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DEERS FROM WĘŻE AND THEIR RELATIONSHIP WITH THE PLIOCENE AND RECENT EURASIATIC CERVIDAE

Study on the Tertiary bone breccia fauna from Węże near Działoszyn in Poland

PART XX*

Contents

Abstract. — Three species of deers, *Procapreolus wenzensis* (Czyżewska, 1960). *Cervus warthae* n. sp. and *Muntiacus polonicus* n. sp. are described from the Pliocene locality Węże near Działoszyn. A new systematics of the subfamily Cervinae is here suggested and its evolution presented. The results of a quantitative analysis of deer remains from the bone breccia of that locality and the palaeontological conclusions drawn from them are also discussed.

INTRODUCTION

The Pliocene fauna from Węże, found by Samsonowicz (1934) was described by many authors. Since 1951, these works have been published in „Acta Geologica Polonica" and „Acta Palaeontologica Polonica".

Deer remains in breccia of the locality Węże occur in considerable quantities. Using only part of the material available, two species of deers, *Cervus (Rusa)* sp. (Czyżewska, 1959) and *Cervocerus wenzensis* (Czyżewska, 1960) have been described so far. Many new specimens, in particular remains of young individuals, were obtained by continued working up. During my visit to the USSR, I studied rich collections of the remains of Pliocene deers from Eastern Europe and Asia, housed at the Palaeontological Institute of USSR's Academy of Sciences in Moscow and at the Zoological Institute of the Ukrainian Academy of Sciences in Kiev. In Leningrad, I was shown a rich osteological collection of Recent deers of the Zoological· Institute of the USSR's Academy of Sciences. Since my previous descriptions of Cervidae from Węże required certain supplements, I resolved to resume this subject.

Węże is the only locality of the Upper Tertiary in Poland which supplied a considerable amount of deer remains. The Tertiary Cervidae are seldom met with in Poland and only as single specimens. A primitive muntjac *Prox furcatus* (now called *Euprox furcatus* (Hensel)) was described by Hensel (1859) from Miocene deposits of Sośnicowice near Gliwice (and not near Opole, as maintained by Thenius, 1959). The occurrence of this species at Nowa Wieś Królewska was mentioned by Wegner (1913). A few teeth of *Palaeomeryx eminens* Meyer were also found in that locality. The antlers of *Euprox furcatus* (Hensel) from Kosów District, USSR, found on the Czarny Czeremosz River, were described by Kiernik (1913). *Euprox furcatus* (Hensel) occurs in the following two forms: a) with high forked antlers, from Sarmatian deposits, and b) with low forked antlers, the latter form met with from Helvetian to late Sarmatian (Thenius, 1948). Both are known in Poland.

In 1959, a layer with Pliocene mammal remains was found at Węże below the cave filled with Upper Pliocene bone breccia (Samsonowicz, 1934). This second locality, containing teeth and fragments of jaws of Cervidae (not described so far), was called Węże II.

In addition to abundant remains of micromammals (Kowalski, 1960), the Upper Pliocene fauna of mammals, from Rębielice Królewskie, contains amount of teeth and jaws of Cervidae.

The terminology of the skull and antlers, used in the present paper, does not deviate in principle from that of my previous works. The terms concerning dentition are similar to those used by Obergfell (1957) in his description of the mandible dentition of Lower Miocene deers. I applied

them also to milk and permanent teeth of the maxilla. The descriptions of teeth are accompanied by diagrammatic drawings.

Measurements were taken by means of a slide gauge or a bow compass with nonius. In the case of some skulls, I could take a measurement of length from basion to the line connecting anterior margins of DP^2 (or P^2), which I called a measurement of skull length. Indexes, referred to this length as a fundamental measurement, were separately calculated for these skulls. Three dimensions of teeth: length, width and height, given in the present paper, are maximum measurements. Indexes of dentition were calculated only for completely unworn teeth and mean measurements — only for adult individuals. Measurements and indexes are explained in text.

A systematics of the family Cervidae with the division into subfamilies is here adopted after Flerov (1952, 1962).

Specimens of the following species of Recent deers from the collections of the Zoological Institute of the USSR's Academy of Sciences in Leningrad and the Zoological Museum of the University of Wrocław (ZMUWr) were used as a comparative material:

— *Muntiacus reevesi* Ogilby, 7 skulls from Eastern China;
— *Muntiacus muntjac* Zimmerman, 5 skulls from Bengal and Southern China;
— *Elaphodus cephalophus* Milne-Edwards, 5 skulls from Central China;
— *Capreolus capreolus* L., 18 skulls from Central Europe;
— *Capreolus pygargus* Pallas, 8 skulls from Siberia;
— *Axis axis* Erxleben, 5 skulls from India;
— *Dama dama* L., 7 skulls from Central Europe;
— *Cervus (Sika) hortulorum* Swinhoe, 18 skulls from Primorski Krai;
— *C. (Rusa) unicolor* Kerr, 12 skulls from India (Assam) and Indochina;
— *C. elaphus bactrianus* Lydekker, 12 skulls from Bukhara;
— *C. elaphus* L., 28 skulls from Central Europe.

Altogether, I had at my disposal 125 skulls of Recent deers.

I have also used the following comparative material of fossil deers:

— *Cervavitus variabilis* Alexeyev from Bessarabia (Palaeont. Inst. Acad. Sci. USSR, Moscow): 14 fragments of maxillae, 11 mandibles and many antlers;
— „*Cervavitus*" *sibiricus* from Pavlodar (the same Institute): 8 fragments of maxillae, 4 mandibles and many antlers;
— *Cervus (Rusa) moldavicus* Janovskaja: a skeleton with a skull of a juvenile individual;
— *Procapreolus ukrainicus* Korotkevitsh from Novo-Ukrainka (Zool. Inst. Ukrain. Acad. Sci., Kiev): 2 fragments of maxillae, 3 mandibles and 2 fragments of antlers;

— *Procapreolus cusanus* Cr. from Andreyevka and Chornaya Loschina (the same Institute): 5 fragments of mandibles and 2 antlers;
— *Procapreolus* from Stavropol, Caucasia (Palaeont. Inst. Acad. Sci. USSR, Moscow): few fragments of jaws and damaged antlers;
— *Pliocervus* from the region on the Kuchurgan River and from Stavropol, Caucasia (the same Institutes in Moscov and in Kiev): 3 fragments of maxillae, 8 mandibles and fragments of antlers;
— *Eostyloceros* and *Muntiacus* (the same Institute in Kiev): a few fragments of antlers;
— *Eucladocerus* (the same Institutes in Moscow and in Kiev): antlers and fragments of jaws;
— *Euprox furcatus* (Hensel) from Nowa Wieś Królewska near Opole (ZMUWr): an antler and five fragments of jaws.

The specimens of deers from Węże, described in the present paper, are housed at the Department of Palaeozoology of the Wrocław University and they are the property of the Polish Academy of Sciences, Museum of the Earth, Warsaw.

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REMARKS ON THE TAXONOMY OF THE SUBFAMILY CERVINAE

In generally accepted systematics, the subfamily Cervinae is divided into several genera (e. g., Simpson, 1945). Since these closely related genera are not grouped together, such a division does not, however, sufficiently differentiate this subfamily and, therefore, in my opinion, a few tribes should be distinguished within it.

Khomenko (1913) distinguished, among Cervidae, the subfamily Pliocervinae, thus emphasizing the primitiveness and a specific character of the deers from Taraklia, Moldavia, which he described. Simpson (1945) assigned these deers to the subfamily Cervinae, which — on account of a close relationship of this group to most Cervinae — is, in my opinion, correct, but I suggest a distinction of the tribe Pliocervini nov. (= Pliocervinae Khomenko, 1913) to which the genus *Cervavitus* Khomenko, 1913 (= *Cervocerus* Khomenko = *Damacerus* Khomenko) with the species *C. variabilis* Alexeyev would be assigned. Close to this tribe I place *Pliocervus* Hilzheimer, 1922 (as incertae sedis) with the species *Pl. matheroni* Gervais, *Pl. pentelici* Dames and *Pl. kutchurganicus* Korotkevitsh. On the other hand, the genus *Procervus* Alexeyev, 1915 cannot be maintained because it is a homonym of *Procervus* Hodgston, 1847. *Cervavitus*, *Cervocerus* and *Damacerus* are stages of the ontogenetic development of a deer of one genus and one species, which was stated by many authors (Flerov & Pidopličko, 1952; Azzaroli, 1953; Halthenorth, 1959). I share Azzaroli's (1953) opinion that the Lower Pliocene deers of China, described by Zdansky (1925 and 1927) and Teilhard de Chardin & Trassaert (1937) as *Cervocerus novorossiae* Khomenko (= *Damacerus bessarabiae* Khomenko), require a repeated study and new generic and specific names. They cannot be assigned to the genus *Cervavitus*. This would also apply to the deers from Kazakhstan (Pavlodar, Selim Djevar) (Borissiak & Belayeva, 1948) which should not be related to the genus *Cervavitus* (Flerov, 1950. *Cervavitus orlovi*). After my study of the remains of the deer from Pavlodar at the Palaeontological Institute in Moscow, I am of the opinion that it fundamentally differs in the structure of its antlers from *Cervavitus* from Eastern Europe. I think, however, that the deers from China and Kazakhstan may continue to be associated with Pliocervini.

On the other hand, the assignment (Dietrich, 1938) of more Recent deers to Pliocervini seems to be unjustified since this is a group of fairly primitive deers. The deer from Jüchsen might be at most a descendant of Pliocervini but, unfortunately, it is very poorly recognized. It is beyond any doubt that the young individual of the deer, described by Böhme (1963) from Upper Pliocene of Kaltensundheim/Rhön, should not have been assigned to Pliocervini. *C. dicranocerus* Kaup from Eppelsheim was also assigned to Pliocervini by Dietrich (1938), who considered it one of

the species of *Cervocerus*. Thenius (1948) is, however, right believing that this is a representative of Cervulinae, i. e., *Euprox dicranocerus* (Kaup), from which Pliocervini are probably derived.

I consider the genus *Pliocervus* to be incertae sedis. Primitive, Lower and Middle Pliocene deers with characters, which are intermediate between those of Pliocervini and primitive Cervini, belong to it.

In more recent systematics the position of roe deers is variously presented and not in all cases emphasizes an indubitable relationship of these deers to other Eurasian deers. Simpson (1945) and after him, Ellermann & Morrison-Scott (1951) distinguish within the subfamily Odocoileinae[1] a separate tribe, Capreolini (= Capreolidae Brooke, 1928), separating roe deers from Cervinae. After Pocock (1923), Azzaroli (1953) distinguishes, next to Cervinae, even a separate subfamily of Capreolinae. According to Flerov (1952, 1962), Cervinae is a larger subfamily, also including roe deers. Such a broader presentation of Cervinae is quite convincing since it includes all more important genera of deer connected by a relationship. I suggest, therefore, to include the tribe Capreolini Simpson with the genera *Procapreolus* Schlosser, 1924 and *Capreolus*. L. in the subfamily Cervinae. I believe that the tribes Pliocervini and Capreolini are related by a common derivation from the ancestors relatively similar to Cervulinae (the genus *Euprox*).

The tribe Cervini is the central, most numerous and most variable group within the subfamily Cervinae. This is a more modern group than Pliocervini and Capreolini. It appears in the Lower Pliocene, but its extensive development takes place as late as middle and upper parts of this period. Cervini are descendants of Pliocervini, to which belong, on the one hand, the deers *Eucladocerus* Falconer and, on the other, Recent genera *Axis* H. Smith, *Cervus* L., *Dama* Frisch and *Elaphurus* Milne-Edwards. The genus *Cervus* (Simpson, 1945) includes several species and has a very wide geographical range. As larger and larger amounts of the fossil material will be collected and more and more thoroughly studied, some Pliocene species will be surely excluded from this genus.

The systematics I suggest is as follows:

Family Cervidae Gray, 1821
Subfamily Cervinae Baird, 1857

A. Tribe Pliocervini (= Pliocervinae Khomenko, 1913)

Middle-sized deers with relatively simple antlers, fixed on long, posteriorly bowed pedicles. Holometacarpalia.

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[1] In addition to roe deers, Simpson also assigns to this subfamily the North and South American deers, as well as elks, reindeers and Hydropotes. I share Azzaroli's (1953) view that this group is not phylogenetically uniform.

Genera assigned: *Cervavitus* Khomenko (= *Cervocerus* Khomenko = *Procervus* Alexeyev), Lower Pliocene.

Incertae sedis: *Pliocervus* Hilzheimer, Lower-Middle Pliocene

B. Tribe Capreolini Simpson, 1945 (= Capreolidae Brooke, 1828)

Skull with elongated parietals and short facial part. Lacrimal fossa middle to very small. Antlers with three tines, the first of them growing up at least above the point half-way the length of beam. Telemetacarpalia (or still holometacarpalia?).

Genera assigned: *Capreolus* Frisch, Pleistocene — Recent, *Procapreolus* Schlosser, Lower to Upper Pliocene.

C. Tribe Cervini Weber, 1928

Skull usually elongated, with mostly large and deep lacrimal fossa. Antlers strongly branched, having more than three tines and mostly mounted on short pedicles. Plesiometacarpalia.

Genera assigned: *Axis* H. Smith (together with *Hyelaphus* Sundewall), Lower Pliocene — Recent, *Cervus* L. (together with *Rusa* H. Smith, *Sika* Sclater, *Rucervus* Hodgson), Middle Pliocene — Recent, *Eucladocerus* Falconer (= *Polycladus* Pomel), Middle Pliocene — Pleistocene, *Dama* Frisch, Pleistocene — Recent, *Elaphurus* Milne-Edwards, Recent.

The following two tribes of large deers differing in specific characters from those, mentioned above, are also assigned to Cervinae:

D. Tribe Alcini Simpson, 1945, with the genera *Alce* Frisch (= *Alces* Gray), Pleistocene-Recent, *Cervalces* Scott and *Libralces* Azzaroli from Pleistocene.

E. Tribe Megacerini Viret, 1961, with the Pleistocene *Megalocerus* Brooke (= *Megaceros* Owen).

EVOLUTION OF THE PLIOCENE CERVINAE

The family Cervidae started in Oligocene with the appearance of small deers of the subfamily Palaeomerycinae which, in the late Miocene, become extinct in Eurasia. Cervulinae (=Muntiacinae), met with in Miocene and Lower Pliocene of Europe, are their descendants, whereas in Asia two genera of Cervulinae have survived until the Recent period. The latter are *Muntiacus* Rafinesque and *Elaphodus* Milne-Edwards. The family Cervinae, which appears in the early Pliocene, is much younger.

Cervulinae which in the late Miocene form two stocks (Flerov, 1950), are ancestors of the Lower Pliocene Cervinae. One of these stocks lead to Recent Cervulinae and the other originated roe deers and the tribe Pliocervini.

In my opinion, some characters representative of Lower Pliocene species of Cervinae — particularly distinct in Pliocervini — such as:

simple antlers with a small number of tines, fixed on long and posteriorly strongly bowed pedicles, a convex profile of skull, fairly large lacrimal fossa, short facial part of skull as compared with the braincase and primitive structure of dentition, are indicative of a still very close relationship to Cervulinae and of a common derivation from Cervulinae. The Miocene *Euprox dicranocerus* (Kaup) may be (Thenius, 1948) a common ancestor of all Pliocervini. *Procapreolus* also seems to be a descendant of this genus.

The representatives of the three tribes of Cervinae: Pliocervini, known only from Lower Pliocene, Capreolini, represented by *Procapreolus*, and Cervini — by *Axis speciosus* Schlosser, are met with already in Lower Pliocene. During the Pliocene period Cervinae gradually acquire a more modern character. Recent genera appear in this group .

The remains of a roe deer of the genus *Procapreolus* were first described by Schlosser (1924) from Mongolia (Ertemte, Olan Chorea, etc.). There were fragments of antlers assigned by Schlosser to two new species, *P. latifrons* and *P. rütimeyeri*. On account of a different structure of antlers than that in roe deers, *P. rütimeyeri* Schlosser was excluded by Korotkevitsh (1963, 1965) from the genus *Procapreolus*.

A deer, at first described (Kadić, 1911) as *C. (Axis) loczyi* Pohlig and assigned by Motl (1939) to the genus *Procapreolus*, occurs in the Pliocene fauna of the coastal region on Lake Balaton, Hungary (Faunyód, Polgardi, Karád, Baltavàr). It has also been found (Thenius, 1948) in Austria. Gaal (1943) mentions this deer from Hatvan together with *P. latifrons* Schlosser. *P. loczyi* is marked by a considerable similarity (Thenius, 1948, 1950) in its antlers and dentition to *P. latifrons*. In my opinion, both these species make up a primitive Lower Pliocene group within the genus *Procapreolus* differing from the rest of species.

Procapreolus may be considered (Korotkevitsh, 1963) an ancestor of the genus *Capreolus*. It is marked by several characters, which are primitive in roe deers, such as, a small middle branch of antlers, small burr, smooth surface of antlers devoid of tubercles, strongly bowed pedicles, as well as cingulum and palaeomeryx fold occurring on molars.

P. ukrainicus Korotkevitsh, described in 1965, from Lower Pliocene of Novo-Ukrainka, Odessa District, USSR, is — like *P. wenzensis* (Czyżewska) — marked by a hight position of the first tine.

The remains of the Upper Pliocene deer *C. cusanus* Cr. (Gervais, 1848—1852; Depéret, 1883; Simionescu, 1930; Heintz, 1966 and others), similar to a roe deer, have for a long time been known mostly from France. Korotkevitsh (1963, 1964) gives a new locality of this deer, i. e. Chornaya Loshchina, Nikolayevskii District, and assigns it to the genus *Procapreolus*, at the same time indicating its less primitive characters as compared with other species of *Procapreolus*. She believes *P. casanus*

to be derived from *P. ukrainicus* and to be most similar to Recent roe deers, particularly so to *Capreolus pygargus* Pallas.

P. wenzensis from Węże is marked by a very primitive — for a roe deer — structure of skull (large lacrimal fossae, long and bowed pedicles of antlers, long parietal region). A slightly outlined palaeomeryx fold occurs on its dentition. I believe that this species developed parallelly to the stock leading to the genus *Capreolus* through *P. ukrainicus* and, subsequently, *P. cusanus*.

Pliocervini were first described by Khomenko (1913) from Taraklia, Moldavia. These were the species, *Cervavitus tarakliensis*, *Cervocerus novorossiae* and *Damacerus bessarabiae*. Another representative of Pliocervini — *Procervus variabilis* — was described by Alexeyev (1915) from Novo-Elizavetovka, Odessa District. Later, these species were considered to be different development stages of *Cervavitus bessarabiae* Khomenko and *Cervavitus variabilis* Alexeyev (Schlosser, 1924; Dietrich, 1938; Flerov & Pidopličko, 1952).

The remains of deers from Honan and Shansi Provinces, China, were described by Zdansky (1925, 1927), who assigned them to *Cervocerus novorossiae* Khomenko (= *Damacerus bessarabiae* Khomenko). Their antlers had not bladelike tines. The bladelike tines are frequent in European Pliocervini. According to Teilhard de Chardin & Trassaert (1937), *Cervocerus novorossiae* from Shansi is marked by a variable structure of antlers. Azzaroli (1953) and Halthenorth (1959) are of the opinion that the species of Pliocervini from Eastern Europe are different than the Lower Pliocene deers from China which, therefore, should be given new specific and generic names. Asian Pliocervini are probably the ancestors of the genus *Axis* (the Lower Pliocene *Axis speciosus* Schlosser is the oldest of them) and *Cervus* (*C. perrieri* Cr.).

In addition to the species of Pliocervini, mentioned above, a deer first described by Gervais (1852) from Mont Lebéron (Vaucluse) as *C. matheroni*, occurred in Lower Pliocene. A similar form is described by Dames (1883) from Lower Pliocene of Pikermi as *C. pentelici*. It was difficult to establish the generic assignment of this deer. It was considered to be *Axis* (Gervais, 1852; Gaudry, 1873) or *Capreolus* (Dawkins, 1878; Dames, 1883; Lydekker, 1898). A new generic name of *Pliocervus* is erected for *C. matheroni* Gervais by Hilzheimer (1922). In some locatities (as, for instance, at Stavropol, Caucasia, USSR), *Pliocervus* accompanies the remains of *Procapreolus* (Vereshchagin, 1959; Korotkevitsh, 1964, 1965, 1966). *Pliocervus* from the southern European part of the USSR (Korotkevitsh, 1964, 1965), considerably differs in the structure of antlers from *Pliocervus matheroni*.

A structure of young antlers, different than that in *Procapreolus*, was found in *Pliocervus kutchurganicus* Korotkevitsh (1965). In my opinion, the antlers of young *Pliocervus* resemble to a certain extent those of
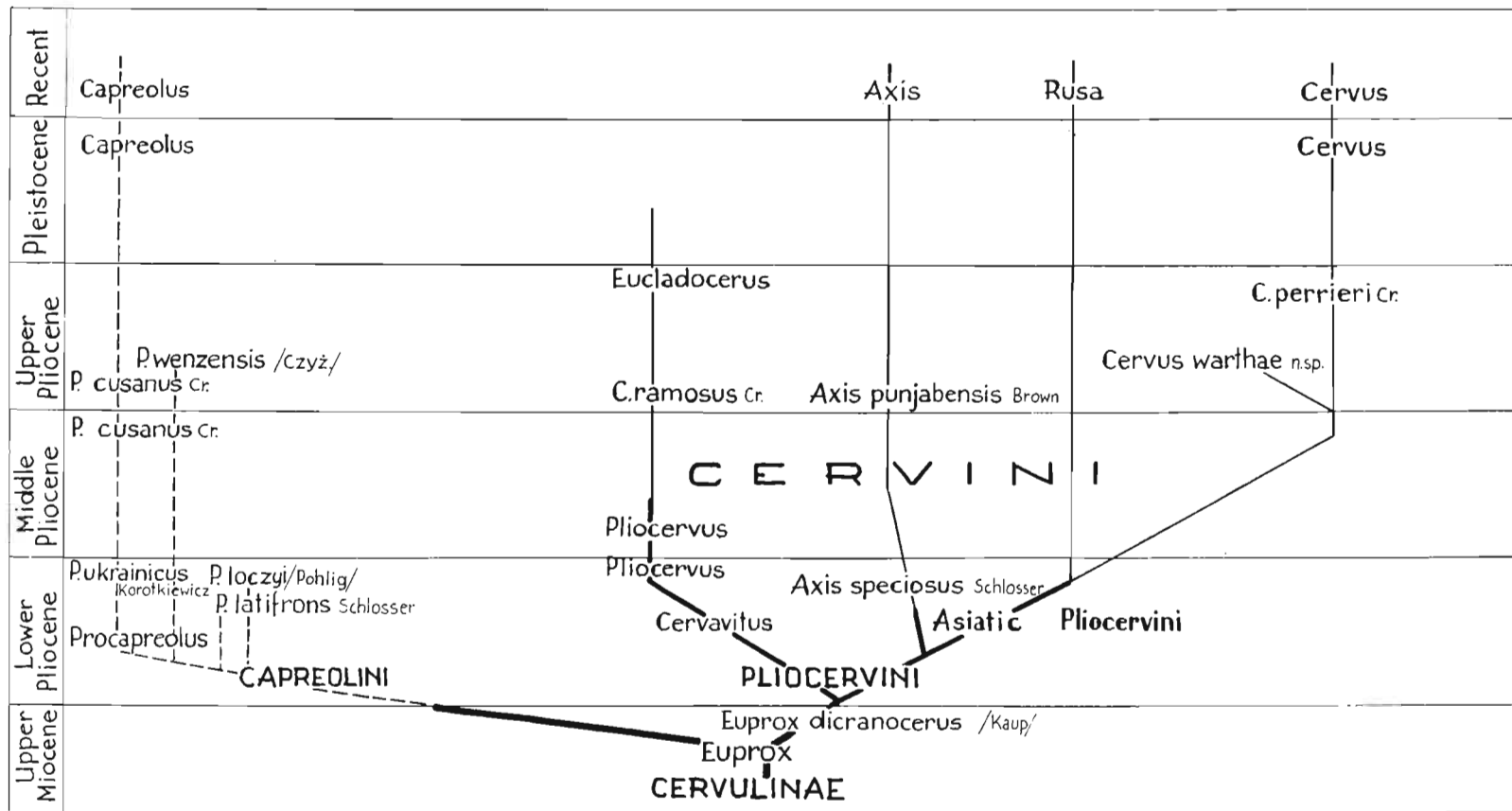
Fig. 1. — Phylogeny of Pliocene Cervinae.

C. elaphus L. Such antlers in *Pliocervus kutchurganicus* has the form of a small fork at the end of the long and almost completely straight beam. In the specimen, described by Korotkevitsh (1965, p. 112, Fig. 4), the antlers have a very poorly developed burr. The branching of the tips of antlers in young individuals is frequently observed in Recent deers. In roe deers, the second antlers have the spines of fork mostly directed upwards, and a strongly developed burr, whereas in *C. elaphus*, under favourable conditions, the tip of the first horn may be also forked, but the antlers of so young individuals have not a normally developed burr. In the structure of antlers of young individuals *Pliocervus*, the representative of Pliocervini is, therefore, related to the tribe Cervini. Within the tribe Pliocervini this genus is more modern than *Cervavitus* (for instance, the lack of the palaeomeryx fold on lower molars). Most species of *Pliocervus* were extinct without leaving any descendants, whereas *Pliocervus matheroni* Gervais may be considered (Depéret, 1890) an ancestor of *C. ramosus* Cr., from which *Eucladocerus* was subsequently derived (Fig. 1).

ZOOGEOGRAPHICAL REMARKS

The history of Pliocene Cervinae is related to the Eurasian area. The Lower Pliocene *Cervavitus* lived in South-eastern Europe, i. e. in Southern Ukraine: Novo-Elizavetovka, Petroverovka, Stratevka, Grebenniki, Novo-Petrovka, Andriashevka, Grossulovo, etc., as well as in Moldavia and Bessarabia: Taraklia, Cimislia, Gura-Galben, etc. (Boryssiak & Belayeva, 1948; Simionescu & Dobrescu, 1941). Hungarian findings from Hatvan (Gaal, 1943) make up the western limit of the range of *Cervavitus*, which probably never exceeded 48° of northern latitude. This deer lived in a warm (but not hot) climate and on the boundary between wood and steppe regions. Its remains occur abundantly, hence we may conclude that these animals formed big herds (Flerov, 1950).

The range of *Pliocervus* in Europe from France to Southern Ukraine is much more extensive than that of *Cervavitus*, but likewise limited only to southern areas.

Procapreolus lived on a vast territory stretching from France and Spain in Western Europe (Heinz, 1966) to the South-eastern Asia (Fig. 2). All locatities of this genus, recognized so far, are distributed within the range of the Recent genus *Capreolus*, but they are concentrated in its southern parts. Węże, Poland, situated north of 51° of northern latitude (11°45″ of longitude), is the northernmost locality of this genus. We may conclude, therefore, that *Procapreolus* lived further south and in a milder
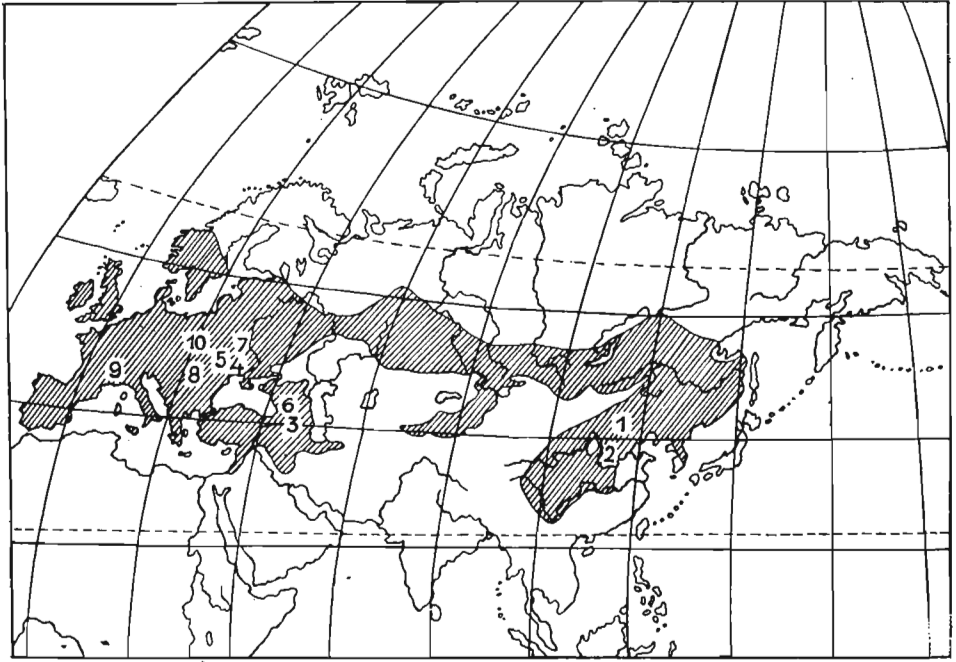
Fig. 2. — The most important localities with the remains of roe deers of the genus
Procapreolus and the present range of occurrence of the genus *Capreolus* (shaded
area).

1 Ertemte, Olan-Chorea and other localities in Inner Mongolia, China (*P. latifrons*
Schlosser); 2 Shansi, China (*P. latifrons* Schlosser); 3 Eldar, Transcaucasia, U.S.S.R.
(*Procapreolus* sp.); 4 Novo-Elizavetovka, Odessa District, U.S.S.R. (*Procapreolus*
sp.) and Novo-Ukrainka, U.S.S.R. (*P. ukrainicus* Korotkevitsh); 5 .Andreyevka,
Chorna Loshchina, Mikolayevsk District, U.S.S.R. (*P. cusanus* Cr.); 6 Caucasian
Stavropol, Rostov District, U.S.S.R. (*Procapreolus* sp.); 7 Kamyanskie, Zaporozhe
District, U.S.S.R. (*Procapreolus* sp.); 8 Fennyód, Polgárdi, Karád, Baltavàr, Hatvan
in the vicinities of Lake Balaton, Hungary; Styria Austria (*P. loczyi* (Pohlig)); 9
Perrier-Étouaires, Neschères and other localities in Auvergne, France (*P. cusanus*
Cr.); 10 Węże near Działoszyn, Poland (*P. wenzensis* (Czyżewska)).

climate than Recent roe deers (like fallow deers, the more primitive of
them *Dama mesopotamica* Brooke and *Dama dama* L.).

The range of the genus *Muntiacus* known so far has been shifted to
the west and north as a result of finding the remains of *Muntiacus
polonicus* n. sp. in Węże and of *M. pliocaenicus* Korotkievitsh in Ukraine.
During the Pliocene period, it certainly lived on much more extensive
areas than at present, since the locality Węże is situated near 51° of
northern latitude and Recent Cervulinae never exceed the 35th parallel
of latitude and do not occur in Northern China. The northern boundary
of the occurrence of *Muntiacus* runs along the watershed of the Hwang
and the Yangtze. Most species of *Muntiacus* live on the areas, situated
south of the 30th parallel. Węże is the northern- and westernmost locality,
where Upper Pliocene Muntiacini have ever been found.

QUANTITATIVE ANALYSIS OF THE OCCURRENCE OF *PROCAPREOLUS WENZENSIS* (CZYŻEWSKA) AND *CERVUS WARTHAE* N. SP. IN WĘŻE

Individual age of specimens was determined on the basis of the state of dentition. Only cheek teeth, i. e., milk teeth, premolars and molars (these teeth were mostly preserved in specimens), were taken into account. The following groups of specimens were distinguished:

I. Only milk teeth present.

II. Milk teeth and the first molar present.

III. Milk teeth and two molars present.

IV. Specimens with visible replacement of cheek teeth.

V. Slightly worn permanent teeth present.

Further groups VI—XI were determined on the basis of a description of dentition in *Cervus elaphus* L. and *Capreolus capreolus* L. (Raesfeld, 1957; Steliński, 1957).

VI. Slightly worn teeth. P_2 worn in the posterior part of the crown. P_3 and P_4 slightly worn, mostly posteriorly. Premolar fossettes visible. Molars with a somewhat sharp-pointed or flat internal edge. M_1 slightly worn on the entire surface. M_2 and M_3 mostly with worn anterior lobes. Fossettes of teeth open.

VII. More strongly worn teeth. Posterior part of P_2 crown worn; P_3 and P_4 with distinct transverse depressions, particularly posteriorly. Premolar fossettes still visible. On M_1, considerably worn, fossettes are closed, and on M_2 and M_3 still widely open.

VIII. The wear of P_2 reaching from the posterior to the anterior part of crown, further than half-way its length. The middle part of crowns in P_3 and P_4 less worn, raised. M_1 strongly worn but fossettes still visible. Edges of internal wall blunt and rounded. M_2 and M_3 fossettes still open. In M_3 even the ultimate lobe is worn.

IX. P_3 and P_4 fossettes in the form of circlets, mastication surface of the crown subflat. M_1 fossettes closed but visible, over the entire length, abrasion surface of the crown leveled. M_2 and M_3 crowns lower than in group VIII.

X. P_3 and P_4 without fossettes; in some cases they occur in the form of dots. Internal edge of M_1 substraight, fossettes — if present — occur in the form of a line, crown surface slightly concave. M_2 and M_3 fossettes closed, internal edge either with indistinct tops or undulating. Abrasion surface of these teeth fairly well leveled.

XI. P_3, P_4 and M_1 crowns completely worn. Traces of fossettes still visible on M_1 and M_2.

A presumable number of individuals was estimated for each group.

It is not in all cases that the dentition of deers is indicative of an individual's age. This may be most accurately determined on the basis of milk teeth and the growth of successive molars (Groups I—IV). The

age of, for instance, a roe deer may be thus determined with a considerable accuracy (Sokolov, 1959), On the other hand, the wear of crowns of cheek teeth and straitening of fossettes often display considerable divergencies, caused by a varying degree of resistance of teeth to abrasion.

Since: 1) both species from Węże are most similar to these Recent deers, that is, *C. warthae* n. sp. to *C. elaphus*, and *P. wenzensis* to *Capreolus capreolus*, and 2) *C. elaphus* and *C. capreolus* are similar in dimensions to both fossil species, I determined the individual age of the specimens from Węże by comparing them with *C. elaphus* and *C. capreolus*.

Particular species of Recent Cervidae considerably differ from each other in their average life time, for instance, the red deer lives about 20 years and roe deer — only somewhat more than 10.

The milk dentition of *C. elaphus* is replaced within 30—32 and of *C. capreolus* — within 16 months. Different tendencies are displayed by these two species (Bromée-Skuncke, 1952). In *C. elaphus*, the period of using milk dentition is extended, and in the roe deer — shortened. Other Eurasian deers display an intermediate trend in this respect. The milk teeth of the ancestors of *C. elaphus* were probably used for a shorter time than 32 months, and of those of the roe deer longer than 16 months. In its morphological characters, *C. warthae* n. sp. from Węże is similar to *C. elaphus* and, therefore, I believe that the replacement of its milk with permanent teeth took place in it within a similar time as in *C. elaphus*.

The tables presented below have been worked out according to the tables of life, used for illustrating the mortality of Recent populations. For the fossil material, this problem was elaborated by Kurtén (1952,

Table 1

Procapreolus wenzensis (Czyżewska) — 100 individuals

Age interval	Age	Number of individuals dying in age interval	Number of all individuals at beginning of interval (2)	Index of mortality
1	2	3	4	5
	months:			%
I	0– 4	20	100	20.0
II	4– 5	41	80	51.3
III	5–12	13	39	33.3
IV	12–16	6	26	23.1
V	16–24	11	20	55.0
	years:			
VI	2– 3	5	9	55.6
VII	3– 5	4	4	100.0

Table 2

Cervus warthae n. sp. — 64 individuals

Age interval	Age	Number of individuals dying in age interval		Number of all individuals at beginning of interval (2)		Index of mortality
1	2	3		4		5
	months:	no.	%	no.	%	%
I	0- 5	19	30	64	100	30.0
II	5-12	8	12	45	70	17.8
III	12-25	2	3	37	58	5.4
IV	25-30	19	30	35	55	54.2
	years:					
V	2.5- 3	3	5	16	25	18.7
VI	3- 5	5	8	13	20	38.5
VII	5- 7	4	6	8	12	50.0
VIII	7- 9	1	1	4	6	25.0
IX	9-11	—	—	3	5	—
X	11-13	2	3	3	5	66.7
XI	13-15	1	2	1	2	100.0

1953, 1958). On the whole, age intervals in such tables are equal to each other. In Tables 1 and 2, unequal periods, determined by the appearance of successive molars, correspond to Groups I—V.

The bones of mammals were accumulated in the cave at Węże during a period which was not accurately determined (Sulimski, 1959; Kowalski, 1960). This period was, however, so long that individuals of the populations which lived in the vicinity of the cave when the process of the accumulation of bones was started, did not survive until the moment when this process was finished, despite the fact that remains are usually quickly accumulated in the localities of this type (a cave with an opening in the top part). Hence, Tables 1 and 2 contain the data on the amounts of individuals which perished at Węże, but no time is given within which this took place.

Figs. 3 and 4 are drawn on the basis of column 3 in Tables 1 and 2 (number of the individuals found). Most individuals of *C. warthae* n. sp. (19.3 per cent) occur in the first (6 month old) and fourth (2—2½ year old) age intervals. Both groups fall to short, 5—6 month periods. On the other hand, there are very few individuals of the third age interval (2.3 per cent) which are 12—25 month old. A few individuals each form intervals of adults.

Most remains of *P. wenzensis* are in the second (41 per cent) and first (20 per cent) age intervals, whereas the smallest number of them — in the seventh age interval.

The differences in the number of individuals of both species in particular groups of age are fairly large, especially in groups I—IV. The greatest differences occur in groups II (*P. wenzensis* — 41 individuals, *C. warthae* n. sp. — 12, difference — 29) and IV (*P. wenzensis* — 6,
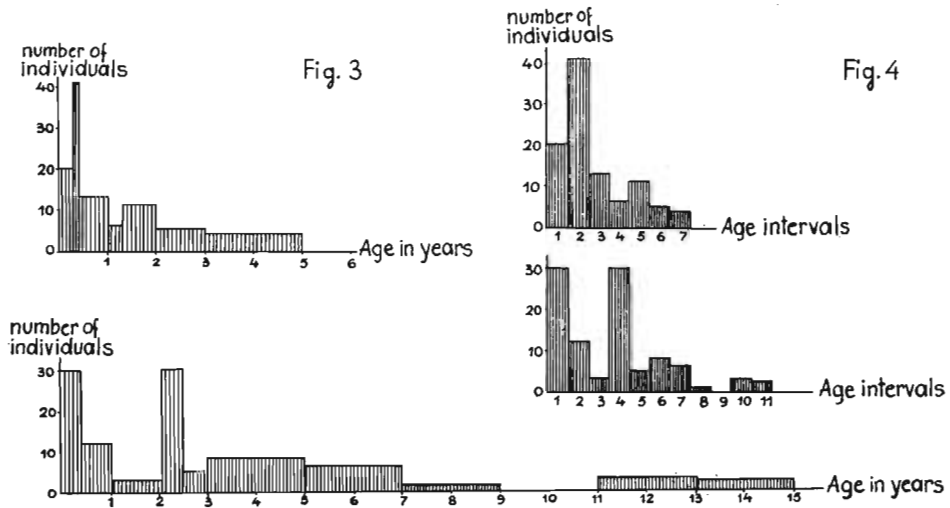

Fig. 3. Diagram of the number of dying individuals in successive age intervals for *Cervus warthae* n. sp. (bottom) and *Procapreolus wenzensis* (Czyżewska) (top) with consideration of the age.

Fig. 4. Diagram of the number of dying individuals in successive age intervals for *Cervus warthae* n. sp. (bottom) and *Procapreolus wenzensis* (Czyżewska) (top).

C. warthae n. sp. — 30, difference — 24), as well as groups I and III (I: *P. wenzensis* — 20, *C. warthae* n. sp. — 30; III: *P. wenzensis* — 13, *C. warthae* n. sp. — 3, difference, in both groups — 10).

The deers which perished at Węże were mostly young individuals, in which the process of the replacement of dentition was not yet completed. Groups I—IV of *P. wenzensis* include 80 per cent of all individuals of this species, those of *C. warthae* n. sp. — 75 per cent. Both deers display different quantitative proportions in the youngest two age intervals. In the case of *P. wenzensis* they comprise 61 per cent, and of *C. warthae* n. sp. — 42 per cent. In addition, group II of *P. wenzensis* is twice as numerous as group I (41 and 20) and in *C. warthae* n. sp. this relation is opposite (12 and 30).

The remains of adult *P. wenzensis* make up 20 per cent of all specimens (groups V—VII) and those of adult *C. warthae* n. sp. 25 per cent (groups V—XI). The bones of a few old individuals of *C. warthae* n. sp. were found, whereas such specimens of *P. wenzensis* were lacking.

Fig. 5 contains survivorship curves (column 4 of Tables 1 and 2) of *P. wenzensis* and *P. warthae* n. sp. In the case of *P. wenzensis*, this curve

reveals a strong decrease during the life time up to the 5th month, which corresponds to a high mortality index (51.3 per cent). Such a high mortality persists also in further age intervals, the curve dropping rather abruptly. The curve of *C. warthae* n. sp. displays a contrast between an almost straight line for 12—25 month old individuals (group III with mortality index of 5.2 per cent) and a violent drop of the curve in group IV (index — 54.5 per cent). A curve for *Ovis dalli dalli* Nelson (Deevey, 1947), shown for the purposes of comparison, testifies to a high mortality of young individuals. The mortality of adults is low but, in the age interval of more than 10 years, its curve suddenly ascends. The curves for *C. elaphus* L. display (Taber & Dasman, 1957, Table 12) small fluctuations of the mortality index of adults, the same as in the case of *Capreolus capreolus* L. (*l. c.*, Table 11). In these species, the mortality index is high in the first year of age and very low — in the second. The curves have also been drawn (Fig. 5) for the populations of *Odocoileus hemionus columbianus* (Richardson), which live in a) evergreen brushwood (chaparral), and b) on the areas made productive after burning out of forests (shrubland). The latter b) population was much more numerous and displayed a higher mortality index (Taber & Dasman, 1957, Tables 9 and 10). The curve of population a) is similar to that of *C. warthae* n. sp. and of b) — to that of *P. wenzensis*.

CONCLUSIONS FROM THE QUANTITATIVE ANALYSIS OF THE REMAINS OF DEERS FROM WĘŻE

At Węże, the bone breccia was formed in a cave situated in calcareous hills. The geological conditions of this locality were described by Samsonowicz (1934), Sulimski (1959) and Kowalski (1960).

The remains of *P. wenzensis* and *C. warthae* n. sp. were almost uniformly distributed over the entire section. During taking out and preparation of the breccia, no visible difference could be observed in the number of remains of both species. Both the upper, red and lower, gray breccia contain the bones of both deers.

At Węże, more individuals of *P. wenzensis* (100) than of *C. warthae* n. sp. (64) were found. The former was probably a more numerous species than the latter. It is clear from the studies of Vagenknecht (1962) who analyzed the destruction of trees in forests by herds of deers depending on the structure of populations (under natural conditions, deers do not cause damage in forests) that the density of primitive populations was small, e. g. ,in the Eastern Carpathians, 2—4 individuals lived on an area of 1,000 ha. Since we do not know the time within which their bones were accumulated, it is difficult to conclude on the density of the Pliocene deer population in the environs of the cave at Węże.
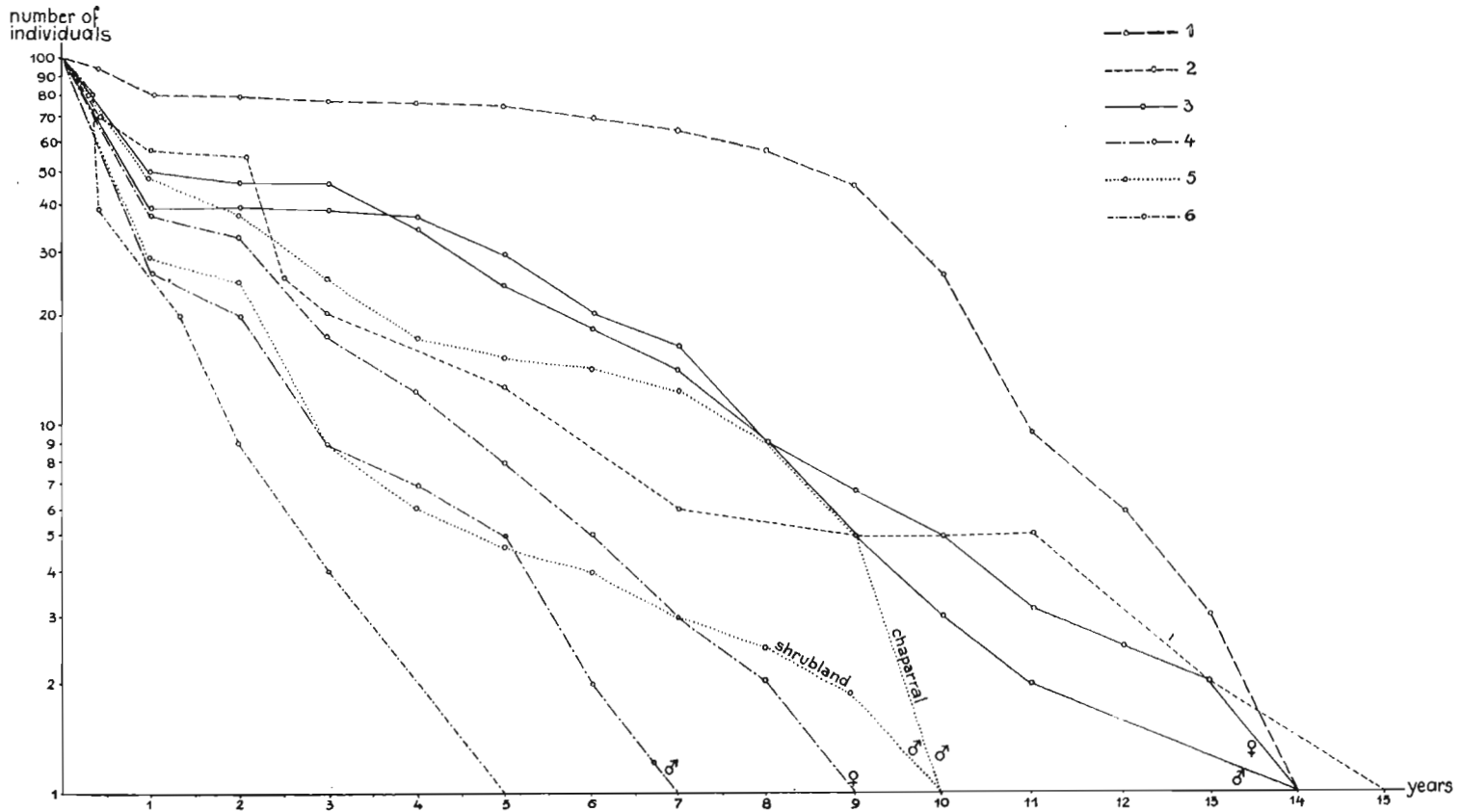
Fig. 5. — Survivorship curve: 1 *Ovis dalli dalli* Nelson, 2 *Cervus warthae* n. sp., 3 *Cervus elaphus* L., 4 *Capreolus capreolus* L., 5 *Odocoileus hemionus columbianus* (Richardson), 6 *Procapreolus wenzensis* (Czyżewska).

At Węże, many bones were found of young (75—80 per cent) and much less of adult individuals. Few old individuals belonged to *C. warthae* n. sp. According to Vagenknecht (1962), primitive populations usually contain a small number of young individuals. Many calves perish in the first year of their life, so that in the spring they represent only about 20 per cent of an entire population (increase = 40—50 and even 60 per cent). The losses of deers in older age intervals are smaller. A particularly great number of calves perish soon after their birth (Darling, 1938). Carnivors (volves, lynxes, foxes, etc.), diseases, accidents (Severcov, 1953; Halthenorth, 1959; Darling, 1938), climatic changes (a big drought, severe winter, etc.; Adams, 1960) are the most frequent causes of the death of deers. Carnivors, found at Węże, were mostly small-sized (except for *Agriotherium*) and probably could not be dangerous to adult deers, but they threatened young individuals.

At Węże, deer bones were accumulated in a cave-trap into which the animals fell by accident (Kowalski, 1960). A certain amount of bones might be also dragged into the case by the streams of water during downpours. The latter remains belonged to the victims of carnivors or to the animals which died of other causes. The remains of deers, collected at Węże, make up only a small percentage of all individuals which died in this locality.

The age of deer remains from Węże is different (very many young individuals) than the age structure of Recent deer populations and than that living in Węże in the Upper Pliocene. The occurrence of quantitative differences between *P. wenzensis* and *C. warthae* n. sp. may be explained by different absolute quantities of them, different modes of life and different cycles of the development of dentition.

Bones of deers are very numerous in the breccia from Węże. The deers stayed on the area surrounding the cave all the year round — the same as Recent deers, which now inhabit extensive forest areas — but their number in different parts of woods varied in individual seasons. In some seasons, there were more of them near the cave (the probability of an accident increases when the population is more numerous).

The number of young individuals (the first age interval) of both species is great (*P. wenzensis* — 20 per cent, *C. warthae* n. sp. — 30 per cent). These are bones of suckling calves, whereas no remains of newborn calves have ever been found in this vicinity. Very young deer calves died in the forest and their delicate bones could not be preserved. Hinds or does, suckling their young, usually stay in woods, preferring such places where they may find sufficient fodder (grass, herbs, etc.) and hide from their enemies. I believe, therefore, that the forest at Węże had many clearings and an abundant undergrowth.

In temperate climate zone, deer calves are born in the late spring, for instance, roe deers are born in May or June, but sometimes, there

are certain deviations from this rule (Steliński, 1957, certain specimens of roe deers at Zool. Inst. USSR Acad. Sci. in Leningrad). In warmer climate zones, calves are born earlier, for instance, *Dama mesopotamica* Brooke in Iran (30—35° of northern latitude) — in March. During the Pliocene period, the region of Węże had a warmer climate than now and, therefore, I conclude that the deers of the first age interval lived in spring and summer.

The remains of the *P. wenzensis* individuals of the second age interval make up 41 per cent and of *C. warthae* n. sp. — 12 per cent. In the case of *P. wenzensis*, the period corresponding to this group was short (for roe deers this is October) and took in the autumn and in *C. warthae* n. sp. these were autumn and winter months. In the late summer, Recent deers change their diet, eat less grass and herbs, and in autumn and winter they live on leaves, young shoots of trees and brush, bark, etc. Herds leave open clearings and pass inside forest areas. In autumn, *C. warthae* n. sp. also left the environs of the cave and earlier than *P. wenzensis* went into dense woods, hence there is a smaller number of the specimens of the second age interval of this species. A high percentage of the representatives of the second age interval of *P. wenzensis* is, in my opinion, caused by frequent accidents which happen when young deers begin to display a certain independence.

The third age interval of *P. wenzensis* fell in autumn, winter and early spring and was less numerous (13 per cent). *P. wenzensis* probably stayed in other parts of the forest. In *C. warthae* n. sp. this age interval amounts only to 3 per cent. In *C. elaphus* L. this is a period longer than a year. Individuals of this age usually migrate together with an entire herd and are sufficiently experienced to avoid traps. It is less probable that the deers of this age interval should permanently stay in other parts of the forest. It is clear from the tables of life for *Odocoileus* (Taber & Dasman, 1957, Tables 9, 10), and roe deer (Table 11) that a smaller number of individuals die at the age of 1—2 years.

The remains of *P. wenzensis* of the fourth age interval (6 per cent) come from the late summer or early autumn. These individuals, older than a year, were already members of the herd and were not led by their mothers. In *C. warthae* n. sp., the fourth age interval (30 per cent) fell in the late summer and autumn (about $2^{1}/_{2}$ years of age). An increase in mortality in this group is related with the rut period. *C. elaphus* prefers open spaces for rutting grounds where a few herds may come together. During such a period, deers are more active and careless, particularly young ones. There were possibilities of lethal mutilations, especially frequent in young and weak individuals. It results from Taber's & Dasman's (1957) tables of life for *Odocoileus* (Tables 9, 10) and roe deers (Table 11) that 2—3 year old individuals die more often than those in preceding age intervals.

In *P. wenzensis* the fifth age interval is more numerous (11 per cent) than in *C. warthae* n. sp. (5 per cent). The first rut, falling during that period, might cause a higher mortality.

DESCRIPTIONS

Family **Cervidae** Gray, 1821
Subfamily **Cervinae** Baird, 1857
Tribe **Capreolini** Simpson, 1945 (= Capreolidae Brooke, 1828)
Genus *Procapreolus* Schlosser, 1924
Procapreolus wenzensis (Czyżewska, 1960)

(Pls. I-IV)

1960. *Cervocerus wenzensis* Czyżewska; T. Czyżewska, Nowy gatunek jelenia...,
   p. 299; Pl. 2, Fig. 2a; Pl. 3.

Material. — Fragments of skulls, upper jaws and mandibles with teeth and detached teeth, assigned to the following age intervals:

   I. Below 1/2 year (in roe deer, 2–4 months). Six fragments of upper jaws, 9 of mandibles and 6 detached teeth. Probable number of individuals — about 20.
   II. About 1/2 year (in roe deer, 5 months). Seven fragments of skulls, 24 of mandibles, 13 upper jaws and 2 teeth. About 41 individuals.
   III. Half-year to a year (in roe deer, 5–12 months). A skull, 12 fragments of mandibles, 3 of upper jaws. Probably 13 individuals.
   IV. More than a year (in roe deer, 12–16 months). A skull, 4 mandibles, 2 upper jaws. Probably 6 individuals.
   V. Below 2 years (in roe deer, 16–24 months). Ten fragments of mandibles, 4 upper jaws. Probably 11 individuals.
   VI. Two-three years (in roe deer, 24–36 months). Three mandibles, 3 upper jaws. Probably 5 individuals.
   VII. Three-five years (in roe deers, the same). Two skulls, 4 fragments of mandibles. Probably 4 individuals.

In addition, there are six skull fragments of adult individuals of an indeterminate age.

The material of *P. wenzensis* does not contain skulls of individuals of the first age interval. In my opinion, the skulls of such young individuals of fossil deers are mostly preserved as separate bones, e. g., upper jaws with teeth. The best preserved specimens of skulls are Nos. 1241I [2],

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[2] This numeration of specimens corresponds to the list of deers from Węże, prepared at the Department of Palaeozoology of the Wrocław University. Roman numerals denote age intervals of specimens. I also used this numeration in my previous works (Czyżewska, 1959, 1960).

370II, 409IV, 345IV and 220VII, whereas the best preserved antlers are those of the specimen No. 220VII (Czyżewska, 1960, p. 295, Pl. 3).

Description. — *Skull* (No. 409IV). Skull without antlers, facial part damaged; nasals, premaxilla and anterior part of maxilla as far as alveolus of DP² — lacking. Except for M² and M³, which grows on the left side, all teeth destroyed. Palate slightly beaten in; both zygomatic arches deformed, the left lacrimal fossa damaged.
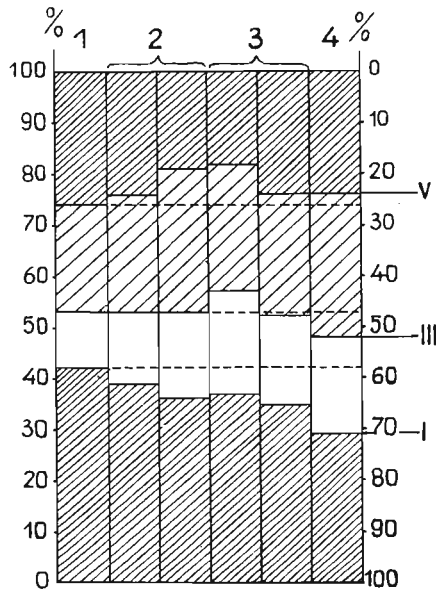

Fig. 6. Diagram of indexes of lengths of the bottom part of skull (indexes: *I* length of basioccipital + basisphenoid; *III* length of palate; *V* length of palatinum). 1 *Procapreolus wenzensis* (Czyżewska), No. 409IV; 2 *Capreolus pygargus* Pallas, specimens ZMUWr Nos. 1669 and 1564; 3 *Capreolus capreolus* L., specimens ZMUWr Nos. 5 and 1653; 4 *Muntiacus muntjak* Zimmermann, ZMUWr No. 45. Scale on the left for index I, on the right for indexes III and V.

This skull is slightly smaller than that of the Sibirian roe deer or the large, European roe deer and pronouncedly smaller than that of muntjac. A distance between basion and a line connecting DP² (medial line) is here called a length (in No. 409IV = 122.3; in roe deer = 112.8 — 129; in *M. muntjak* Zimmermann = 108). This measurement, which could not be taken on other specimens of *P. wenzensis*, is a basis for most indexes calculated for this skull.

Basioccipital and basisphenoid are long and narrow (lenght of skull to length of basioccipital and basisphenoid = 42.6; length to width of basioccipital and basisphenoid = 51.9) like in roe deers (34.9 — 39.3; 52.2 — 63.5) and in muntjac short and wide (29.6 and 87.5) (Fig. 6).

The following foramina are visible on specimen No. 409IV: foramen opticum, f. palatinum maj., f. ovale, f. lacerum ant., f. lacerum post., f.

stylomastoideum and f. hypoglossi (= condyloideum ant.). Their position is the same as in roe deers.

As in roe deers, the osseous palate is short and wide; in muntjac it is long and narrow. An elongate depression is visible in the anterior part of palate. Palatinum short. The row of cheek teeth of this skull and of the skulls of roe deers is slightly arcuate, in muntjac — more straight.

In lateral view, the skull No. 409IV has a convex forehead and convex, posteriorly inclined parietals. The profile line of the frontal in the medial plane is bent near the supraorbital foramen and mildly convex posteriorly, resembling the skulls of young roe deers and C. elaphus and of adult Axis axis Erxleben, but conspicuously differs from the profiles of adult Rusa, fallow deers, Axis porcinus Zimmermann and C. elaphus.

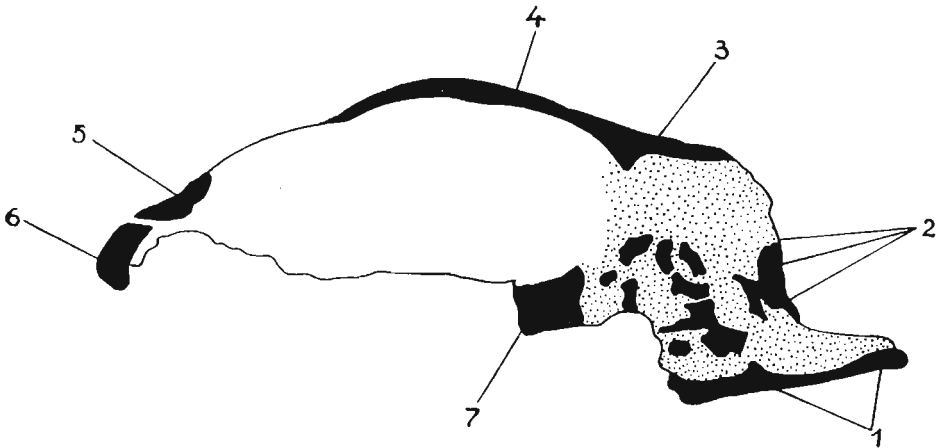Fig. 7. — *Procapreolus wenzensis* (Czyżewska). Longitudinal section of skull No. 124II, ca. ×0.8. *1* maxillae, *2* fragments of turbinals of maxilla, *3* incisura ethmoidalis, *4* frontal, *5* parietal, *6* occipital, *7* praesphenoid.

In relation to the skull length the frontal is short (in No. 409IV — 57.4; in roe deer — 51.2 — 53.1); in muntjac this index is much larger (72.2). The width of the frontal between supraorbital foramina is larger than that in the skulls compared (forehead wide and short) (Fig. 8). Behind orbits, the frontals of *P. wenzensis* and roe deers are wide, in muntjac — much narrower (the ratio of the lenght of the frontal to its width behind orbits in No. 409IV amounts to 73.6, in roe deers to 79.6 — 91.7, in *M. muntjak* to 69.2).

The skull region behind orbits in No. 409IV is long; parietals longer than in larger skulls of roe deers (in No. 409IV = 49, in roe deers = 35–42). The skull length index for the length of parietal in No. 409IV = 40.2, in roe deers 27.1 — 35.4, in *M. muntjak* 35.2. A considerable length of parietals is undoubtedly a primitive character.

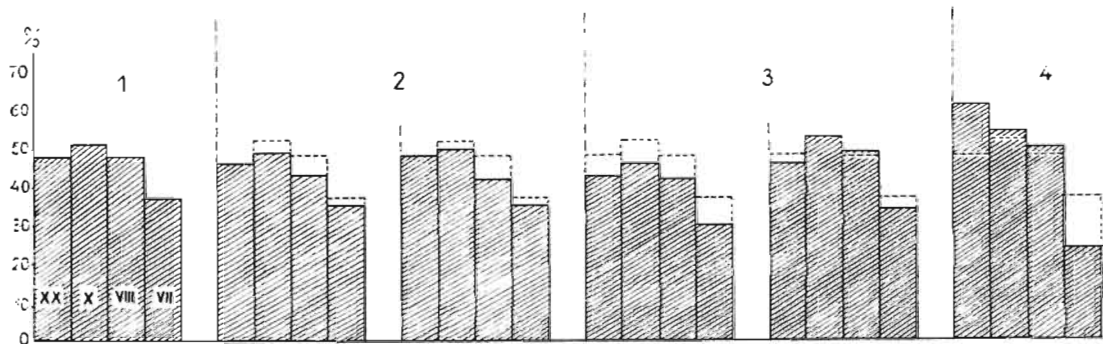Very sligthly outlined temporal lines are visible on the skull No. 409IV.

Fig. 8. Diagram of indexes of the width of skull (indexes: *XX* width of occiput, *X* width of parietal, *VIII* width of frontal behind orbits, *VII* width of frontal between supraorbital foramina). 1 *Procapreolus wenzensis* (Czyżewska), No. 409IV; 2 *Capreolus pygargus* Pallas, specimens ZMUWr Nos. 1669 and 1564; 3 *Capreolus capreolus* L., specimens ZMUWr Nos. 5 and 1653; 4 *Muntiacus muntjak* Zimmermann, ZMUWr No. 45.

In roe deer or *C. elaphus*, these lines are much more distinct even on the skulls of young individuals. The temporal jaw muscle in *P. wenzensis* was, therefore, less strongly developed than in roe deer or *C. elaphus*.

The width-length index of parietal in No. 409IV amounts to 76.6, whereas in roe deer to 58.3 — 66.7 and in *M. muntjak* to 64.5.

The braincase of No. 409IV is high ,the skull length-height index amounting to 48.4 (in *M. muntjak* to 47.6, in roe deer to 38.8 — 45.1). Maxilla below orbit is low (index for No. 409IV = 17.7, for roe deer = = 26.0–26.6, for *M. muntjak* = 23.6). These indexes distinguish *P. wenzensis* from roe deers and muntjac (Fig. 9).

Lacrimal fossa of the specimen No. 409IV is longer and deeper than that in roe deers and smaller than in muntjac. The facial part of the
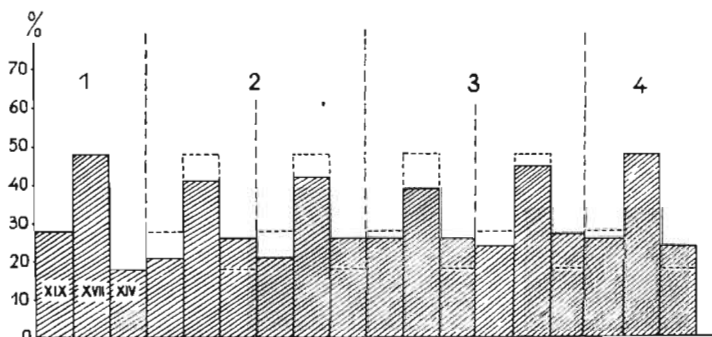

Fig. 9. Diagram of indexes of the height of skull (indexes: *XIX* height of occiput, *XVII* height of the skull, *XIV* height of maxilla). 1 *Procapreolus wenzensis* (Czyżewska), No. 409IV; 2 *Capreolus pygargus* Pallas, specimens ZMUWr Nos. 1669 and 1564; 3 *Capreolus capreolus* L., specimens ZMUWr Nos. 5 and 1653; 4 *Muntiacus muntjak* Zimmermann, ZMUWr No. 45.

lacrimal is more spacious than in roe deer and smaller than in muntjac. Both lacrimal foramina, which are not situated inside orbit, are visible on the margin of lacrimal fossa. Finding the lacrimal opening inside the orbit of the specimen No. 220VII (Czyżewska, 1960) was caused by the fact that this specimen was damaged. Lacrimal fossa is situated over M^1 and posterior part of DP^4, whereas in roe deer — over DP^4 and in an adult muntjac it stretches from M^1 to P^2.

Occiput high (index for No. 409IV = 28.2, for *C. pygargus* Pallas = = 20.7, for *C. capreolus* = 25.0 and for *M. muntjak* = 25.9) and narrow. Its width in roe deers is much the same, whereas muntjac has a much wider occiput. Occipital condyles of No. 409IV are much wider and more triangular than in roe deers, in which their sides are almost parallel. Paroccipital process wide, fairly massive, its length being unknown. Supraoccipitals and exoccipitals of No. 409IV are not yet fused like in young roe deers.

Other specimens of skulls of adult individuals. A strongly bent margo interalveolar, with its margins of the left and right side very near each other, is visible on the specimen No. 220VII (the smallest distance — 14, in *Muntiacus reevesi* — 5.0–7.6, in *M. muntjak* — 6.8–12.5 and in *Elaphodus cephalophus* — 13.2–16.7). In Cervinae, distances between these margins are larger, in roe deers — intermediate.

Auditory bulla (specimen No. 171) is not very large, with smooth surface, convex, not projecting above basioccipital. External auditory meatus elongate, without crest (the anterior-posterior length of auditory bulla = 23, the largest width = 17.8, the length of auditory meatus = = 24.5).

Fragments of nasalia of the skull No. 220VII are in such a position, as if their posterior margin did not reach the line connecting anterior margin of orbits, as is the case of the skulls of Cervulinae and *Axis*. In Cervinae these bones do reach the line connecting the margins of orbit. Nasals of the specimen No. 220VII are poorly preserved, but there is a possibility of the displacement of bones, which does not allow one to determine their position. I think that this position might be as primitive as in Cervulinae.

The medial length of the frontal, known for young individuals, reaches 71 and for the specimen No. 345IV it amounts to 64. The width of the frontal between supraorbital foramina amounts to 40–47, averaging 43.7, and in a contraction behind orbits to 51.0–65.5, averaging 57.4. Frontal of *P. wenzensis* was longer than that of *Muntiacus reevesi* and roe deers, and shorter than in the rest of Recent deers. Smaller widths of the frontal are recorded in *Elaphodus cephalophus*, *Muntiacus* and roe deers (Fig. 10).

The length-width indexes of the frontal between supraorbital foramina and in the contraction behind orbits amount, for the specimen No. 345IV,

to 62.5 and 79.7. Roe deers and *C. elaphus bactrianus* Lydekker with wide frontals have the former index high, whereas in muntjacs and *Elaphodus cephalophus*, which have a narrow frontal, it is low. The latter index
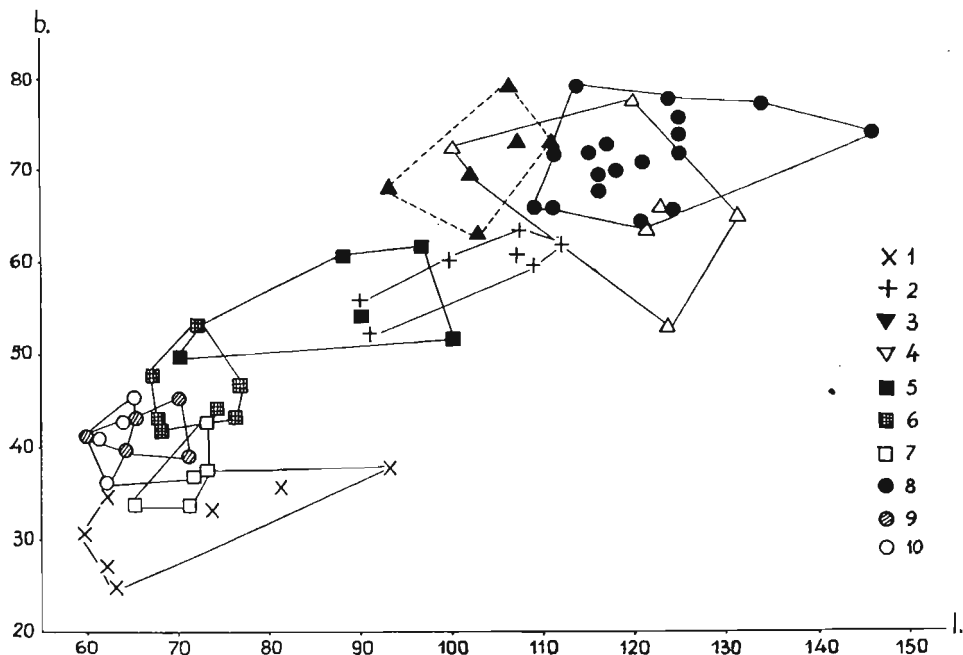

Fig. 10. — Diagram of the dimensions of the frontal: width between supraorbital foramina (on the left) and length (bottom). 1 *Capreolus*, 2 *Procapreolus wenzensis* (Czyżewska), 3 *Cervus elaphus* L., 4 *Elaphodus cephalophus* Milne-Edwards, 5 *Dama dama* L., 6 *Axis axis* Erxleben, 7 *C. (Rusa) unicolor* Kerr, 8 *C. elaphus bactrianus* Lydekker, 9 *C. (Sika) hortulorum* Swinhoe, 10 *Muntiacus*.

is, in *M. muntjak* and *E. cephalophus*, lower and in *M. reevesi* (80.7) and Cervinae (more than 85.9, behind orbits frontals wide) — high.

Recent Cervulinae and Cervinae have different dimensions and indexes of the frontal. Muntjacs and *Elaphodus cephalophus* (Cervulinae) have their frontals narrow, as compared with their length (the index of the length to the width between supraorbital foramina amounts to 39.7–59.3, the highest one being in *Elaphodus*). The ratio of the length of the frontal to its width behind orbits is in these deers relatively low (60.5–86.1). Cervinae have frontals wider in relation to their length; the first index is more than 50, the mean of the second varies from 85.9 to 121.5. In the indexes of the frontal, *P. wenzensis* differs from Cervulinae (a much wider frontal), the first index being higher and the second fairly high as for Cervinae, but lower than the average in Cervinae. An intermediate value of the second index testifies to the primitivity of *P. wenzensis* (Fig. 10). Supraorbital sulcus is narrow, deep, clearly outlined, posteriorly slightly tapering and bending towards the middle. The anterior extension

of this sulcus is very slight. This region considerably resembles the skull of a roe deer. Orbit margin conspicuous.

A fragment of the skull of a young male deer (No. 471II) has a preserved lower part of the pedicle of horn. Slightly worn milk teeth and M^1 make up the dentition of this specimen. Such a dentition occurs in 5-month old roe deers and 5 to 10-month old *C. elaphus* L. The first antlers begin to develop in the fifth month of life of a roe deer, i. e. in October (Steliński, 1957), occurring in the form of a swelling on the forehead in the individuals which already have M^1 teeth. The development of the pedicles of antlers takes further three months, so that the first horns appear in February, when the individuals of the third age group have two molars. In *C. elaphus* (Raesfeld, 1957), the first pedicles of antlers are developed in winter of the first year of life (January-February) and in such individuals M^2 is growing, and M^1 has already certain traces of wear. The antlers of the spiked stage are formed at the end of the first year of life (May-September). In young *P. wenzensis*, the pedicles of horns were developed during the same period as in roe deers, and earlier than in *C. elaphus*.

In adult males, pedicles of antlers are situated on the sides of forehead widely a part, slightly diverging outwards, strongly bowed backwards and resemble those of *C. pygargus* Pallas. The inclination of pedicles in *P. wenzensis* was, however, stronger than in roe deers, but not so strong as in muntjac. In specimen No. 220VII, an angle between the lower margin of lacrimal fossa and anterior surface of pedicle amounts to 30°, in *C. elaphus* to 50°, in *C. pygargus* to 40° and in *Muntiacus muntjak* less than 20°.

The length of parietal, which in specimen No. 345IV amounts to 43.6, is larger than that in *Muntiacus reevesi* Ogilby and in roe deers. Other deers have longer parietals. The index: the medial length of the frontal to the length of the parietal in the skull No. 345IV amounts to 68.1; in adult Recent deers this figure varies from 39.7 to 81.6. Low indexes (less than 60, short parietal) are recorded in *M. muntjak, C. elaphus* and *C. capreolus*, medium ones (60–70) — in *M. reevesi, Sika* and *C. elaphus bactrianus* and high ones (more than 70) — in *Elaphodus cephalophus, C. pygargus* Pallas, *Axis axis* Erxleben, *Dama dama* L. and *C. (Rusa) unicolor* Kerr. The index of the specimen No. 345IV is intermediate between that met with in *C. capreolus* (59.4) and *C. pygargus* (72.3). The tendency is observed in deers of shortening of the part of braincase behind orbits, with a simultaneous elongation of the facial part of skull. Long parietals in *P. wenzensis* are indisputably a primitive character.

The upper jaw, usually preserved in its part below orbit and lacrimal, is relatively low (in No. 345IV — 24 and in No. 220VII — 25). The jaws of Cervulinae are lower (13.6–22.7) and high (more than 35) in the Siberian

roe deer, fallow deer, *Sika*, *Rusa* and *C. elaphus*. (The index: the length of frontal to the height of maxilla amounts in No. 345IV to 37.5, whereas in *M. reevesi* and *Elaphodus cephalophus* — to 20.3–30.8, and in *Axis axis* to 31.3–35.7). An index similar to that of *P. wenzensis* is displayed by *M. muntjak* (37.5–40.8) and in other Cervinae it is much higher as, for instance, in roe deer, fallow deer, *C. elaphus bactrianus*, in which it amounts to more than 60.

Facial tuber of the upper jaw is conspicuous. Maxilla of *P. wenzensis* only to a slight extent forms the lower part of the lacrimal fossa. Upper margin of maxilla is turned down to the inside of fossa. Lacrimal fossae characteristic of Cervulinae and Cervinae are fairly sizeable, whereas in roe deers, whose lacrimal is small, lacrimal fossae are poorly developed. Lacrimal fossa of *P. wenzensis* is triangular and separated from lacrimal hiatus by a straight edge similar to that in *C. elaphus*. The length of lacrimal fossa in the specimen No. 345IV amounts to 25 and in No. 220VII — to 27.5, the height resp. 19 and 24, depth — 8 and 10. The boundaries of lacrimal fossa in roe deer, *Axis axis* and fallow deer are indistinct. In roe deer it is short (11.0–15.6). Other deers have lacrimal fossae longer or of the same length as that in *P. wenzensis*. The height of the fossa in roe and fallow deers is smaller. Shallower fossae are recorded only in roe deers. The index of the length-depth ratio of lacrimal fossa amounts in *P. wenzensis* to 32 (in specimen No. 345IV) and 36.4 (in 220VII). In Recent deers this index varies within limits of 23.1 and 73.5, and in roe deers (shallow fossa), *Axis axis* and fallow deer it is less than 30. Fossae of medium depth are recorded in muntjacs, *P. wenzensis*, *Sika* and *C. elaphus*. *Elaphodus cephalophus* and *C. (Rusa) unicolor* have the deepest fossae. In *P. wenzensis* lacrimal fossa stretches from halfway the

Fig. 11 — *Capreolus pygargus* Pallas, longitudinal section through the skull, ZMUWr No. 202, ca × 0.75.

length of P^3 to halfway the length of M^2. In adult roe deers it is situated over M^1, P^4 and, in *C. elaphus*, over P^4, M^1 and M^2, and in *C. (Rusa) unicolor* over P^3, P^4 and M^1.

Thin and delicate bones are revealed by the sections of skulls of *P. wenzensis*. An angle between the palatal plate of maxilla and a line connecting the ethmoidal incisura of the frontal with the anterior margin of praesphenoid amounts to (specimen No. 124) 47°, in *C. pygargus* 49° and in *C. elaphus* 53°. In Cervulinae, the ethmoidal incisura of the frontal is situated on the line of the anterior margin of orbit (*M. muntjak*), in *C. pygargus* — halfway the length of orbit, in *C. elaphus* — on the line of the posterior margin of orbit ,and in *P. wenzensis* — identically as in roe deers (Figs. 7 and 11).

Mandible (Fig. 12 a-d). All mandibles of *P. wenzensis* are incomplete. Diastema is preserved in four specimens only. The best preserved specimens are Nos. 419I, 414II, 487IV and 220VII.

A distance between the posterior margin of M_3 and the posterior margin of the canine alveolus is called here the length of mandible (in No. 487IV, it amounts to 124.6 and in No. 220VII — to 134).

The mandible of *P. wenzensis* is longer than those of roe deers and muntjac and has a longer diastema. The index of ratio of the length of mandible to its height behind P_4 amounts for No. 487IV to 13 and for No. 220VII to 14.8. In roe deers it is much the same (13.6–15.7) and in muntjac somewhat higher (17.9) because of its shorter and higher mandible. In No. 487IV, the index of the length of mandible to the length of diastema amounts to 41.4, in 220VII to 42.7, and in muntjac to 43.5. Roe deers, with a short diastema, have a very low index (33.0–39.7). A short diastema is a primitive character.

The height of mandible behind M_3 amounts, in adult *P. wenzensis* (No. 440VII) to 27.0; in muntjacs, *Elaphodus cephalophus*, roe and fallow deers, as well as *Axis axis* the mandible is lower. The lowest mandibles are recorded in *M. reevesi* (9.8) and the highest — in *C. elaphus bactrianus* (42). Muntjacs and roe deers have low mandibles (up to 20 mm), while those of medium height (20–30 mm) occur in *Rusa*, fallow deers, *Sika*, *C. elaphus*, *Axis axis* and *P. wenzensis* and high (30–45 mm) ones in big *Sika* and *C. elaphus*.

The thickness of mandible behind M_3 amounts in No. 440VII to 11.8 and in Nos. 487IV and 220VII — to 13.0. In Recent deers it varies within limits of 6.8 and 22.0. Thin mandibles (up to 8 mm) occur in *M. reevesi* and in some of *M. muntjak*, those of medium thickness (8–16 mm) -– in *P. wenzensis*, some of *M. muntjak*, *Elaphodus cephalophus*, roe deers, *Rusa*, fallow deers, *Sika* and *Axis axis* and thick (more than 16 mm) ones are met with in grown up *Sambars* and *C. elaphus*.

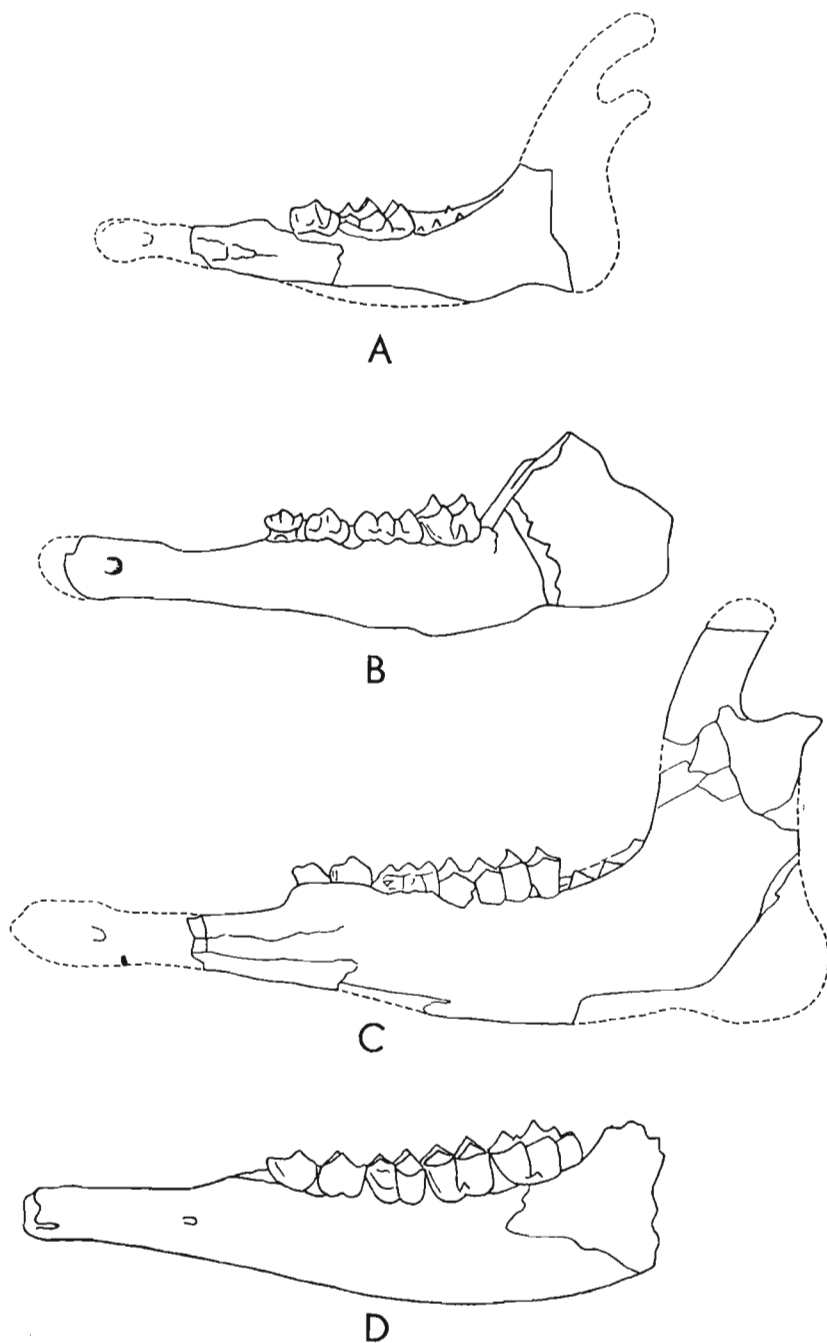The height of mandible in *P. wenzensis* considerably decreases

Fig. 12. — *Procapreolus wenzensis* (Czyżewska), fragments of left mandibles, ca. × 0.75. *A* partial reconstruction, No. 419I; *B* No. 424II; *C* partial reconstruction, No. 370IV; *D* No. 440VII.

anteriorly. The ratio of height behind M_3 to that behind P_4 amounts, in No. 487IV, to 64.2. In adult individuals, this mandible is thin, e. g., in No. 440VII, the height-thickness ratio amounts to 43.7. In Recent deers, this index fluctuates within limits of 46.8 and 80.5, the highest being in roe (58.8–66.2) and fallow deers (56.3–80.5).

The mandibles of *P. wenzensis* have a praemasseteric incisure (Nos. 419I, Fig. 12a). Angular process of the mandible is rounded and strongly shifted posteriorly (No. 415IV). Condyle of mandible — roller-like (No. 305), with almost parallel side walls. Temporal process (No. 370IV, Fig. 12c) delicate and narrow. The structure of this region indicates that the temporal muscle was weak since the temporal process is small, masseter and musculus pterygoideus were strong since praemasseteric incisure is present, horizontal ramus of mandible is thick and angular process of mandible is prominent. *P. wenzensis* could not widely open its jaws (large masseter) which did not hinder it from plucking soft and succulent leaves, grass and green shoots. It was different, however, in the case of dry and hard fodder and, therefore, it ate much less bark and twigs of trees.

Dentition (Fig. 13). Milk teeth of the mandible. DP_2: length 6.5–8.5, width 3.7–4.3, height to 4.3. In *M. reevesi*, DP_2 is smaller but slightly higher, in *C. capreolus* — shorter and approximately the same in width, in *C. pygargus* — of a similar length and width. Recent deers have higher DP_2. The ratio of the length of DP_2–DP_4 teeth to the length of DP_2 in specimen No. 383II amounts to 21.7 and in No. 419I to 25.3. In *P. wenzensis*, DP_2 is long as compared with the length of the row of milk teeth (in roe deers, 17.9). Protoconid prominent, coulisse [2] and [3] form parallel, oblique folds of dentine and enamel. DP_2 in specimens Nos. 290I and 424II are larger and have more differentiated crowns with longer coulisse[2] and [3], whereas in specimens Nos. 425I and 383II they are smaller and with quite short coulisses.

DP_3: Structure the same as that of DP_2, but elements of crown are much more distinct and larger. Coulisse[1] (situated across the crown) and anterior lingual cusp — present. A straight coulisse, inclined posteriorly and reaching metaconid, grows up from a large cardinal labial cusp. Length 8.8–11.3, width 4.7–5.9, height to 6.7. In *M. reevesi*, DP_3 teeth are lower and smaller, in *M. muntjak*, *Elaphodus cephalophus* and roe deers — of similar dimensions. Posterior part of the DP_3 crown — differentiated. In specimens Nos. 260II, 440II and 140II the posterior lingual cusp is separate, coulisse[3] not being fused with it. These are slightly worn teeth. In other specimens coulisse[3] is connected with entoconid. On abraded teeth, closed fossettes are formed in the posterior and middle parts of crown. Very strongly abraded teeth have a smooth surface.
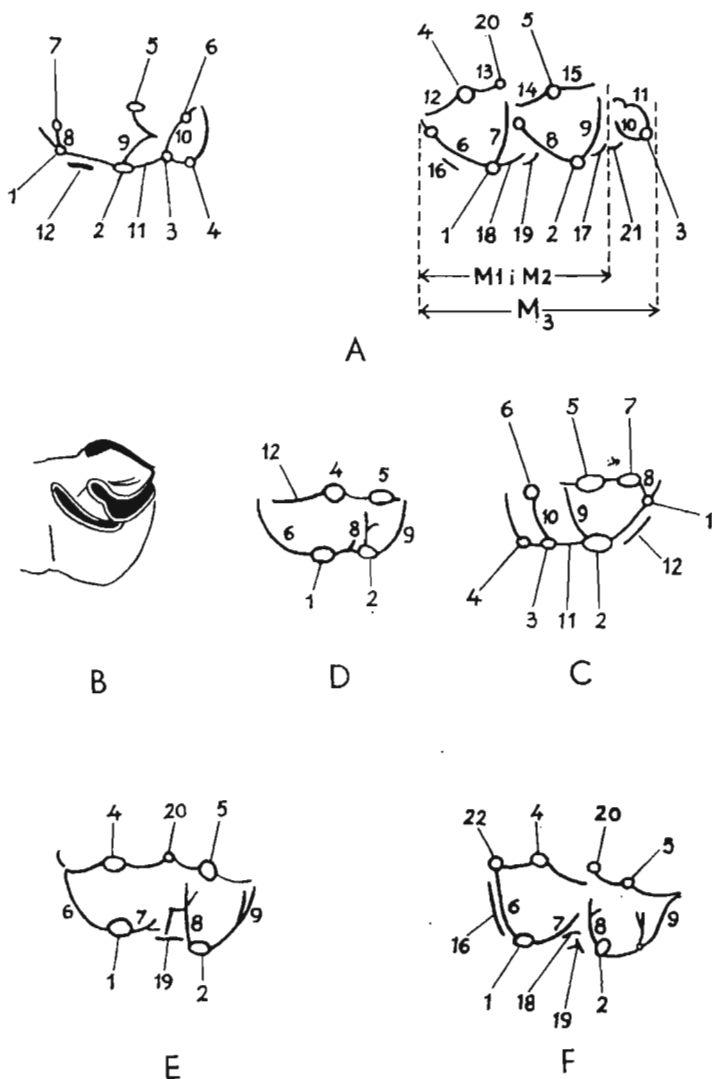
Fig. 13. — *A* simplified diagram of the structure of teeth in deers according to Obergfell (1951): premolars of the mandible (left). molars (right). Dentition of *Procapreolus wenzensis* (Czyżewska). *B* anterior lobe of DP$_4$, No. 290I, ca × 3. *C–F* diagrams of structure of: *C* of P$_4$, *D* of DP^2, *E* DP^3, *F* DP^4.

Premolars: *1* a cusp from which coulisse$_1$ runs, *2* cardinal cusp of labial wall (protoconid), *3* a cusp from which coulisse$_3$ runs, *4* posterior cusp of labial wall (hypoconid), *5* cardinal lingual cusp (metaconid), *6* posterior lingual cusp (entoconid), *7* anterior lingual cusp (paraconid), *8* coulisse$_1$, *9* coulisse$_2$, *10* coulisse$_3$, *11* counterpart of palaeomeryx fold, *12* anterior list.

Molars: *1* cusp on lobus$_1$, *2* cusp on lobus$_2$, *3* cusp on lobus$_3$, *4* cusp on lobus$_1$, *5* cusp on lobus$_2$, *6* praespina$_1$, *7* postspina$_1$, *8* praespina$_2$, *9* postspina$_2$, *10* praespina$_3$, *11* postspina$_3$, *12* praeala$_1$, *13* postala$_1$, *14* praeala$_2$, *15* postala$_2$, *16* anterior list, *17* posterior list, *18* palaeomeryx fold, *19* medianstyle (-stylid)$_1$, *20* mesostyle (-stylid), *21* medianstyle (-stylid)$_2$, *22* protostyle.

DP_4: Length 14.0–16.8, width 5.9–8.2, height to 8.0. In *M. reevesi* it is smaller and lower, in *Elaphodus cephalophus* — shorter, lower and of a similar width. *M. muntjak* and roe deers have DP_4 similar dimensions, except for height which in muntjac is smaller. Mesostylid$_1$ and $_2$, which is subject to rapid wear, occur on unworn DP_4 teeth of *P. wenzensis*. Lingual walls of lobes diagonal to the long axis of the tooth, particularly so on lobe$_2$. Labial walls of lobe$_1$ are bent at an angle exceeding 90°, postspina$_1$ situated almost parallel to the long axis of the tooth and — on further lobes —at an acute angle. A palaeomeryx fold (No. 290I, Fig. 13B, and No. 471I) is visible on lobe$_1$ of slightly worn teeth. Fossette of lobe$_1$ is posteriorly broadly connected with lobe$_2$. A postspina$_1$ — praespina$_2$ connection occurs on DP_4, whereas there is no connection between postala$_1$ and praespina$_2$. Medianstylid$_2$ present on all teeth, medianstylid$_1$ — variable in size from a sligthly marked to middle–sized. Anterior and posterior list occur on anterior and posterior parts of the tooth. DP_4 is rapidly worn: in the fourth age interval crowns are very low, fossettes contracted and cusps considerably blunted.

The length of the DP_2–DP_4 row of *P. wenzensis* amounts to 32.7 and is much the same as that in *M. muntjak* and *C. pygargus*.

Permanent dentition of the mandible. Permanent teeth of the mandible in *P. wenzensis* are low-crowned and have strongly inclined walls (Czyżewska, 1960).

P_2 and P_3 are similar in structure and size to DP_2 and DP_3. Internal wall of P_4 forms an elongate cardinal lingual cusp (metaconid). A closed cavity occurs in the anterior part of this tooth, which is similar to P_4 of roe deer (Fig. 13C).

Medianstylids of molars middle-sized, anterior and posterior lists present. A palaeomeryx fold — slightly marked on unworn M_1 and M_2. The length of the P_2–M_3 row = 73.

The length-height index of the P_4 crown (in No. 220VII–65.2 and in No. 440VII–69.7) is in Recent deers, the lowest in *M. muntjak* (60.2, low P_4) and the highest in *Sika* (108.4) and *Rusa* (120.3). This index of M_3 (in No. 220VII–50 and in No. 440VII–60.7) is the lowest also in *M. muntjak* (45.6, low M_3) and the highest in *Rusa* (73.3).

Milk dentition of the upper jaw. In deers, these teeth are four-cusped (Weber, 1928, *v.* II, after Stehlin, 1910). On the labial side, there are paracone and metacone, and on the lingual side — protocone and metaconule (with a tendency to a stronger molarization than that in the teeth of the mandible) (Fig. 13 D-F).

The length of the DP^2–DP^4 row, amounting in *P. wenzensis* to 29.0–32.7, approaches that in *Elaphodus cephalophus* and *C. capreolus*.

DP^2 simple in structure. Few plates of dentine and enamel occur inside fossette. Internal and posterior parts are subject to strong wear,

particularly wide surface being formed on the posterointernal wall. Length 8.5–12.7, width 6.3–8.9, height to 6.9.

DP[3] is marked by a bifurcation of lingual walls (postspina[1], praespina[2], postspina[2]), variable structure of medianstyle[1] and occurrence of mesostyle. A strong medianstyle[1] reinforces the crown of DP[3] between the anterior, lower and elongate, and the posterior, higher lobe. In this place, the tooth is abraded by the cusps of the anterior lobe of DP$_4$. The anterior and internal walls of the crown are the most strongly abraded parts. Length 10.9–13.6, width 7.8–10.7, height to 7.9.

DP[4] has a strong proto- and mesostyle. Size of anterior list variable. Medianstyle[1] present. Lingual walls bifurcated. Length 10.5–13.4, width 9.4–13.0, height to 8.8.

Smaller milk teeth occur in *M. reevesi* and of a similar size — in *M. muntjak*, *Elaphodus cephalophus* and roe deers.

Permanent dentition of the upper jaw in *P. wenzensis* is marked by the presence of upper canines. An alveolus of a canine is visible in the specimen No. 220VII. Posteriorly inclined enamel plates occur in crown fossettes of upper premolars. Medianstyle lacking. The length of the P[2]–M[3] row fluctuates within limits of 63 and 74 and is slightly larger than that in roe deers.

Discussion. — It is clear from the description of the structure of *P. wenzensis* that this is not a representative of Cervulinae, from which it differs in the shape of antlers and the structure of skull and dentition (wide and short forehead, widely spaced and shorter pedicles of horns which are less bowed posteriorly and are oval in cross section, higher upper jaws, less bent interalveolar margo, narrower and higher occiput and long parietals). Canines are present, but their size is not large, P$_4$ molar-like. *P. wenzensis* and Cervulinae have large lacrimal fossae, but in Cervulinae they are rounded and in *P. wenzensis* subtriangular. Both Cervulinae and *P. wenzensis* have low teeth crowns which are primitive in character.

P. wenzensis differs from most Cervinae, except roe deers, in the structure of antlers, its first tine being set relatively high above the burr and in the shape of the cranium (a convex profile of the frontal, shape of a supraorbital fossa, earlier formation and different shape of horn pedicles, stronger bend of interalveolar margo, elongation of the parietal, etc.). On the other hand, *P. wenzensis* resembles Cervinae in a wide frontal, medium height of maxilla, the same as in primitive Cervinae such as *Axis axis* and *C. (Rusa) unicolor*, a similar shape and size of lacrimal fossae (except for *Axis axis*, fallow and roe deer) and certain characters of dentition, e.g. presence of upper canines and molarization of P$_4$.

Some Pliocene species of deers had antlers of the same type as

P. wenzensis, i.e. three-tined and with the first fork set high above the burr (such antlers also occur in roe deers). These were *Cervavitus*, *Pliocervus* and *Procapreolus*. *Pliocervus* and *Procapreolus* are known only for the fragments of their antlers and jaws with teeth, whereas the structure of their skulls and limbs remains unknown.

The similarity of *P. wenzensis* to *Cervavitus* (= *Cervocerus* Czyżewska, 1960) is expressed in the structure of skull and teeth (i.e. a wide frontal, position of horn pedicles, large size of lacrimal fossae, presence of upper canines, low crowns of cheek teeth and presence of the palaeomeryx fold). However, I have previously (Czyżewska, 1960) given attention to several essential differences. Now, after having studied the collection of *Cervavitus* from the environs of Odessa and from Moldavia, I believe that *P. wenzensis* is not a representative of the genus *Cervavitus*. Lacrimal foramina of *Cervavitus* are situated inside and on the margin of orbit (*C. variabilis* Alexeyev), whereas both these foramina in *P. wenzensis* occur only on the margin of orbit, which I found on a new, better preserved material. Unlike the horns from Węże, pedicles of antlers in *Cervavitus* are thicker and longer, antlers form bladelike, flattened tines (*C. variabilis*). Horn tines of Pliocervini from Asia (Teilhard de Chardin & Trassaert, 1937) are longer and differently set on the beam than those in *P. wenzensis*. The first of them is nearer the burr and the distance between the first and second tine is much larger than that in *P. wenzensis*. The terminal fork of horns of Pliocervini from Asia is of the adaptive and that of *P. wenzensis* — inadaptive type. The dentition of *Cervavitus variabilis*, strongly similar in size and structure, has a massive palaeomeryx fold which, on the other hand, does not occur in Asian Pliocervini. Common character of *P. wenzensis* and Pliocervini are primitive and may testify to their derivation from closely related forms of Cervulinae.

The horns of *Pliocervus* are longer and thicker than those of *P. wenzensis*. Their first branch grows up from a lower place and the distance between the first and second branch is larger, tines are long and the surface of the beam is furrowed with many longitudinal grooves. In *P. wenzensis*, branches are short and the surface of horns almost completely smooth. The teeth of both these deers are strongly similar to each other, but *Pliocervus* has not even a trace of the palaeomeryx fold.

The horns of *Procapreolus latifrons* Schlosser from Mongolia and China were mounted on shorter pedicles than those in *P. wenzensis*, the diameter of burr was longer, beam above burr thicker and the diameter below the first tine identical with that above burr. The first branch of the antlers of *P. latifrons* grows up from a lower place than in *P. wenzensis* and the index of the ratio of the distance between burr and the first branch to the diameter of the beam above burr (= 26.3) is much higher than in *P. wenzenzis* (in No. 220VII it amounts to 12.9). The

distance between the first and second branch of antlers in *P. latifrons* is unknown. *Procapreolus loczyi* (Pohlig) from Hungary is similar to *P. latifrons*. In both these species, the positions of the first tine of antlers and thickness of beam are similar to each other. The distance between the first and second branch in *P. loczyi* is very long (equalling the distance between the burr and the first tine), whereas in other species of *Procapreolus* it is much shorter. The index of the ratio of the distance between the burr and the first tine to the distance between the first and second branch amounts in *P. loczyi* to 100 and in *P. wenzensis* (No. 220VII) to 62.6. On account of a lower position of the first branch and considerable thickness of beam, *P. latifrons* and *P. loczyi* make up a specific group of the genus *Procapreolus*.

Korotkevitsh (1965a) believes that the structure of antlers in *P. loczyi* is similar to that in the genus *Pliocervus*. Indeed, there occurs a certain similarity in the shape of horns of both these deers, but the horns of *P. loczyi* are equally similar to those of *P. latifrons*. The antlers of *P. loczyi* are smaller than the horns of *Pliocervus* and its primitive dentition has the palaeomeryx fold and cingulum, who do not occur in *Pliocervus*. I think that till the explanation of the taxonomic position of *P. loczyi*, it would be adviseable to maintain this species in a group of Pliocene roe deers.

Procapreolus ukrainicus Korotkevitsh from Novo-Ukrainka (Korotkevitsh, 1963, 1965) is marked by a high position of the first tine of antlers (in *P. wenzensis*, No. 220VII — 147 and in *P. ukrainicus* — 150) with the thickness of beam being much the same as that in *P. latifrons*. The index of the ratio of the distance between the burr and the first tine to the diameter of beam above the burr is low (in juveniles — 13.6, in adults — 16.4, in *P. wenzensis*, No. 220VII — 12.9). The distance between the first and second branch in *P. ukrainicus* (56.5–78.0) is smaller than in *P. wenzensis* (90.0–95.0) and the index of the ratio of the distance between the first branch and burr to the distance between the first and second branch of full-grown antlers comes to 50. The horns of *P. ukrainicus* have many grooves running along the surface of beam, whereas the ribbing of the horns of *P. wenzensis* is less distinct.

The species of *Procapreolus* mentioned above differ from *P. wenzensis* in a primitive dentition, i.e., a deep palaeomeryx fold on lower and a thick cingulum on upper molars. According to Korotkevitsh (1963, 1964, 1965), the genus *Procapreolus* also includes *Cervus cusanus*. In addition to France, this species is met with in Southern Ukraine (Chornaya Loshchina, Mikolayevskii District) and in Northern Caucasia (Caucasian Stavropol), where it occurs in Pliocene deposits. *P. cusanus* and *P. ukrainicus* have antlers of the same type, but the dentition of *P. cusanus* is of a more modern type (a very poorly developed palaeomeryx fold, slight bifurcation of internal walls of upper molars, small cingulum). *P. cusa-*

nus takes a position intermediate between the species of Lower Pliocene *Procapreolus* and Pleistocene and Recent roe deers of the genus *Capreolus* (*Capreolus pygargus* Pallas).

Within the genus *Procapreolus*, the structure of cranium is known only in *P. wenzensis*. If, judging by the structure of its antlers, pedicles and dentition, these are deers related to Recent roe deers, in particular to *Capreolus pygargus*, the structure of cranium of *Procapreolus* should be similar to that of a Recent roe deer. *P. wenzensis* has upper canines, a fairly large lacrimal fossa, a larger and smooth auditory bulla with a long external auditory meatus and an upper jaw of a medium height. In these characters it is more primitive than roe deers. Roe deers are characterized by an elongation of the parietal region, which in *C. pygargus* is longer (index — 77.6) than in *C. capreolus* (67.3). *P. wenzensis* takes an intermediate place (index — 69) between both these species of roe deers and, therefore, despite the similarity in the structure of antlers and dentition to *P. ukrainicus* and *P. cusanus*, considered to be ancestors of roe deers, *P. wenzensis* is not an ancestor of *C. pygargus*. This is a species of an Upper Pliocene stock *Procapreolus*, developed parallel to *P. ukrainicus* and *P. cusanus* and which preserved several characters common with Pliocervini. This stock became extinct without any descendants.

<div align="center">

Tribe **Cervini** Weber, 1928

Genus *Cervus* L.

Cervus warthae n. sp.

(Pls. V-VIII)

</div>

1959. *Cervus* (*Rusa*) sp.; T. Czyżewska, *Cervus* (*Rusa*) sp. ..., p. 418, Pl. 1, Figs. 2, 3.

    Holotype: Skull No. 1VI; Pl. V, Fig. 1.

    Locality: Węże near Działoszyn, Upper Pliocene.

    Derivation of the name: *warthae* — after the Warta River, on which the locality of Węże is situated.

Diagnosis. — Dimensions slightly smaller than those of *C.* (*Rusa*) *unicolor* and *C. elaphus*. Antlers branched, the first tine mounted near the burr, hooklike and together with the beam forming a right angle. Beam slightly bent between tines. P_4 primitive in structure. Anterior and posterior lobes of upper premolars clearly separated. Forehead high and convex, skull particularly wide behind orbits. Lacrimal fossa middle--sized. Auditory bulla small, with smooth surface.

Material. — Skull No 1VI is a holotype. The remaining specimens are fragments of skulls, upper jaws and mandibles with teeth and detached teeth. They belonged to the following age intervals:

I. Younger than half a year (in the case of *C. elaphus* — 2–4 months).

Seven fragments of skulls, 3 upper jaws with teeth and 9 mandibles. Probably 19 individuals.

II. Below one year (*C. elaphus* — 5–11 months). Four fragments of skulls, 3 upper jaws with teeth and a mandible. Probably 8 individuals.

III. One to two years (*C. elaphus* — 12–28 months). A skull and 2 mandibles with teeth. Probably 3 individuals.

IV. About $2^{1}/_{2}$–3 years (*C. elaphus* — about $2^{1}/_{2}$ years). Probably 19 individuals.

Other specimens belonged to adult individuals (3-year old to aged). These were 3 fragments of skulls, 9 mandibles and 6 upper jaws with teeth. Probably 16 individuals.

Description. — Skulls Nos. 1VI, 407II and 370I. The best preserved are: the skull No. 1VI, a skull of an adult male (Czyżewska, 1959) and skulls of young individuals Nos. 407II and 370I. All skulls without antlers and anterior parts of jaws. Specimen No. 1VI lacking the left side of facial region, occiput and part of braincase. Specimen No. 407II has almost no bones of the upper part, the base and side parts being also damaged. Orbits and lacrimal fossae lacking. Skull No. 370I has no occiput and braincase floor.

Skull No. 1VI is smaller than that of *C. elaphus* and *C. (Rusa) unicolor*, but larger than that of *C. (Sika) hortulorum* Swinhoe. The length of skull is designed by the distance between basion and a line connecting DP^2 (P^2) (in the middle). In the case of a damaged specimen No. 1VI, this is a distance between posterior margin of the parietal and P^3. In the skulls of deers this dimension is most similar to the distance between basion and the line connecting DP^2 (P^2) (in No. 1VI–201, in No. 407II–147, 73.1 per cent of the size of an adult individual).

The base of braincase in *C. warthae* n. sp. is long (the ratio of the length of skull to the length of base amounts in No. 1VI to 40.3 and in No. 407II to 47.6). A similar index occurs in *C. elaphus* (41.4), whereas roe deers and *M. muntjak* have lower indexes.

The following foramina are preserved in the specimen No. 1VI: f. sphenoorbitale and f. opticum, and in No. 407II: f. sphenoorbitale, f. ovale, f. postglenoideum and f. acusticus externus.

The length of palate to P^2 in No. 1VI amounts to 85, in young *C. warthae* n. sp. — to 61 (in No. 407II — 71.8 per cent of the size of an adult) and to 52.6 (in No. 370I — 61.2 per cent). The width of palate of the specimen No. 1VI is unknown, in young individuals it amounts to 50 (No. 407II) and 48 (No. 370I). The palate is short and in young individuals also wide (the ratio of the length of skull to the length of palate amounts in No. 1VI to 42.3 and in No. 407II to 41.5; the length to the width of palate, in No. 407II — 82.0, in No. 370I — 92.3). Adult Recent deers have longer and narrower palates, particularly so in the case of *M. muntjak*. The row of check teeth slightly bent.

The frontal of the skull No. 1VI is high and steep. The line of profile is similar to that of young *C. elaphus* or adult *Axis axis*, which gives it a primitive character. Anteriorly of supraorbital foramen, supraorbital sulcus is fairly wide (in No. 370I and 1VI). The length of the frontal of No. 1VI amounts to 88 and of a young *C. warthae* n. sp. — to 73 (82.9 per cent of the size of an adult). In relation to the length of skull, frontal is short. Its length amounts in No. 1VI to 43.8, in *C. (Rusa) unicolor* to 53.3, in *C. elaphus* to 55,7, in roe deer to 51.3–53.1 and in *M. muntjak* to 72.2. The width of the frontal between supraorbital foramina amounts in No. 1VI to 52.0 and in No. 370I to 42.5 (81.7 per cent of the size of an adult). In relation to the length of skull, frontal is narrow in this place: in 1VI — 26.0, in *C. (Rusa) unicolor* — 30.3 and in *C. elaphus* — 32.6, but much wider in a contraction behind orbits: in No. 1VI — 48.4, in *C. (Rusa) unicolor* — 42.0 and in *C. elaphus* — 43.5.

The index of the ratio of length of the frontal to its width between supraorbital foramina does not differ *C. warthae* n. sp. from other species of the genus *Cervus*. The index of the ratio of length of the frontal to its width in a contraction behind orbits is very high (in No. 1VI — 110.0 and in No. 370I — 104.1). Frontals are wide behind orbits. In Recent deers this index does not exceed 100, in *M. muntjak* amounting to 69.2 which is a very low index.

Specimen No. 1VI has parts of horn pedicles adhering to the skull, the length of this fragments amounting to 54 and 59. Judging by the dimensions of pedicles, the antlers of this specimen were strongly developed.

Parietals have the following dimensions: No. 1VI, length 56.0, width 77.8; No. 370I, length 42.0 (75 per cent of the size of an adult), width 72.0 (92 per cent of the size of an adult). The index of the ratio of the length of skull to the length of the parietal is low (in No. 1VI — 27.9). Similar indexes are in *C. (Rusa) unicolor* (27.2) and *C. (Sika) hortulorum* (27.8) and a lower one in *C. elaphus* (23.4). The index of the length-width ratio of the parietal is in No. 1VI — 71.9 and in a young skull — 58.3. As compared with Recent deers, it is high.

Nasals not preserved. The anterior margin of the frontal, observed on a few specimens, indicates that, like in *Sika*, *Cervus* and *Dama*, nasals reached anterior edges of orbits.

In an adult *C. warthae* n. sp., the height of maxilla above P^4 amounts to 46 and in young ones — to 30 (in No. 407II, 65.2 per cent of the size of an adult) and to 28 (in No. 370I, 62.4 per cent). As compared with the length of skull, this height is medium and, in *Rusa* and *C. elaphus*, lower (in No. 1VI — 22.9, in *C. (Rusa) unicolor* — 15.4 and *C. elaphus* — 17.6).

The margin of the right lacrimal fossa bordering on lacrimal hiatus is narrow (No. 1VI). Among deers of the genus *Cervus*, *Rusa* and *Sika* have

a narrow and *C. elaphus* a swollen margin of lacrimal hiatus, the same as is the case of fallow deers (Knottnerus-Meyer, 1907). The upper lacrimal foramen is situated on the margin of orbit.

The height of braincase, i. e. a distance between the posterior end of praesphenoid and bregma amounts in No. 1VI to 74.0. In lateral view, this skull seems to be high. The index of the length-height ratio of this skull, amounting to 36.8, is identical with that of *C. elaphus* and slightly lower than in *Rusa* and *Sika*.

Other skulls. Specimen No. 347I has a preserved interalveolar margo. The distance between margins is larger (21.6) than the length of DP^4 (17.2). They are more widely spaced than in *C. elaphus* juv. (20.6, length of DP^4 19.0). In the specimen No. 348II, this distance is smaller (16.0).

The row of cheek teeth is slightly curved. A longitudinal depression (No. 348II) runs anteriorly and through the middle of palate. The naso--pharyngeal canal is fairly long (in No. 348II more than 13 mm).

The width of the braincase base (No. 362, probably an adult individual) at the level of tubera muscularia amounts to 28.5 and the width of foramen magnum — to 26.0 (Nos. 362 and 407II).

Auditory bulla (Nos. 362 and 403I) does not protrude above the basioccipital tubera muscularia. Dimensions: No. 362 — 22.4 $\times$ 19; No. 403I — 24.0. Muscular process, directed anteriorly and downwards, prominent. The wall on the side of the paroccipital process is convex. External auditory meatus long. Paroccipital process has a wide (17.0) base.
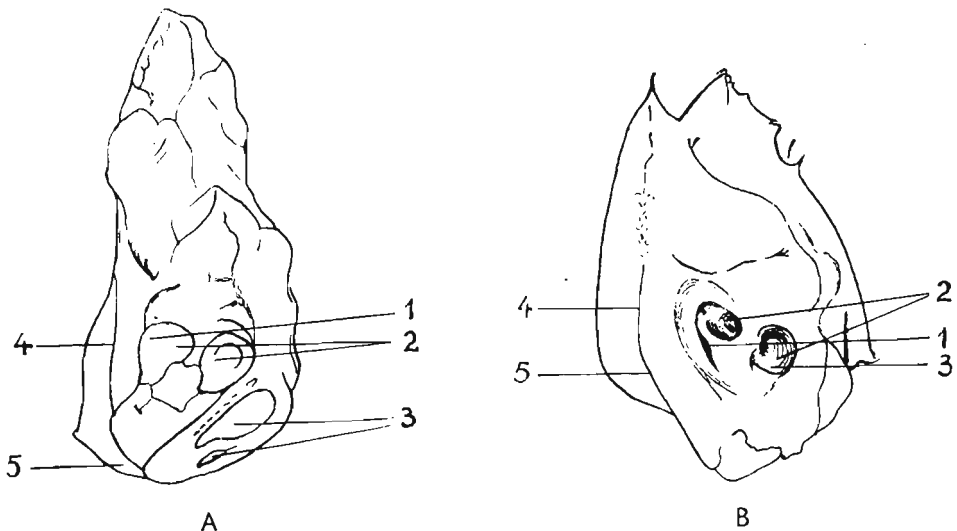

A   B

Fig. 14. — Petrosum dextrum, medial surface, ca. $\times$ 2. *A Cervus warthae* n. sp., damaged lower and posterior part, No. 403; *B Capreolus capreolus* L., ZMUWr No. 202. *1* canalis facialis, n. VII, *2* meatus acusticus internus, n. VII and VIII, *3* cochlea, *4* crista petrosa, *5* hiatus canalis facialis, n. VII.

The largest length of a fragment of the right petrosum (in No. 403I) amounts to 16.6 and the largest width — to 30.5. Openings of internal auditory meatus are visible on petrosum. Since they are situated in an extended depression, this region is slightly damaged. An opening of facial canal occurs in the anterior upper part of this depression. Crista petrosa, an area of the attachment of tentorium membranaceum, sharply outlined, distinct, straight and similar to that of *C. elaphus* (an adult male) or *Axis porcinus* (a young individual). In the European roe deer (an adult male), this crest is less distinct and the upper surface of petrosum more convex. Hiatus canalis facialis (branch of n. II) (Fig. 14*A* and *B*) is visible on the upper surface of petrosum.

Mandible. Almost complete mandibles of *C. warthae* n. sp. are observed in specimens Nos. 469I, 370IV (Fig. 15*A*), 411I, 495II (Fig. 15*B*.) and 363VII (Fig. 16*A*). Temporal process is visible in specimen No. 495II. The length of mandible (a distance between the last cheek tooth and the anterior margin of the canine alveolus) was measured on specimens Nos. 411I, 495II and 363VII.
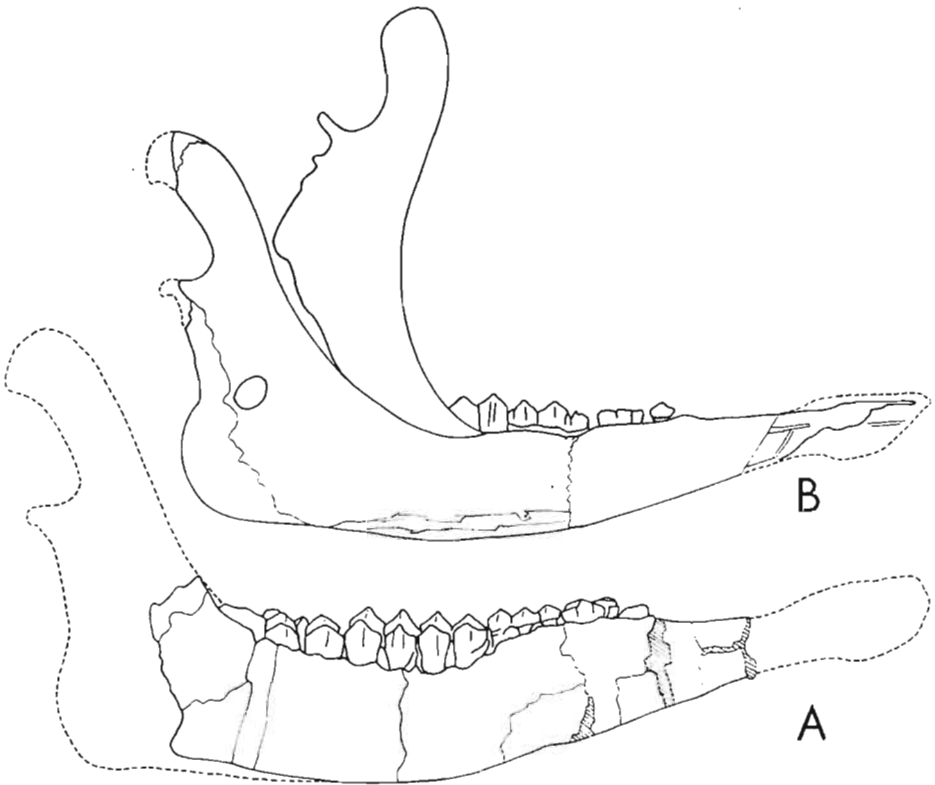

Fig. 15 — *Cervus warthae* n. sp., fragments of right mandibles ca. × 0.5. *A* partial reconstruction, No. 370IV; B No. 495II, posteriorly — ramus of the left mandible.

The mandible of an adult *C. warthae* n. sp. is shorter than that of *C. elaphus* and *C. (Rusa) unicolor*. Its diastema is of a similar length as in *Rusa,* but shorter than in *C. elaphus*. The mandible is lower than in *C. elaphus* and *Rusa* and much the same in thickness. An adult *C. warthae* n. sp. has a high (more than 30 mm behind M_3) and thick (more than 16 mm) mandible similar to those of *Rusa* and *C. elaphus*. In young specimens, mandible is medium in height and thickness (Fig. 16*B*). The index of the ratio of the length of mandible to the length of diastema is in young *C. warthae* n. sp. (38.1) similar to that in *C. elaphus* and higher than in *Rusa* (35.8). Young individuals of *C. warthae* n. sp. had relatively longer diastemae (47.6 and 47.4).

Incisura praemasseterica is visible on specimen No. 495II, angular process is rounded and shifted posteriorly. Condyle of mandible is set high. Articular region wide (in No. 337–42.7), temporal process fine. Like *P. wenzensis*, *C. warthae* n. sp. had a poorly developed temporal muscle and a strong masseter and m. pterygoideus internus.

Dentition. Milk teeth of the mandible. The length of the DP_2 — DP_4 row, which in No. 441II amounts to 46.5, is smaller than that in *Rusa* and *C. elaphus*.

DP_2: length 9.8–10.4, width 6.0–6.4, height to 7.0. Crown is primarily formed by external cardinal cusp, which, through a short coulisse $_2$, is
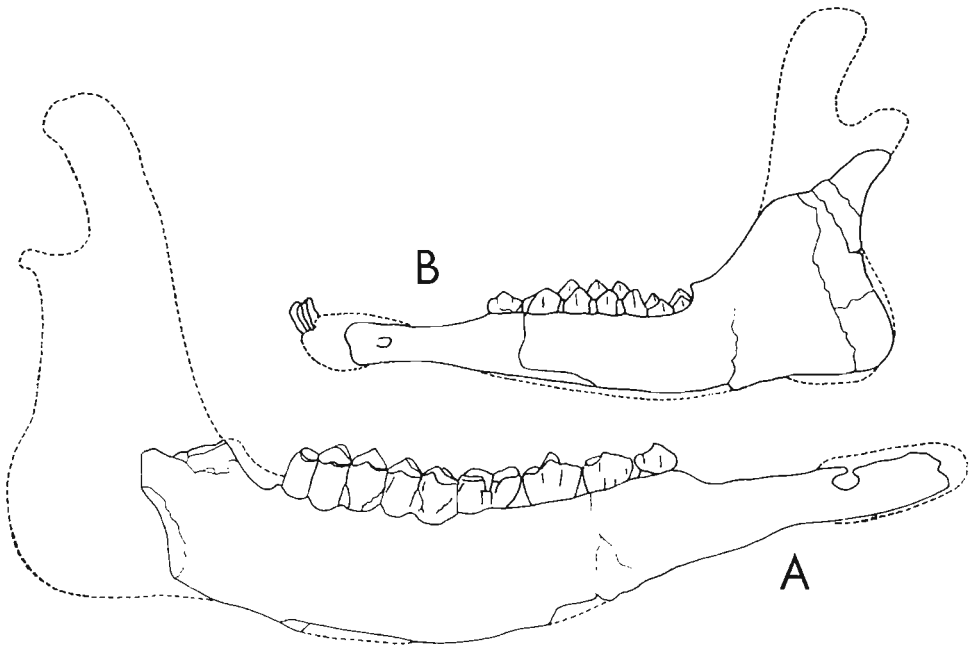

Fig. 16. — *Cervus warthae* n. sp., partly reconstructed fragments of mandibles, ca. × 0.45. *A* No. 363VII, right mandible; *B* No. 88I, left mandible.

connected with cardinal lingual cusp. Size of cusps variable (in No. 411I — very small, in No. 469I — higher and clearly separated). In all cases, coulisses are strongly developed although short. The index of ratio of the DP_2–DP_4 length to the length of DP_2 amounts, like in *C. elaphus*, to 23.0.

DP_3: length 14.8–16.0, width 7.4–9.5, height to 10.5. This tooth is similar to that of *C. elaphus*. Anterior lingual cusp distinct, cardinal lingual cusp connected with posterior cusp to form an internal wall in the posterior part of crown. A wide and deep fossette occurs between the anterior and cardinal cusp. A complete coulisse $_3$ is lacking on an unworn DP_3, in this place there occurs a short spur inclined posteriorly. This spur may be connected (No. 469I) with the posterior lingual cusp and close a recess between both cusps (Figs. 17, 19A).

DP_4: length 21.9–25.3, width 9.8–11.2, height to 11.7. Medianstylids $_1$ and $_2$ strongly developed. Recess of anterior lobe posteriorly open (postspina $_1$ does not reach postala $_1$); internal walls fairly smooth, mesostylid visible on completely unworn teeth. Anterior list small. DP_4 is subjects to a rapid wear, fossettes are strongly contracted as early as in the 2nd age interval (Fig. 17).

The index of the ratio of the DP_2-DP_4 to DP_4 length, amounting to 47.3, is much the same in most Cervinae.

Permanent dentition of the mandible. The length of the P_2–M_3 row (in No. 363VII amounting to 110.0) is similar to that in *C. (Rusa) unicolor*, whereas in *C. elaphus* this row of teeth is longer.

P_2: length 12.0–12.2, width 7.4–7.6, height to 9.0. Cardinal labial cusp large, cardinal lingual cusp very small. Coulisses slightly outlined. This tooth wears in late age stages.
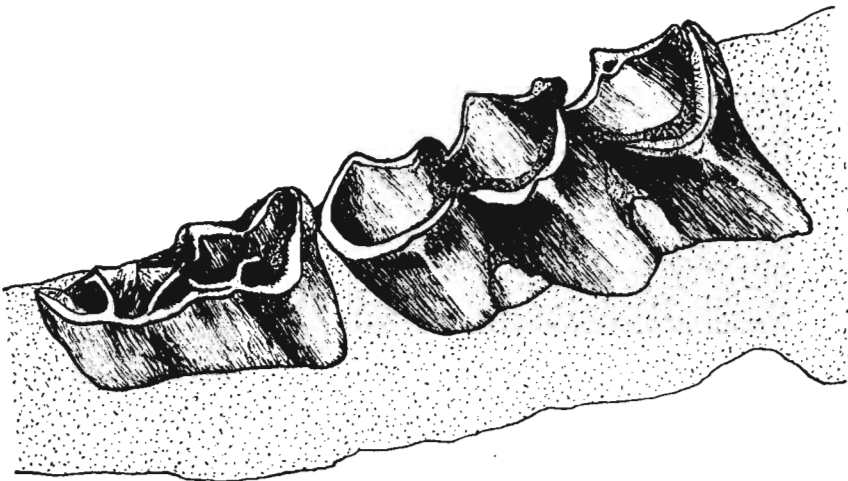

Fig. 17. — *Cervus warthae* n. sp., DP_3 and DP_4, No. 448I, ca. $\times$ 2.5.

A spacious recess (Fig. 19B) is situated on P_3 and P_4 between cardinal and anterior cusp on the lingual side. Both these teeth are similarly shaped, but P_3 is smaller. Dimensions: P_3 — length 15.8–16.7, width 8.0–10.7, height to 14.5; P_4 — length 16.6–16.8, width 10.8–12.0, height to 14.5. The length-height ratio of P_4 (73.8–87.4) indicates that P_4 is of a medium height, the same as in *C. elaphus*. Index of the length of P_2–M_3 to the length of P_2 amounts in *C. warthae* n. sp. to 11.2 and *C. elaphus* to 10.1–11.8. The length of the P_2–P_4 row in *C. warthae* n. sp. (42.0) is similar to that in *Sika* and *Rusa*.

Molars of *C. warthae* n. sp. are high, but lower than those in *Rusa*. Medianstylids $_1$ and $_2$ and anterior list — present. The index of length to height of M_3 amounts to 72.2 (a high crown), much the same as in *Rusa*, whereas *Sika* and *C. elaphus* have lower indexes. The index of the length of the row of cheek teeth to the length of M_3 amounts in *C. warthae* n. sp. to 33.9. In Cervulinae, this index is low (15–27.9), in Cervinae it amounts to more than 20, and in *C. elaphus* — to 32.8 (the highest). In *C. warthae* n. sp., the surface of the enamel of teeth is wrinkled, in particular on molars.

Milk dentition of the upper jaw. This dentition is similar to the teeth of *C. elaphus*. The length of the DP^2–DP^4 row, amounting to 49.7 is nearly the same as in *C. elaphus* and *C. (Rusa) unicolor*.

DP^2: length 15.6, width 11.2, height to 11.3. On the lingual side, postspina^1 and praespina^2 are short so that they do not close the opening of the crown fossette (on slightly worn teeth). Praespina^2 forked (Fig. 18).

DP^3: postspina^1 short, medianstyle present. Anterior list, varying in size from very slight to strongly developed, on some teeth overlapping the internal side of the anterior lobe (Nos. 350I, 351I, 403I). Length 17.9, width 14.8, height to 15.3 (Fig. 18).

DP^4: a strong mesostyle occurs in the external wall. Anterior list present in all cases. Postspina ^{1} and ^{2} forked. Medianstyle occurs between lobes. Length 17.2, width 16.7, height to 14.8 (Fig. 18).

Permanent dentition of the upper jaw The structure of premolars is uniform: all crowns have two lobes each. The anterior labial cusp of P^2
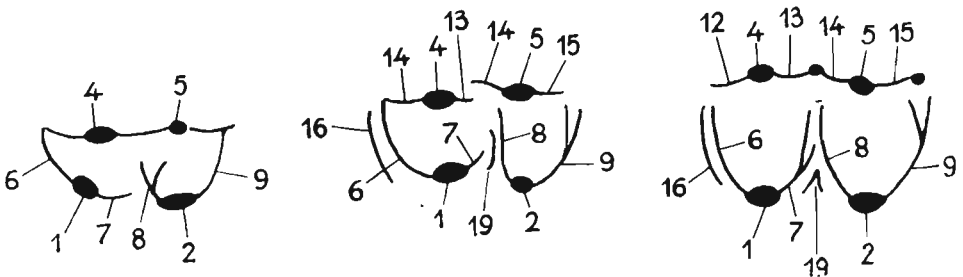

Fig. 18. — *Cervus warthae* n. sp., diagram of teeth, from the left: DP^2, DP^3 and DP^4 according to No. 370I. Explanations — in Fig. 13.

is much larger than the posterior one and it makes up the main part of the labial wall. Praespina[2] short, forked, forming a spur which is directed towards the interior of the tooth. Postspina [1] short. Length of P^2 — 15.0, width — 14.5, height to 14.4 (Fig. 19C). Protostyle present on P^3. Praespina[2] forming a spur, which is also directed towards the interior of the tooth, but nearer the posterior wall than in P^2. Length of P^3 — 14.4, width 16.3, height to 17.0 (Fig. 19D). The recess of the lingual wall of P^4 shallow, on worn teeth almost invisible. Protostyle and posterior list present. Length of P^4–13.8, width 18.0, height to 17.3. The length to height index reaches in P^4–111.7 (in No. 494VI) and is lower than in *Sika* and *C. elaphus bactrianus* Lydekker (124.6 and 131.7 resp.).

The length-height index of M^3 reaches in specimen No. 494VI – 92.1. The length of the P^2–M^3 row amounts to 98.0–100.0 and of the P^2–P^4 row — to 46.0–49.0. As compared with the length of all cheek teeth, these are of considerable lengths.

Discussion. — On the basis of a part of the material found at Węże, *C. warthae* n. sp. was described (Czyżewska, 1959) as *C. (Rusa)* sp. The antlers of this deer, fragmentarily preserved (*l. c.*, pp. 406–407) have a distinct sculpture of the lower part of shaft, a round burr formed by a single row of tubercles (No. 312), the first fork set directly above the burr and turned outwards aside of the beam at an angle of 110°. The beam is also turned outwards and slightly bent just above the burr. The first tine has a characteristic, bent point. Other branches grow up (two or three of them) at an acute angle to the beam. In the place of bifurcation the beam is slightly flattened.

In view of considerable dimensions of its antlers and structure of skull, *C. warthae* n. sp. was assigned to Cervini. *C. warthae* n. sp. is most similar to Recent *C. (Rusa) unicolor* and *C. elaphus.* In this discussion, I take into account only those species of Pliocene deers, whose antlers have the first tine set directly above the burr.

The deers of the genus *Eucladocerus* differ from *C. warthae* n. sp. in large dimensions and much larger antlers having many ramifications.
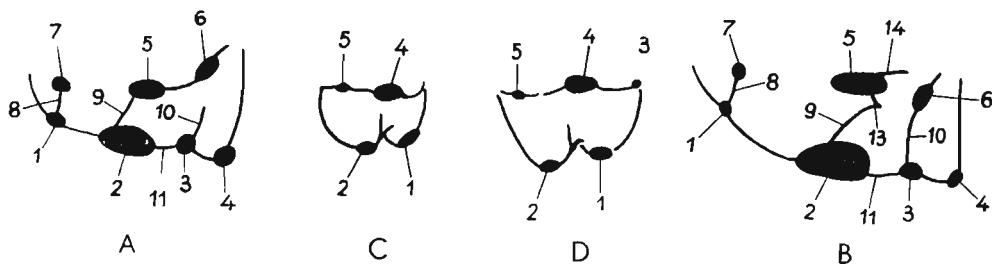

Fig. 19. — *Cervus warthae* n. sp., diagrams of teeth: *A* DP₃ according to No. 448I; *B* P₄ according to No. 52IVB; *C* P² according to No. 259V; *D* DP³ according to No. 259V· Explanation — in Fig. 13.

Some of them even have fairly low mounted first tine, but in more of them it is situated so near the burr as in *C. warthae* n. sp.

C. perrieri Cr. from Etouaires (Depéret, 1883; Dawkins, 1878; Lydekker, 1898; Heintz, 1966) is similar to *C. warthae* n. sp. in the position and shape of the first tine and bend and cross section of its shaft, but its antlers are smaller and devoid of a tubercle near the burr. *C. warthae* n. sp. also differs from *C. arvernensis* Cr. (Depéret, 1883) in smaller dimensions narrow frontal and cross section of the antler beam.

Dama nestii eurygonos F. Major from Valdarno (Azzaroli, 1948) has antlers with the first tine set low. The structure of the skull and dentition in *C. warthae* n. sp. is, however, different than that in fallow deers (a long row of cheek teeth, large lacrimal pits).

C. warthae n. sp. displays a certain similarity to *Axis punjabensis* Brown, which is expressed in the manner of mounting the first tine, size of auditory bulla and a general shape of the skull. However, its teeth differ from those of *Axis* (Brown, 1926; Colbert, 1935).

C. warthae n. sp. differs from the Pliocene species recognized so far. In my opinion, as concerns its systematic position, this is an early representative of the genus *Cervus*. Deers of the genus *Cervus*, from which Pleistocene ancestors of *C. elaphus* were derived, appeared in the Upper Pliocene. Since the number of antler ramifications of *C. warthae* n. sp. is unknown, this species cannot be assigned to any subgenus of *Cervus*. The structure of its skull and dentition relates it to *Rusa* and *C. elaphus*, but, on the other hand, it differs from them in a shorter frontal, low index of the width of frontal between supraorbital foramina, considerable width of cranium behind orbits, high index of the width-length ratio of the parietal, higher upper jaw and lower and shorter mandible.

<center>

Subfamily **Cervulinae** Sclater, 1870
Tribe **Muntiacini** Weber, 1928
Genus *Muntiacus* Rafinesque, 1815
Muntiacus polonicus n. sp.
(Pl. VIII, Figs. 3, 4)

</center>

Holotype: A fragment of the left mandible with teeth, No. 99IV, Pl. VIII, Figs. 3 and 4.

Locality: Węże near Działoszyn, Upper Pliocene.

Derivation of the name: *polonicus* — from Poland.

Diagnosis. — A small deer, similar in size to *M. reevesi* Ogilby. Lower molars devoid of the palaeomeryx fold and cingulum. Milk teeth of the mandible primitive. Mandible thick and, as compared with Recent Muntiacini, of a medium height.

Material. — A fragment of the left horizontal ramus of the mandible with DP_3, DP_4 and M_1–M_3 (specimen No. 99IV) is a holotype. A fragment of the horizontal ramus of the mandible with M_1 and M_2 (No. 154). A molar of the upper jaw (No. 254). These specimens are parts of the collection of the Polish Academy of Sciences, Museum of the Earth, No. VIII/Vm–353.

Description. — Specimen No. 99IV is an incomplete mandible, its anterior part being broken off before the alveolus of DP_2 and posterior part behind M_3. Dentition consists of worn but still well preserved milk teeth DP_3 and DP_4, alveolus of DP_2 and molars M_1–M_3. Lower margin of mandible arcuate. Incisura praemasseterica present. In transverse section, ramus of mandible is broader in its upper part and narrower at the bottom, internal surface of ramus slightly concave. Dimensions are given in Table 3.

Table 3

Muntiacus polonicus n. sp. — measurements (in mm)

Measurement	Specimens	
	No. 99IV	No. 154
DP_2 length	7.0	—
width	4.0	—
height	—	—
DP_3 length	7.0	—
width	4.5	—
height	3.8	—
DP_4 length	11.6	—
width	5.3	—
height	4.1	—
M_1 length	10.0	9.0
width	6.5	—
height	6.6	7.4
M_2 length	11.1	10.1
width	7.3	7.0
height	6.7	6.8
M_3 length	13.7	15.0
width	7.4	7.0
height	8.8	7.0
Length of:		
DP_2–DP_4	25.4	—
M_1–M_3	34.0	34.0
DP_2–M_3	59.0	—
Height of mandible:		
near DP_4	14.8	—
„ M_3	16.8	17.7
Width of mandible:		
near DP_4	9.2	—
„ M_3	10.5	9.6

DP$_3$: Labial wall, formed by a large cardinal cusp (protoconid), passes into a small anterior lingual cusp. Coulisse$_2$ runs posteriorly from the cardinal cusp and unites with the cardinal lingual cusp, situated along the crown. Since a spacious fossette occurs between the cardinal and anterior cusp, the internal wall is not complete. The opening of fossette between coulisses $_2$ and $_3$ is posteriorly closed by the cardinal lingual cusp, which contacts the posterior lingual cusp. A fossette between coulisse$_3$ and the posterior wall of the tooth is open (Figs. 20A and 21B). In
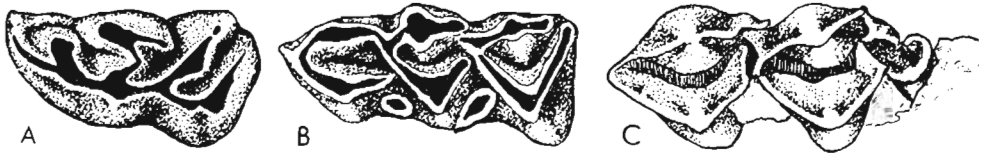

Fig. 20. — *Muntiacus polonicus* n. sp., dentition, No. 99IV, ca. $\times$ 4; A DP$_3$, B DP$_4$, C M$_3$.

relation to its length, DP$_3$ of *M. polonicus* n. sp. is wide; both species of muntjac and *Elaphodus cephalophus* have narrower DP$_3$ teeth.

DP$_4$: Anterior lobe smaller and narrower than the next two, its labial wall is rounded since postspina$_1$ descends posteriorly and is situated parallel to the long axis of the tooth. Fossette of anterior lobe is still open. Medianstylids $_1$ and $_2$ present. Labial walls of lobes $_2$ and $_3$ pointed. Mesostylid present (Figs. 20B and 21A).

M$_I$ and M$_2$: Externall walls have sharp edges. Lingual cusps pointed. Medianstylid completely unworn. Mesostylid present. Enamel lists, reaching the labial wall, occur on anterior walls. Palaeomeryx fold lacking.

M$_3$: Cusp of the third lobe shifted towards lingual side (Fig. 20C).

Milk teeth and molars of *M. polonicus* n. sp. have identical dimensions as those of *M. reevesi* and smaller than in *M. muntjak*, *Elaphodus cephalophus* and *C. capreolus*. The structure of teeth of *M. polonicus* n. sp. does not differ from that of Recent muntjacs. The length of the DP$_2$–DP$_4$ row is much the same as in *M. reevesi*, the length of the row of molars — as in muntjacs and *Elaphodus*, but smaller than in roe deers.

Mandibles of *M. reevesi* are lower and narrower and of *M. muntjak*, *Elaphodus* and roe deers higher and broader than in *M. polonicus* n. sp. The ratio of the height of mandible near DP$_4$ to the height near M$_3$, which in *M. polonicus* n. sp. amounts to 88.1, is similar to this index recorded for *M. muntjak*. The index of the ratio of the height of mandible near M$_2$ to the length of the DP$_2$–M$_3$ row, which in *M. polonicus* n. sp. amounts to 28.5, is almost identical in *M. muntjak* (29.1), the same as for the height of mandible near DP$_4$ (25.1 for both species). In *M. reevesi* this

index is lower (23.9) and in *Elaphodus* — higher (27.7). The mandible of *M. polonicus* n. sp. near M₃ is narrower than in *M. muntjak*, whereas its thickness near DP₄ is, in both species, almost identical. *M. reevesi* and *Elaphodus* have thinner mandibles.
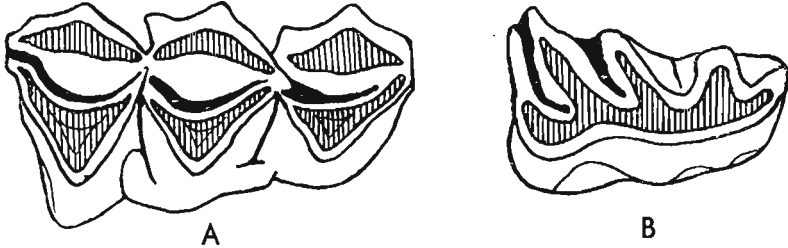

Fig. 21. — *Capreolus capreolus* L., ZMUWr No. 3, ca × 4; *A* DP₄, *B* DP₃.

Discussion. — Small dimensions and shape of mandible (bottom margin arcuate, ramus of mandible low, presence of incisura praemasseterica) indicate that specimens Nos. 99IV and 154 represent Cervulinae. Deers of this group are very rare in Poland. One Miocene species only, i. e., *Euprox furcatus* (Hensel) from the environs of Gliwice, Silesia (Hensel, 1859) and Opole (Wegner, 1913), is recorded. In Pliocene of Europe, Dicrocerini are represented only by the genus *Palaeoplatycerus* Pacheco from Spain. In Asia, they survived till the Lower Pliocene (*Dicroceros* Lartet, *Stephanocemas* Colbert). *Platycemas* Teilhard de Chardin & Trassaert is limited only to the Pliocene of Asia. Muntiacini, phylogenetically younger than Dicrocerini, in Pliocene had the following four representatives: *Eostylocerus* Zdansky, *Paracervulus* Teilhard & Trassaert, *Metacervulus* Teilhard & Trassaert, and *Muntiacus* Rafinesque. It is generally assumed that the species of the genus *Cervulus* (= *Muntiacus*) are not met with in the Tertiary of Europe (e. g., Hilzheimer, 1922).

Eostylocerus from China is marked by large dimensions (Zdansky, 1925, Pl. 9, Fig. 4; length of the P₂–M₃ row — ca. 98.0 and of the M₁–M₃ row — ca. 60; No. 99IV — 59.0 and 34.0 resp.). In Europe, it occurs in Pliocene of Moldavia (Taraklia) and of the Kuchurgan River valley (Korotkevitsh, 1964, 1965).

Paracervulus from China was described by Teilhard & Trassaert, who, however, did not characterize its dentition. *C. australis* de Serres (Montpellier, Roussillon; Depéret, 1890), which was much larger than *M. polonicus* n. sp. (the length of the M₁–M₃ row amounts in No. 99IV to 34.0 and in *Paracervulus australis* — to 45.0–52.0) was assigned to this genus. The dentition of *P. australis*, in particular its premolars, is very similar to that of roe deers.

Metacervulus from China (Teilhard & Trassaert, 1937) is also larger than *M. polonicus* n. sp. (length and width of M_3 in No. 99IV–13.7 and 7.4, and those in *Metacervulus capreolinus* Teilhard & Trassaert — 18.0 and 10.7; length of the $M-_1M_3$ row in No. 99IV–34.0 and in *M. capreolinus* — 47.0). *M. capreolinus* has three-tined antlers which is exceptional in Cervulinae.

In Europe, Pliocene muntjac was found in the Kuchurgan River valley, Odessa District. That was a fragment of antlers of *Muntiacus pliocenicus* Korotkevitsh. Korotkevitsh (1965) believes that *Muntiacus* occurred in Eastern Europe in the late Miocene and early Pliocene and that *M. pliocenicus* was the last representative of Cervulinae on the territory of Europe. Muntjacs from later periods are recorded only in Asia.

For the reasons, listed below, I think that the material, here described should be assigned to the new species of the genus *Muntiacus* Rafinesque:

1) These are the remains of a very small deer; there are no Eurasian representatives of Cervinae of such dimensions. In its size it corresponds to *M. reevesi* (length of the M_1–M_3 row amounting in No. 99IV to 34.0, in *M. reevesi* — to 32.6–34.0 and, according to Hooijer (1951) — to 31.0–38.0).

2) Shape and dimensions of mandibles are identical with those in *Muntiacus reevesi* and *M. muntjak*.

3) Molars of mandibles are devoid of the palaeomeryx fold and cingulum, the same as all species of *Muntiacus*, DP_3 has a primitive, considerably differentiated structure which in Cervinae is much simpler. Anterior lobe of DP_4 is also built in a primitive way.

4) Mandible of the specimen No. 99IV has simultaneously all the three molars and milk teeth, whose crowns are still very well preserved. Functioning of the latter teeth simultaneously with all molars has not been ever recorded in Cervinae, whose milk teeth are lost and premolars appear when M_3 begins to grow (in *Muntiacus* or *Elaphodus*, as I had ample opportunity to find many times, milk teeth persist after growing up of M_3, the same as in the mandible No. 99IV).

5) The locality of Węże is of Upper Pliocene age and it is situated far from the areas, which now are and in Pliocene were inhabited by the species of the genus *Muntiacus* (fossils, known from the Quaternary of Asia). *M. pliocenicus* Korotkevitsh, known from Pliocene of Europe, is older than the muntjac from Węże. So, I assign the latter to the new species *Muntiacus polonicus* n. sp., which is marked by dimensions approaching those of *M. reevesi* and whose mandible is thick and of medium height, as compared with the representatives of Recent Muntiacini.

Although they are few, finding the remains of *Muntiacus* at Węże

extends the range of the genus *Muntiacus* far to the west and north. Since Recent muntjacs are inhabitants of areas with a tropical or subtropical climate, the presence of *Muntiacus polonicus* n. sp. at Węże is indicative of a warm climate. Recent muntjacs live in forests and brushwood. *M. polonicus* n. sp. is a later representative of Cervulinae in Europe than *Muntiacus* and *Eostylocerus* from the Kuchurgan River valley.

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TERESA CZYŻEWSKA

JELENIE Z WĘŻÓW KOŁO DZIAŁOSZYNA NA TLE PLIOCEŃSKICH I WSPÓŁCZESNYCH JELENI EURAZJATYCKICH

Streszczenie

Z pliocenu Wężów opisano poprzednio (Czyżewska, 1959, 1960) dwa gatunki: *Cervus (Rusa)* sp. i *Cervocerus wenzensis*, na podstawie części okazów wydobytych z brekcji. Nowy i bogaty materiał jest podstawą ponownego opracowania.

Autorka niniejszej pracy proponuje wprowadzenie podziału podrodziny Cervinae na plemiona:

A. Pliocervini (= Pliocervinae Khomenko), zaliczając tu *Cervavitus* Khomenko i jako incertae sedis *Pliocervus* Hilzheimer;

B. Capreolini Simpson (= Capreolidae Brooke) wraz z *Capreolus* Frisch i *Procapreolus* Schlosser:

C. Cervini Weber; do plemienia tego należą: *Axis* H. Smith, *Cervus* L., *Eucladocerus* Falconer, *Dama* Frisch i *Elaphurus* Milne-Edwards;

D. Alcini Simpson; należą tu: *Alce* Frisch, *Cervalces* Scott i *Libralces* Azzaroli:

E. Megacerini Viret, z rodzajem *Megaloceros* Brooke.

Autorka podkreśla pierwotny charakter Pliocervini w ramach podrodziny Cervinae i niewątpliwy związek plemienia Capreolini z jeleniami Eurazji. Przedstawiony w pracy obraz ewolucji plioceńskich Cervinae wskazuje na bliskie pokrewieństwo Pliocervini i Capreolini; autorka omawia ponadto filogenezę rodzaju *Procapreolus*, Pliocervini i plioceńskich Cervini.

Węże są najdalej na północ wysuniętym stanowiskiem rodzaju *Procapreolus*. Stwierdzenie występowania w Wężach rodzaju *Muntiacus* przesuwa daleko na zachód i północ linię zasięgu tego rodzaju.

W pracy przedyskutowano zagadnienie śmiertelności kopalnej populacji jeleni z Wężów. Wykonano analizę ilościową szczątków tych jeleni, sporządzając tabelę życia, używaną do ilustrowania śmiertelności populacji współczesnych. Wykresy krzywych przeżywania zestawiono z analogicznymi krzywymi kilku współczesnych przedstawicieli parzystokopytnych. Autorka wyciąga wnioski, dotyczące populacji kopalnej z Wężów, sposobu życia i charakteru środowiska.

Opisano budowę czaszki i uzębienia *Procapreolus wenzensis* (= *Cervocerus wenzensis* Czyżewska). Budowa czaszki *Procapreolus* nie była dotychczas znana. Czaszka tego jelenia podobna jest do czaszki sarny i charakteryzuje się dużą prymitywnością, na co wskazują długie i nachylone nasady rogów, wypukłe czoło, długa mózgoczaszka, głęboki i duży dół łzowy, gładka *bulla tympani* i występowanie górnych kłów.

DIAGNOZY NOWYCH GATUNKÓW

Cervus warthae n. sp.
(Pl. V-VII; Pl. VIII, Fig. 1-2)

Rozmiary nieco mniejsze od *Cervus (Rusa) unicolor* i *C. elaphus* L. Poroże rozgałęzione; pierwsze odgałęzienie, osadzone blisko róży, ma kształt haczykowaty i tworzy z łodygą kąt rozwarty. Łodyga lekko wygięta między odgałęzieniami. P_4 o budowie pierwotnej. Płat przedni i tylny przedtrzonowców górnych wyraźnie oddzielony. Czoło wysokie i wypukłe, czaszka szczególnie szeroka za orbitami. Dół łzowy średniej wielkości. *Bulla tympani* mała, o gładkiej powierzchni.

Muntiacus polonicus n. sp.
(Pl. VIII, Fig. 3-4)

Mały jeleń o rozmiarach *Muntiacus reevesi* Ogilby. Dolne trzonowce bez fałdy paleomeryksowej i *cingulum*. Zęby mleczne żuchwy o budowie pierwotnej. Żuchwa gruba i średniej wysokości w porównaniu ze współczesnymi Muntiacini.

ТЕРЕСА ЧИЖЕВСКА

ОЛЕНИ ИЗ ВЕНЖЕ БЛИЗ ДЗЯЛОШИНА (ПОЛЬША) И ИХ СООТНОШЕНИЕ С ПЛИОЦЕНОВЫМИ И СОВРЕМЕННЫМИ CERVIDAE

Резюме

Из плиоценовых осадков в местности Венже близ Дзялошина, на основании экземпляров найденных в брекчии, описано ранее (Чижевска, 1959, 1960) два вида: *Cervus (Rusa)* sp. и *Cervocerus wenzensis*. Новый и обильный материал является основанием вторичного изучения.

Автор настоящей работы предлагает ввести подразделение подсемейства
Cervinae на племена:

A. Pliocervini (= Pliocervinae Khomenko), включая сюда *Cervavitus* Khomenko
    и как incertae sedis — *Pliocervus* Hilzheimer.

B. Capreolini Simpson (= Capreolidae Brooke), вместо с *Capreolus* Frisch и *Pro-
    capreolus* Schlosser.

C. Cervini Weber; к этому племени принадлежат: *Axis* H. Smith, *Cervus* L.,
    Eucladocerus Falconer, *Dama* Frisch и *Elaphurus* Milne-Edwards.

D. Alcini Simpson; принадлежат здесь: *Alce* Frisch, *Cervalces* Scott и *Libralces*
    Azzaroli.

E. Megacerini Viret, с родом *Megaloceros* Brooke.

Автором подчеркивается первичный характер Pliocervini в пределах под-
семейства Cervinae и несомненную связь племени Capreolini с оленями Евразии.
Представленная в работе схема эволюции плиоценовых Cervinae указывает на
близкое родство Pliocervini и Capreolini; автором обсуждается также филогенез
рода *Procapreolus*, Pliocervini и плиоценовых Cervini.

Венже являются наиболее на север выдвинутым пунктом нахождения рода
Procapreolus. Нахождение рода *Muntiacus* в Венжах перемещает пределы рас-
пространения этого рода далеко к северу и западу.

В работе обсуждается вопрос смертности ископаемой популяции оленей из
Венжев. На основании количественного анализа ископаемых остатков этих
оленей составлено таблицу продолжительности жизни, применяемую для иллю-
страции смертности современных популяций. Графики кривых проживания
сопоставлено с аналогическими кривыми нескольких современных представи-
телей двукопытных. Автор делает выводы относительно структуры ископаемой
популяции из Венжев, образа жизни и характера среды.

Описано строение черепа и зубной системы *Procapreolus wenzensis* (= *Cervo-
cerus wenzensis* Czyżewska). Строение черепа *Procapreolus* не было до сих пор
известно. Череп этого оления очень примитивный, что проявляется в таких
чертах как: длинные и наклоненные основания рогов, выпуклый лоб, длинный
мозгочереп, глубокая и большая предглазничная впадина (*fossa lacrimalis*),
гладкий слуховой пузырь (*bulla tympani*) и наличие верхних клыков.

ДИАГНОЗЫ НОВЫХ ВИДОВ

Cervus warthae n. sp.

(Пл. V—VII; Пл. VIII, фиг. 1—2)

Размеры меньшие чем у C. (*Rusa*) *unicolor* и C. *elaphus*. Порожье разветвлен-
ное, первая развилка близко розетки, крючкообразная и со стебелем образует
тупой угол. Стебель слегка выгнутый между развилками. P_4 о примитивном
строении. Передняя и задняя пластина верхних предкоренных зубов четко от-
делены. Лоб высокий и выпуклый, череп особенно широкий за орбитами. Пред-
глазничная впадина средних размеров. Слуховой пузырь малый, с гладкой
поверхностью.

Muntiacus polonicus n. sp.
(Пл. VIII, фиг. 3—4)

Малый олень размеров *M. reevesi* Ogilby. Нижние коренные зубы без палео-мерыксовой складки и *cingulum*. Молочные зубы челюсти имеют примитивное строение. Челюсть толстая и средней высоты в сравнении с современным Muntiacini.

PLATES

Plate I

Procapreolus wenzensis (Czyżewska), skull No. 409IV, top view; × 1.

Plate II

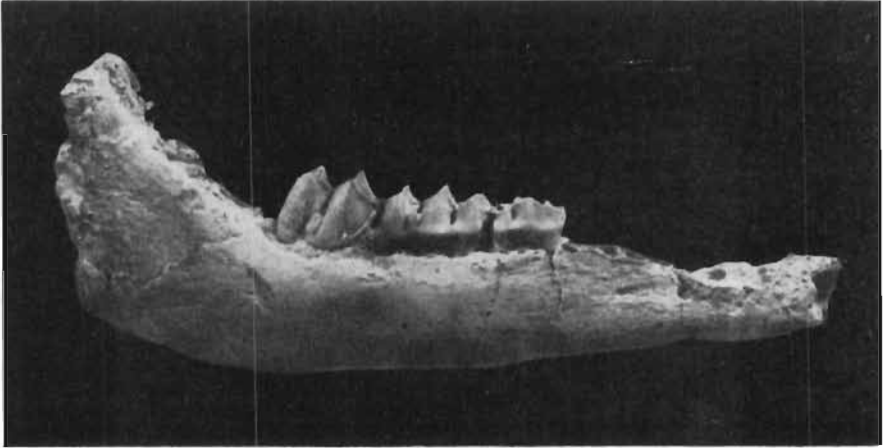*Procapreolus wenzensis* (Czyżewska), skull No. 409IV, viewed from palate; × 1.

Plate III

Procapreolus wenzensis (Czyżewska), skull No. 409IV, viewed from the left; ✕ 1.

1

2

3

Plate IV

Procapreolus wenzensis (Czyżewska)

Fig. 1. Left mandible, No. 419I, lingual side; × 1.
Fig. 2. Right mandible, No. 414II, labial side; × 1.
Fig. 3. Right mandible, No. 414II, lingual side; × 1.

Plate V

Cervus warthae n. sp.

Fig. 1. Skull No. 1VI, top view; ca. $\times$ 0.75.
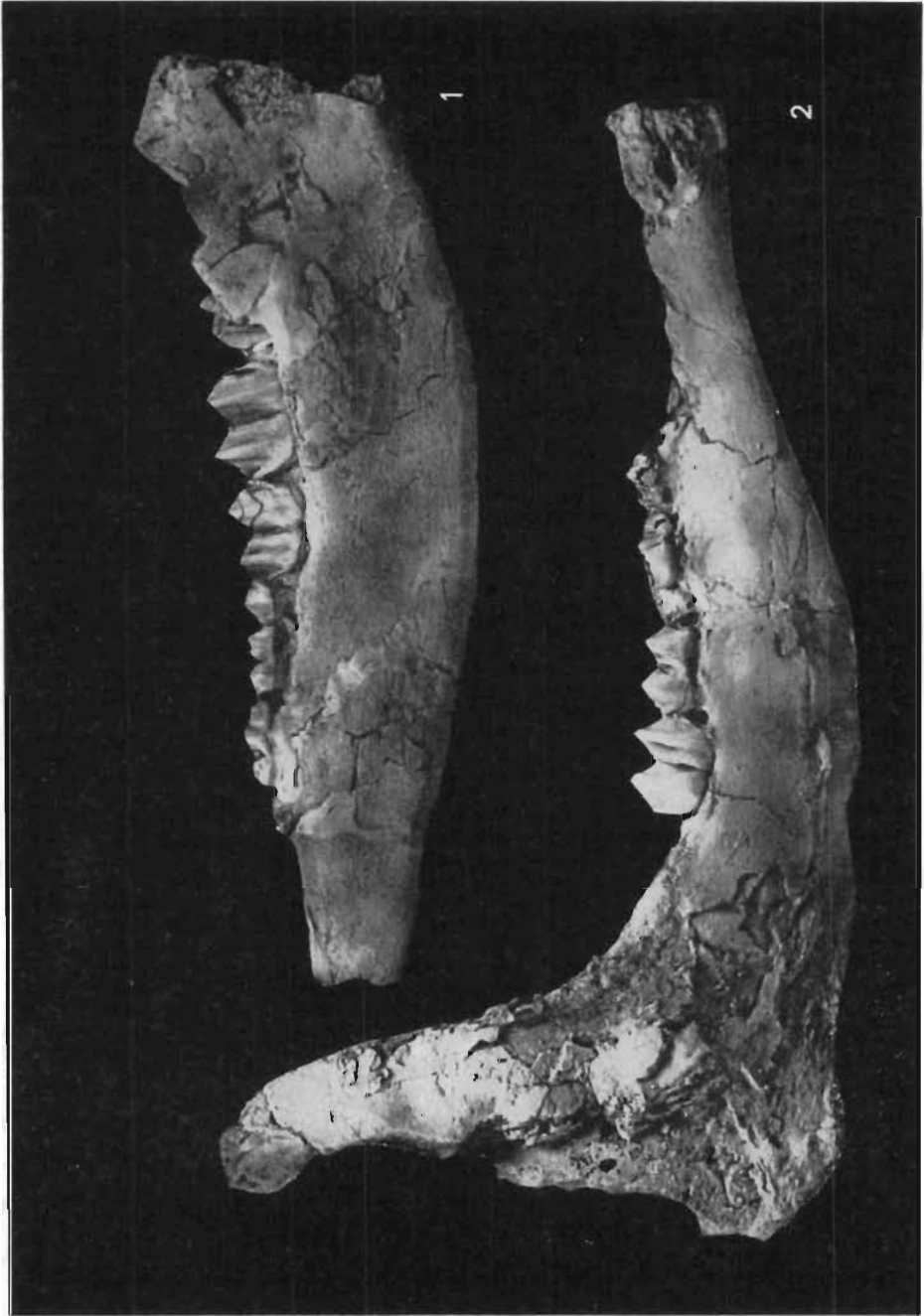Fig. 2. Right mandible, No. 370IV, labial side; $\times$ 0.75.

1

2

Plate VI

Cervus warthae n. sp.

Fig. 1. Right mandible, No. 370IV, lingual side; × 0.75.
Fig. 2. Left mandible, No. 495II, lingual side; × 0.75.

Plate VII

Cervus warthae n. sp.

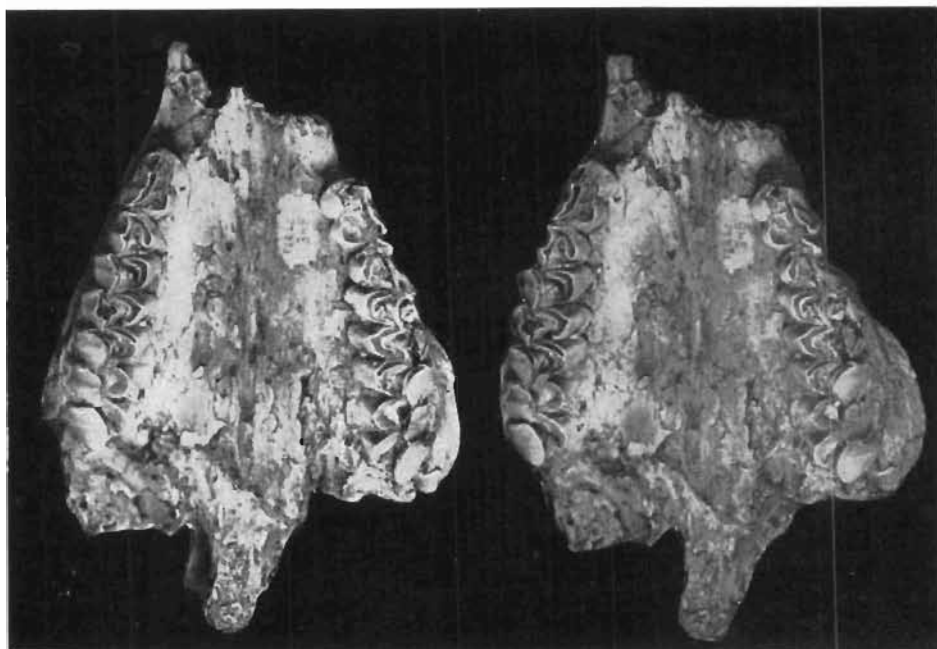Fig. 1. Right mandible, No. 363VII, lingual side; × 0.75.
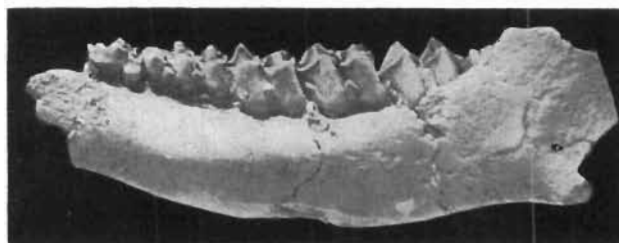Fig. 2. Right mandible, No. 363VII, labial side; × 0.75.

1

2

3

4

Plate VIII

Cervus warthae n. sp.

Fig. 1. Fragment of skull, No. 348II, viewed stereoscopically from palate; × 0.5.
Fig. 2. Left mandible, No. 448I, viewed from the surface of wear of teeth, × 1.

Muntiacus polonicus n. sp.

Fig. 3. Left mandible, No. 99IV, viewed from labial side; × 1.
Fig. 4. Left mandible, No. 99IV, viewed from lingual side; × 1.