margin of P_4 are very inexpressive in *Vulpes vulpes,* while in *Alopex lagopus* they are more pronounced (cited almost literally according to J. N. WOLDŘICH 1880).

Already G. HAGMANN (1899) regarded Woldřich's distinguishing features as doubtful; I myself can state from my own experience that these features are quite unusable. When premolars have been preserved in the jaw, the shape of P_3 may serve as a fairly reliable distinctive feature, as in *Alopex lagopus* an additional cusp is developed on P_3, so that the shape of P_3 resembles that of P_2, while in the common fox *Vulpes vulpes* a second minor cusp is developed behind the chief cusp, so that its shape approaches that of the 4th premolar. In the arctic fox, P_4 is relatively shorter than that of the common fox, so that both cusps as well as the talonide stand out much more strikingly. In the jaw of arctic fox the premolars relatively tightly follow each other, only with small interstices between them or without gaps at all; often there is a sign of a coulisse arrangement of teeth (the axis of the tooth cown is not parallel with that of the jaw — in contrast to the premolars of the common fox which are aligned relatively loosely, the axis of their crown always being parallel with that of the jaw).

Metrically, the lower teeth of the arctic fox differ from those of the common fox only in individuals of the same geological age; in such a case the differences in size are quite pronounced, but in general the teeth sizes of both species fairly approach each other. In studying the differences in size within *Alopex lagopus,* the difference between arctic foxes of the Early Würm (interstadial „$W_{1/2}$") and of the Main Würm is very distinct (see text-tables 16 and 17). The lower teeth of Early

Text-table 15 **Metrical data on lower canine teeth of the arctic fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown			Height of crown		
			variation range	number of specimens	average	variation range	number of specimens	average	variation range	number of specimens	average
Alopex lagopus	Tromsö	Recent	7.1—8.6	3	7.7	4.0—4.8	3	4.4	11.2—14.4	3	13.1
Alopex lagopus	Pekárna	W_3	6.4—7.4	2	6.6	3.9	2	3.9	8.8—12.5	2	10.7
Alopex lagopus	Pod hradem	W_3	7.3—7.4	2	7.4	4.3—4.4	2	4.4	12.0—13.5	2	12.8
—	—	$W_{2/3}$	—	—	—	—	—	—	—	—	—
—	—	W_2	—	—	—	—	—	—	—	—	—
Alopex lagopus	Pekárna	$W_{1/2}$	6.5—7.1	3	7.0	3.5—4.7	3	4.2	11.5—11.8	2	11.7
Alopex lagopus	Pod hradem	$W_{1/2}$	7.8	1	7.8	4.0	1	4.0	11.5	1	11.5
Alopex lagopus	Turská M.	$W_{1/2}$	7.3	1	7.3	3.9	1	3.9	10.6	1	10.6
„Leucocyon lagopus fossilis"	Čertova díra	Not determined	6.6—7.7	19	7.2	3.8—4.6	19	4.1	12.0—15.3	9	13.6
„Leucocyon lagopus fossilis"	Sudslavice	Not determined	7.5	1	7.5	4.4	1	4.4	13.0	1	13.0
„Vulpes minor"	Sudslavice	Not determined	6.5—8.7	8	7.1	3.9—4.6	8	4.1	14.0—19.9	8	15.8
„Vulpes meridionalis"	Sudslavice	Not determined	5.9—8.0	9	7.2	2.9—4.9	9	4.1	9.7—15.0	7	12.4

Text-table 16 **Metrical data on P_4 of the arctic fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Alopex lagopus	Tromsö	Recent	7.0—8.8	3	8.2	4.1—4.4	3	4.2
Alopex lagopus	Pekárna	W_3	7.6—8.0	11	8.5	2.8—3.6	11	3.2
Alopex lagopus	Pod hradem	W_3	7.9—8.0	2	8.0	3.3—3.5	2	3.4
Alopex lagopus	Šipka II	$W_{2/3}$	9.6	1	9.6	3.9	1	3.9
Alopex lagopus	Pod hradem	W_2	7.9	1	7.9	2.7	1	2.7
Alopex lagopus	N. drátenická	W_2	7.8	1	7.8	2.7	1	2.7
Alopex lagopus	Pekárna	$W_{1/2}$	7.3—8.8	4	8.0	3.0—3.4	4	3.3
Alopex lagopus	Pod hradem	$W_{1/2}$	7.8—8.4	4	8.0	2.7—2.8	4	2.8
Alopex lagopus	Švédův stůl	$W_{1/2}$	8.5	1	8.5	3.7	1	3.7
Alopex lagopus	Turská Maštal	$W_{1/2}$	7.4—7.8	2	7.6	2.9—3.0	2	3.0
„Leucocyon lagopus fossilis“	Čertova díra	Not determined	7.0—9.1	9	8.4	2.5—3.2	9	2.9
„Leucocyon lagopus fossilis“	Pekárna	Not determined	7.7—8.7	3	8.3	2.3—3.2	3	2.8
„Leucocyon lagopus fossilis“	Sudslavice	Not determined	8.6—9.3	2	8.9	2.8—3.8	2	3.3
„Vulpes meridionalis“	Čertova díra	Not determined	7.8—9.0	8	8.3	2.7—3.6	8	3.2
„Vulpes meridionalis“	Sudslavice	Not determined	8.2	1	8.2	2.7	1	2.7
„Vulpes minor“	Čertova díra	Not determined	8.6—9.6	6	9.0	3.0—4.3	6	3.5

Text-table 17 **Metrical data on M_1 of the arctic fox (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Alopex lagopus	Tromsö	Recent	12.1—13.3	3	12.9	5.2—5.7	3	5.4
Alopex lagopus	Pekárna	W_3	11.4—14.1	12	12.7	3.6—5.4	12	4.4
Alopex lagopus	Pod hradem	W_3	12.3—13.5	2	13.9	4.5	2	4.5
Alopex lagopus	Šipka II	$W_{2/3}$	13.0—14.6	2	13.8	4.3—6.0	2	5.2
Alopex lagopus	Pod hradem	W_2	13.0	1	13.0	4.3	1	4.3
Alopex lagopus	N. drátenická	W_2	12.8	1	12.8	4.2	1	4.2
Alopex lagopus	Pekárna	$W_{1/2}$	12.1—14.3	4	13.4	3.8—4.8	4	4.3
Alopex lagopus	Pod hradem	$W_{1/2}$	12.2—13.0	4	12.6	3.8—3.9	4	3.9
Alopex lagopus	Turská Maštal	$W_{1/2}$	12.7	1	12.4	3.8	1	3.8
„Leucocyon lagopus fossilis“	Čertova díra	Not determined	13.2—14.8	6	14.1	3.9—4.8	6	4.4
„Leucocyon lagopus fossilis“	Pekárna	Not determined	12.5—12.9	2	12.7	3.7	2	3.7
„Leucocyon lagopus fossilis“	Sudslavice	Not determined	12.1	1	12.1	4.1	1	4.1
„Vulpes meridionalis“	Čertova díra	Not determined	11.8—13.0	8	12.6	3.4—4.9	8	4.3
„Vulpes meridionalis“	Sudslavice	Not determined	12.6	1	12.6	3.9	1	3.9
„Vulpes minor“	Čertova díra	Not determined	12.5—15.2	7	13.9	4.0—5.2	7	4.6

Würmian arctic foxes are clearly smaller although the calculated mean values somewhat distort the results (the number of specimens from which these have been calculated varies between 1 to 12 specimens). I regard the graphs shown in figs 14 and 15 as much more instructive and directive.

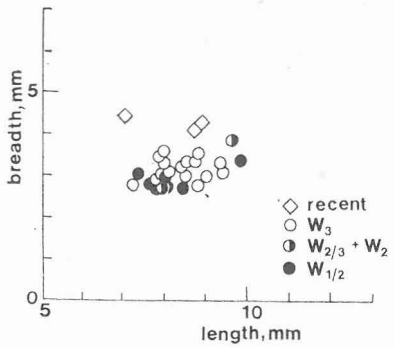


Fig. 14 Length/breadth ratio of the crown of P_4 of the arctic fox (*Alopex lagopus*).

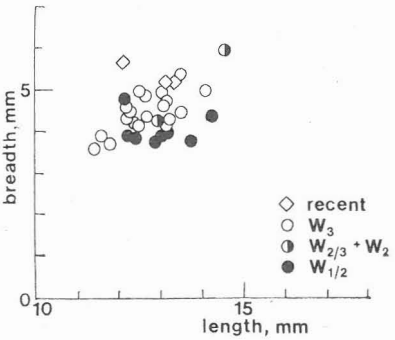


Fig. 15 Length/breadth ratio of the crown of M_1 of the arctic fox (*Alopex lagopus*).

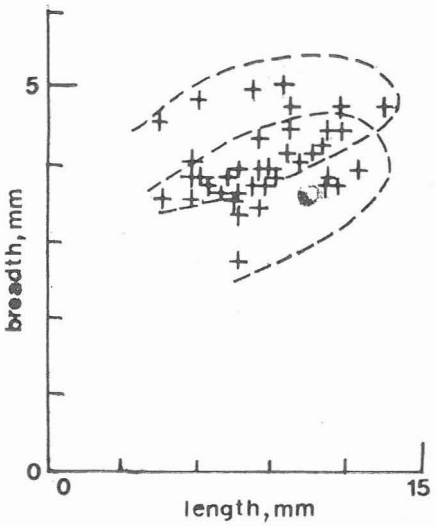


Fig. 16 Length/breadth ratio of the crown of M_1 in stratigraphically undated arctic foxes from the Pekárna Cave.

A division of the „spectrum" of data analogous to that of geologically dated finds may also be observed in the undated finds of foxes without geological dating (fig. 16). Naturally, the result is hypothetical and may be misleading (the influence of sexual dimorphism cannot be ruled out), but it is not excluded that in this material, from the Pekárna cave, devoid of detailed dating, individuals of different geological ages occur (i.e. from the Early and Late Würm).

I tried to compare the results obtained from the dated material with those obtained by measuring Woldřich's species *Leucocyon lagopus fossilis*, *„Vulpes meridionalis"* and *„Vulpes minor"*. In general it may be stated that the metrical values of *Leucocyon lagopus fossilis* correspond to those of the arctic foxes *Alopex lagopus* from the younger Würmian stadials „W_2" and „W_3", while those of *Vulpes meridionalis* correspond to those of arctic foxes *Alopex lagopus* from the interstadial „$W_{1/2}$". These conculsions also clearly follow from text-table 16 and 17, and still more instructively from the comparison of the graph in fig. 17 with that in fig. 15. The stratigraphic position of *Vulpes minor* cannot be so equivocally defined as that of the two above-mentioned species.

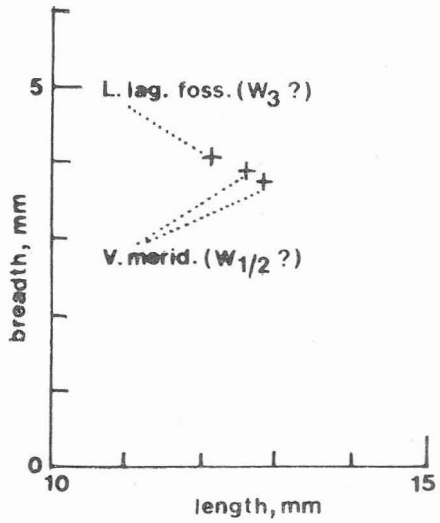


Fig. 17 Length/breadth ratio of the crown of M_1 of the arctic foxes from Sudslavice.

The P_4 and M_1 of recent arctic foxes are larger than the teeth of the same kind in Würmian foxes. This statement has been confirmed by the well-known progressive and permanent increase of the dimensions of arctic foxes, which is usually explained by Bergmann's rule of the increasing bodily size due to transition from a warm to a cold climate.

In investigating mandibles I have obtained results analogous to those found on lower teeth. Analogously as in common foxes, I measured the height of the mandible in front of P_1, between P_3 and P_4 and below M_1. The results obtained were still more marked than those in common foxes as shown on the diagram in fig. 18. Although in the diagram the positions of various individuals of the same geological age are considerably heterogeneous, a certain accumulation of the Early Würmian arctic foxes may be observed in the lower part of the field of the graph, while the foxes of the Main Würm are distributed randomly over the whole field, predominating in its upper part. The recent foxes occupy roughly the centre of the graph. In general, in the Main Würm a strengthening of mandibles can be observed in arctic foxes, which may even exceed

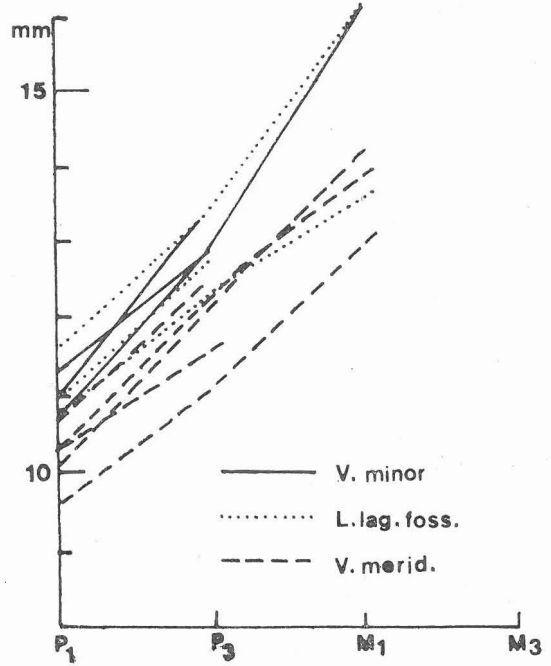


Fig. 19 Height variations of mandibles in stratigraphically undated arctic foxes from the Čertov díra Cave.

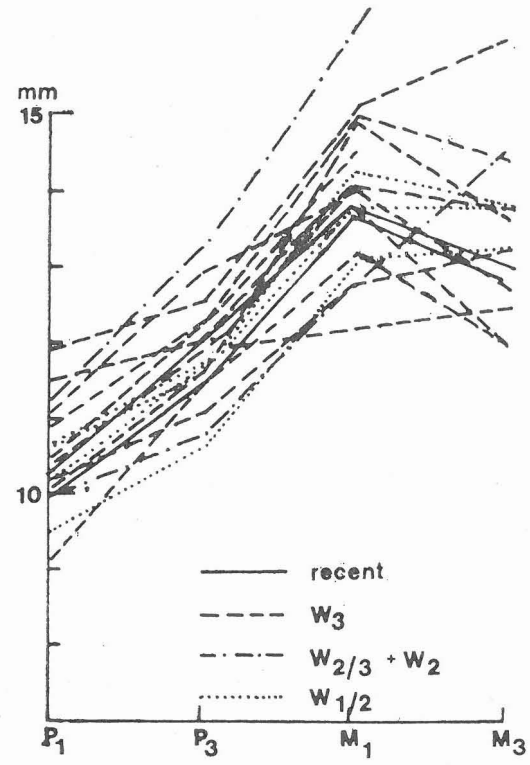


Fig. 18 Height variations of mandibles of the arctic fox (*Alopex lagopus*).

that of recent foxes. This increasing size of mandibles may be explained by the general trend to increasing size of arctic foxes during the Early Würm. But these dimensional differences may also be interpreted ecologically. There are relatively great differences between the fauna of the Early Würm and that of the Main Würm (see above the Introduction). Changes take place in the composition of species of the mammal macro- and microfauna, and changes have also been recognized in the species composition of the gastropod fauna. These changes must necessarily have also appeared in the diet of foxes, and it is possible that the change in the specific composition of the prey caused strengthening of the biting apparatus.

From the Čertova díra cave several mandibles of foxes (from Maška's collection) were available for my investigation. However, they were not stratigraphically dated, and were designated by Woldřich's names of species. When I had plotted the height of the mandibles up to their extreme limits taken from the graph shown in fig. 18, I obtained a very interesting graph presented in fig. 19. The accumulation of the values for *Vulpes meridionalis* in the lower part of the field and those for *Leucocyon lagopus fossilis* in its upper part is striking. Thus here too what I have stated in the conclusion of my description of the lower teeth holds the same. The values of *Vulpes mbinor* agree in this case with the range of data of *Leucocyon lagopus fossilis.*

Postcranial skeleton. In the material studied, the postcranial skeleton was represented by a large number of specimens, but most of the fragments were not stratigraphically assigned.

Shoulder blade (scapula). Of shoulder blades, mostly parts from the nearest vicinity of the cavitas glenoidalis have been preserved, which, in addition, were mechanically damaged. I had at my disposal 8 fragments from the Čertova díra cave, 5 from the Pekárna cave, and 1 from the Šipka cave — all without stratigraphic dating. As with the common fox, it was not possible to read from these fragments characteristic morphological features.

Arm bone (humerus). Of arm bones of arctic foxes 49 specimens were available, of which only two are stratigraphically dated. Summarizing, it may be stated that all dimensions of Würmian arctic foxes are relatively smaller than those of the recent ones (see text-table 18). I do not present graphs for this bone, as a poor result only could be obtained from an undated material. Woldřich's *„Leucocyon lagopus fossilis"* from Sudslavice does not deviate from the dimensions variation range of arctic foxes. The size ranges of both foxes do not coincide and the latter is only shifted to the upper limit of the values, of recent arctic foxes, and thus confirming the conclusions drawn in the study of teeth. The fragment of a humerus from the Výpustek cave, determined as belonging to *Vulpes meridionalis,* approaches by its dimensions the arm bone of a corsac from the Býčí skála cave.

The differentiation between a humerus of the artic fox and that of the common fox is relatively easy on the basis of metrical data, as the

humerus of arctic fox is evidently smaller. The dinstancion of both humeri on a morphological basis has been mentioned in the chapter on the arm bone of the common fox.

Text-table 18
Metrical data on the arm bone (humerus) of the arctic fox (in mm)

Locality	Age	Total length	Anterioposterior breadth of proximal head	Transverse breadth of proximal head	Transverse breadth of diaphyse	Transverse breadth of distal head
Tromsö	Recent	114.6	22.3	16.0	6.6	17.8
Tromsö	Recent	107.4	20.6	14.8	6.6	17.2
Tromsö	Recent	106.0	19.3	13.6	6.6	16.2
Pekárna	W_3	—	—	—	6.6	17.2
Pod hradem	$W_{1/2}$	—	—	—	6.2	16.0
Sudslavice	Würm	110.0	22.3	15.5	7.5	16.4

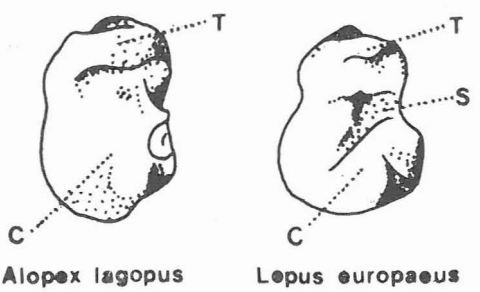


Fig. 20 Comparison between the proximal heads of humerus in the arctic fox and the hare. — (Orig.)
T = tuberculus maius;
C = joint surface of proximal head;
S = groove separating the joint surface from tuberculus maius.

Very frequent and probable confusion is possible in isolated proximal heads of the humeri of the common fox and the hare. Although the distal heads of these bones are morphologically and metricaly so different that no confusion is posible, the proximal heads are metrically nearly equal. For a morphological differentiation a shallow groove in the hare humerus running between tuberculum maius of the proximal head and the surface proper of the joint is a reliable distinguishing feature. Neither in the arctic fox nor in the common fox is this groove developed (see fig. 20). On the material studied I could check the reliability of this feature which helped me to exclude the proximal heads of hare humeri erroneously attributed to arctic fox.

S p i n d l e b o n e (radius). Compared with the spindle bone of the common fox, the radius of the arctic fox is generally smaller. I give the

results of the measurements in text-table 19; they agree with the data given by V. GROMOVA (1950). The material dated stratigraphically in greater detail was scanty, and from the individual data no general conclusions can be drawn.

Text-table 19
Metrical data on the spindle bone (radius) of the arctic fox (in mm)

Locality	Age	Total length	Transverse breadth of proximal head	Anterioposterior breadth of proximal head	Transverse breadth of diaphyse	Transverse breadth of distal head
Tromsö	Recent	108.6	10.7	6.7	7.0	14.3
Tromsö	Recent	101.2	9.9	6.0	6.4	13.4
Tromsö	Recent	98.1	9.7	5.7	6.6	12.7
Pod hradem	W_3	—	9.8	6.0	—	—
Šipka	$W_{2/3}$	—	—	—	6.6	12.0
Pod hradem	$W_{1/2}$	—	10.2	6.9	7.0	—

E l b o w b o n e (ulna). The elbow bone available has yielded very few metrical data; stratigraphic assignment of the material studied was lacking throughout. According to V. GROMOVA (1950) the elbow bone of the arctic fox can be morphologically distinguished from that of the common fox on the basis of the following criteria:

1. The central part of the diaphysis is mostly strongly flattened, so that the largest (i.e. the anterio-posterior — note by J. BENEŠ) diameter rarely attains less than 140 % of the section perpendicular to it i.e. transverse section — note by J. BENEŠ).

2. The posterior part of the processus olecrani is raised only slightly; in the common fox the dorsal points are highly raised, to the same levels as that or the olecranon itself, and between the posterior points and the olecranon there is a saddle-like depression. I do not regard the abovementioned feature as very useful because the processus olecrani is very often mechanically damaged; but I consider the metrical differences to be much more indicative.

The elbow bone of the arctic fox may sometimes be confused with that of the hare, especially if the fossil material is fragmentary. Both these bones may be relatively easily distinguished according to the configuration of the volar surface; the incisura radialis of the arctic fox projects into a distinct process which is missing on the elbow bone of the hare. The volar surface below the incisura radialis is smooth in the artic fox, while in the hare it shows edges (connection with spindle bone — see fig. 21).

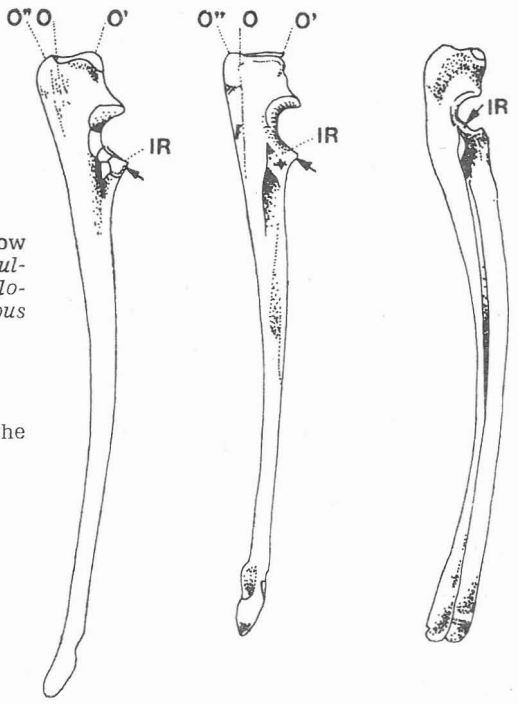


Fig. 21 Comparison between the elbow bones in the common fox (*Vulpes vulpes*), the arctic fox (*Alopex lagopus*) and the hare (*Lepus europaeus*). — (Orig.)
O = processus olecrani;
O' = dorsal points;
O" = olecranon;
IR = incisura radialis of the bone.

Carpal bones (ossa carpi, carpalia), metacarpal bones (ossa metacarpalia) and phalanges. I was obliged to omit all these bones as well as the whole axial skeleton in my elaboration for the same reason as in the case of common fox, because in the material at my disposal, these parts of the skeleton were represented by such an insignificant number of specimens or were absent throughout that it was not possible to draw any conclusions.

Pelvic bones. In the material studied only fragments of pelvic bones were present. Just as in the common fox, in the pelvises mostly only acetabula could be measured. No stratigraphically dated material was available.

Thigh bone (femur). Only some stratigraphically undated fragments of thigh bones of the arctic fox were at my disposal. Compared with V. GROMOVA'S (1950) data, in my measurements a certain difference occurred — on the recent and fossil materials higher values than those given by V. Gromova were obtained. The resulting data are, however, insufficient for any kind of conclusion.

Shin bone (tibia). In the material studied, shin bones were very numerous (109 specimens) but fragmentary; complete specimens were rare. Except for two specimens, this material was devoid of detailed stratigraphic data. The metrical data obtained are given in text-table 20. Isolated proximal heads of shin bone of the arctic fox may often be and are confused with those of the hare; so much more that the sizes of both

Text-table 20
Metrical data on the shin bone (tibia) of the arctic fox (in mm)

Locality	Age	Total length	Anterioposterior breadth of proximal head	Transverse breadth of proximal head	Transverse breadth of diaphyse	Anterioposterior breadth of distal head	Transverse breadth of distal head
Tromsö	Recent	134.5	22.9	21.0	7.0	9.0	14.9
Tromsö	Recent	124.0	21.2	19.8	7.0	8.8	13.4
Tromsö	Recent	122.0	20.0	18.8	7.0	9.3	13.4
Pekárna	W_3	—	—	—	7.8	11.0	14.9
Pekárna	W_3	—	—	—	7.5	10.7	14.6

heads are mostly equal. For discerning them the following characteristics can be given as reliable distinctive features:

1. the ratio of the anterio-posterior breadth to the transverse breadth of the proximal head of the shin bone of the hare is roughly 1 : 1, while in the arctic fox the anterio-posterior breadth distinctly exceeds the transverse breadth;

2. the plantar surface below the proximal head of the arctic fox is smooth, while in hare it shows edges (see fig. 22).

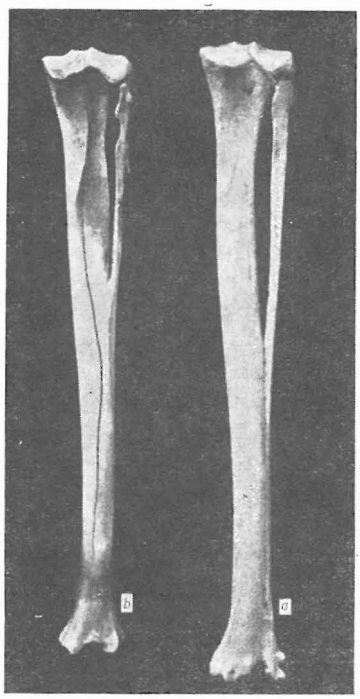


Fig. 22 Comparison between the plantar surfaces of the shin bone in the arctic fox (a) and the hare (b). (Foto J. Chlumský.)

Outer postaxial bone (fibula). Only fragments of fibula occurred in the material studied. These could not be elaborated either morphologically or metrically.

Sole bones. Some usable metrical data were yielded only by the tals (talus bone) and the heel bone (calcaneus). The results essentially correspond to the dimensions reported by V. GROMOVA (1950). The other sole bones occurred only sporadically if at all in the material studied.

Ecology

Biotope. The recent arctic fox is a characteristic representative of tundra fauna. It penetrates farther into the forest zone only during bad winter weather. However, its specialization to an extremely cold climate appeared as late as in the Middle Würm or possibly even later. This may be concluded from the fact that the Early Würmian foxes still occur among the cold steppe fauna together with the common fox *Vulpes vulpes*. A. LIEBUS (1933) was not yet able to explain this phenomenon; he thought that mixed fox materials of different ages or of cross-breeds between both these species are involved. During the Main Würm, the arctic fox appears as a typical element of the fauna of stadials („Rangifer-Lemming-Alopex-Fauna" according to H. W. MATTHES 1962).

It seems that with advancing adaptation to cold climate the quantitative representation of arctic foxes increased among the Würmian mammal fauna. In the stratigraphically dated material studied, the arctic fox from the interstadial „$W_{1/2}$" is represented by 21 specimens, that from the beginning of the Main Würm („W^2") by 3 specimens, that from the interstadial „$W_{2/3}$" by 7 specimens and that from the last stadials („W_3") by 30 specimens. The numbers are naturally distored by the numbers of specimens from individual localities; this distortion is especially clearly seen on the material from the interstadial „$W_{1/2}$" where a large collection of bones from the „Pod hradem" cave renders the number of specimens disproportionally large in relation to those from other localities. In contrast it may be stated that R. MUSIL (1955) has established that among the specimens from the Pavlov locality („W_3") arctic foxes represent 21% of the entire osteological material (common fox about 12%), while in the Dolní Věstonice („$W_{2/3}$") material the bones of both these fox species together make up about 17—25 % only of the osteological material. Among the fossil bones from the Early Würmian localities, those of arctic foxes represent a still smaller proportion (J. BENEŠ).

Geographic distribution. At the present time, the arctic fox is spread in the tundra and tundra-forest zones in the northernmost parts of Europe. However, during the Late Pleistocene the arctic fox was also widespread in Central Europe, occurring in the west as far as to the Pyrenees and the Côte d'Azur and in the east to the Crimea and the southern boundary of Siberia (BOULE 1919; BOULE, VILLENEUVE 1927, STEHLIN, DUBOIS 1933) — see fig. 23. During the Late Würm and Early Holocene the arctic fox retreated to the north, following glaciers (or, more precisely, periglacial areas); it seems that this retreat has been continuing until today. A. NEHRING (1890) reports 60° of northern latitude and

A. G. NOVIKOV (1956) 68° of northern latitude to be southern boundary of the occurrence of arctic foxes.

Stratigraphic range: Late Pleistocene (Würm?) to Recent.

Fig. 23 Geographic distribution of the arctic fox (*Alopex lagopus*) in the Pleistocene (2) and at the present time (1). (Orig.)

Final notes

1. It is not yet clear where the lower boundary of the stratigraphic distribution of arctic foxes should be placed. Just as with the common fox (*Vulpes vulpes*), this is due to the so far insufficient knowledge of the development of foxes during Middle Pleistocene. Most authors report foxes from the Würm glacial onward only. J. VAŇURA (1942, 1943) has described finds of endocrania of arctic foxes from the travertines of the Eemian interglacial in Tučín near Přerov. K. KOWALSKI (1959) records the finds of arctic foxes from the cave sediments near Ojców in Poland, assigned to the Riss stage; the determination of the age is, however, uncertain.

2. The Early Würmian arctic foxes are smaller than those of the Main Würm. In addition to the general trend of development toward increasing bodily size, the progressing adaptation af arctic foxes to a cold climate also played a role here, this itself also contributing — according to Bergmann's rule — to the increase of bodily size. This tendency for growth to a larger size evidently advanced gradually during the whole Würm stadial up to the Holocene. For this reason recent arctic foxes (*Alopex*

lagopus), contrary to the common fox (*Vulpes vulpes*), are larger in size than Würmian arctic foxes.

3. I tried to confront the results obtained by the study of stratigraphically dated bones of arctic foxes *Alopex lagopus* with the data obtained on the material determined as Woldřich's „species" *Leucocyon lagopus fossilis, Vulpes meridionalis, Vulpes moravica* and *Vulpes minor.* There has been a great vagueness and confusion about these species; I think that J. N. Woldřich and his contemporaries were uncertain about them.

Breadth of palate has been suggested by J. N. WOLDŘICH (1878) as a diagnostic feature of the „species" *Vulpes moravica.* Already J. KAFKA (1900) doubted the existence of „*Vulpes moravica*" as a separate species. H. C. Stehlin (STEHLIN, DUBOIS 1933) compared it with the arctic fox. According to S. I. OGNEV (1931), the breadth of a fox palate varies with the age and sex of the individual, being larger in the male than in the female. As I have shown in text-table 11, the breadth of palate of Woldřich's „*Vulpes moravica*" from Sudslavice is only 0,3 mm (!) greater than that of „*Leucocyon lagopus fossilis*" from the same locality; for this reason I do not regard the distinctive feature by Woldřich as sufficient for the creation of a separate species. As the further morphological and metrical features of the species „*Vulpes moravica*" do not deviate from the characteristics of the arctic fox *Alopex lagopus,* I agree with Stehlin's opinion, and consider the remain of Woldřich's „*Vulpes moravica*" to be a skull fragment of a robust individual (perhaps male) of the arctic fox *Alopex lagopus.*

The species „*Leucocyon lagopus fossilis*" has been determined by J. N. WOLDŘICH (1878) on the basis of the dimensions of canine teeth. He writes: „The canines are too massive for *Vulpes meridionalis* (sensu WOLDŘICH nec NORDMANN — note by J. BENEŠ) and *Vulpes moravica* but more slender than those of *Leucocyon lagopus* GRAY from Labrador, especially the roots being weaker". Numerical data and illustration are absent. A. NEHRING (1880) cites Woldřich's „species" with a query, and G. HAGMANN (1899) rejects it throughout regarding it as superfluous. F. BAYER (1905) gives this Woldřich's species as a synonym of *Alopex lagopus* (LINNÉ). In text-table 12 I summarized the results of the measurements of upper canines of the arctic foxes from Woldřich's collections (localities Čertova díra and Sudslavice), from Klíma's collection (Pekárna cave — det. R. Musil) and Musil's collection (Pod hradem locality) and of the measurements on the recent arctic foxes from Tromsoe. The table shows that there are not substantial differences between Woldřich's „species" and *Alopex lagopus.* Only the values obtained by measuring the crown heights of canine teeth differ to a considerable extent, but in this case these differences may be attributed to the insufficient reliability of this measurement, as I have mentioned above. But it should also be taken into consideration that in canids the development of canine teeth depends on the age and sex of the individual (DUERST-BERN 1926). Thus I do not regard the dimensions of a canine tooth as a sufficient diagnostic feature for the creation of a separate species.

The species „*Vulpes minor*" and „*Vulpes meridionalis*" (sensu WOLDŘICH nec NORDMANN, 1858!) are defined by J. N. WOLDŘICH (1878) on

the basis of metrical differences only. Fig. 17 shows diagrammatically the metrical values of M_1 of the foxes from Sudslavice. When this diagram is compared with that in fig. 15, we see that „*Vulpes meridionalis*" falls within the field of Early Würmian arctic foxes while „*Leucocyon lagopus fossilis*" into that of the arctic foxes of the Main Würm. Several similar cases may be given even on further materials; the values are almost equal. I assume that J. N. Woldřich has discovered metrical differences between Early Würmian and Late Würmian foxes. But in Woldřich's time nothing was yet known of the existence of several glacials, so much less of the existence of stadials. J. N. Woldřich could not therefore interpret correctly the differences stated; he overestimated them, elevating to species what he could have regarded as races (varieties) or, at most, subspecies. He defined his species rather vaguely. My conclusions are also supported by K. J. Maška's approach to the determination of species. Although he accepted Woldřich's determination of the material and his designation of „species", it was with hesitation only; he was certainly sufficiently acquainted with the material which was determined by J. N. Woldřich himself. But, of course, this cannot be said of other authors who not knowing the material found, understood Woldřich's species in the way which suited their purpose.

Summarizing it may be stated that Woldřich's species *Leucocyon lagopus fossilis*" corresponds to the arctic foxes of younger Würm stadials („W_2" and „W_3"). The species „*Vulpes meridionalis*" and „*Vulpes minor*" are synonyms of the Early Würmian (interstadial „$W_{1/2}$") arctic foxes *Alopex lagopus.*

The term „*Vulpes minor*" is evidently a term opposite to „*Vulpes maior*" which already by J. N. Woldřich was taken for a synonym of *Vulpes vulpes*; for this reason too, „*Vulpes minor*" is to be regarded as a synonym of *Alopex lagopus.*

Alopex corsac (LINNÉ, 1768) — steppe corsac
(figs 9 and 10)

1768 *Canis corsac* LINNAEUS, Syst. nat., 12, 3, p. 223.
1850 *Canis corsac* EVERSMAN, Estestv. ist. Orenb. kraja, 2, p. 33—34.
1931 *Vulpes corsac* OGNEV, Zvery vost. Evr. i sev. Azii, 2. p. 346.
1941 *Cynalopex corsac* KRETZOI, Ann. mus. natur. hung., 34, p. 124.
1951 *Vulpes corsac* ELLERMAN et MORRISON-SCOTT, Checklist of Palaearc. and Ind. Mammals, p. 223.
1956 *Vulpes corsac* NOVIKOV, Chiščnye mlek. fauny SSSR, p. 67.
1975 *Alopex corsac* HANÁK et HERÁŇ, Lynx IV, p. 45.

Holotype: Not determined (the species is described according to a specimen found between the rivers Ural and Irtyš, USSR).
Stratum typicum: Holocene (Recent, 18th century).
Locus typicus: Not determined.

Diagnosis of species (NOVIKOV 1956): Skull relativelly small, the facial part being relatively shorter than that of *Vulpes vulpes.* Crista sagittalis and crista occipitalis weakly developed. Outer cristae frontales externae extending almost parallely from processi zygomatici

of frontal bones, fusing posteriorly and delimiting a wide lyre-shaped or triangular platform (see fig. 24). Canine teeth relatively longer than in *Vulpes vulpes*. Lower premolars and molars often reduced in number up to six. Limbs relatively longer than those of *Vulpes vulpes*.

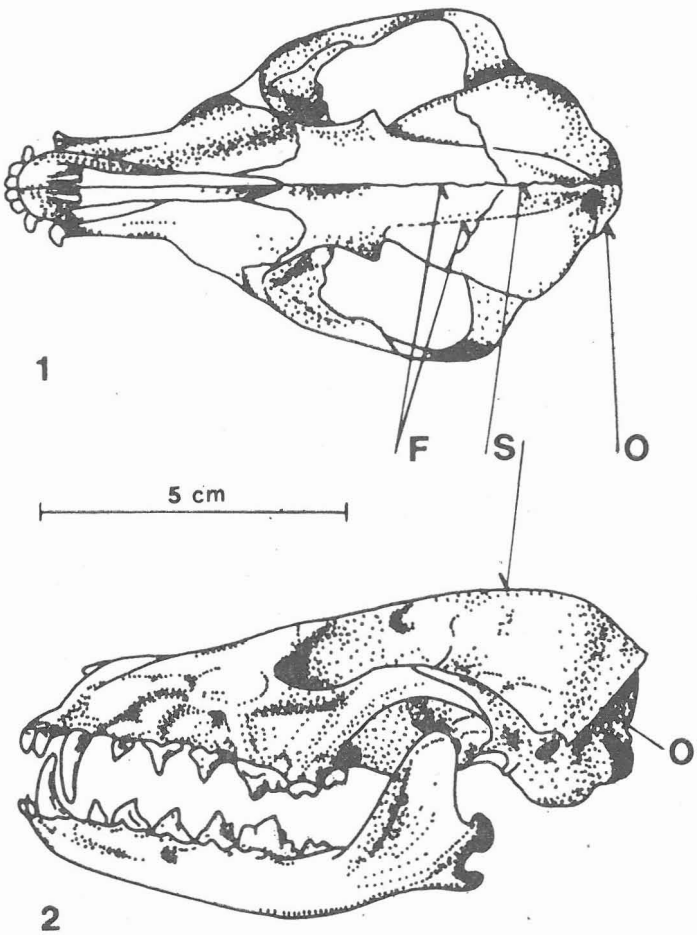


Fig. 24 Skull of the steppe corsac (*Alopex corsac*).
(According to G. A. NOVIKOV, 1956 — adapted)
1 = norma vertialis; F = cristae frontales externae;
2 = norma lateralis; S = crista sagittalis;
O = crista occipitalis.

Extended diagnosis (J. BENEŠ): Internal cusps of M^1 (protocone and hypocone — see fig. 25) connected by a ridge, talon shorter than breadth of crown on the tie-line of interal cusps (as in *Alopex lagopus*). Longitudinal axis of the crown of premolars parallel with that of

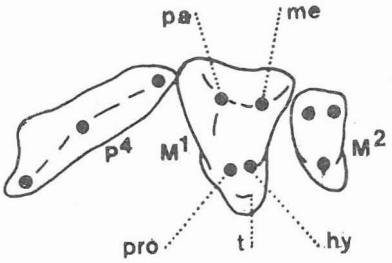


Fig. 25 Scheme of the structure of upper teeth (P^4—M^2) of the steppe corsac (*Alopex corsac*). — (Orig.)
pa = paracone; pro = protocone;
me = metacone; hy = hypocone;
t = talon.

the mandible (as in *Vulpes vulpes*). Lower carnassial (M_1) with an additional cusp on the lingual side of the crown between metaconide and entoconide as in *Vulpes vulpes.* First lower premolar (P_1) and last molar (M_3) fairly frequently strongly reduced to a very small peg-shaped tooth up to 1×1 mm in size. Bones of limbs are morphologically reminiscent of the arctic fox *Alopex lagopus,* though strikingly smaller.

Material studied: Left maxilla with M^1 and M^2 from the Pekárna cave (Absolon's collection), left arm bone (humerus) from the Býčí skála cave (Musil's collection), right spindle bone (radius) from the Býčí skála cave (Musil's collection); further bones not determined with certainty: left mandible from the Pekárna cave (Absolon's collection) and right spindle bone (radius) from the same locality (Absolon et Czižek's collection). For comparison, a corsac skull from the correlation collection of the Department of Palaeontology of the Moravian Museum, Brno, was used.

Description of the material studied

Skull. Skull specimens — except one — were absent in the material studied, so that noting substantial can be reported. The same case is with the corcac's upper teeth. The morphological observations are given in the extended diagnosis of the species, the metrical data obtained by measuring a fragment of maxilla from the Pekárna cave, and a recent corsac's skull are given in text-tables 21 and 22. In general it may be stated that the dimensions of the upper teeth of the corsac do not attain the variation range of the arctic fox's upper teeth. The lower teeth of corsac — irrespective of the uncertain mandible from the Pekárna cave — did not occur in the material studied. The comparison of the lower teeth of a recent corsac with those of the common fox and the arctic fox are given in the diagnosis of the species.

Postcranial skeleton. Of the postcranial skeleton, only one arm bone (humerus) and two spindle bones (radii) were available for my study. The metrical data are given in text-table 23 (for the humerus) and in text-table 24 (radius). The results are shown of the comparison between the measurements of the fossil material and those of the recent material obtained by V. GROMOVA (1950) and by R. MUSIL, who measured the recent osteological material in the Department of Zoology of the Museum of the Academy of Sciences of the USSR, Leningrad (unpublished). Summarizing it may be stated that the metrical data which I have established on the fossil material are higher than those given by

Text-table 21 **Metrical data on P^4 of the steppe corsac (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Alopex corsac	Not determined	Recent	10.4	1	10.4	5.1	1	5.1
Alopex corsac	Pekárna	Würm	12.1	1	12.1	5.5	1	5.5
Alopex lagopus	Tromsö	Recent	11.0—12.0	3	11.5	4.6—5.0	3	4.7

Text-table 22 **Metrical data on M^1 of the steppe corsac (in mm)**

Species	Locality	Age	Length of crown			Breadth of crown		
			variation range	number of specimens	average	variation range	number of specimens	average
Alopex corsac	Not determined	Recent	6.3	1	6.3	8.4	1	8.4
Alopex corsac	Pekárna	Würm	6.9	1	6.9	8.7	1	8.7
Alopex lagopus	Tromsö	Recent	7.0—7.6	3	7.3	9.6—10.0	3	9.8

V. Gromova, but relatively agree with the dimensions measured by R. Musil. No other conclusions can be drawn on the basis of such a small amount of material.

Text-table 23
Metrical data in the arm bone (humerus) of the steppe corsac (in mm)

Locality	Age	Total length	Anterioposterior breadth of proximal head	Transverse breadth of proximal head	Transverse breadth of diaphyse	Transverse breadth of distal head	Author of measurement
Býčí skála	Würm	94.0	20.0 ?	13.0 ?	6.0	15.0	J. Beneš
Not given	Recent	82.0	18.5	13.5	—	13.5	V. Gromova
Leningrad	Recent	92.5	19.6	12.9	5.6	15.6	R. Musil

Text-table 24
Metrical data on the spindle bone (radius) of the steppe corsac (in mm)

Locality	Age	Total length	Transverse breadth of proximal head	Anterioposterior breadth of proximal head	Transverse breadth of diaphyse	Transverse breadth of distal head	Anterioposterior breadth of distal head	Author of measurment
Býčí skála	Würm	89.7	8.9	5.6	6.7	12.2	5.8	J. Beneš
Pekárna	Würm	95.9	8.3	5.6	6.6	12.7	6.8	J. Beneš
Not given	Recent	77.5	8.0	—	5.3	10.4	—	V. Gromova
Leningrad	Recent	—	8.6	5.4	5.6	11.2	6.5	R. Musil

Ecology

Biotope. The recent steppe corsac is a typical inhabitant of steppes and semi-deserts, penetrating into forest-steppes but only when it occurs abundantly. It lives in foothills, avoiding forest, growths of bushes and reeds, areas worked agriculturally and densely populated areas. It feeds on steppe rodents and birds, and preys on aquatic birds and eggs and young from bird nests (NOVIKOV 1956).

About fossil corsacs nothing more is known than that they lived during the Late Pleistocene in steppe areas with a continental climate (J. BENEŠ).

Geographic distribution. The geographic distribution of recent steppe corsac depends on the geographic range of steppe regions.

In Europe they live around the Caspian Sea and only rarely do they penetrate to the Azov and peri-Caucasus areas (NOVIKOV 1956). In Asia they are widespread in the zone of steppes and semi-deserts from the Caspian Sea to Mongolia and China (J. BENEŠ).

Fossil corsacs are known to have lived in Central Europe overlapping to South-Europe (see the Final notes). The northern boundary of their distribution area in Europa is not known.

Stratigraphic range: Late Pleistocene (Würm?) to Recent.

Final notes

There are but few reports on steppe corsacs. It is assumed that in the Late Pleistocene they came from Asia to Europe. A. NEHRING (1889) has reported finds from Germany (without detailed stratigraphic dating), M. BOULE (1919) has recorded a find from the Grimaldi Cave ($W_{1/2}$ or W_2), H. C. STEHLIN (1933) has described a find from Cotencher Cave (Early Würm). J. KAFKA (1900) reports some rather problematic finds from the Srbská sluj cave (probably interstadial „$W_{1/2}$") and Lochkov (without stratigraphic dating). R. MUSIL (1961) has described the find of a mandible from the Švédův stůl cave (vague stratigraphy) which could belong to an arctic fox or a steppe corsac. From the finds known so far I can judge that steppe corsacs never formed a quantitatively important part of European mammal fauna, occurring rather sporadically and probably during a limited time interval. In contrast to the hitherto handed down idea that they penetrated to Europe during the Last Würmian stadial together with other elements of Asian fauna, there is the evidence that the stratigraphically rather precisely dated or datable finds derive from the interstadial „$W_{1/2}$". With respect to this, steppe corsacs cannot be regarded as a species typical of the Last Würmian stadial, but rather of the Earlier Würmian interstadials.

CONCLUSION

The results of this paper can be summarized as follows:

1. From the material investigated it follows that Early Würmian foxes are smaller than those of the Main and Late Würm, both *Vulpes vulpes* and *Alopex lagopus*. This conclusion is based especially on the metrical values obtained by measuring teeth and also parts of the postcranial skeleton (the latter values are not so marked as the postcranial bones were much less numerous in the material studied). The increase of dimensions may be explained partly by the general tendency for growth to considerable size partly by Bergmann's rule of increasing dimensions of the body during the passage from a warm into a cold climate. A certain role may also be played by biologico-ecological dependences. The Early/Main Würm boundary at the end of the interstadial „$W_{1/2}$" also represents an important faunal boundary. Natural conditions change, and so do the representation of individual species as well as the number of their individuals. The changes in the specific composition and number of minor mammals were necessarily reflected in the mode of life of foxes and their acquisition of food; these changes also influenced the trend of

their general bodily development. It was not and could not be the aim of this paper to establish the extent to which the above-mentioned factors participated in the changes in the build of foxes' bodies at the Early/Main Würm boundary. This would require a special investigation of the changes of the composition of the minor vertebrate fauna and also the changes of further natural factors.

2. The common fox *Vulpes vulpes* from the Main Würm has yielded metrical data pointing rather to the subspecies *Vulpes vulpes vulpes* than the subspecies *Vulpes vulpes crucigera.* The foxes of the latter species appear in Europe as late as in the Holocene.

3. In the material studied I could ascertain the presence of three species of foxes: *Vulpes vulpes* (LINNÉ), *Alopex lagopus* (LINNÉ) and *Alopex corsac* (LINNÉ). Woldřich's „species" of Pleistocene foxes are based on the metrical differences between Early Würmian and Middle Würmian foxes. J. N. Woldřich did not know this stratigraphic dependence, nor could he know it at his time. He overestimated the difference established in measurements, using them as the basis for the characterization of separate species. His species *„Vulpes vulgaris fossilis"* may be identified with *Vulpes vulpes* of the Main Würm, *„Vulpes meridionalis"* sensu WOLDŘICH 1878 is the arctic fox *Alopex lagopus* of the Early Würm, *„Leucocyon lagopus fossilis"* and *„Vulpes minor"* correspond to the arctic fox *Alopex lagopus* of the Main Würm (*„Vulpes minor"* being evidently opposite to *„Vulpes maior"*; the latter name was regarded by J. N. Woldřich as a synonym of *„Vulpes vulgaris fossilis"*. This explanation is substantiated by the metrical data obtained on the material determined by J. N. Woldřich or K. J. Maška). The above statement given under 3. is of restricted stratigraphic validity only, as J. N. Woldřich did not clearly identify his „species" himself being uncertain in classifying them. *„Vulpes moravica"* does not morphologically differ from *Alopex lagopus,* its distinguishing feature proposed by J. N. Woldřich not deviating from the breadth variation rate of the palate, obtained by measuring arctic foxes, *Vulpes moravica* is therefore a robust individual of *Alopex lagopus.* Woldřich's species *„Canis Mikii"* is invalid throughout, having been erroneously identified on the basis of the jaws of an old individual of *Vulpes vulpes.*

4. I was able to identify with certainty the steppe corsac *Alopex corsac* in two cases only. Except these two finds I have found still other bones in the material studied, which could belong to a small individual of the arctic fox or corsac. On the basis of these facts I can state that the corsac appears, in the Würmian fauna of the Moravian and Bohemian karsts although sporadically only perhaps during a limited time span. In contrast to the idea generally accepted so far, that corsacs penetrated into Central Europe at the close of the Würmian glacial, I conclude that corsacs may be regarded rather as a species typical of the Earlier Würmian interstadial.

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JOSEF BENEŠ

WÜRMSKÉ LIŠKY ČESKÉHO A MORAVSKÉHO KRASU

V práci jsou uvedeny výsledky výzkumu mladopleistocénních lišek z würmských jeskynních sedimentů Českého a Moravského krasu. Zkoumaný materiál pochází jednak ze sbírek Národního muzea v Praze, jednak ze sbírek Moravského muzea v Brně. Pozornost jsem věnoval hlavně měření zubů a kostí lišek a srovnání výsledků měření se stratigrafickými údaji. Vedle metriky jsem věnoval pozornost i morfologickému rozlišování kostí jednotlivých druhů lišek, případně i kostí jiných druhů savců, které lze snadno s kostmi lišek zaměnit (hlavně rod *Lepus).* U materiálů ze starších sběrů, hlavně z kolekce Woldřichovy a Maškovy, jsem se blíže zabýval materiálem, označovaným Woldřichovými názvy *„Vulpes meridionalis"*, *„Vulpes moravica"*, *„Vulpes minor"*, *„Vulpes vulgaris fossilis"* a *„Leucocyon lagopus fossilis"*. Byla to práce časově náročná, ale, jak se ukázalo, nebyla marná. Důležité výsledky shrnuji do těchto bodů:

1) Ze zkoumaného vyplývá, že lišky raného würmu jsou menší než lišky hlavního a pozdního würmu, a to jak u druhu *Vulpes vulpes,* tak u druhu *Alopex lagopus.* Tyto závěry vyplynuly hlavně z metrických údajů, získaných měřením zubů, ale projevují se i na postkraniální kostře, i když ne tak výrazně, protože postkraniální kostra byla ve zkoumaném materiálu zastoupena v mnohem omezenějším počtu kostí. Zvětšování rozměrů mladopleistocénních lišek je možno vysvětlit jednak všeobecným trendem vývoje, směřujícím ke zvětšení tělesných rozměrů, jednak Bergmannovým pravidlem o přibývání tělesných rozměrů při přechodu z teplého do chladného podnebí. Určitý vliv tu budou mít i závislosti biologicko-ekologické. Rozhraní raného a hlavního würmu na konci interstadiálu „$W_{1/2}$" (interstadiál „Podhradem" sensu R. MUSIL — K. VALOCH, 1966 nebo „Hengelo" sensu Th. HAMMEN et al., 1967) je i velkým rozhraním faunistickým. Mění se přírodní poměry i druhové a početní zastoupení jednotlivých druhů. Změny v druhovém složení a v početním zastoupení různých menších savců se musely nezbytně odrazit i ve způsobu života a v získávání potravy lišek a tyto změny pak ovlivňovaly i směr jejich celkového tělesného vývoje. Zjišťovat jak a do jaké míry se tito činitelé podíleli na změnách tělesné stavby lišek na rozhraní raného a hlavního würmu (případně i v dalších obdobích) není a nemohlo být součástí této práce, protože si to vyžádá specielní výzkum změn složení drobné obratlovčí fauny i změn dalších přírodních činitelů.

2) Liška obecná *Vulpes vulpes* (Linné) z hlavního würmu se metricky projevuje spíše jako poddruh *Vulpes vulpes vulpes* (LINNÉ), který žije v současné době v severní Evropě, než jako poddruh *Vulpes vulpes crucigera* (BECHSTEIN), který žije v současné době ve střední Evropě. Tento poddruh se objevuje ve střední Evropě až v holocénu.

3) Ve zkoumaném materiálu jsem měl možnost konstatovat přítomnost tří druhů lišek: *Vulpes vulpes* (LINNÉ), *Alopex lagopus* (LINNÉ), a *Alopex corsac* (LINNÉ). Další druhy, které stanovil J. N. Woldřich na podkladě metrické rozdílnosti lišek raného a středního würmu, jsou neplatné. J. N. Woldřich neznal a ve své době ani znát nemohl stratigrafické závislosti a zjištěné metrické rozdíly přecenil. Druh *Vulpes vulgaris fossilis* WOLDŘICH je možno identifikovat s liškami *Vulpes vulpes* (LINNÉ) z hlavního würmu. *Vulpes meridionalis* WOLDŘICH (nec NORDMANN, 1858) je polární liška *Alopex lagopus* (LINNÉ) z raného würmu. *Leucocyon lagopus fossilis* WOLDŘICH a *Vulpes minor* WOLDŘICH jsou polární lišky *Alopex lagopus* (LINNÉ) z hlavního würmu. *„Vulpes minor"* je zřejmě antipod *„Vulpes maior"*, kteréžto označení považuje J. N. Woldřich za synonymum pro *„Vulpes vulgaris fossilis"*. Dokladem pro tato vysvětlení jsou metrické údaje získané na materiálu, určovaném J. N. Woldřichem nebo K. J. Maškou. Získané výsledky mají jen omezenou stratigrafickou platnost, protože sám J. N. Woldřich si se svými „druhy" nevěděl dobře rady a nijak zvlášť je neidentifikoval. *Vulpes moravica* WOLDŘICH se morfologicky neliší od *Alopex lagopus* (LINNÉ). Ani Woldřichem uváděný rozlišovací znak „šířka patra" se nevymyká z variačních šířek, získaných měřením patra polárních lišek. *Vulpes moravica* WOLDŘICH je tedy jen silným jedincem lišky *Alopex lagopus* (LINNÉ). *„Canis Mikii"* je zcela neplatný druh, stanovený J. N. Woldřichem na čelisti velmi starého jedince lišky *Vulpes vulpes* z jeskyně Čertova díra. Už K. J. Maška, ačkoliv tento Woldřichův „druh" do jisté míry uznával, zanechal u Woldřichova typového materiálu lístek s nápisem: „Woldřichův slavný pes Canis Mikii, ale podle mého soudu pouze velká l i š k a (podtrženo K. J. Maškou — pozn. J. Beneš) Vulpes vulgaris — 5. 6. 1887 Maška".

4) Korsaka *Alopex corsac* (LINNÉ) jsem mohl s jistotou určit jen ve dvou případech. Kromě těchto dvou nálezů jsem ve zkoumaném materiálu našel ještě několik kostí, které by mohly patřit buď malému jedinci polární lišky nebo korsakovi; přesnější identifikace nebyla možná. Na základě všech zjištěných faktů mohu konstatovat, že korsak se ve würmské fauně Českého a Moravského krasu sice vyskytuje, ale v míře více než sporadické a snad i v časovém úseku velmi omezeném. Proti představě, že korsaci pronikli do střední Evropy na konci würmské doby ledové, docházím k závěru, že korsaka je nutno považovat spíše za druh, typický pro starší würmské interstadiály („$W_{1/2}$", případně i pro dobu starší).

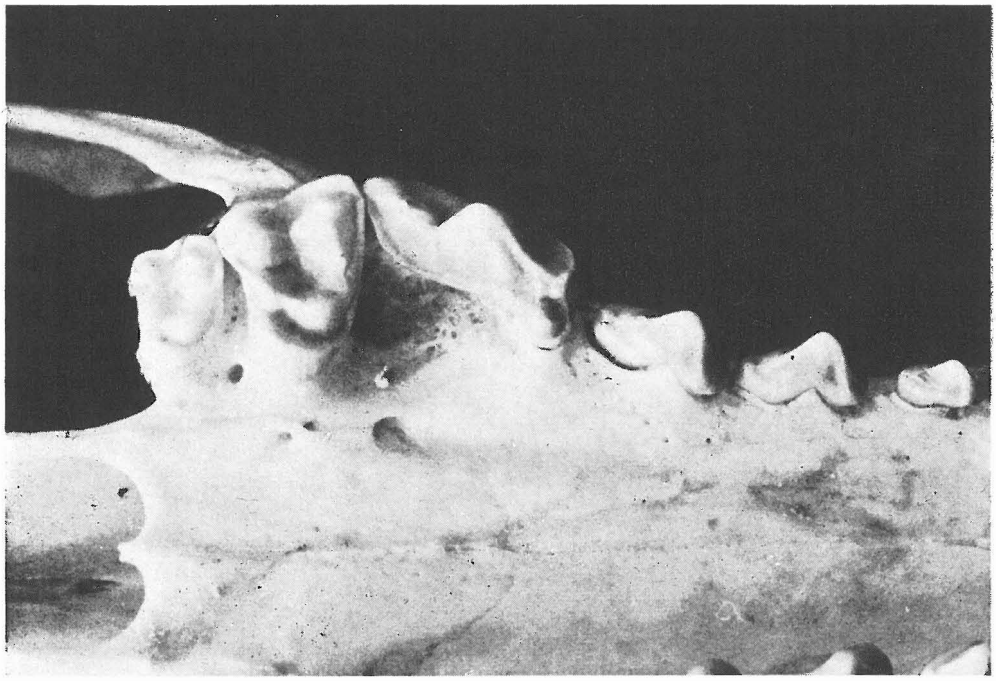
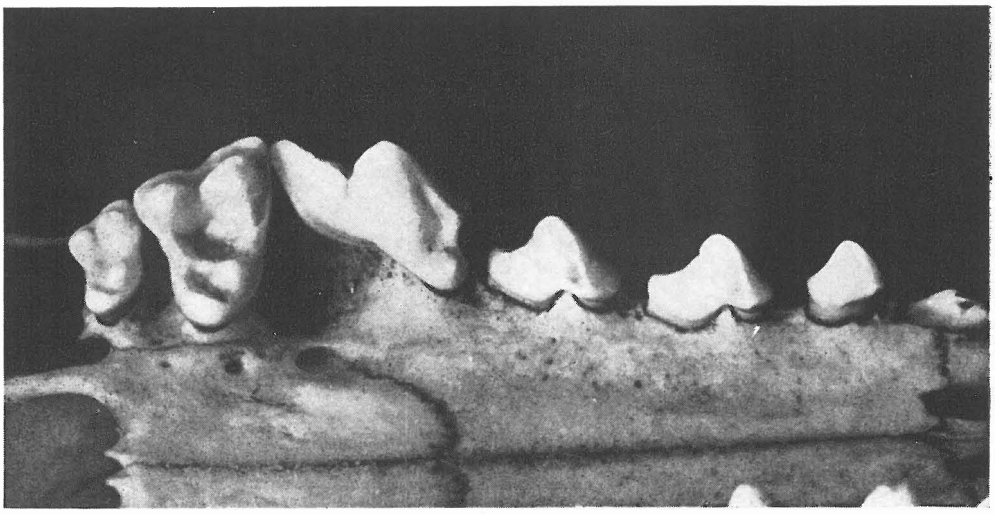


Fig. 1 Upper teeth of the common fox (*Vulpes vulpes*) from Bánská Bystrica. (Collection of the National Museum, Prague. — Foto J. Chlumský.)

Fig. 2 Upper teeth of the arctic fox (*Alopex lagopus*) from Tromsö (Collection of the Moravian Museum, Brno. — Foto J. Chlumský.)



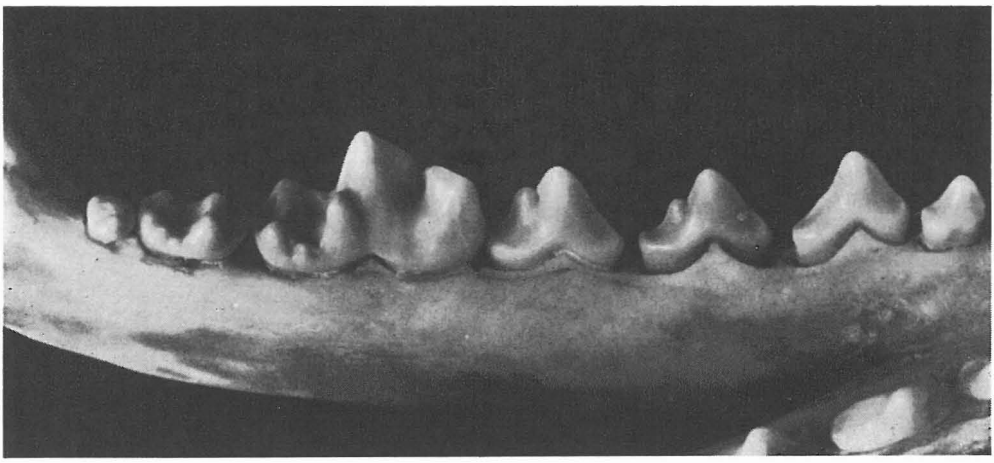


Fig. 1 Lower teeth of the common fox (*Vulpes vulpes*) from Bánská Bystrica. (Collection of the National Museum, Prague. — Foto J. Chlumský.)

Fig. 2 Lower teeth of the arctic fox (*Alopex lagopus*) from Tromsö. (Collection of the Moravian Museum, Brno. — Foto J. Chlumský.)