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Fossil *Leporidae* from the Pliocene and Pleistocene of Poland

[Plates I—VII and 30 text-figures]

Kopalne *Leporidae* z pliocenu i plejstocenu Polski

Ископаемые *Leporidae* из плиоцена и плейстоцена Польши

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INTRODUCTION

The *Lagomorpha* BRANDT, 1855 include, according to the present state of science, 30 fossil and 19 modern genera (GUREYEV, 1964). This not very numerous group of mammals, however uniform it seems to be in respect of systematics, has presented much difficulty to systematists and palaeontologists since as early as the middle of the last century. The problems that the studies on fossil lagomorphs have hitherto been concentrated on can be arranged in three groups.

The first and most numerous of them comprises the problems concerning the morphology and description of new species. These problems constitute the basis of most papers on the *Lagomorpha*, especially of those of the early period. Such studies are based on remains of skulls and teeth, while the other elements of the skeleton are usually described only in general outlines. Papers giving detailed descriptions and analyses of long bones of the skeleton from the viewpoint of biomechanics are rare. The first trials of this kind can be found in the studies by COPE (1884) and MAJOR (1899). Of the latest papers dealing widely, in addition to the skull, with the morphology of the skeleton in the *Lagomorpha*, those by WOOD (1940) and DAWSON (1958) should be mentioned.

Phylogenetic-systematic problems, especially those connected with the origin of leporids, make up the second group. They have been discussed continuously starting from LLIGER (1811) and WATERHOUSE (1842), who were the first to take note of distinction of the *Leporidae* GRAY 1821 and *Ochotonidae* THOMAS 1897 from the remaining rodents. The suggestion of TULLBERG (1897)

and GIDLEY (1912) that the *Lagomorpha* are possibly descended from some groups of mammals other than rodents, e. g., from primitive insectivores, discussed also by other investigators (among them HARTMAN, 1925 and SIMPSON, 1945), who on the whole unanimously rejected the rodents as ancestors of lagomorphs, was eventually crystallized in WOOD's hypothesis (1957) on the origin of lagomorphs from the *Condylarthra*. The homology of tooth cusps was one of the basic problems in the research after phylogenetic relationships of lagomorphs to the other mammals (EHIK, 1926; BURKE, 1934; WOOD, 1940, and others). The discovery of new fossil forms prompted DICE (1917, 1929) to make attempts to systematize all living and extinct species of the *Lagomorpha*. In this he was followed by BURKE (1941) and recently by GUREYEV (1964), who, besides presenting a new division of the *Lagomorpha*, drew up the pedigree of all their genera. Much attention was given to systematics and phylogeny within smaller systematic units by KORMOS (1934), DAWSON 1958 — phylogeny of leporids), and HIBBARD (1963 — among other things, evolutionary line of the *Leporidae* TROUSSART, 1880).

The third and least numerous group consists of palaeozoogeographical problems, such as transcontinental migrations of some species and their groups (SIMPSON, 1947) or the distribution of fossil species given by many authors.

Summing up, the fossil *Lagomorpha* are a fairly well-known group. There is, however, a lack of detailed studies on variation (individual and evolutionary) in it, the familiarity with which would certainly make a systematic revision of different related species or genera possible. Apart from a relatively poor knowledge of the morphology of the skeleton, except for the skull, little is also known of the dentition of young animals, especially of deciduous teeth (with the exception of the fragmentary data given by WOOD (1940) and KORMOS (1934), which are of great importance for the studies of phylogenetic relations.

▲The blank pages of the history of the *Lagomorpha* fill up slowly as the new fossil faunae are discovered. The Pliocene and Pleistocene faunae found in Poland in recent years (at Węże near Działoszyn, Rebielice Królewskie near Kłobuck, Kadzielnia in Kielce, and Kamyk near Częstochowa), of which nearly all the groups of vertebrates have already been worked out (KOWALSKI, 1958a, 1960a, 1960b; SULIMSKI, 1959, 1964; MLYNARSKI, 1962), contained very abundant remains of leporids.

The dominating form of these faunae is *Hypolagus brachygnathus* KORMOS, 1934, resembling the genus *Lepus* LINNAEUS, 1785 in some characters. It is one of the 11 species of the genus *Hypolagus* DICE, 1917, occurring in North America, Asia and Central Europe. The earliest known species of this genus are from the middle Miocene of North America (DAWSON, 1958). It is characteristic of the genus *Hypolagus* that it nowhere survived beyond the middle of the Pleistocene. Though *Hypolagus brachygnathus* was recorded from several localities of Central Europe (Table I), the knowledge of this species

Table 1

European localities of fossil hares of the genera *Hypolagus* and *Pliolagus* with regard to their stratigraphy after particular authors

<i>Hypolagus brachygnathus</i> KORMOS, 1934	Hungary		
	Beremend	lower Cromerian	KORMOS, 1934
	Csarnota	lower Cromerian	KRETZOI, 1941
	Nagyharsanyhegy	upper Cromerian	KRETZOI, 1956
	Villany	upper Pliocene	KORMOS, 1934
		early Pleistocene	KRETZOI, 1956
	Kislang	Villafranchian	KRETZOI, 1954
	Roumania		
	Betfia Episcopia (Püspökföld)	lower Pleistocene	KRETZOI, 1941
	Yugoslavia		
	Podumci	early Pleistocene	KOWALSKI, 1958
	Netherlands		
	Tegelen	early Pleistocene	SCHREUDER, 1937 BERNSEN and SCHREUDER, 1934
	Germany		
	Sackdillinger Höhle	Forest-Bad Fauna	
	Gundersheim	(= Cromerian)	HELLER, 1930
		upper Pliocene	HELLER, 1936
	Poland		
	Weże	upper Pliocene	KOWALSKI, 1962a
<i>Hypolagus</i> sp.	Rebiełice Król.	upper Pliocene	KOWALSKI, 1962b
	Kadzielnia	early Pleistocene, be- ginning of intergl. Günz-Mindel	
	Kamyk	early Pleistocene, end of intergl. Günz-Mindel	KOWALSKI, 1960a
	Czechoslovakia		
	Hajnačka	lower Villafranchian	FÉJFAR, 1961
	Ivanovce	upper Pliocene (Astian)	FÉJFAR, 1961
<i>Pliolagus beremendensis</i> KORMOS, 1934, <i>Pliola- gus tothi</i> KRETZOI, 1941	Hungary	upper Pliocene	KORMOS, 1934b
	Villany-Kalkberg	early Pleistocene	KRETZOI, 1956
	Beremend	lower Cromerian	KRETZOI, 1956
	Csarnota	lower Cromerian	KRETZOI, 1956
	Rumania		
	Betfia	lower Pleistocene	KRETZOI, 1941
<i>Pliolagus</i> cf. <i>tothi</i> KRETZOI, 1941	Poland		
	Kadzielnia	early Pleistocene (beginning of intergl. Günz-Mindel)	KOWALSKI, 1958

has hitherto been confined to the fragments of mandibles and maxillae (KORMOS, 1934; KRETZOI, 1956; KOWALSKI, 1958a), and only some of the limb bones (SCHREUDER, 1937). The finding of very abundant remains of *Hypo-*

lagus brachygnathus in the four faunae, differing in geological age, from the Pliocene and Pleistocene of Central Poland permitted a close examination of the skull, permanent and milk teeth, as well as the limb skeleton, and made it possible to gain knowledge of various forms of variation, especially those of the dentition. These problems are the subject of the present paper. According to KORMOS (1934), KRETZOI (1941), and KOWALSKI (1958a), in the early Pleistocene faunae and in some older ones *Hypolagus brachygnathus* occurs occasionally along with other similar species of the genus *Pliolagus* KORMOS, 1934. The matter of systematic distinction between the genera *Pliolagus* and *Hypolagus* is put to revision in this paper.

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I. MATERIAL AND METHOD

MATERIAL

The basic fossil material used for this study includes the remains of two species of the family *Archaeolaginae*, DICE 1929: *Hypolagus brachygnathus* KORMOS, 1934 and *Pliolagus tothi* KRETZOI, 1941. Both these species occur in abundance in the Polish faunae from the Pliocene (Węże near Działoszyn and Rębielice Królewskie near Kłobuck) and those of the early Pleistocene (Kadzielnia Quarry in Kielce and Kamyk near Częstochowa). Their occurrence in the fauna from Kadzielnia has been described by KOWALSKI (1958a).

The fauna of Węże, geologically the oldest, has been referred to the Pliocene (KOWALSKI, 1962a). Its specific composition allows the presumption that the environment, inhabited by a large number of mammals and reptiles, was a steppe one. The breccia bearing remaining of many animal species including numerous bones of leporids was strongly cemented with calcite, and the clay in which these remains were embedded was red in colour and of the nature of „terra rossa“. The following remains were used for the study of leporids:

- skull — 4 incomplete (damages to occipital region or partial lack of skull base);
- mandible — 68 fragmentary rami with part of teeth missing;
- maxilla — 16 fragments without some teeth and often with palatine preserved;
- single teeth — P_3 -52, P_4 -40, M_1 -42, M_2 -42, M_3 -28, P^2 -40, P^3 -25, P^4 -15, M^1 -18, M^2 -17, M^3 -8, lower incisors — 52, upper incisors — 34;
- scapula — 5 bones; one of them nearly complete, 4 with neck-and-socket region preserved;
- humerus — 7 proximal and 8 distal ends with fragmentary shafts;
- radius — 8 proximal and 5 distal ends;
- ulna — 12 proximal ends;
- innominate — 8 fragments of acetabular region;
- femur — 15 distal ends with fragmentary shafts;
- tibia — 10 proximal and 9 distal ends with fragments of shafts;
- calcaneus — 21 bones, of which 18 complete;
- talus — 16 bones, of which 10 complete.

In addition, numerous fragments of phalanges, metacarpals and metatarsals, as well as very fragmentary remains of vertebrae were preserved.

The fauna of Rebielice Królewskie is geologically younger than that of Węże and its age is regarded as Upper Pliocene (KOWALSKI, 1960b). Part of its remains represent species associated with water (numerous amphibians and *Desmana kormosi* SCHREUDER, 1940). The bones, contrary to those from the breccia of Węże, were found in soft red clay, not cemented with calcite. Out of the abundant remains of the *Leporidae* the following were used for study:

- mandible — 40 incomplete rami without articular processes and some of the teeth;
- maxilla — 30 fragments lacking in some teeth;
- single teeth — P_3 -50, P_4 -42, M_1 -52, M_2 -24, M_3 -14, P^2 -35, P^3 -30, P^4 -26, M^1 -29, M^2 -25, M^3 -4, lower incisors — 48, upper incisors — 40;
- scapula — 10 fragments of neck-and-socket region with spine partly preserved;
- humerus — 7 proximal and 16 distal ends with shafts partly preserved;
- ulna — 18 proximal ends with fragments of shafts;
- innominate — 10 fragments of acetabular region;
- femur — 7 proximal and 10 distal ends with shafts partly preserved;
- tibia — 4 proximal and 14 distal ends with fragmentary shafts;
- calcaneus — 36 bones, of which 34 complete;
- talus — 37 bones, of which 32 complete.

There were also large numbers of phalanges, metacarpals, metatarsals, and fragments of vertebrae.

The fauna discovered in the quarry of Kadzielnia is referred to the early Pleistocene; in all probability, it dates from the Günz-Mindel interglacial

(KOWALSKI, 1958a). The occurrence of such genera as *Muscardinus* KAUP, 1829 and *Glis* BRISSON, 1762 in this fauna indicates the presence of a forest along with open areas at the time of its origin. Here again the bones of leporids form a very large proportion of the remains of numerous amphibian, reptilian, and mammalian species identified. Those used in the present study are as follows:

- mandible — 40 rami without articular processes; 36 of them with nearly complete dentition;
- maxilla — 15 fragments with incomplete dentition;
- single teeth — P_3 -66, P_4 -66, M_1 -70, M_2 -56, M_3 -50, P^2 -36, P^3 -37, P^4 -21, M^1 -28, M^2 -42, M^3 -2, lower incisors — 71, upper incisors — 36;
- scapula — 12 fragments of neck-and-socket region;
- humerus — 10 proximal and 32 distal ends with shafts partly preserved;
- radius — 12 proximal and 6 distal ends with shafts partly preserved;
- ulna — 29 proximal ends with fragments of shafts;
- innominate — 36 fragments of acetabular, iliac, and pubic regions;
- femur — 35 proximal and 14 distal ends with shafts partly preserved;
- tibia — 8 proximal and 16 distal ends with fragmentary shafts;
- calcaneus — 24 bones, of which 20 complete;
- talus — 14 bones, of which 9 complete.

Moreover, the material includes some fragments of metacarpals and metatarsals, as well as a few remains of vertebrae.

The geological age of the fauna represented by the remains collected at Kamyk is the youngest of the four faunae from Central Poland, and these remains probably come from the end of the Günz-Mindel interglacial (KOWALSKI, 1960a). On the basis of its specific make-up this fauna is considered to be a steppe one. The bones of leporids are fairly well preserved; however, there are no large fragments of the skull. Out of the remains of leporids identified the following were dealt with in this study:

- mandible — 16 damaged rami without articular processes;
- maxilla — 5 fragments with palate bones partly preserved;
- single teeth — P_3 -50, P_4 -68, M_1 -52, M_2 -70, M_3 -66, P^2 -90, P^3 -48, P^4 -38, M^1 -47, M^2 -23, M^3 -10, lower incisors — 59, upper incisors — 56;
- scapula — 14 fragments of neck-and-socket region;
- humerus — 42 distal and 4 proximal ends with fragments of shafts;
- radius — 45 proximal and 6 distal ends with fragments of shafts;
- ulna — 27 proximal ends with shafts partly preserved;
- innominate — 7 fragments of acetabular region, 5 fragments of ilium;
- femur — 6 proximal and 6 distal ends with shafts partly preserved;
- tibia — 4 proximal and 18 distal ends with shafts partly preserved;
- calcaneus — 48 bones, of which 31 complete;
- talus — 12 bones, of which 10 complete.

Besides the above-mentioned remains, in all these localities there were also permanent teeth of young individuals at various stages of development, their total number being 85. Special attention should be given to the fact of finding 120 specimens of milk cheek teeth at Rębielice Królewskie and Kadzielnia.

The colouration of the deposits bearing the bones at Kadzielnia and Kamyk is not so red as in the case of those at Weże and Rębielice. The clay at Kadzielnia is reddish-brown and that at Kamyk brown-yellow.

Each of the breccias discussed in this paper was formed by accumulation of animal bones either in a cave (Weże) or in deep funnels and other similar karst formations, which probably made natural traps for animals, and existed for a long time, at least several thousand years. Thus, remains of animals of various ages were accumulated in them. As for the manner of accumulation, it may be supposed that most likely it was not selective.

Nine nearly complete mandibles and 2 fragmentary maxillae (among them also the holotype) of *Hypolagus gromovi* GUREEV, 1963 from the Upper Miocene of Moldavia were used for comparison. These specimens were lent me from the Museum of the Zoological Institute, Academy of Sciences, Lenin-grad, U.S.S.R. My comparative material comprised also 12 fragments of mandibles and maxillae of *Hypolagus brachygnathus* KORMOS, 1934 from the early Pleistocene fauna of Betfia in Roumania, received from the Zoological Department of the National Museum in Budapest. The specimens of *Pliolagus beremendensis* KORMOS, 1934, including its holotype, come from the same collection, while the remains of *Pliolagus tothi* KRETZOI, 1941 were obtained from the collection of the Institute of Geology in Budapest.

Besides, at the examination of the teeth of *Hypolagus brachygnathus* I used specimens of the following fossil species as comparative material: *Agispelagus simplex* ARGYLOPULO, 1940 from the Lower Miocene of Kazakhstan, *Procaprolagus vetustus* (BURKE, 1941), and *Procaprolagus mongolicus* GUREEV, 1960, the last two from the middle Oligocene of Mongolia. The specimens of these species are in the possession of the Museum of the Palaeontological Institute, Academy of Sciences, Moscow, U.S.S.R.

The fossil specimens were compared with the skeletons of the wild rabbit *Oryctolagus cuniculus* (LINNAEUS, 1758) and the brown hare *Lepus europaeus* PALLAS, 1778. A series of 32 skulls of the wild rabbit from the collection of the Anatomical Institute, Central College for Agriculture, Warsaw, and a series containing the same number of skulls of the hare from the collection of the Mammals Research Institute, Polish Academy of Sciences, Białowieża, were used for this purpose. The hares came from the northern regions of Poland. The bones of skeleton of the fossil species were compared with the corresponding elements of the skeletons of 8 wild rabbits and 8 brown hares. Both the skulls and the whole skeletons of the recent species belonged to adult individuals, whose growth process had been completed.

Fifty skulls of the variable hare *Lepus timidus* LINNAEUS, 1758 from two

different climatic zones of Asia were used to illustrate variation in measurements of recent hares with climate. The specimens of this series were measured in the Zoological Museum of the Lomonosov University in Moscow.

MEASURING METHODS

Measurements were taken by means of a vernier caliper and dividers to an accuracy of 0.1 mm. Very small objects, such as milk teeth and their parts, were measured using a micrometer eyepiece allowing an accuracy of 0.01 mm. Missing lengths of the skeletal bones were restored in approximation by the reconstruction of the bones; photographs of bony fragments of adult specimens taken to the same scale were used for this purpose. In particular cases, e. g., for the examination of the curvature of teeth, radiograms were employed.

Some measurements, especially those of the teeth, were put to a statistical analysis, using the standard formulae and methods of calculation in statistics.

Considerable defectiveness of bones of the fossil species and the consequent difficulties in taking some of the measurements made it necessary to establish a number of new measuring points, varying from the conventional ones in some cases. Where the use of methods accepted in osteology was possible I used the measuring conventions adopted by DÜRST (1930). Many papers on leporids lack any descriptions of the position of the measuring points on the bones, which makes a comparison of the data given by different authors impossible. To avoid this in the future, a list of measurements taken during this study is presented and provided with their respective well-defined measuring points on the bones.

MEASUREMENTS OF SKULL

Width of neurocranium — distance between both Eurion points;
breadth of frontal — distance between the medialmost points on the margins of the frontal;

length of frontal — Nasion-Bregma distance;

breadth of nasal — distance between points of contact of the nasal, frontal, and intermaxillary;

greatest span of maxillae — distance between the lateralmost points of the maxillary bones;

length of maxillary diastema — distance between the most orally situated point of the alveolus of P² and the posteriormost point of the alveolus of the posterior incisor;

length of incisive foramina — distance between the anteriormost point of the foramina and the point of intersection of the line connecting both their

posterior borders and the perpendicular to this line passing through the above-mentioned anteriormost point;

width of incisive foramina — measured along the line connecting the anterior borders of the alveoli of P²;

width 1 of posterior nares — along the line running between M¹ and P⁴;

width 2 of posterior nares — along the tangential line to the posterior border of the alveoli of M³;

length of palate — least anteroposterior length of the palatal bridge;

breadth of palate — distance between lingual borders of the alveoli of P³;

length of base of zygomatic process of maxilla — least anteroposterior length on the ventral side;

length of mandibular diastema — distance between the anteriormost point of the alveolus of P₃ and the posteriormost point of the alveolus of the lower incisor;

distance from mental foramen to masseteric impress — distance between the anteriormost point of the impress and the posterior border of the foramen (= distance *f*);

height of mandible between P₄ and M₁ — measured on the lingual side;

thickness of mandible in the same place — measured in the frontal plane.

Ratios of measurements:

$$\frac{\text{length of palate}}{\text{breadth of palate}} \cdot 100$$

$$\frac{\text{length of upper tooth row}}{\text{length of maxillary diastema}} \cdot 100$$

$$\frac{\text{width of incisive foramina}}{\text{length of incisive foramina}} \cdot 100$$

$$\frac{\text{width 2 of posterior nares}}{\text{width 1 of posterior nares}} \cdot 100$$

$$\frac{\text{width 1 of posterior nares}}{\text{span of maxillae}} \cdot 100$$

$$\frac{\text{width 2 of posterior nares}}{\text{breadth of palate}} \cdot 100$$

$$\frac{\text{breadth of frontal}}{\text{length of frontal}} \cdot 100$$

$$\frac{\text{length of lower tooth row}}{\text{length of mandibular diastema}} \cdot 100$$

$$\frac{\text{length of mandibular diastema}}{\text{distance } f} \cdot 100$$

MEASUREMENTS OF TEETH

Lower incisors (I)

Width — at the posterior border of the biting surface;

thickness — as above;

$$\text{ratio of measurements: } \frac{\text{thickness}}{\text{width}} \cdot 100.$$

Upper incisor (I), anterior pair

Width — at the posterior border of the biting surface;

thickness — as above;

distance of the top groove from the medial margin of the tooth (*b*);

ratios of measurements:

$$\frac{\text{thickness}}{\text{width}} \cdot 100 \qquad \frac{b}{\text{width}} \cdot 100$$

Lower cheek teeth

Length of mandibular tooth row — distance between the anteriormost point of the alveolus of P_3 and the posteriormost point of the alveolus of M_3 .

P_3 :

length — greatest anteroposterior measurement;

width — greatest mediolateral measurement;

least distance of the posterior external enamel fold from the medial margin of the tooth (*l*).

P_4 , M_1 , M_2 , M_3 :

length — as above;

width of trigonid — greatest mediolateral measurement;

width of talonid — as above;

ratios of measurements:

$$\frac{\text{length}}{\text{width}} \cdot 100 \text{ (for } P_3) \qquad \frac{\text{length}}{\text{width of trigonid}} \cdot 100$$

$$\frac{\text{width of talonid}}{\text{width of trigonid}} \cdot 100 \qquad \frac{l}{\text{width}} \cdot 100 \text{ (for } P_3).$$

Upper cheek teeth

Length of maxillary tooth row — distance between the anteriormost point of the alveolus of P^2 and the posteriormost point of the alveolus of M^3 .

P^2 :

length — as for P_3 .

width — as for P_3 .

P^3 , P^4 , M^1 , M^2 :

length — greatest anteroposterior measurement;

width of anterolophid — greatest mediolateral measurement;

width of posterolophid — greatest mediolateral measurement.

M³:

length — as for P₃;

width — as for P₃;

ratios of measurements:

$$\frac{\text{length}}{\text{width}} \cdot 100 \text{ (for P}^2 \text{ and M}^3\text{)}$$

$$\frac{\text{length}}{\text{width of anterolophid}} \cdot 100$$

$$\frac{\text{length}}{\text{width of posterolophid}} \cdot 100$$

$$\frac{\text{width of posterolophid}}{\text{width of anterolophid}} \cdot 100.$$

MEASUREMENTS OF BONES OF THE POSTCRANIAL SKELETON

Scapula

Least width of neck — measured in the sagittal plane;

shorter diameter of glenoid cavity — from the vertex of the medial angular bend in the margin of the cavity at the base of the coracoid process perpendicularly to the ventral margin of the cavity;

longer diameter of glenoid cavity — greatest measurement perpendicular to the previous one;

coracoid-glenoid distance — minimum distance between the ventral margin of the coracoid and the anterior section of the margin of the glenoid cavity;

ratios of measurements:

$$\frac{\text{shorter diameter of glenoid cavity}}{\text{longer diameter of glenoid cavity}} \cdot 100$$

$$\frac{\text{coracoid-glenoid distance}}{\text{shorter diameter of glenoid cavity}} \cdot 100.$$

Humerus

Width of trochlea — distance between the medialmost and the lateralmost points of the respective medial and lateral epicondyles;

width of medial sulcus of trochlea — distance between the distalmost points of the medial and intermediate crests;

height of medial crest — from the distalmost point of the medial condyle situated at the base of the medial crest to the distalmost point of the medial crest;

width of greater tuberosity — measured at the height of the distal end of the bicipital groove perpendicularly to the shaft;

height of greater tuberosity — from its apex to the lateralmost point of the deltoid tubercle;

transverse width of head — measured at the base on the dorsal side;

length — greatest measurement;

ratios of measurements:

$$\frac{\text{width of medial sulcus}}{\text{width of trochlea}} \cdot 100$$

$$\frac{\text{height of medial crest}}{\text{width of trochlea}} \cdot 100$$

$$\frac{\text{width of greater tuberosity}}{\text{height of greater tuberosity}} \cdot 100.$$

Radius

Thickness of proximal epiphysis — greatest, measured along the medial sulcus;

width of proximal epiphysis — greatest, measured along a mediolateral line;

thickness of distal epiphysis — greatest, measured along an antero-posterior line;

width of distal epiphysis — greatest, measured along a mediolateral line;

ratios of measurements:

$$\frac{\text{thickness of proximal epiphysis}}{\text{width of proximal epiphysis}} \cdot 100$$

$$\frac{\text{thickness of distal epiphysis}}{\text{width of distal epiphysis}} \cdot 100.$$

Ulna

Width of olecranon — distance between the posteriormost points on the anterior and posterior edges;

height of olecranon — distance between the ventralmost point of the tuberculum anconaeum and the dorsalmost point of the olecranon;

ratio of measurements:

$$\frac{\text{width of olecranon}}{\text{height of olecranon}} \cdot 100.$$

Innominate bone

Diameter of acetabulum — greatest diameter.

Femur

Transverse diameter of shaft in the proximal portion of the bone — measured in the terminal section of the labium laterale at the height of the gluteal tuberosity;

sagittal diameter of shaft — measured as above;
 spread of condyles — distance between the lateralmost point of the lateral epicondyle and the medialmost point of the medial epicondyle;
 width of patellar groove — measured at its mid-length;
 width of intercondylar notch — greatest measurement;
 ratios of measurements:

$$\frac{\text{width of intercondylar notch}}{\text{width of patellar groove}} \cdot 100 \qquad \frac{\text{transverse diameter of shaft}}{\text{spread of condyles}} \cdot 100.$$

Tibia

Width of proximal epiphysis — distance between the medialmost point of the medial condyle and the lateralmost point of the lateral condyle;
 width of distal epiphysis — distance between the medialmost point of the tibial malleolus and the lateralmost point of the fibular malleolus;
 thickness of distal epiphysis — measured along the lateral sulcus;
 ratio of measurements:

$$\frac{\text{thickness of distal epiphysis}}{\text{width of distal epiphysis}} \cdot 100.$$

Calcaneus

Total length — distance between the posteriormost point of the tuber calcanei and the anteriormost point of the facet for the cuboid;
 width — distance between the lateralmost point of the tibiofibular facet and the medialmost point of the sustentaculum tali;
 length of tuber calcanei — distance between the posteriormost points of the tibio-fibular facet and the tuber calcanei, on the lateral side;
 length of body of calcaneus — distance between the anteriormost point of the facet for the cuboid and the anteriormost point of the tibio-fibular facet;
 ratios of measurements:

$$\frac{\text{width}}{\text{total length}} \cdot 100 \qquad \frac{\text{length of tuber calcanei}}{\text{total length}} \cdot 100$$

Talus

Total length — distance between the posteriormost point situated on the bottom of the trochlear groove and the anteriormost point of the facet for the navicular;

length of collum — distance between the anteriormost point situated on the bottom of the trochlear groove and the anteriormost point of the facet for the navicular;

ratio of measurements:

$$\frac{\text{length of collum}}{\text{total length}} \cdot 100.$$

In addition to the measurements described above, measurements of length made on the basis of reconstructions were applied in the case of long bones of the limbs. These are always the greatest lengths; in the tables of measurements they are defined as „lengths from reconstruction“. In contrast with the other measurements they are charged with a relatively great error, reaching up to 5%.

II. MORPHOLOGY OF THE SKELETON OF *HYPOLAGUS* *BRACHYGNATHUS* KORMOS

SKULL

The present description of the skull is based on 4 incomplete specimens from the Weże breccia and numerous small fragments from the faunae of Rebielice, Kadzielnia, and Kamyk. Only remains of adult individuals (Pl. I, 1, 2, 3) with strongly obliterated sutures were used for description and reconstruction.

As far as its size is concerned, the skull of *Hypolagus brachygnathus*, especially if derived from later geological periods, holds an intermediate position between the modern wild rabbit and the brown hare; however, it more resembles the skull of the hare in dimensions. The corresponding elements of the skulls from different geological periods show some differences in size, there being a tendency to growth with time. A general tendency shown by the skeleton of this species to increase in size, especially in the geologically younger faunae, is discussed in detail on p. 62. Owing to the incompleteness of the skulls from Weże, the measurements of their lengths have been given up as being too inaccurate.

The descriptions of distinctive bone characters of *Hypolagus brachygnathus* presented below concern only the elements that in a characteristic way make these bones different from or similar to the corresponding bones in other species, above all in *Lepus europaeus* and *Oryctolagus cuniculus*.

Frontal

The supraorbital process is, like that in the modern hare, triangular in shape. The well-developed posterior (postorbital) part of this process comes off the remaining portion of the frontal laterally (Fig. 1 a, b, c), while the anterior

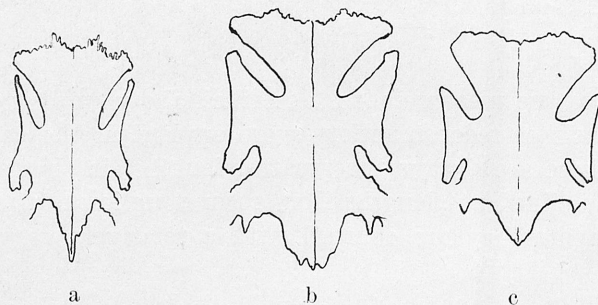


Fig. 1. Frontal of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c)

(preorbital) part closely approaches the anterosuperior margin of the orbit. The width to length ratio of this bone does not show any pronounced divergencies from those in the modern hare and wild rabbit.

Intermaxillary

The posterior end of this bone extends on the dorsum of the skull nearly as far as the posterior border of the nasal. In the modern hare and wild rabbit the intermaxillary does not reach this border, whereas in *Hypolagus schreuderi*,

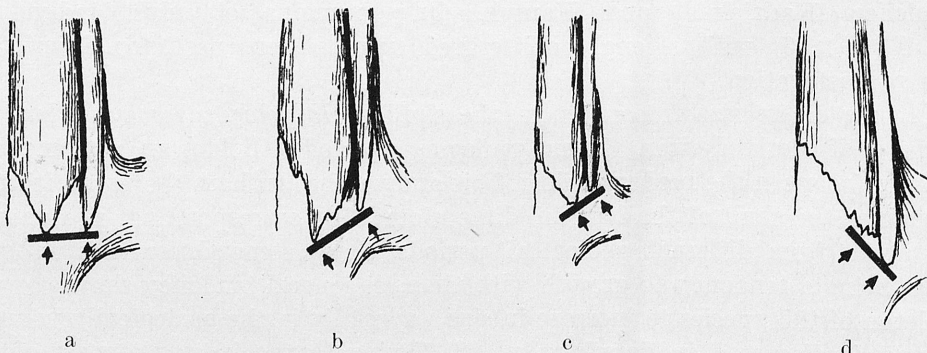


Fig. 2. Topographical relation of the intermaxillary to the nasal in *Hypolagus brachygnathus* (a), *Lepus europaeus* (b), *Oryctolagus cuniculus* (c), *Hypolagus schreuderi* (d)

as will be seen from TEILHARD'S drawing (1940), goes far beyond it (Fig. 2 a, b, c). There is less fenestration on the lateral side of this bone in *Hypolagus brachygnathus* than in the modern species.

Maxilla

In *Hypolagus brachygnathus* the ventral anteroposterior dimension of the zygomatic process of the maxilla is relatively larger than those in the recent hare and wild rabbit.

Zygomatic arch

The anterior part of the zygomatic arch, close to the zygomatic process of the maxilla, is robust and its measurements equal and, occasionally, exceed the absolute measurements of the corresponding part in the recent hare (Pl. I, 1a, b, c).

Palatine

The anteroposterior length of the bony bridge of the palate, consisting of the proper palate bone and the palatine process of the maxilla, is large, relatively larger than in the hare, and its length to width ratio approximates to that in the wild rabbit (Table 2a; Pl. I, 2a, b, c). The posterior nares, wide in the region of the palatal bridge, become somewhat narrower posteriorly in *Hypolagus brachygnathus* and the wild rabbit, as shown by the ratios of their two diameters (Table 2c). Besides, the shape of this foramen differs considerably from its shape in the hare and wild rabbit (Pl. I, 3a, b, c).

The incisive foramen is similar to that in the hare, whereas in the wild rabbit it is relatively much larger.

Diastemae

In *Hypolagus brachygnathus* the anterior (facial) part of the skull is strongly shortened, which is connected with a considerable, in comparison with the modern species, shortening of the maxillary and mandibular diastemae (Pl. I, 1a, b, c). The ratios of their lengths to the lengths of the diastemae in other species are given in Table 2c.

Tympanic bulla

The tympanic bulla of *Hypolagus brachygnathus* is worse developed than that of the modern hare and wild rabbit.

Other morphological details of the skull, connected with the dentition, such as the degree of curvature of the incisors and their relation to the diastemae, general shape of the tooth rows, etc., will be discussed in further sections of this paper.

Table 2 a

Measurements of skull of *Hypolagus brachygnathus* in comparison with other species of the genus *Hypolagus* as well as *Lepus europaeus* and *Oryctolagus cuniculus*. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements

		<i>Hypolagus brachygnathus</i>			<i>Hypolagus gro-movi</i>	<i>Hypolagus schreuderi</i>	<i>Lepus europaeus</i>	<i>Oryctolagus cuniculus</i>
		Weże	Rebielice	Kadzielnia				
length of palate	M	6.38	7.23	7.40	6.4	—	5.93	6.33
	O. R. N	5.7—7.4 12	6.5—8.1 10	6.9—8.3 5	— 1	—	4.8—7.4 32	5.6—7.3 18
breadth of palate	M	13.10	12.86	—	—	—	14.11	10.61
	O. R. N	12.2—14.2 7	11.8—13.8 8	—	—	—	12.9—15.9 32	9.8—11.8 18
length of maxillary tooth row	M	17.86	18.09	17.93	—	16.67	17.73	13.81
	O. R. N	17.0—19.6 7	17.7—19.2 10	17.6—18.2 3	—	16.0—17.0 3	16.6—19.2 32	12.6—15.2 18
length of base of zygomatic process	M	6.02	6.73	6.75	6.8	—	5.12	4.3
	O. R. N	5.4—7.4 13	5.8—7.2 14	5.7—7.6 11	— 1	—	4.7—6.2 32	3.9—4.6 18
length of maxillary diastema	M	21.15	—	—	—	—	29.54	22.34
	O. R. N	20.0—21.3 2	—	—	—	—	27.3—31.8 32	20.0—23.8 18
length of incisive foramina	M	21.30	—	—	—	—	28.51	21.92
	O. R. N	19.9—22.7 3	—	—	—	—	26.2—30.7 32	21.4—24.0 18

width of incisive foramina	M	8.57	—	—	—	—	11.84	7.07
	O.R.	8.7—9.2	—	—	—	—	10.9—13.7	6.5—7.8
	N	3	—	—	—	—	32	18
width 1 of posterior nares	M	8.40	—	—	—	—	11.80	5.75
	O.R.	7.4—8.9	—	—	—	—	10.3—13.0	5.2—6.2
	N	3	—	—	—	—	32	18
width 2 of posterior nares	M	6.50	—	—	—	—	11.8	4.47
	O.R.	6.2—6.9	—	—	—	—	10.7—12.9	4.1—5.0
	N	3	—	—	—	—	32	18
greatest span of maxillae	M	20.73	—	—	—	—	22.53	16.80
	O.R.	20.4—20.7	—	—	—	—	21.4—23.7	16.2—18.2
	N	3	—	—	—	—	32	18
breadth of nasal	M	17.77	—	—	—	—	22.50	14.62
	O.R.	16.4—17.9	—	—	—	—	21.8—22.9	13.9—15.3
	N	3	—	—	—	—	32	18
breadth of frontal	M	13.93	—	—	—	13.5	13.92	12.14
	O.R.	13.6—14.4	—	—	—	—	13.0—15.0	11.8—13.0
	N	3	—	—	—	3	32	18
length of frontal	M	33.3	—	—	—	—	31.54	25.71
	O.R.	—	—	—	—	—	30.9—32.1	24.8—26.3
	N	2	—	—	—	—	32	18
width of neurocranium	M	27.00	—	—	—	3.0	30.62	26.00
	O.R.	2	—	—	—	—	29.8—31.3	25.6—27.0
	N	—	—	—	—	3	32	18

Table 2 b

Comparison of mandibular measurements of various species of the genus *Hypolaqus* with those of *Lepus europaeus* and *Oryctolagus cuniculus*.
 N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; * — after SCHREUDER (1937), ** — after
 TEILHARD (1940)

		<i>Hypolaqus brachygnathus</i>								<i>Hypolaqus schreuderi</i> **	<i>Hypolaqus gr-moni</i>	<i>Lepus europaeus</i>	<i>Oryctolagus cuniculus</i>
		Węże	Rebielice	Kadzielnia	Kamyk	Tege-len *	Bełtfa	Vil-lany	Bere-mend				
length of diastema	M	16.07	16.45	16.93	—	—	18.82	20.50	20.10	20.50	19.58	24.26	17.38
	N	11	5	7	—	—	6	1	4	5	6	32	18
	O.R.	15.2-17.5	15.5-17.4	15.7-17.5	19.0-20.8	—	18.1-20.6	—	19.3-20.5	21.5-26.0	18.7-20.7	22.1-26.4	16.3-18.4
length of tooth row	M	17.51	17.40	16.93	18.4	—	16.8	17.40	17.25	17.30	19.60	19.96	14.38
	N	8	6	7	2	—	1	2	2	5	5	32	18
	O.R.	16.9-18.7	17.1-18.8	16.8-18.9	—	—	—	—	—	17.0-18.0	19.0-20.1	18.5-21.2	14.2-16.0
distance <i>f</i>	M	19.75	18.13	18.8	19.25	21.0	18.05	20.20	20.10	—	20.16	24.52	14.71
	N	3	4	3	2	1	2	1	3	—	7	32	18
	O.R.	18.2-21.3	17.2-18.6	18.7-18.9	—	—	—	—	19.8-20.6	—	18.7-20.8	22.6-25.7	13.5-16.2
height of mandible	M	14.49	15.21	14.9	15.12	15.1	15.4	15.70	14.33	—	17.07	15.18	12.49
	N	13	14	14	9	1	5	2	4	—	7	32	18
	O.R.	14.0-16.3	14.8-15.9	14.6-15.7	14.9-15.3	—	4.8-15.8	—	14.2-14.4	—	15.1-18.5	14.0-16.7	11.9-13.8
thickness of mandible	M	5.77	6.03	5.89	6.16	5.9	5.75	5.70	5.76	—	—	5.89	4.65
	N	22	14	20	9	—	4	2	4	—	—	32	18
	O.R.	5.2-6.4	5.8-6.5	5.4-6.4	5.8-6.4	—	5.7-5.8	—	5.5-6.3	—	—	5.2-6.4	4.3-4.9

Table 2c

Ratios of measurements of the skull and mandible of *Hypolagus brachygnathus* in comparison with other species

	<i>H. brachygnathus</i>			<i>H. schreuder</i>	<i>H. gro-movi</i>	<i>L. eu-ropae-us</i>	<i>O. cuni-culus</i>
	Weże	Rebie-lice	Ka-dziel-nia				
$\frac{\text{length of palate}}{\text{breadth of palate}} \cdot 100$	—	56.0	—	—	—	42.0	59.5
$\frac{\text{lenght of upper tooth row}}{\text{length of maxillary diastema}} \cdot 100$	—	84.3	—	—	—	60.2	61.8
$\frac{\text{width of incisive foramina}}{\text{length of incisive foramina}} \cdot 100$	40.1	—	—	—	—	41.5	31.3
$\frac{\text{width 2 of posterior nares}}{\text{width 1 of posterior nares}} \cdot 100$	77.5	—	—	—	—	100.0	78.4
$\frac{\text{width 2 of posterior nares}}{\text{span of maxillae}} \cdot 100$	31.2	—	—	—	—	52.4	26.6
$\frac{\text{width 2 of posterior nares}}{\text{breadth of palate}} \cdot 100$	49.7	—	—	—	—	83.7	42.5
$\frac{\text{breadth of frontal}}{\text{length of frontal}} \cdot 100$	41.8	—	—	—	—	44.2	47.0
$\frac{\text{length of mandibular diastema}}{\text{distance } f} \cdot 100$	108.8	105.8	100.0	70.6	100.1	82.3	82.7
$\frac{\text{length of lower tooth row}}{\text{length of mandibular diastema}} \cdot 100$	81.4	—	—	—	97.1	98.9	18.5



DENTITION

DESCRIPTION AND MEASUREMENTS

Permanent Dentition

The cheek teeth M₁ and M₂ resemble each other so much that, when isolated, they were hard to distinguish and consequently they have not hitherto been used for measurements. However, an observation of a large number of single

teeth of adult specimens has revealed a set of distinctive characters, namely their being curved in different planes and having talonids differing in shape. These characters can be tabulated as follows:

Curvature		talonid shape on the side of wear surface	
frontal plane	sagittal plane		
P ₄ curved laterald	no curve	slightly convex on lingual side	
M ₁ very slightly curved lateral	slightly curved posterad		
M ₂ no curve	strongly curved posterad	distinctly convex on lingual side	

The upper and lower cheek teeth of *Hypolagus brachygnathus* are hypsodont and in adult specimens they are, as a rule, of the shape of irregular prisms (Pl. III, 1a; Pl. IV, 1a, b, c). As a result, the pattern of enamel folds on the wear surface of a tooth repeats in its deepest radical portion. This phenomenon not only makes the reconstruction of the configuration of the enamel easier, when the crown is destroyed, but can also be used to determine whether some occasional divergencies from the typical pattern of enamel in the crown are casual, or whether they took rise in early developmental stages of the tooth.

The ever-growing incisors of the mandible and maxilla, like the cheek teeth, show a prismatic structure, but have chisel-like endings of their gnawing surfaces. As will be seen from the observations of numerous isolated teeth and the radiograms of specimens varying in age, the prismatic structure of the teeth is characteristic only of adult specimens. The teeth of young individuals are more or less truncated pyramids in shape. The enamel pattern at the base of such a tooth is copied, diminished and usually somewhat deformed, in the crown (Pl. III, 1b; Pl. IV, 5a, b).

Out of the upper cheek teeth only P⁴ and M¹ give some difficulty when isolated. In about 75% of cases it is possible to distinguish them from each other on the basis of the ratio of the greatest mediolateral width of the anterolophid

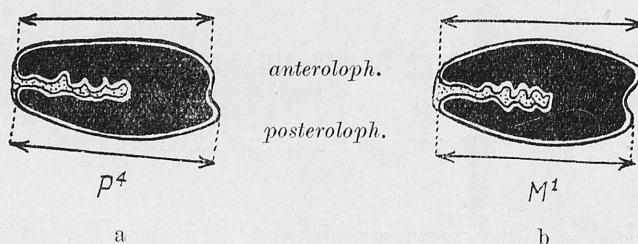


Fig. 3. Comparison of widths of the anterolophid (a) and posterolophid (b) on P⁴ and M¹

to that of the posterolophid: the anterolophid of P^4 is somewhat narrower than the posterolophid, while in M^1 this relation is generally inverse (Fig. 3a, b). An observation of these teeth standing together *in situ* shows that in a fairly large number of cases (25%) the measurements of the anterolophids and posterolophids of P^4 and M^1 are subequal. Then the distinction of these teeth from each other in isolation is impossible, because the differences in degree of curvature between P^4 and M^1 are imperceptible.

Lower Cheek Teeth

The position of the lower cheek tooth row in relation to the long axis of the mandibular ramus and the shape of its wear surface in *Hypolagus brachygnathus* are the same as in the modern hare and wild rabbit.

In all the leporids known so far P_3 differs considerably in structure from the remaining lower cheek teeth. The division of its crown into the trigonid and the talonid, used by some authors (e. g., Wood, 1940), is here of smaller practical significance than in the other lower cheek teeth and, consequently, in my measurements and description of this tooth I use the terms: the length and width of crown. The shape of the crown in the horizontal plane resembles a triangle having more or less rounded vertices (Pl. III, 2a, b, c; Fig. 4). The enamel surrounding the dentine forms a thin layer varying in thickness in different regions of the tooth. The thickness of enamel generally decreases towards the alveolar end. The same is also true of all the other cheek teeth. On the medial and posterior walls of the crown the enamel forms a nearly uniform thin layer, which thickens laterad.

In adult specimens there are two enamel folds on the anterolateral side, a shallow anterior fold and a deep posterior one (Fig. 4). The anterior fold is simple in shape and approximates to the right angle. The posterior fold cuts into the dentine as deep as about half the greatest width of the tooth and is directed somewhat towards its posteromedial margin. The anterior wall of the fold is made of a very thick layer of enamel, which, however, in the bottom of the fold becomes so thin that at the passage on to the posterior wall it can hardly be told from the dentine. The posterior wall of the fold, slightly convex anterad, is either completely smooth or it shows some undulation, which most frequently passes into irregular crenulation in the medial portion (Pl. III, 2c; Fig. 4). Both of the folds are well filled with cement, which covers the whole anterolateral wall of the tooth, sometimes forming a thick layer along the posterolateral edge.

In P_4 , M_1 and M_2 a very deep fold of enamel squeezes in between the trigonid and the talonid from the lateral side and reaches as far as the medial wall of

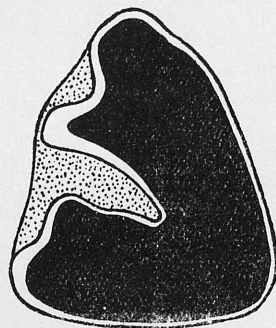


Fig. 4. Wear surface of the crown of P_3 of *Hypolagus brachygnathus*

the tooth. The anterior wall of this fold is strongly thickened, whereas the posterior one is very thin and occasionally slightly and irregularly wavy. The angle of the fold is filled with cement.

The thin posterior wall of the fold shows, as a rule, three types of configuration: 1) entirely smooth line, 2) irregular waviness, and 3) distinct, more or less regular, crenulation, particularly well visible in the medial region (Fig. 5).

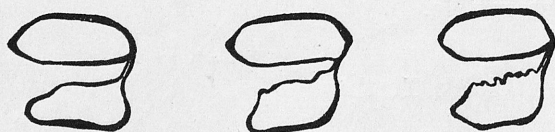


Fig. 5. Wear surface of the crowns of P_4 , M_1 and M_2 of *Hypolagus brachygnathus*



Fig. 6. Wear surface of the crown of M_3 of *Hypolagus brachygnathus*

Table 3a

Measurements of lower premolars of *Hypolagus brachygnathus*. N — number of specimens; M — arithmetic mean; O. R. — range of measurements; s — standard deviation; V — coefficient of variation; W — Weże; R — Rębiełice; K — Kadzielnia; Ky — Kamyk

			N	M	O. R.	s	V
P_3	length	W	52	3.29 ± 0.018	3.0—3.6	0.13 ± 0.012	3.9 ± 0.38
		R	30	3.53 ± 0.053	3.2—3.5	0.29 ± 0.037	8.5 ± 1.05
		K	66	3.32 ± 0.017	2.9—3.6	0.14 ± 0.012	4.1 ± 0.36
		Ky	50	3.59 ± 0.025	3.0—4.0	0.18 ± 0.018	5.0 ± 0.50
	width	W	52	3.20 ± 0.026	2.8—3.7	0.19 ± 0.019	5.9 ± 0.58
		R	30	3.21 ± 0.024	2.9—3.4	0.13 ± 0.017	4.0 ± 0.52
		K	66	3.24 ± 0.018	2.9—3.6	0.15 ± 0.013	4.8 ± 0.42
		Ky	50	3.42 ± 0.031	2.8—3.8	0.22 ± 0.022	6.5 ± 0.65
	distance l	W	52	1.17 ± 0.017	0.9—1.5	0.12 ± 0.012	9.6 ± 0.95
		R	30	1.19 ± 0.018	0.9—1.4	0.10 ± 0.014	8.6 ± 1.05
		K	66	1.24 ± 0.017	0.9—1.5	0.14 ± 0.012	10.9 ± 0.94
		Ky	50	1.33 ± 0.021	0.9—1.6	0.15 ± 0.015	11.3 ± 1.13
P_4	length	W	40	3.28 ± 0.022	3.1—3.7	0.14 ± 0.016	4.3 ± 0.48
		R	24	3.22 ± 0.033	2.9—3.6	0.16 ± 0.023	4.9 ± 0.71
		K	66	3.23 ± 0.019	2.8—3.8	0.16 ± 0.014	4.8 ± 0.42
		Ky	68	3.35 ± 0.018	2.9—3.6	0.15 ± 0.013	4.4 ± 0.38
	width trigonid	W	40	3.78 ± 0.039	3.3—4.3	0.24 ± 0.027	6.5 ± 0.72
		R	24	3.88 ± 0.047	3.4—4.2	0.23 ± 0.033	6.0 ± 0.91
		K	66	3.93 ± 0.022	3.5—4.3	0.18 ± 0.016	4.7 ± 0.41
		Ky	68	3.91 ± 0.023	3.4—4.4	0.19 ± 0.016	5.0 ± 0.43
	width talonid	W	40	2.99 ± 0.019	2.8—3.2	0.12 ± 0.014	3.9 ± 0.44
		R	24	2.88 ± 0.039	2.6—3.2	0.19 ± 0.028	6.7 ± 0.97
		K	66	2.94 ± 0.022	2.6—3.3	0.18 ± 0.017	6.1 ± 0.53
		Ky	68	3.15 ± 0.022	2.6—3.5	0.18 ± 0.015	5.7 ± 0.49

Table 3b

Measurements of lower molars of *Hypolagus brachygnathus*. Abbreviations as in Table 3a

			N	M	O. R.	s	V
M ₁	length	W	42	3.26 ± 0.028	2.9—3.9	0.18 ± 0.020	5.5 ± 0.59
		R	23	3.21 ± 0.035	2.9—3.5	0.17 ± 0.025	5.3 ± 0.78
		K	70	3.20 ± 0.018	2.6—3.5	0.15 ± 0.013	4.7 ± 0.39
		Ky	52	3.43 ± 0.019	3.2—3.7	0.14 ± 0.014	4.0 ± 0.36
	width trigonid	W	42	3.72 ± 0.031	3.2—4.2	0.20 ± 0.022	5.5 ± 0.60
		R	23	3.89 ± 0.061	3.3—4.3	0.29 ± 0.042	7.5 ± 1.12
		K	70	3.88 ± 0.025	3.3—4.4	0.21 ± 0.018	5.4 ± 0.46
		Ky	52	3.88 ± 0.019	3.4—4.2	0.14 ± 0.014	3.7 ± 0.36
	width talonid	W	42	2.69 ± 0.022	2.5—3.1	0.14 ± 0.015	5.2 ± 0.55
		R	23	2.68 ± 0.025	2.4—2.9	0.12 ± 0.017	4.7 ± 0.69
		K	70	2.72 ± 0.020	2.3—3.2	0.17 ± 0.014	6.4 ± 0.54
		Ky	52	3.11 ± 0.042	2.8—3.4	0.30 ± 0.030	9.6 ± 0.95
M ₂	length	W	42	3.22 ± 0.015	3.0—3.9	0.10 ± 0.011	3.2 ± 0.35
		R	16	3.14 ± 0.043	2.8—3.4	0.17 ± 0.030	5.3 ± 0.95
		K	56	3.18 ± 0.020	2.8—3.5	0.15 ± 0.014	4.7 ± 0.44
		Ky	70	3.41 ± 0.019	3.1—3.9	0.16 ± 0.014	4.8 ± 0.41
	width trigonid	W	42	3.61 ± 0.038	3.2—4.3	0.25 ± 0.027	6.7 ± 0.73
		R	16	3.69 ± 0.060	3.2—4.1	0.24 ± 0.042	6.6 ± 1.16
		K	56	3.73 ± 0.031	3.2—4.1	0.23 ± 0.022	6.1 ± 0.54
		Ky	70	3.73 ± 0.021	3.4—4.3	0.18 ± 0.015	4.8 ± 0.41
	width talonid	W	42	2.88 ± 0.022	2.6—3.2	0.14 ± 0.015	4.9 ± 0.53
		R	16	2.81 ± 0.045	2.5—3.1	0.18 ± 0.032	6.3 ± 1.08
		K	56	2.79 ± 0.025	2.4—3.2	0.19 ± 0.018	6.8 ± 0.64
		Ky	70	3.02 ± 0.020	2.6—3.3	0.17 ± 0.014	5.5 ± 0.47
M ₃	length	W	28	1.99 ± 0.023	1.7—2.2	0.12 ± 0.016	6.2 ± 0.83
		R	14	1.98 ± 0.020	1.8—2.1	0.08 ± 0.014	3.9 ± 0.74
		K	50	1.92 ± 0.021	1.6—2.4	0.15 ± 0.015	8.0 ± 0.80
		Ky	66	2.31 ± 0.015	1.9—2.5	0.12 ± 0.010	5.2 ± 0.44
	width trigonid	W	28	2.00 ± 0.032	1.7—2.3	0.17 ± 0.023	8.3 ± 1.12
		R	14	2.03 ± 0.026	1.8—2.2	0.10 ± 0.019	5.1 ± 0.97
		K	50	2.03 ± 0.024	1.6—2.4	0.17 ± 0.017	8.2 ± 0.82
		Ky	66	2.31 ± 0.019	2.0—2.7	0.16 ± 0.014	7.0 ± 0.61
	width talonid	W	28	1.25 ± 0.007	1.0—1.5	0.03 ± 0.004	2.5 ± 0.33
		R	14	1.36 ± 0.019	1.2—1.5	0.07 ± 0.014	5.2 ± 0.98
		K	50	1.27 ± 0.018	0.9—1.7	0.13 ± 0.013	10.8 ± 1.08
		Ky	66	1.57 ± 0.099	1.3—1.7	0.08 ± 0.007	5.3 ± 0.46

M_3 is much simpler in shape than the other lower cheek teeth. Its trigonid and talonid retain their distinctness and are united all along the tooth only with a cement layer varying in thickness from specimen to specimen. Both the trigonid and the talonid have the shape of cylinders deformed in varying degrees. The trigonid is flattened in the frontal plane, while the talonid shows a slight flattening on the anterior side (Fig. 6). The thickenings of enamel can be seen in both parts of the tooth on the medial and lateral sides.

Among the M_3 specimens examined there were some single teeth in which the dentine and enamel of the posterior side of the trigonid were connected with those of the anterior side of the talonid, this connection taking place on the lingual side. As a result, an enamel fold, analogous with those observed in the other molar teeth, was formed. Such specimens were found in the material from Kadzielnia and Kamyk.

Upper Cheek Teeth

The border line of the wear surface in the upper tooth row of *Hypolagus brachygnathus* is concave on the medial side, while it is straight or slightly convex in the modern hare and wild rabbit. In *Hypolagus brachygnathus* this character seems to be connected with a larger angle between both mandibular rami than in the modern forms.

In shape P^2 differs remarkably from the other upper cheek teeth. It bends in the sagittal plane so that its anterior and posterior walls bulge forward. At the half-width of the anterior wall the enamel forms a deep fold cutting in as far as one-third or, occasionally, a half of the length of the crown. After sinking into the dentine, the fold extends towards the lateroposterior margin of the tooth. Somewhat more externally to this fold on the anterior wall of the tooth there is another shallower recess of enamel, which forms a groove running all along the tooth (Pl. III, 4a, b). The portion of enamel separating these two folds, as well as that on the anteromedial margin, is strongly thickened. In other regions of the crown the enamel layer is thin. Cement fills both the folds, and its thick layer covers the anterior, medial, and lateral walls of the tooth.

The enamel of the upper premolars and molars (except for M^3) is thick on the anterior wall of the anterolophid. On the posterior and external (buccal) sides the enamel layer becomes very thin and occasionally it cannot be found at all, whereas on the medial side it thickens again and sinking into the dentine forms a deep fold, the so-called hypostria. In the frontal plane the anterior and posterior walls of this fold are wavy to various degrees. This results in characteristic crenulations of the anterior and posterior margins of the hypostria on the wear surface of the teeth (Fig. 7).

The following types of shape of hypostriae were found in P^3 , P^4 , M^1 , and M^2 :

1. pronounced crenulation of both margins,

2. only one margin with pronounced crenulation,
3. irregular waviness of both margins without pronounced crenulation, and
4. both margins almost quite smooth.

Types 2 and 3 were most frequently present in the teeth under study. Crenulation was most often lacking on the posterior margin of P^4 . The diverse shapes of hypostria are presented in Fig. 7.

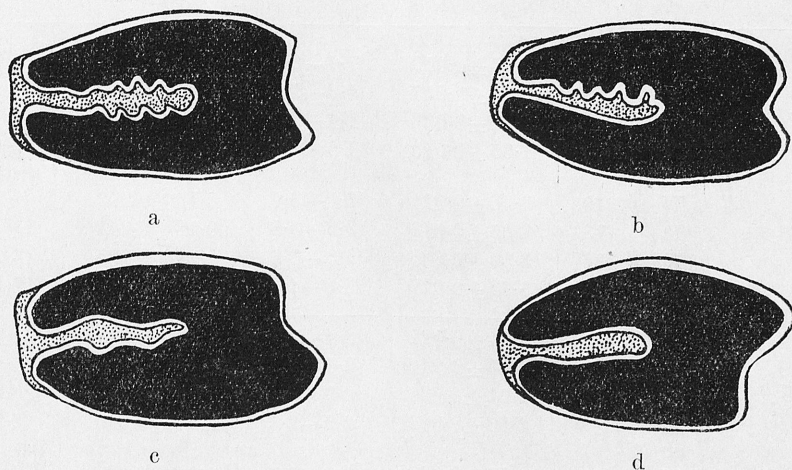


Fig. 7. Examples of different structures of the hypostriae on P^3 , P^4 , M^1 and M^2 of *Hypolagus brachygnathus*. a — crenulation of both margins; b — only one margin crenulated; c — irregular waviness of both margins; d — both margins almost smooth

In *Hypolagus brachygnathus* M^3 is always present, though it is very rarely preserved whole. It is simple and cylindrical in structure and very small. A very thin layer of enamel surrounds the pillar of dentine without showing any pattern at all (Pl. IV, 3).

Incisors

The ever-growing incisors of *Hypolagus brachygnathus* have their walls parallel to each other similarly to what is found in all lagomorphs. The character distinguishing them from the incisors of the modern hare and wild rabbit is their massiveness (see Table 6c on p. 33).

Despite the shortening of the facial portion of the skull in *Hypolagus brachygnathus* the curvatures of its lower and upper incisors are almost identical with those in the modern hare. The radius of curvature of the lower incisors is 16.0—17.6 mm (on the average 17.1 mm) in *Hypolagus brachygnathus* and 16.4—17.9 mm (on the average 17.3 mm) in the hare, while the radius of curvature of the upper incisors is respectively 10.0—10.9 mm and 9.9—11.0 mm (averages: 10.5 and 10.2 mm). Thus, it is impossible to tell the teeth of both these species apart on the basis of their curvatures. The remark made by KOWALSKI (1958a) that the curvature of the lower incisors of *Hypolagus brachy-*

Table 4a

Measurements of upper premolars of *Hypolagus brachygnathus*. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; s — standard deviation; V — coefficient of variation; W — Weże; R — Rębielice; K — Kadzielnia; Ky — Kamyk

			N	M	O. R.	s	V
P ²	length	W	40	1.82 ± 0.019	1.4—2.0	0.12 ± 0.014	6.4 ± 0.72
		R	13	1.81 ± 0.017	1.6—1.9	0.06 ± 0.012	3.2 ± 0.63
		K	36	1.72 ± 0.033	1.4—2.4	0.20 ± 0.024	11.0 ± 1.29
		Ky	90	1.85 ± 0.015	1.6—2.2	0.14 ± 0.011	7.4 ± 0.55
	width	W	40	3.40 ± 0.025	3.0—3.7	0.16 ± 0.018	4.7 ± 0.53
		R	13	3.65 ± 0.049	3.3—3.8	0.18 ± 0.041	4.9 ± 0.96
		K	36	3.39 ± 0.035	2.8—3.8	0.21 ± 0.025	6.2 ± 0.73
		Ky	90	3.71 ± 0.027	3.2—4.3	0.26 ± 0.019	7.1 ± 0.53
P ³	length	W	25	2.64 ± 0.022	2.4—2.9	0.11 ± 0.014	4.2 ± 0.54
		R	14	2.63 ± 0.040	2.4—2.9	0.15 ± 0.028	5.8 ± 1.11
		K	37	2.61 ± 0.026	2.3—2.9	0.16 ± 0.019	6.2 ± 0.72
		Ky	48	2.56 ± 0.022	2.2—2.8	0.15 ± 0.015	5.9 ± 0.60
	width anteroloph	W	25	4.22 ± 0.037	3.9—4.7	0.19 ± 0.025	4.6 ± 0.60
		R	14	4.45 ± 0.040	4.2—4.8	0.15 ± 0.028	3.4 ± 0.64
		K	37	4.26 ± 0.032	3.9—4.9	0.20 ± 0.023	4.8 ± 0.56
		Ky	48	4.53 ± 0.033	4.1—4.9	0.23 ± 0.024	5.0 ± 0.51
	width posteroloph	W	25	5.10 ± 0.040	4.9—5.6	0.20 ± 0.026	4.0 ± 0.52
		R	14	5.26 ± 0.051	5.0—5.7	0.19 ± 0.036	3.7 ± 0.70
		K	37	5.06 ± 0.035	4.6—5.5	0.21 ± 0.024	4.2 ± 0.49
		Ky	48	5.25 ± 0.026	4.9—5.7	0.18 ± 0.018	3.5 ± 0.36
	length	W	15	2.79 ± 0.054	2.4—3.2	0.21 ± 0.038	$7.4 \pm 1.34^*$
		R	20	2.77 ± 0.040	2.5—3.3	0.18 ± 0.035	5.8 ± 0.92
		K	21	2.75 ± 0.028	2.5—3.0	0.13 ± 0.020	4.9 ± 0.75
		Ky	38	2.78 ± 0.029	2.4—3.3	0.18 ± 0.021	6.5 ± 0.75
	width anteroloph	W	15	4.92 ± 0.077	4.2—5.5	0.30 ± 0.055	6.1 ± 1.13
		R	20	4.96 ± 0.058	4.2—5.6	0.26 ± 0.041	4.7 ± 0.74
		K	21	5.06 ± 0.037	4.8—5.4	0.17 ± 0.026	3.4 ± 0.52
		Ky	38	4.74 ± 0.041	4.4—5.3	0.25 ± 0.029	5.2 ± 0.59
	width posteroloph	W	15	5.06 ± 0.054	4.7—5.6	0.21 ± 0.038	4.2 ± 0.76
		R	20	5.10 ± 0.058	4.8—5.7	0.26 ± 0.041	4.7 ± 0.74
		K	21	5.14 ± 0.039	4.7—5.5	0.18 ± 0.028	3.4 ± 0.52
		Ky	38	5.01 ± 0.036	4.3—5.5	0.22 ± 0.025	4.5 ± 0.52

gnathus is larger than that in *L. europaeus* was probably caused by the fact that the diastema of the former species is remarkably shortened and along with the robustness of the incisors makes them look like being more strongly

Table 4b

Measurements of upper molars of *Hypolagus brachygnathus*. Abbreviations as in Table 4a

			N	M	O. R.	s	V
M ¹	length	W	18	2.60 ± 0.057	2.3—3.1	0.24 ± 0.040	9.4 ± 1.56
		R	25	2.65 ± 0.040	2.2—3.1	0.20 ± 0.029	7.5 ± 1.06
		K	28	2.76 ± 0.023	2.5—3.0	0.12 ± 0.016	4.4 ± 0.59
		Ky	47	2.73 ± 0.026	2.4—3.1	0.18 ± 0.019	6.6 ± 0.68
	width anteroloph	W	18	4.84 ± 0.078	4.2—5.3	0.33 ± 0.055	6.8 ± 1.14
		R	25	4.91 ± 0.064	4.3—5.3	0.32 ± 0.045	6.5 ± 0.92
		K	28	5.15 ± 0.038	4.8—5.5	0.20 ± 0.027	3.8 ± 0.51
		Ky	47	4.88 ± 0.039	4.4—5.3	0.27 ± 0.028	5.5 ± 0.57
	width posteroloph	W	18	4.71 ± 0.085	4.1—5.3	0.36 ± 0.060	7.7 ± 1.06
		R	25	5.01 ± 0.058	4.7—5.5	0.29 ± 0.041	5.8 ± 0.83
		K	28	5.03 ± 0.040	4.6—5.4	0.21 ± 0.028	4.1 ± 0.55
		Ky	47	4.76 ± 0.046	4.2—5.2	0.32 ± 0.033	6.7 ± 0.69
M ²	length	W	17	2.31 ± 0.027	2.1—2.5	0.11 ± 0.019	4.9 ± 0.85
		R	11	2.37 ± 0.018	2.3—2.6	0.06 ± 0.013	2.6 ± 0.55
		K	42	2.36 ± 0.022	2.1—2.9	0.14 ± 0.015	5.8 ± 0.63
		Ky	23	2.39 ± 0.025	2.2—2.6	0.12 ± 0.018	4.9 ± 0.72
	width anteroloph	W	17	4.32 ± 0.051	4.0—4.7	0.21 ± 0.036	4.8 ± 0.83
		R	11	4.61 ± 0.066	4.2—4.9	0.22 ± 0.047	4.8 ± 1.01
		K	42	4.58 ± 0.040	4.2—5.0	0.26 ± 0.028	5.6 ± 0.61
		Ky	23	4.61 ± 0.042	4.2—4.9	0.20 ± 0.029	4.4 ± 0.65
	width posteroloph	W	17	3.95 ± 0.044	3.6—4.2	0.18 ± 0.031	4.4 ± 0.76
		R	11	4.07 ± 0.051	3.9—4.5	0.17 ± 0.036	4.2 ± 0.89
		K	42	4.11 ± 0.031	3.6—4.5	0.20 ± 0.022	4.8 ± 0.52
		Ky	23	4.01 ± 0.038	3.6—4.3	0.18 ± 0.027	4.5 ± 0.66
M ³	length	W	8	1.26 ± 0.018	1.2—1.3	0.05 ± 0.013	3.8 ± 0.95
		R	—	—	—	—	—
		K	—	—	—	—	—
		Ky	10	1.53 ± 0.019	1.4—1.6	0.06 ± 0.013	4.2 ± 0.94
	width	W	8	1.85 ± 0.018	1.8—1.9	0.05 ± 0.013	2.7 ± 0.68
		R	—	—	—	—	—
		K	—	—	—	—	—
		Ky	10	2.18 ± 0.028	2.1—2.4	0.09 ± 0.020	4.1 ± 0.91

bent. The arrangement of the lower incisors and their topographical relation to the lower cheek tooth row in *Hypolagus brachygnathus* and in the modern hare are shown in the radiograms of their mandibles (Pl. IV, 1a, b).

The cross-sections of the upper and lower incisors made at the height of

the posterior margin of the wear surface are offered for comparison in Pl. IV, 2a, b. In shape, the sections agree with the indices of massiveness calculated for these teeth.

Table 5

Measurements of incisors of *Hypolaemus brachygnathus*. Abbreviations as in Table 4a

			N	M	O. R.	s	V
I upper	width	W	52	3.41 ± 0.022	3.1—3.7	0.16 ± 0.016	4.7 ± 0.46
		R	38	3.37 ± 0.031	3.1—3.9	0.19 ± 0.022	5.7 ± 0.65
		K	71	3.44 ± 0.019	3.2—3.8	0.16 ± 0.013	4.7 ± 0.45
		Ky	59	3.42 ± 0.025	3.0—4.1	0.19 ± 0.017	5.4 ± 0.49
	thickness	W	52	2.84 ± 0.025	2.5—3.2	0.18 ± 0.017	6.2 ± 0.61
		R	38	2.76 ± 0.025	2.4—3.2	0.18 ± 0.021	6.7 ± 0.77
		K	71	2.88 ± 0.021	2.5—3.3	0.18 ± 0.015	6.3 ± 0.53
		Ky	59	2.81 ± 0.016	2.6—3.1	0.12 ± 0.011	4.4 ± 0.41
I lower	width	W	34	3.34 ± 0.027	3.0—3.7	0.16 ± 0.019	4.8 ± 0.58
		R	27	3.22 ± 0.025	3.0—3.4	0.13 ± 0.018	4.1 ± 0.56
		K	36	3.29 ± 0.012	3.0—3.7	0.13 ± 0.015	4.1 ± 0.48
		Ky	56	3.25 ± 0.025	2.8—3.7	0.19 ± 0.018	5.8 ± 0.55
	thickness	W	34	2.21 ± 0.015	2.1—2.4	0.09 ± 0.011	4.0 ± 0.49
		R	27	2.19 ± 0.025	1.9—2.4	0.13 ± 0.017	6.0 ± 0.82
		K	36	2.19 ± 0.012	1.8—2.4	0.13 ± 0.015	5.7 ± 0.67
		Ky	56	2.14 ± 0.017	1.9—2.5	0.13 ± 0.012	6.1 ± 0.58
	distance <i>b</i>	W	34	1.30 ± 0.010	1.1—1.4	0.06 ± 0.007	4.9 ± 0.59
		R	27	1.17 ± 0.023	0.9—1.4	0.12 ± 0.016	10.7 ± 1.46
		K	36	1.17 ± 0.013	1.0—1.4	0.08 ± 0.009	6.7 ± 0.79
		Ky	56	1.25 ± 0.013	1.0—1.6	0.10 ± 0.009	8.1 ± 0.77

Permanent Cheek Teeth of Juveniles

These teeth, unlike the teeth of adult specimens, have their walls unparallel and resemble truncated pyramids in general outlines. Basing on the enamel pattern and the degree of obliquity of walls one can distinguish three stages in the development of these teeth:

Stage 1 — immediately after the tooth has broken through the gum — crown irregularly folded by knobs of unworn enamel (Pl. IV, 5a); distinct tuberous structure of teeth particularly well visible in upper cheek teeth and P_3 ; enamel pattern at tooth base only partly developed, crenulation slight; wall obliquity very pronounced (Pl. IV, 5a).

Stage 2 — crown with evident traces of wear, but its original enamel is still

Table 6 b

Ratios of measurements of upper cheek teeth of *Hypolaqus brachynathus*. Abbreviations as in Table 6 a

	P ²			P ³			P ⁴			M ¹			M ²			M ³		
	W	R	Ky	W	R	Ky	W	R	Ky	W	R	Ky	W	R	Ky	W	R	Ky
$\frac{\text{length}}{\text{width}} \cdot 100$	54.3	49.7	50.9	46.9	—	—	—	—	—	—	—	—	—	—	—	—	—	52.6
$\frac{\text{length}}{\text{width anteroloph}} \cdot 100$	—	—	—	—	62.9	59.1	61.4	—	57.8	—	53.8	49.2	53.8	51.5	52.3	—	53.7	52.1
$\frac{\text{length}}{\text{width posteroloph}} \cdot 100$	—	—	—	—	52.1	49.9	51.8	—	55.8	—	53.5	42.8	55.3	58.3	53.0	—	58.6	58.3
$\frac{\text{width posteroloph}}{\text{width anteroloph}} \cdot 100$	—	—	—	—	120.8	118.3	118.4	—	103.6	—	100.5	114.7	97.4	88.4	98.4	—	91.6	90.7

Table 6c

Ratios of measurements of upper and lower incisors of *Hypolagus brachygnathus*. Abbreviations as in Table 6a

	I upper				I lower			
	W	R	K	Ky	W	R	K	Ky
$\frac{\text{thickness}}{\text{width}} \cdot 100$	66.40	67.93	66.41	67.03	81.66	81.86	83.98	81.89
$\frac{\text{distance } b}{\text{width}} \cdot 100$	39.06	36.21	35.49	38.86	—	—	—	—

partly preserved on the wear surface and therefore it forms additional folds and islets, occurring besides the enamel folds typical of the given tooth; enamel pattern at tooth base nearly completely developed, crenulation distinct; wall obliquity still very distinct, as well (Pl. IV, 5b).

Stage 3 — crown with typical enamel pattern same as at tooth base only to a little smaller scale owing to the still existing obliquity of walls.

Towards the end of stage 3 the walls become parallel and the enamel pattern of the crown and that of the tooth base become almost analogical.

The taper of walls is a character peculiar only to young specimens. With the teeth set in their alveoli, it is hard to observe the taper of walls and this difficulty becomes greater, the more advanced is the developmental stage of the teeth. When the mandibular and maxillary fragments of leporids are strongly fossilized and it is difficult to determine the young individual age of specimens from the structure of the surface of teeth, the parallelism of tooth walls or its lack (which can easily be disclosed, e. g. by help of radiograms) is the character that makes it possible to distinguish juveniles of one species from adults of another similar but smaller one.

The observation of developmental stages 2 and 3 of young teeth together with the additional enamel formations characteristic of these stages and the taper of walls is of great importance during the systematic revision of the genus *Pliolagus* (p. 69).

Milk Teeth

The milk teeth of fossil lagomorphs have been described by many authors. Some of these authors tried to establish the terminology of their cusps, homologizing them with different elements of teeth in the mammals of other orders (BURKE, 1941; EHIK, 1926; WOOD, 1940).

No detailed description of deciduous and permanent teeth of juvenile *Hypolagus* has been presented hitherto, except for a short mention and drawing

of DM_3 of *Hypolagus brachygnathus* from Episcopia (middle Cromerian) given by KORMOS (1934).

The milk teeth of *Hypolagus brachygnathus* under study have been found in the material from Rebielice Królewskie (80 specimens) and that from Kadzielnia (3 specimens). They are DM_3 , DM_4 , DM^2 , DM^3 , and DM^4 and, unlike the permanent teeth, show apparent differentiation into crown and roots.

Two types of roots appear in a tooth at the same time:

1. the conic type and
2. the trough-shaped one.

Conic roots are to be seen in DM_4 , DM^3 , DM^4 , and partly in DM_3 and DM^2 (Pl. IV, 6a). They are short, conically bent, and closed at ends. In DM^3 and DM^4 two such roots are present on the buccal side and one on the lingual side of each tooth; in the case of DM_4 two roots are situated under the anterior wall of the trigonid and the third grows out on the lateral side, at the base of the talonid.

The trough-shaped roots occur only in DM_3 and DM^2 (Pl. IV, 6b, c). They are generally elongated (2—3 times as long as the height of the crown), have a pronounced depression on the medial side, and are the extensions of the crowns in the direction of their alveoli. In DM_3 there is one long root of this type going off the trigonid base on the anterior side. The other root, at the base of the talonid, on the external side, is short, sometimes coneshaped. The elongated trough-shaped tooth of DM^2 is the extension of the anterior and lingual walls of the crown, while the other root, conic in shape, is present on the buccal side of the tooth (Pl. IV, 6b).

The presence of long trough-shaped roots in DM_3 and DM^2 (Pl. IV, 6b, c), whose shape is suggestive of the hypsodont one, precedes the appearance of the proper hypsodonty characteristic of the permanent dentition of *Hypolagus brachygnathus*.

The height of crown in the deciduous teeth varies with the degree of wear. The wearing of the crown discloses different forms of enamel pattern successively (Pl. IV, 7a, b, c), the description of which is given below.

DM_3 has two enamel folds on the buccal side of the crown: the shallow anterior fold and the deeper posterior one. These are also present in P_3 . In shape, the anterior fold corresponds to the analogous fold in P_3 , the posterior one being far shallower than its pendant in P_3 (Pl. IV). Special attention should be given to the presence of the third fold in DM_3 (Pl. IV, 7a), it squeezes deep into the dentine on the lingual side and its deepest portion lies close to the posterior external fold. Owing to these characters the enamel pattern of DM_3 in *Hypolagus brachygnathus* resembles that of P_3 in *Pliolagus beremendensis* and in the genus *Alilepus* DICE, e. g. in *Alilepus hungaricus* KORMOS, 1934 (Fig. 8). The likeness of DM_3 to the specimens so far reckoned in *Pliolagus beremendensis* is due to the presence of an enamel fold on the internal (lingual) side of P_3 , particularly well visible at the lower end of the tooth, in the last mentioned species.

As results from an observation of a large number of specimens, the crown of DM_3 of *Hypolagus brachygnathus* has a potentiality to change its enamel pattern by wear, because the third (middle) fold mentioned above does not reach below the half height of the crown. When the wear is heavy and involves

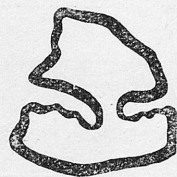


Fig. 8. P_3 of *Alilepus hungaricus* (after KORMOS)

the lower half of the crown, the shape of DM_3 is the same as in the permanent P (Pl. IV, 7 c). The anteroposterior measurements of DM_3 are proportionally larger than the corresponding measurements of P_3 (cf. Table 7b).

The structure of DM_4 , like that of P_4 , is clearly bipartite: the higher anterior portion corresponds to the trigonid and is separated from the lower posterior portion, corresponding to the talonid, by a deep enamel fold cutting in on the buccal side. The talonid is proportionally broader than in P_4 . The anterior wall of the trigonid is often convex and forms an additional thickening on the buccal side (Pl. IV, 4). It is hard to determine its homology with other cusps, because my material is lacking in milk teeth in the stage of eruption.

The enamel of the posterior wall of the trigonid shows a characteristic convexity, directed towards the talonid. It is usually situated at about one-third of the trigonid width from the external side (Pl. IV, 4). It was not found in the permanent teeth of *Hypolagus brachygnathus*, but occurs in *Agispelagus simplex*, *Procaprolagus maximus*, and *Procaprolagus orlovii* from the Oligocene. In P_4 and M_1 this convexity is very pronounced, and the enamel in this place is usually very thin or even quite wanting. The above-mentioned species have been grouped by GUREYEV (1960) in the subfamily *Agispelaginae*, from which, in his opinion, also the group *Hypolagus* was derived. Thus, the occurrence of this character in the deciduous dentition of *Hypolagus* confirms (besides other arguments given by GUREYEV) the soundness of this hypothesis on the origin of *Hypolagus* from the *Agispelaginae*.

The pattern of the wear surface of DM^2 is similar to that of P^2 , to which it corresponds. Of the two enamel folds cutting into the dentine from the anterior side of the crown of P^2 , only one, the medial, appears clear-cut in DM^2 (Pl. IV, 6b). Its depth varies within wide limits: in many cases it hardly covers a quarter of the length of the crown and equally often extends in the dentine far beyond half the length. On the anterior wall of the tooth the fold appears as a groove running vertically from the wear surface towards the root. The other, more externally situated, fold of P^2 has its counterpart in the form of a very shallow depression in a few specimens of DM^2 .

The distinction between DM^3 and DM^4 is possible on the basis of the anterolophid to posterolophid width ratio. In mediolateral diameter the antero-

lophid of DM^3 is smaller than the posterolophid. Both these elements are subequal in DM^4 . The hypostriae of DM^3 and DM^4 are very short, sometimes extend hardly a quarter of the way across the teeth. Some specimens of these teeth have additional elliptic or crescent islets of enamel lying more externally on the extension line of the hypostria (Fig. 9). They arise in the place where a con-

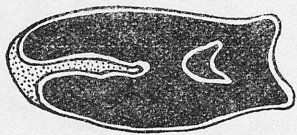


Fig. 9. Crescent islet of enamel on DM^3 of *Hypolagus brachygnathus*

spicuous cusp, in some cases reaching deep into the dentine towards the radical portion of the tooth, is being worn. Topographically, these islets always lie in the region corresponding to the outermost portion of the hypostria in the permanent teeth. The relationship between these two elements in the deciduous and permanent teeth seems to be undoubtful: the enamel islets of DM^3 and DM^4 constitute the „rudiments“ of the complete hypostriae of P^3 and P^4 , though they have not been found in their original form in the permanent dentition of adult specimens of *Hypolagus brachygnathus* so far.

It is known from the data given by WOOD (1940) and DAWSON (1958) that the process of reduction of these forms of enamel in favour of the elongating hypostria took place in the permanent dentition of the fossil Miocene leporids. At early stages of wear the permanent cheek teeth of *Archeclagus ennisianus* (COPE, 1881) have still these crescent enamel islets. The changes in enamel pattern coincided with a distinct molarization of the upper premolars. Also some of the early developmental stages of the permanent teeth of *Hypolagus*

Table 7a

Measurements of lower milk teeth of *Hypolagus brachygnathus* from Rebielice

	DM_3	DM_4	DM^2	DM^3	DM^4
length	2.02	1.85	0.95	1.35	1.38
width	1.57	—	1.64	—	—
width trigonid	—	1.79	—	—	—
width talonid	—	1.54	—	—	—
width anteroloph	—	—	—	1.84	2.25
width posteroloph	—	—	—	2.24	2.31
number of specimens (N)	28	28	29	15	12

brachygnathus show remains of enamel in the form of crescents during the first period of wearing.

The amount of cement in the milk teeth of *Hypolagus brachygnathus* is very small in comparison with that in the permanent teeth. It fills only the deepest enamel folds, never appearing on the walls of teeth. The deep folds of DM₃ contain comparatively most cement of all the milk teeth.

Table 7b

Ratios of measurements of milk teeth of *Hypolagus brachygnathus* in comparison with those of corresponding permanent teeth. Material from Rebielice

	P ₃	DM ₃	P ₄	DM ₄	P ²	DM ²	P ³	DM ³	P ⁴	DM ⁴
length width · 100	104·8	128·7	—	—	49·7	57·9	—	—	—	—
length width trigonid · 100	—	—	82·9	103·7	—	—	—	—	—	—
width trigonid width talonid · 100	—	—	74·2	86·0	—	—	59·1	73·0	—	61·6
length width anteroloph · 100	—	—	—	—	—	—	49·9	60·2	—	59·8
width posteroloph width anteroloph · 100	—	—	—	—	—	—	118·3	121·4	—	102·9

MORPHOLOGICAL CHANGES IN THE DENTITION OF *HYPOLAGUS BRACHYGNATHUS* FROM THE MIDDLE PLIOCENE TO THE EARLY PLEISTOCENE

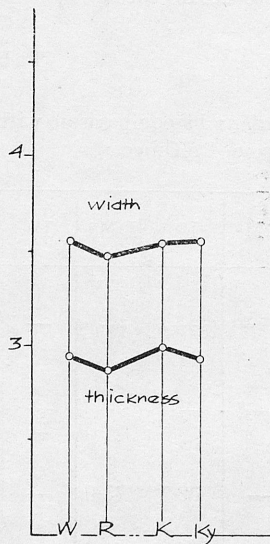
A comparatively large number of specimens of teeth of *Hypolagus brachygnathus* from faunae varying in geological age gives an opportunity to trace the morphological changes occurring in the dentition during the periods intervening these faunae.

Changes in the Size of Teeth

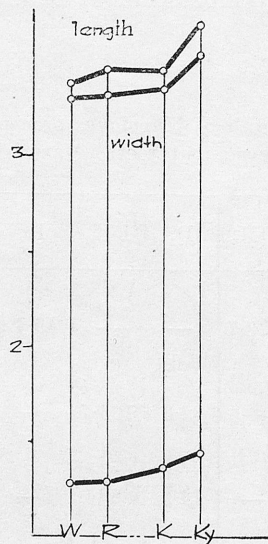
Figs. 10—21 show the changes in absolute values of 2 or 3 selected measurements of teeth: the length of crown (in the sagittal plane), the widths of trigonid and talonid in the lower teeth, and the widths of anterolophid and posterolophid in the upper teeth, arranged according to the localities from the geologically oldest fauna (Weże) to the youngest one (Kamyk).

The changes in measurements (except for P_3) are not continuous. Nevertheless, as to the lower cheek teeth it can be stated that

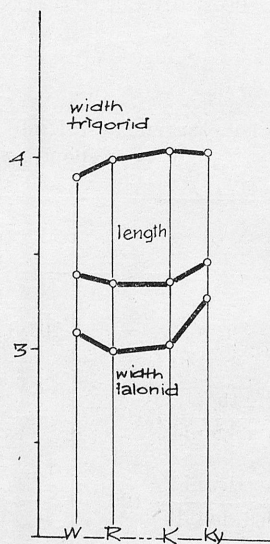
1. generally speaking, there is an increase in size of particular parts of teeth coming from the faunae extremely remote from each other; this increase is found in the length of crown, which has a bearing on the increase of length



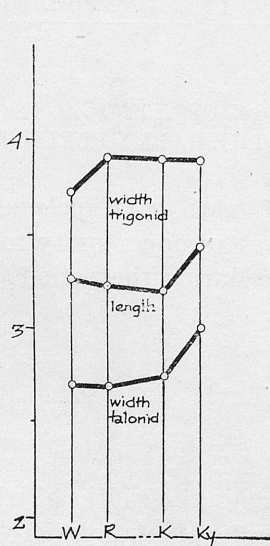
J lower
Fig. 10



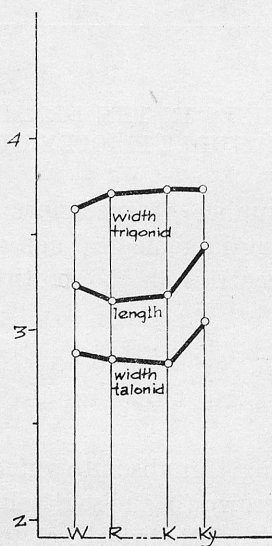
P₃
Fig. 11



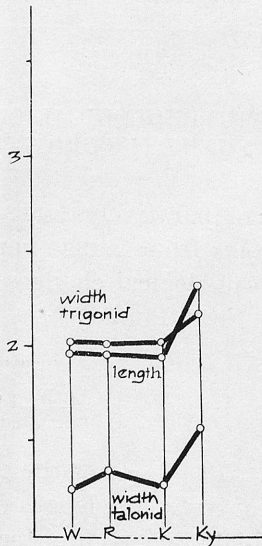
P₄
Fig. 12



M₁
Fig. 13



M₂
Fig. 14



M₃
Fig. 15

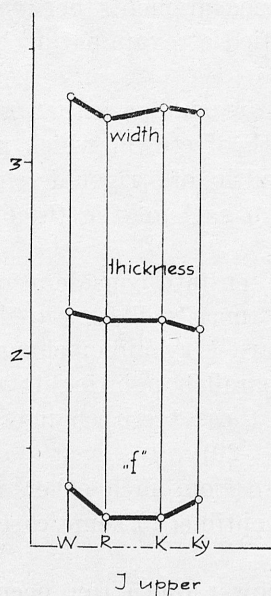


Fig. 16

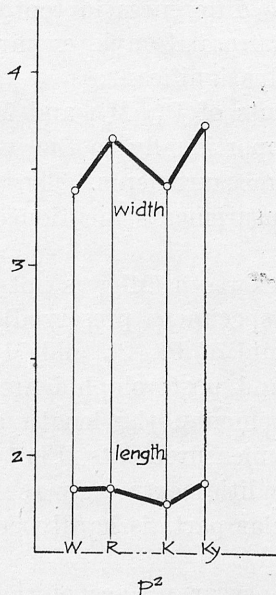


Fig. 17

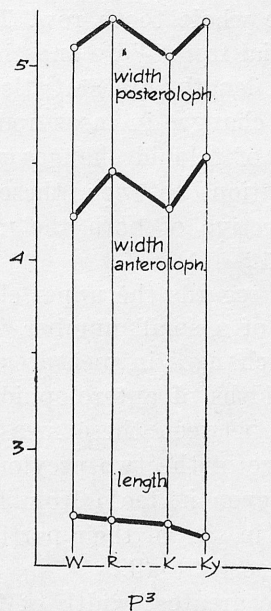


Fig. 18

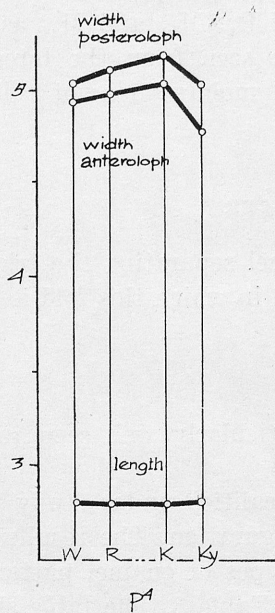


Fig. 19

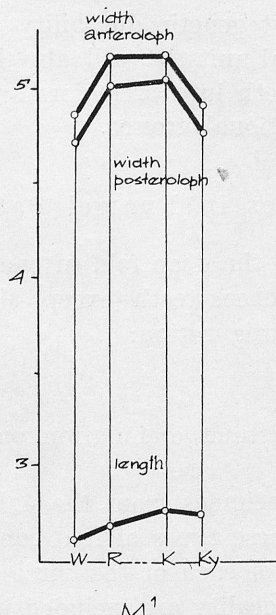


Fig. 20

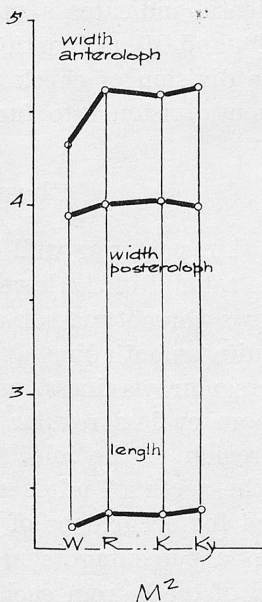


Fig. 21

Fig. 10—21. Changes in the measurements (in millimeters) of teeth of *Hypolagus brachygnathus* from the fauna of Weže to that of Kamyk

of the whole tooth row. The differences in tooth measurements between the material from Weże and that from Kamyk, exemplified at examination by the crown length, are statistically significant;

2. changes in measurements of P_4 , M_1 , and M_2 are similar in nature: the width of talonid changes proportionally to the width of crown, which proves correlation between these measurements. The width of trigonid changes irrespective of both the measurements mentioned in each of the three cases (Fig. 12—14).

As regards the upper cheek teeth (M^3 was not taken into consideration because of a small number of specimens preserved) it may well be stated that

1. changes in measurements of P^3 , P^4 , and M^1 are very alike: changes in the widths of anterolophid and posterolophid are parallel, pointing to correlation between these measurements; the length of these teeth changes irrespective of the two previous measurements (Fig. 18—20);

2. even in teeth from localities extremely remote from each other an increase in size of their particular parts is hardly perceptible, in some cases not to be seen at all.

The greatest width of the wear surface of the lower tooth row occurs in P_4 , M_1 , and M_2 and in the case of the upper tooth row in P^3 , P^4 , and M^1 . The uniformity of changes in the measurements of particular parts of teeth within either of these groups points to a close functional relationship of teeth in this group, and perhaps also between the groups. The correlativity of changes in certain measurements with time, found only in some groups of lower and upper teeth, indicates a great genetic durability of P_4 , M_1 , and M_2 , as well as P^3 , P^4 , and M^1 as functional units. It will also be seen from the foregoing that the division of cheek teeth into premolars and molars does not coincide with their division into functional groups.

Changes in Enamel Pattern

The thin posterior wall of the deep fold of enamel separating the trigonid from the talonid in the lower cheek teeth (except M_3 , in which this fold is lacking) shows three types of configuration:

1. quite smooth line,
2. irregular waviness, and
3. more or less regular distinct crenulation particularly well seen in the medial region of the fold.

All the teeth of adult specimens from the 4 localities under study were examined for occurrence of these types of fold configuration. The results presented as a percentage share of each of the three types of enamel pattern in the total of teeth from each locality are included in Table 8. The table shows that during the interval between the fauna from Weże and that from Kamyk there was a tendency to simplification of the shape of this fold (Pl. III, 2; Fig. 22 a, b, c). It consisted in a gradual change of crenulation into wavy or

smooth lines, or a change of wavy lines into smooth ones. This trend is particularly pronounced in P_3 . The data obtained from the table should be treated as informative of the direction of changes and not of their exact quantitative proportions. However, the one-direction tendency common to all lower cheek teeth examined allows us to regard it as very probable that the samples from the particular localities are fairly representative of the character in question.

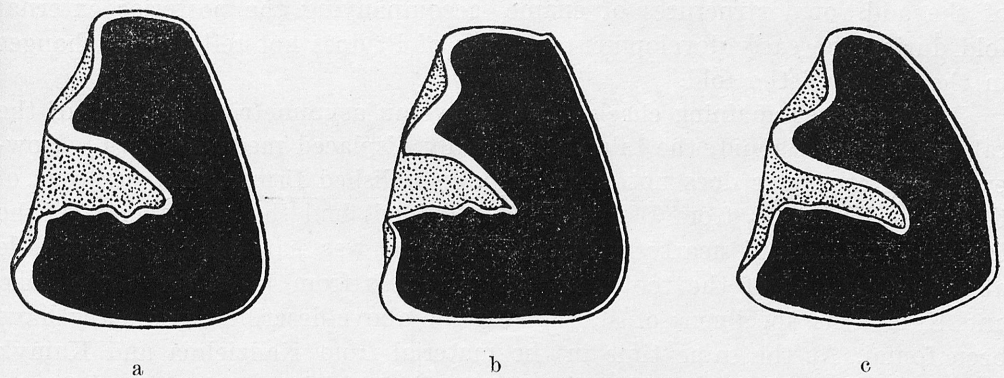


Fig. 22. Surface of typical P_3 of *Hypolagus brachygnathus* from different localities. a — P_3 with crenulation of the fold (Weże); b — P_3 with irregular waviness of the fold (Rębielice); c — P_3 with smooth line of the fold (Kamyk)

Table 8.

Three types of structure of the enamel fold between trigonid and talonid in *Hypolagus brachygnathus*. Percentage share of each of the three types of enamel pattern in the total number of specimens of each tooth in each breccia. Symbols: — smooth line of fold; $\nabla\nabla\nabla\nabla$ line irregularly wavy; $\wedge\wedge\wedge\wedge$ fold crenulated

	Weże			Rębielice			Kadzielnia			Kamyk		
	—	$\nabla\nabla$	$\wedge\wedge$	—	$\nabla\nabla$	$\wedge\wedge$	—	$\nabla\nabla$	$\wedge\wedge$	—	$\nabla\nabla$	$\wedge\wedge$
P_3	7.0	32.0	61.0	17.5	52.5	30.0	80.0	15.0	5.0	86.0	12.5	1.5
P_4	80.0	18.0	2.0	78.0	22.0	0	86.0	14.0	0	85.0	15.0	0
M_1	84.0	16.0	0	90.5	9.5	0	90.0	10.0	0	87.0	13.0	0
M_2	63.0	37.0	0	71.0	29.0	0	78.0	22.0	0	89.5	10.5	0

Special attention was given to P_3 , in which the depth of the posterior external fold is an important systematic character used, among other characters, as a basis for the division of the *Leporidae* into subfamilies (DICE, 1917, 1929). In *Hypolagus brachygnathus* this fold extends two-thirds of the way across the tooth. The fold is very deep and touches the medial wall of the tooth in modern leporids. In some fossil genera, e. g., in *Pratilepus* HIBBARD, 1939, four additional enamel formations developed between this fold and the medial wall, making it possible to trace the evolution of the fold (HIBBARD, 1963). Similar struc-

tures appear occasionally in the early developmental stages of P_3 of *Hypolagus brachygnathus* as well (p. 30). Therefore it seemed purposeful to find whether this species showed also a tendency to changes in the depth of the fold. The ratios of the smallest distance between the posterior external fold and the medial margin of P_3 to the width of this tooth are given for geologically varying localities in Table 6a. This ratio has undergone no changes. Consequently, the appearance of the additional structures of enamel accompanying the posterior external fold during the early developmental stages of P_3 does not reflect any changes in the depth of the fold.

M_3 , like the remaining cheek teeth, shows an asymmetrical position of the talonid to the trigonid: the talonid is usually displaced mediad (Fig. 6). However, this character does not seem to be established firmly. Ten per cent of the specimens of M_3 from Weże (of 70 examined) had the arrangement of the trigonid and talonid nearly symmetrical, which was particularly well visible at the lower end of the tooth. In the materials from Rebielice, Kadzielnia, and Kamyk no specimens of M_3 showing the above-described symmetry have been found. At the same time in the material from Kadzielnia and Kamyk a number of specimens of M_3 were observed in which a connection between the trigonid and the talonid was established in the form of a „bridge“ of dentine and enamel fold described in the previous section (Pl. III, 3a, b). This fold varies in length; sometimes it extends only halfway across the tooth, in extreme cases it reaches to the layer of enamel on the medial side of the tooth. These observations suggest that in M_3 there occurred the process of assimilation of this tooth to P_4 , M_1 , and M_2 . In the latter teeth a corresponding enamel fold always reaches as far as their medial layer. In some forms, more primitive than *Hypolagus*, e. g., in those of the genus *Palaeolagus* LEIDY, 1856, this fold is considerably shallower. On the other hand, its occurrence almost

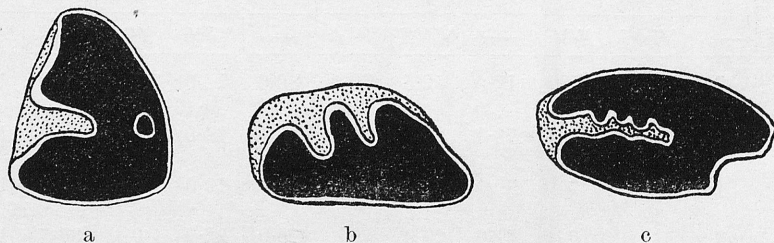


Fig. 23. Individual variation of enamel pattern in some teeth of *Hypolagus brachygnathus* a — P_3 with additional enamel islet (from Kamyk); b — P_2 having two deep enamel folds (from Weże); c — M_2 with strongly shortened posterolophid (from Kadzielnia)

in statu nascendi in M_3 of *Hypolagus brachygnathus* indicates that the original coalescence between the enamel of the trigonid and that of the talonid of P_4 , M_1 , and M_2 did not take place along the medial walls of these teeth, but more laterally, in the centre of the dentine pillar.

Different cases of individual variation of particular teeth are compared in Fig. 23.

CORRELATIONS OF TOOTH MEASUREMENTS IN *HYPOLAGUS*
BRACHYGNATHUS, *LEPUS EUROPAEUS*, AND *ORYCTOLAGUS CUNICULUS*

The dentition of various fossil and modern leporid species as a rule varies distinctly only in the extreme teeth of the lower and upper rows, whereas the remaining teeth represent a common type of structure. It results from the genetically fixed relations between the measurements of teeth. In spite of the uniformity of shape in the whole group of teeth of various species, the relations between the measurements of these teeth are not identical. A comparison of these relations in various species may provide us with additional information on the differences and resemblances existing between them. SIMPSON and ROE (1960) and, above all, KURTÉN (1953) pointed out that such a comparison can be carried out basing on the rule of correlation of measurements of particular teeth established by them. According to this rule, called the „rule of neighbourhood“ by KURTÉN, the strongest correlation generally occurs between the measurements of neighbouring teeth of a row (e. g., P^3 and P^4 , M_1 and M_2 , etc.). The more distant the teeth are from each other, the more the correlation decreases.

The coefficient r , computed for all possible combinations of tooth pairs, is the measure of the strength of correlation. The coefficients r calculated for a selected character (or characters), e. g., the length of crown, are compiled into a correlation table. The values of r are calculated by the formula commonly applied in statistics. For convenience, the values of z , the distribution of which is not, *ipso facto*, a statistically normal curve, are converted to the values z of FISHER, whose distribution is normal and properties allow a direct comparison of correlations in samples from various populations.

In the present study the coefficients of correlation and the corresponding values z of FISHER have been calculated for suitable pairs of teeth of the lower row in *Hypolagus brachygnathus*, *Lepus europaeus*, and *Oryctolagus cuniculus*. Since the material used for such comparisons must be as homogeneous in respect of origin and geological age as possible, the specimens of *Hypolagus brachygnathus* from the early Pleistocene breccia of Kadzielnia were used as samples. Out of this material, however, only the mandibles, 36 in number, with their teeth preserved and so making calculation possible, were used for the analysis, there being an unsufficient number of maxillary specimens with well-preserved upper cheek tooth rows for statistical purposes.

The character considered here is the length of crown, and the correlative pairs cover all possible combinations of the teeth of the lower cheek row, from P_3 to M_3 . The results of the examination of the correlations in the three species mentioned above are offered in Tables 9a, b, c. The coefficient r may take any value between -1 and $+1$. In the case of a positive correlation, and it is the sort of correlations that we have to do in these considerations, its value lies between 0 and $+1$. The closer the correlation, the more closely the value approaches 1 . The values of the coefficients of statistically insignificant correlations are given in parentheses (with a probability of 95%).

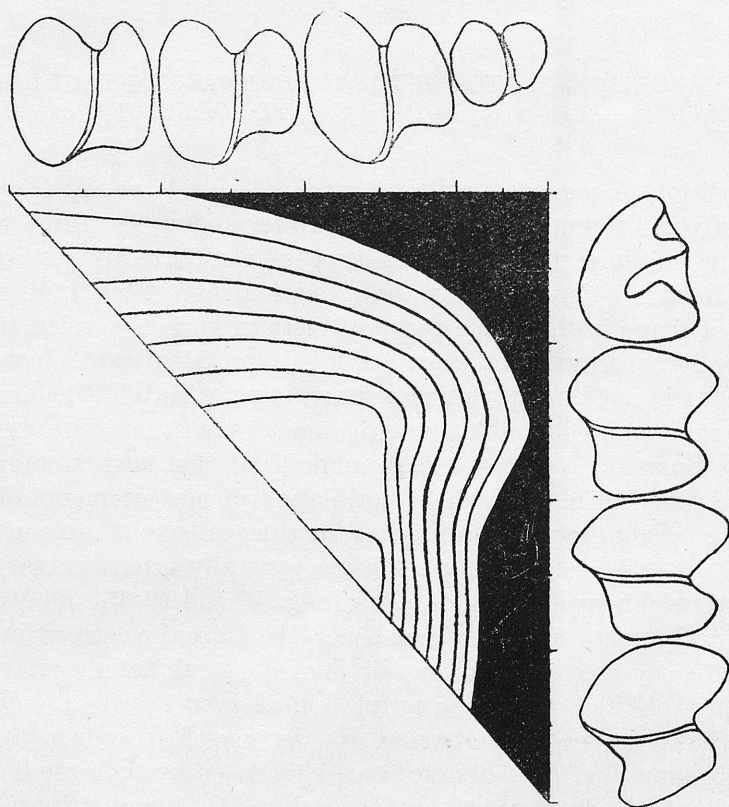


Fig. 24

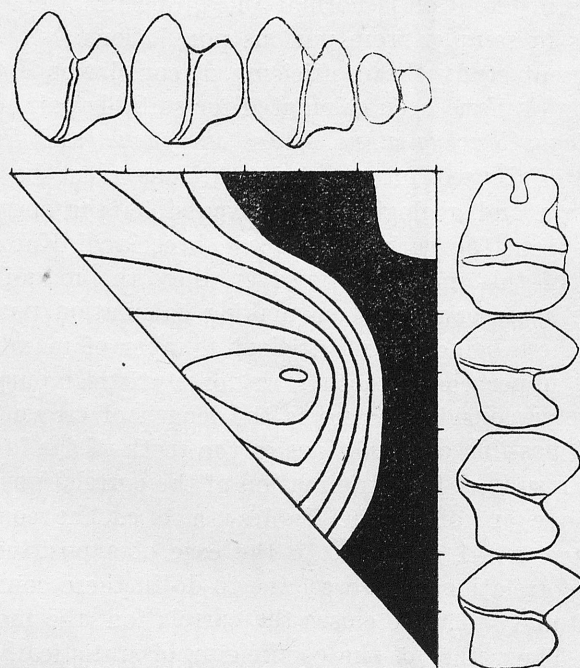


Fig. 26

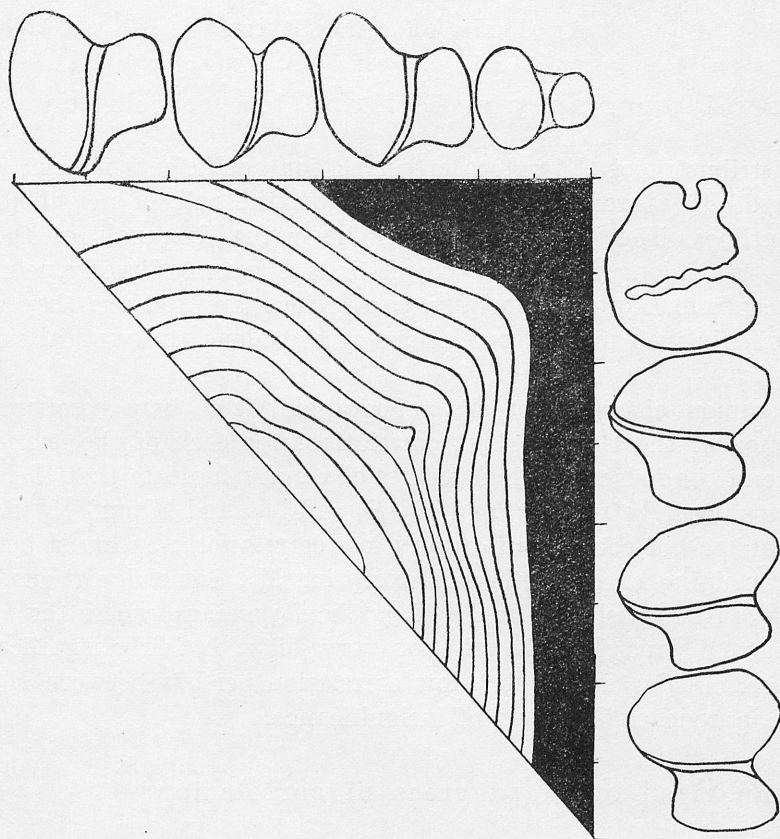


Fig. 25

Figs. 24—26. Correlation fields of measurements for the teeth of the lower row in *Hypolagus brachygnathus* (24), *Lepus europaeus* (25) and *Oryctolagus cuniculus* (26). Contour lines every 0.1 of FISHER's value z . Black fields — not significant correlations or none at all

The coefficients of correlation presented in the tables become particularly telling if the relations existing between them are demonstrated in the form of a graph (Figs. 24, 25 and 26), showing the „topography“ of the distribution of high and low correlations. The data for the graphs were obtained from the tables described above. In the graph the sizes of fields corresponding to the particular teeth are proportional to the lengths of their crowns. The straight lines connecting the middles of the teeth intersect in points, to which the values z from the table are assigned. Intermediate values, at intervals of 0.1, were found by interpolation on the sections of lines between the points for which the values of z were determined, and then points having the same value were connected. The picture thus obtained resembled hypsometric contour lines with intervals of 0.1. The test of significance for these correlations showed that the coefficients r for which the corresponding values of z equal 0.40 represent an insignificant correlation (very low or none at all). In the graphs the areas of insignificant correlations are blackened.

Analysis of correlations

a. General topography of high and low correlations

The distribution of the values of correlation coefficients is clearly characteristic in all the three cases. It corroborates the rule of neighbourhood in general outlines. The highest values lie near the diagonals of the graphs (Figs. 24—26), along which the correlations between directly neighbouring teeth concentrate. More peripherally correlations are weaker; they are quite lacking, or only insignificant correlations spread along the vertical side of the graph.

The common character of the topographic fields here compared is the concentration of the three highest correlations for each of the species in the same place of the fields. The high values of r and z indicate that the strongest relationships occur between P_4 and M_1 , P_4 and M_2 , and M_1 and M_2 in all these species. The lack of correlation or very low correlation was found between M_3 and the remaining cheek teeth, not excepting M_2 . Some deviation from this can be seen in two cases: 1. in *Hypolagus brachygnathus*, where the value of r for the pair M_3 and P_4 , though not very high, is fairly significant; 2. in *Oryctolagus cuniculus*, in which a low correlation persists between M_3 and P_3 , though it approaches the limit of insignificance.

b. Comparison of the degrees of correlations

The degree of correlation is a characteristic quality in the particular species. It will be seen from the tables and graphs that *Oryctolagus cuniculus* is generally characterized by a lower degree of correlation compared with *Lepus europaeus* and *Hypolagus brachygnathus*. This difference is particularly well visible in the case of the coefficients of correlations between P_4 , M_1 , and M_2 . In *Oryctolagus cuniculus* only one value of r (for M_2 and P_4) exceeds 0.75, whereas in the remaining species there are values of 0.80—0.92 in the group of high correlations. In consequence, the graphs for *Hypolagus brachygnathus* and *Lepus europaeus* show a great density of contour lines and greater „steeps“ than in *Oryctolagus cuniculus*.

c. Characteristics of the highest correlations

There are also differences between the species within the group of high correlations. Here, the most uniform correlations occur in *Hypolagus brachygnathus* and the least uniform ones in *Oryctolagus cuniculus* (see Fig. 24, 26). *Hypolagus brachygnathus* and *Lepus europaeus* show the strongest correlations between M_1 and P_4 as well as between M_1 and M_2 , *Oryctolagus cuniculus* only between M_2 and P_4 . In the group examined the correlation between M_1 and P_4 excites attention: it is generally high in all the three species, in each of them

Table 9 (a, b, c).

Coefficients r of correlation and values z of FISHER for dimensions of lower teeth in *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c)

a)		P ₄	M ₁	M ₂	M ₃	
	z	0.62	0.62	0.46	[0.15]	P ₃
	r	0.55	0.55	0.43	[0.15]	
		z	1.16	1.13	0.54	P ₄
		r	0.82	0.81	0.49	
			z	1.22	[0.22]	M ₁
			r	0.84	[0.22]	
				z	[0.20]	M ₂
				r	[0.20]	
		P ₄	M ₁	M ₂	M ₃	
	z	0.82	0.91	0.52	[0.30]	P ₃
b)	r	0.68	0.72	0.48	[0.29]	
		z	1.59	1.13	[0.34]	P ₄
		r	0.92	0.81	[0.33]	
			z	1.47	[0.39]	M ₁
			r	0.90	[0.37]	
				z	[0.39]	M ₂
				r	[0.37]	
		P ₄	M ₁	M ₂	M ₃	
	z	0.68	0.65	[0.34]	0.41	P ₃
	r	0.59	0.57	[0.33]	0.39	
		z	0.91	1.02	[0.26]	P ₄
c)		r	0.72	0.77	[0.25]	
			z	0.73	[0.30]	M ₁
			r	0.62	[0.29]	
				z	[−0.07]	M ₂
				r	[−0.07]	

being, however, different. Significant differences were found here between *Hypolagus brachygnathus* and *Oryctolagus cuniculus* on one side and *Lepus europaeus* on the other ($t \geq 1.73$ corresponding to a probability of 95% or more). The correlations between M₂ and P₄ are practically the same for all the species. The differences in the correlation coefficients for M₁ and M₂ are not significant between *Hypolagus brachygnathus* and *Lepus europaeus* ($t \approx 0.88$; which corresponds to a probability of 60—70%), fairly significant between *Hypolagus brachygnathus* and *Oryctolagus cuniculus* ($t \approx 1.52$ corresponding to a probability of about 90%) and significant between *Oryctolagus cuniculus* and *Lepus europaeus* ($t \approx 2.33$ corresponding to a probability of 95%).

d. Characteristics of medium and low correlations

In the group of correlations of a medium degree special attention should be given to the relations between P₃ and the remaining cheek teeth on account of its being evidently distinct from the other teeth. The correlation between

P_3 and P_4 only partly confirms the rule of neighbourhood. The values of r are not high here and they do not differ clearly between the species (the seeming difference between *Hypolagus brachygnathus* and *Oryctolagus cuniculus* on one side and *Lepus europaeus* on the other is not significant ($t \approx 0.73$ corresponding to a probability of 50—60%).

It should be emphasized that there is no clear correlation of M_3 with the remaining teeth, which can be observed in each of the species. *Hypolagus brachygnathus* and *Oryctolagus cuniculus* exhibit only slight correlation between M_3 and P_4 or M_3 and P_3 . In the case of M_3 and M_2 there is even no tendency to correlation, which is evidenced by the great „steep“ in the contour lines at the proper place of the topographic field in the graphs.

The biological significance of correlations in the sizes of teeth will be dealt with in the Discussion (p. 71).

LIMB BONES

DESCRIPTION AND MEASUREMENTS

Scapula

The reconstruction of the whole outline of the scapula of *Hypolagus brachygnathus* was possible owing to the scapular blade preserved at Weże. Since the complete removal of the blade from its rocky matrix threatened with the destruction of the whole bone, part of the description is based on the impression of this bone in a rocky fragment broken away and strictly fitting to one side of the scapular blade (Pl. V, 1).

The angle formed by the anterior and the posterior margin of the blade is $48^\circ (\pm 3^\circ)$ against $43^\circ (\pm 3^\circ)$ in *Lepus europaeus* and only $35^\circ (\pm 3^\circ)$ in *Oryctolagus cuniculus*.

The neck of the scapula is, proportionally, somewhat shorter and broader than that in *Lepus europaeus*. The scapula of *Hypolagus brachygnathus*, like that of *Lepus europaeus*, is divided by the spine into two parts unequal in area. Thus, the supraspinous fossa is smaller than the infraspinous fossa in *Hypolagus brachygnathus*. In *Oryctolagus cuniculus* the difference in area between these fossae is still more striking. *Hypolagus brachygnathus* and *Oryctolagus cuniculus* have the coracoid process longer than it is in *Lepus europaeus*.

In the fossil material the acromion process was not preserved in any specimen of the scapula. Single fragments of its terminal portion do not vary in shape from the corresponding parts in the modern hare and wild rabbit.

Index 1 (Table 10b), showing the shape of the glenoid cavity, is almost identical for *Hypolagus brachygnathus* and *Oryctolagus cuniculus*. In contrast with them *Lepus europaeus* has this cavity widened mediolaterally.

Index 2 (Table 10b) characterizes the anterior elongation of the coracoid process. It is different in each of the three species, *Hypolagus brachygnathus* coming nearer to *Oryctolagus cuniculus* in this respect than to *Lepus europaeus*.

Table 10a

Measurements of scapula. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rebielice; K — Kadzielnia; Ky — Kamyk

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>
		M	O. R.	N	M	M
width of neck	W	5.45	5.2—5.7	5	7.9	5.2
	R	6.10	5.8—6.3	8		
	K	6.24	5.9—6.5	7		
	Ky	6.63	6.2— 6.9	14		
shorter diameter of glenoid cavity	W	5.09	4.9— 5.2	4	8.2	5.0
	R	5.91	5.7— 6.1	8		
	K	5.98	5.8— 6.2	7		
	Ky	6.19	5.8— 6.4	14		
longer diameter of glenoid cavity	W	8.51	8.3— 8.7	5	12.2	8.2
	R	9.68	9.2—10.1	8		
	K	9.77	9.2—10.1	7		
	Ky	10.36	9.6—11.1	14		
coraco-glenoid distance	W	3.51	3.2— 3.6	5	3.2	3.0
	R	4.20	4.0— 4.4	8		
	K	4.10	4.0— 4.4	7		
	Ky	4.22	3.9— 4.4	14		

Table 10b

Ratios of measurements of scapula. Abbreviations as in Table 10a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{shorter diameter of glenoid cavity}}{\text{longer diameter of glenoid cavity}} \cdot 100$	W	59.8	67.2	60.9
	R	61.1		
	K	61.2		
	Ky	59.7		
2. $\frac{\text{coraco-glenoid distance}}{\text{shorter diameter of glen. cav.}} \cdot 100$	W	68.9	39.2	60.1
	R	71.1		
	K	68.5		
	Ky	68.2		

Humerus

The proximal epiphysis of the humerus much resembles in shape the epiphysis of this bone in *Lepus europaeus* and *Oryctolagus cuniculus*. Only the bicipital groove attracts attention, being here shorter and shallower than in the other two species.

Table 11a

Measurements of humerus. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rębielice; K — Kadzielnia; Ky — Kamyk; * length from reconstruction

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>	<i>H. schreuderii</i>
		M	O. R.	N	M	M	M
width of trochlea	W	9.75	9.0—10.4	8	11.9	8.6	12.1
	R	10.75	10.0—12.0	15			
	K	10.42	10.0—10.9	12			
	Ky	11.33	10.9—12.3	40			
width of medial sulcus of trochlea	W	3.95	3.7— 4.2	8	5.4	4.7	—
	R	4.13	4.0— 4.5	15			
	K	4.23	3.9— 4.5	12			
	Ky	4.56	4.0— 5.1	40			
height of medial crest	W	1.10	0.8— 1.3	8	2.5	1.2	—
	R	1.00	0.7— 1.3	15			
	K	1.11	0.8— 1.4	12			
	Ky	1.51	1.2— 1.8	40			
width of greater tuberosity	W	9.64	9.4— 9.9	5	10.7	6.7	—
	R	—	—	—			
	K	—	—	—			
	Ky	11.05	—	2			
height of greater tuberosity	W	14.65	14.4—15.0	5	23.0	14.0	—
	R	—	—	—			
	K	—	—	—			
	Ky	17.45	—	2			
transverse width of head	W	10.90	10.1—11.2	7	15.2	9.6	—
	R	12.24	11.7—12.4	8			
	K	11.50	11.4—11.6	3			
	Ky	12.50	—	1			
length	W	74.0*	—	—	105.1	61.1	96.6
	R	76.0*	—	—			
	K	80.0*	—	—			
	Ky	92.0*	—	—			

Table 11b

Ratios of measurements of humerus. Abbreviations as in Table 11a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{width of medial sulcus}}{\text{width of trochlea}} \cdot 100$	W	40.4	45.5	55.0
	R	38.5		
	K	40.7		
	Ky	40.3		
2. $\frac{\text{height of greater tuberosity}}{\text{width of greater tuberosity}} \cdot 100$	W	65.8	46.5	47.8
	R	—		
	K	—		
	Ky	63.2		
3. $\frac{\text{height of medial crist}}{\text{width of trochlea}} \cdot 100$	W	11.2	21.1	13.8
	R	9.4		
	K	10.5		
	Ky	13.2		

The terete impress, in contrast with that in *Oryctolagus cuniculus* or *Lepus europaeus*, is slightly marked and has the shape of a shallow rounded depression. The deltoid tubercle and the deltoid crest are better developed and more elongate than they are in *Oryctolagus cuniculus* and *Lepus europaeus* (Pl. V, 2a, b, c). Somewhat above the deltoid tubercle there is occasionally an accessory tubercle, which is lacking in *Lepus europaeus* and *Oryctolagus cuniculus*. The medial epicondyle is more elongate than in the last-mentioned species, and the supra-trochlear foramen is, in contrast with them, very variable in size (from 0.9 to 3.6 mm), sometimes even completely closed.

Index 1 (Table 11a), defining the relative span of the crests of the trochlea, makes it possible to distinguish *Hypolagus brachygnathus* from *Oryctolagus cuniculus* unambiguously (Table 11b; Pl. V, 3a, b, c).

Indices 2 and 3 (Table 11b) characterize the massiveness of the epiphyses. The large relative breadth of the greater tuberosity makes the upper epiphysis robuster than it is in *Lepus europaeus* and *Oryctolagus cuniculus*. *Hypolagus brachygnathus* and partly *Oryctolagus cuniculus* owe the dull massive shape of the trochlea to a relatively poorer development of the medial crest than in *Lepus europaeus*.

Ulna

The proximal epiphysis with the olecranon process is generally the best preserved portion of the ulna. The section of the shaft contiguous to the proximal epiphysis is visibly bent posterad, forming a small protuberance on the posterior margin of the bone at the height of the articular facet for the radius. No such

Table 12 a

Measurements of ulna. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rębiełice; K — Kadzielnia; Ky — Kamyk

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>
		M	O. R.	N	M	M
width of olecranon	W	7.50	7.0— 8.2	10	11.9	7.0
	R	7.88	7.5— 8.3	14		
	K	7.42	7.1— 7.6	9		
	Ky	9.20	8.8— 9.8	25		
height of olecranon	W	8.10	7.3— 8.7	10	11.7	7.8
	R	8.55	7.7— 8.9	9		
	K	8.20	7.8— 8.4	9		
	Ky	9.77	9.2—10.2	25		
length	W	—	—	—	124.5	71.0
	R	82.5*	—	—		
	K	83.0*	—	—		
	Ky	—	—	—		

bend is to be seen in *Lepus europaeus* and *Oryctolagus cuniculus*. The length to width ratio of the olecranon process (Table 12b differs from this ratio in the other two species, indicating the elongated shape of the process (Pl. V, 4a b, c). The lateral margin of the semilunar incisure is sometimes interrupted in the middle by a slight groove furrowing the articular facet and passing on to the lateral surface of the olecranon process. This groove is hardly marked in *Oryctolagus cuniculus* and completely lacking in *Lepus europaeus*. Below the semilunar incisure the anterolateral surface of the shaft is flattened or, at most, slightly concave. In this place *Oryctolagus cuniculus* and *Lepus europaeus* have a clear-cut trough-shaped depression, running along the shaft and being a trace of the fairly close contact of the ulna with the radius (Pl. VI, 1a, b, c).

Table 12b

Ratios of measurements of ulna. Abbreviations as in Table 12a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
$\frac{\text{width of olecranon}}{\text{height of olecranon}} \cdot 100$	W	92.6	101.7	89.1
	R	92.2		
	K	90.5		
	Ky	94.2		

Radius

On the border of the articular facet on the posterior side of the proximal epiphysis there is a small protruding denticle closing the depressed troughshaped portion of the articular facet. (Pl. VI, 2) In some specimens this „denticle“ is badly visible. It is present in *Lepus europaeus* (Pl. VI, 2b), but not in *Oryctolagus cuniculus*. The relief of the surface of the shaft on the side of its contact with the ulna is poorer than it is in the two last-mentioned species. The shaft of this bone is more massive than in the modern hare and wild rabbit.

Indices 1 and 2 (Table 13b) indicate the massiveness of the epiphyses. The proximal epiphysis is relatively broader (robuster) in *Hypolagus brachygnathus* and *Lepus europaeus*. In the relative thickness of the distal epiphysis *Hypolagus brachygnathus* much resembles *Oryctolagus cuniculus* but differs considerably from *Lepus europaeus*.

Table 13 a

Measurements of radius. N — number of specimens; M — arithmetic mean; O. R. — observed range measurements; W — Weże; R — Rebielice; K — Kadzielnia; Ky — Kamyk

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>	<i>H. schreuderii</i>
		M	O. R.	N	M	M	M
thickness of proximal epiphysis	W	3.51	3.1—3.7	8	5.9	3.9	—
	R	—	—	—			
	K	3.59	3.3—3.7	12			
	Ky	4.82	4.6—5.3	45			
width of proximal epiphysis	W	7.10	6.8—7.3	8	9.7	6.3	—
	R	—	—	—			
	K	7.08	6.4—7.5	12			
	Ky	7.77	7.1—8.1	45			
thickness of distal epiphysis	W	5.11	4.9—5.3	5	6.2	4.4	—
	R	—	—	—			
	K	5.34	5.1—5.6	6			
	Ky	5.82	5.6—5.9	6			
width of distal epiphysis	W	6.68	6.4—6.8	5	10.7	6.1	—
	R	—	—	—			
	K	7.12	6.8—7.4	6			
	Ky	7.76	7.4—8.0	6			
length	W	—	—	—	113.0	61.1	93.2
	R	—	—	—			
	K	—	—	—			
	Ky	—	—	—			

Table 13 b

Ratios of measurements of radius. Abbreviations as in Table 12 a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{thickness of proximal epiphysis}}{\text{width of proximal epiphysis}} \cdot 100$	W	49.5	60.7	61.8
	R	—		
	K	50.8		
	Ky	52.0		
2. $\frac{\text{thickness of distal epiphysis}}{\text{width of distal epiphysis}} \cdot 100$	W	76.3	59.7	72.2
	R	—		
	K	75.1		
	Ky	74.8		

Innominate

The parts of the innominate showing the best state of preservation are the acetabular and iliac regions. The iliac crest is a well-developed convex thickening running along the long axis of the iliac wing. This crest is considerably less visible in *Oryctolagus cuniculus* and hardly visible at all in *Lepus europaeus*.

The presence of the supraacetabular tuberosity, in which the iliac crest ends in the acetabular region, is particularly distinctive. In contrast with what is found in *Lepus europaeus*, this tuberosity is big and juts beyond the convex surface of the ilium, just as in *Oryctolagus cuniculus*, though in the last species it is not so well developed.

The articular facet for the sacrum is variable, generally semilunar in shape. The surface area of the iliac wing is larger, proportionally, than in *Lepus europaeus* and *Oryctolagus cuniculus*. In adult specimens of *Hypolagus brachy-*

Table 14

Measurements of innominate bone. N—number of specimens; M—arithmetic mean
O. R.—observed range of measurements; W—Weże; R—Rębielice; K—Kadzielnia;
Ky—Kamyk

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>
		M	O. R.	N	M	M
diameter of acetabulum	W	8.69	8.4—8.9	6	11.4	8.2
	R	8.81	8.2—9.4	9		
	K	9.18	8.9—9.5	8		
	Ky	10.57	9.9—11.5	7		

gnathus and *Oryctolagus cuniculus* the acetabular incisure forms a deep groove crossing the surface of the acetabulum and directed towards the ischium. In *Lepus europaeus* the acetabular incisure is, proportionally, far narrower and it is occasionally partitioned by a thin bony bridge occurring on its surface.

Femur

The great and small trochanters as well as the shaft of the femur are robust than in *Oryctolagus cuniculus* and *Lepus europaeus*.

Above the condyles the posterior surface of the distal epiphysis is covered

Table 15 a

Measurements of femur. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rębielice; K — Kadzielnia; Ky — Kamyk; * — length from reconstruction

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>	<i>H. schreuder</i>
		M	O. R.	N	M	M	M
transverse diameter of shaft	W	—	—	—	9.7	6.2	—
	R	7.35	7.0— 7.6	6			
	K	7.42	6.9— 7.7	12			
	Ky	8.83	8.2— 9.2	4			
sagittal diameter of shaft	W	—	—	—	8.9	6.1	—
	R	7.01	7.0— 7.3	7			
	K	7.20	7.0— 7.8	12			
	Ky	7.65	7.2— 8.5	4			
spread of condyles	W	15.01	14.6—15.3	10	19.2	13.0	—
	R	15.11	14.4—15.8	10			
	K	15.60	14.6—15.8	12			
	Ky	17.20	18.8—17.5	4			
width of patellar groove	W	5.40	5.1— 5.6	10	7.2	5.1	—
	R	5.21	5.0— 5.3	9			
	K	5.40	5.0— 5.7	12			
	Ky	6.30	6.2— 6.5	4			
width of intercondylar fossa	W	5.33	4.9— 5.5	10	7.1	4.3	—
	R	5.33	5.0— 5.8	9			
	K	5.38	4.9— 5.7	11			
	Ky	5.81	5.4— 5.9	4			
length	W	—	—	—	134.0	83.4	123.6
	R	93.0*	—	—			
	K	96.0*	—	—			
	Ky	109.0*	—	—			

Table 15 b

Ratios of measurements of femur. Abbreviations as in Table 15 a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{width of intercondylar fossa}}{\text{width of patellar groove}} \cdot 100$	W	98.8	98.5	84.3
	R	102.3		
	K	99.4		
	Ky	93.1		
2. $\frac{\text{sagittal diameter of shaft}}{\text{spread of condyles}} \cdot 100$	W	—	50.5	47.0
	R	48.6		
	K	47.5		
	Ky	51.3		

with prominent tuberosities, which in *Oryctolagus cuniculus* and *Lepus europaeus* are remarkably more poorly developed (Pl. VI, 4a, b, c).

Index 1, (Table 15a) expressing the relative width of the intercondylar notch, shows no differences between *Hypolagus brachygnathus* and *Lepus europaeus*, but points to a mediolateral shortening of this notch in *Oryctolagus cuniculus*.

Index 2 (Table 15b) characterizes the massiveness of the distal epiphysis. It does not distinguish *Hypolagus brachygnathus* from the other two species.

Tibia

The lateral condyle of the proximal epiphysis in *Hypolagus brachygnathus* little exceeds the medial condyle in size. In *Oryctolagus cuniculus* and *Lepus europaeus* this difference between the condyles is greater. The intercondylar eminence is more pronounced than in *Oryctolagus cuniculus* and *Lepus europaeus* (Pl. VI, 3a, b, c). The anterolateral and medial surfaces of the middle section of the shaft are slightly convex in *Hypolagus brachygnathus*. More peripherally this convexity increases, blurring the three-sided structure of the shaft, which becomes a slightly flattened cylinder here. In the distalmost portion, just above the distal epiphysis, the shaft approximates to a tetragon in cross-section. In *Oryctolagus cuniculus* and *Lepus europaeus* the shaft is angular throughout its length; in the peripheral region this quality is better visible in *Oryctolagus cuniculus* than in *Lepus europaeus*. In *Hypolagus brachygnathus* the anterior side of the distal epiphysis is flattened, in the other two species it is evidently convex, particularly so in *Lepus europaeus*.

Table 16 a

Measurements of tibia. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rębielice; K — Kadzielnia; Ky — Kamyk; * — length from reconstruction

		<i>H. brachygnathus</i>			<i>L. euro- paeus</i>	<i>O. cuni- culus</i>	<i>H. schreu- deri</i>
		M	O. R.	N	M	M	M
width of proximal epiphysis	W	16.90	16.5—17.3	9	21.1	14.5	19.2
	R	17.02	16.8—17.2	4			
	K	17.22	16.8—17.7	5			
	Ky	20.56	19.9—21.4	3			
width of distal epiphysis	W	12.70	12.4—13.1	9	16.3	12.3	15.9
	R	13.06	12.6—13.8	14			
	K	13.56	12.8—13.9	6			
	Ky	14.93	13.9—15.6	18			
thickness of distal epiphysis	W	6.36	6.0— 6.6	9	9.3	5.5	—
	R	6.50	6.1— 6.8	13			
	K	6.61	6.0— 6.9	8			
	Ky	7.65	7.4— 7.9	18			
length	W	103.0*	—	—	151.1	90.5	136.8
	R	—	—	—			
	K	108.0*	—	—			
	Ky	120.5*	—	—			

Table 16 b

Ratios of measurements of tibia. Abbreviations as in Table 16 a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
$\frac{\text{thickness of distal epiphysis}}{\text{width of distal epiphysis}} \cdot 100$	W	50.1	57.3	44.6
	R	49.8		
	K	48.7		
	Ky	51.2		

Talus

The medial crest being well developed, the trochlea of the talus more resembles the trochlea of *Oryctolagus cuniculus* than that of *Lepus europaeus*. The trochlear groove in *Hypolagus brachygnathus* is deeper than in the other two species.

The index of the relative length of the neck of the talus determines the intermediate position of *Hypolagus brachygnathus* in this respect between *Lepus europaeus* and *Oryctolagus cuniculus* (Table 17b). Owing to the great variability of the tibia in *Hypolagus brachygnathus* this index must be treated with reserve.

Table 17a

Measurements of talus. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rębelice; K — Kadzielnia; Ky — Kamyk

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>
		M	O. R.	N	M	M
total length	W	13.01	12.8—13.3	12	17.1	11.4
	R	14.61	14.1—15.1	10		
	K	14.82	13.5—15.2	9		
	Ky	15.73	15.1—16.5	32		
length of collum	W	8.72	8.3—8.9	12	10.4	8.0
	R	8.83	8.0—9.3	10		
	K	10.30	8.7—10.5	9		
	Ky	10.74	10.2—12.2	32		

Table 17b

Ratios of measurements of talus. Abbreviations as in Table 17a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{length of collum}}{\text{total length}} \cdot 100$	W	67.1	60.7	70.1
	R	60.4		
	K	69.4		
	Ky	68.3		

Calcaneus

On the lateral surface of the tuber calcanei of *Hypolagus brachygnathus*, at the height of the facet for the tibia there occurs a longitudinal depression with one or two small foramina for blood vessels in its bottom. In *Oryctolagus cuniculus* and *Lepus europaeus* this depression has the shape of a distinct groove running all along the lateral surface of the tuber calcanei; moreover, in *Lepus europaeus* the above-mentioned foramen lies at about the half-length of the tuber calcanei.

The posterior facet for the talus consists of a medial part and a lateral part, separated by a clear-cut groove (sulcus calcanei). The medial part, situated on the sustentaculum talare, is larger than the lateral part or equal to it. In *Oryctolagus cuniculus* and *Lepus europaeus* this relation is reverse: the medial

Table 18 a

Measurements of calcaneus. N — number of specimens; M — arithmetic mean; O. R. — observed range of measurements; W — Weże; R — Rębielice; K — Kadzielnia; Ky — Kamyk

		<i>H. brachygnathus</i>			<i>L. europaeus</i>	<i>O. cuniculus</i>
		M	O. R.	N	M	M
total length	W	26.33	25.5—27.9	18	35.5	23.5
	R	27.13	25.5—28.4	31		
	K	28.52	27.4—30.0	20		
	Ky	32.04	30.0—34.4	34		
width	W	11.25	10.0—12.4	18	14.2	10.0
	R	11.18	10.5—11.8	31		
	K	11.66	10.4—12.5	20		
	Ky	13.04	12.0—13.9	34		
length of tuber calcanei	W	12.32	11.5—13.5	18	15.7	9.9
	R	12.37	12.9—13.9	31		
	K	12.75	11.9—13.5	20		
	Ky	15.12	14.0—16.8	34		
length of body	W	9.75	11.7—13.4	18	13.0	8.8
	R	9.77	9.5—10.0	31		
	K	10.38	9.7—11.3	20		
	Ky	12.34	11.5—13.9	34		

Table 18 b

Ratios of measurements of calcaneus. Abbreviations as in Table 18 a

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{width}}{\text{length}} \cdot 100$	W	42.8	40.0	42.4
	R	41.3		
	K	40.9		
	Ky	40.7		
2. $\frac{\text{length of tuber calcanei}}{\text{total length}} \cdot 100$	W	46.8	44.2	42.1
	R	45.5		
	K	44.8		
	Ky	47.1		

part is generally smaller than the lateral. Owing to this fact the sustentaculum talare is convex more medially in *Hypolagus brachygnathus* than in both recent species (Pl. VII 1a, b, c).

The anterior facet for the talus is smaller in *Hypolagus brachygnathus* than in *Oryctolagus cuniculus* and *Lepus europaeus*.

The calcanei of the three species cannot be told from each other on the basis of the length to width ratio (index 1, Table 18b).

Neither does index 2 (Table 18b), characterizing the relative length of the tuber calcanei, vary distinctly from one species under study to another.

The fact that in various species the measurements of the calcaneus maintain uniform proportions will be further considered in respect of its usefulness for estimation of the body size of some leporids (p. 78).

Cuboid

The facet of the cuboid for the calcaneus is narrower, proportionally, than in *Oryctolagus cuniculus* and *Lepus europaeus*.

Navicular

The projecting ventral portion of this bone is robuster than in *Lepus europaeus* and *Oryctolagus cuniculus*.

Metacarpals, metatarsals, and phalanges

The epiphyses of the metacarpals and metatarsals are strongly built. In robustness they exceed the same bones in *Lepus europaeus*. Like the phalanges, they show the same morphological characters as the corresponding bones of *Lepus europaeus* and *Oryctolagus cuniculus*.

LENGTH RATIOS OF THE LIMB BONES

The length ratios of the particular sections of limbs have been tabulated for comparison. Since these lengths in the fossil species are known not from direct measurements but from reconstructions, their values bear errors ranging from 3 to 5%. Consequently, in the comparison of the values of indices offered in Table 19 only the differences exceeding 5% can be treated as significant.

As will be seen from this comparison, *Hypolagus brachygnathus* differs from *Lepus europaeus* (partly also from *Oryctolagus cuniculus*) in its arm being relatively longer compared with the forearm. On the other hand, it does not differ from *Lepus europaeus* in the ratio of the partial length of the fore-limb to that

of the hind-limb (index 5, Table 19). In comparison with these species *Oryctolagus cuniculus* has the fore-limbs relatively shorter than the hind-limbs. No significant differences can also be found between *Hypolagus brachygnathus* and *Lepus europaeus* as regards the proportions of the humerus and femur.

Index 5, showing in general that the fore-limb is as much shorter than the hind-limb in *Lepus europaeus* as in *Hypolagus brachygnathus*, compares with similar indices for *Hypolagus schreuderi* TEILHARD DE CHARDIN (TEILHARD DE CHARDIN, 1940). This author compared *Hypolagus schreuderi* with a recent member of *Lepus* from Manchuria (species not given). In the calculation of this ratio he used the radius in the place of the ulna (it was impossible in my case to reconstruct the radius on the basis of my material). The index thus calculated amounts to 71.0 for *Hypolagus schreuderi* and to 70.0 for *Lepus* from Manchuria. The value of the index in the present study is different, because, as mentioned above, I used the ulna for computation. However, it points to the same fact in both cases: the degree of shortening of the fore-limb in relation to the hind-limb is the same in *Hypolagus* as in *Lepus*.

Table 19

Length indices of bones of limbs. W — Weże; R — Rebielice; K — Kadzielnia; Ky — Kamyk

		<i>H. brachygnathus</i>	<i>L. europaeus</i>	<i>O. cuniculus</i>
1. $\frac{\text{femur}}{\text{tibia}} \cdot 100$	W	—		
	R	90.2		
	K	89.0	88.7	92.2
	Ky	90.4		
2. $\frac{\text{humerus}}{\text{ulna}} \cdot 100$	W	—		
	R	92.0		
	K	96.0	84.3	86.0
	Ky	—		
3. $\frac{\text{humerus}}{\text{femur}} \cdot 100$	W	—		
	R	81.7		
	R	83.3	78.4	73.3
	Ky	84.0		
4. $\frac{\text{ulna}}{\text{tibia}} \cdot 100$	W	—		
	R	79.9		
	K	76.9	82.4	78.5
	Ky	—		
5. $\frac{\text{humerus} + \text{ulna}}{\text{femur} + \text{tibia}} \cdot 100$	W	—		
	R	80.8		
	K	79.9	80.5	73.6
	Ky	—		

CHANGES IN SIZE IN THE SKELETON OF *HYPOLAGUS BRACHYGNATHUS* IN THE PERIOD FROM THE UPPER PLIOCENE TO THE END OF THE FIRST INTERGLACIAL

A comparison of the measurements of various elements of the skeleton of *Hypolagus brachygnathus* from different geological periods shows that their sizes changed with time. These changes are manifested in the growth of absolute measurements of the skeletal elements and then they also affected the over-all measurements of the body. The greatest growth in size in the samples from the chronologically „neighbouring“ faunae occurs in the Kadzielnia-Kamyk interval. It is a relatively short period as compared with the time span separating it from the middle Pliocene and, as will be seen from the data given by KOWALSKI (1958a—1960a), it corresponds approximately to the Günz-Mindel interglacial. The increase in size in the Weże-Rebiełice and Rebiełice-Kadzielnia periods is small; it lies close to the significance-insignificance demarcation line, as shown by the test of significance of the differences t for the calcaneus. Thus, the increase in the size of body of *Hypolagus brachygnathus* in the period from the middle Pliocene to the end of the first interglacial is not continuous.

The value of growth varies with the size of bones, the larger the size, the higher the value, which is illustrated by black stripes on the right-hand side of Fig. 27.

III. SYSTEMATIC POSITION OF THE GENUS *PLIOLAGUS* KORMOS

THE HISTORY OF THE DESCRIPTION OF SPECIES BELONGING TO THE GENUS *PLIOLAGUS* KORMOS

In 1917 DICE divided the family *Leporidae*, which was hard to systematize, into three subfamilies: *Palaeolaginae*, *Archaeolaginae*, and *Leporinae*. The division was based on the structure of the first lower premolar (P_3), which has two, an internal and an external, deep enamel folds (giving it the distinctive shape of an hour-glass) in the first group, only one, external, fold extending at most halfway across the tooth in the second group, and the same external fold reaching as far as the medial wall of the tooth in the third group (Fig. 28).

Basing on DICE's division KORMOS (1934) distinguished three genera of the fossil hares from the early Pleistocene of Central Europe: the first represented by *Hypolagus brachygnathus* KORMOS with distinct characters of the *Archaeolaginae*, the second including *Pliolagus beremendensis* KORMOS, which had characters both of the *Archaeolaginae* and of the *Palaeolaginae*, and the third genus, *Lepus*, a typical member of the *Leporinae*.

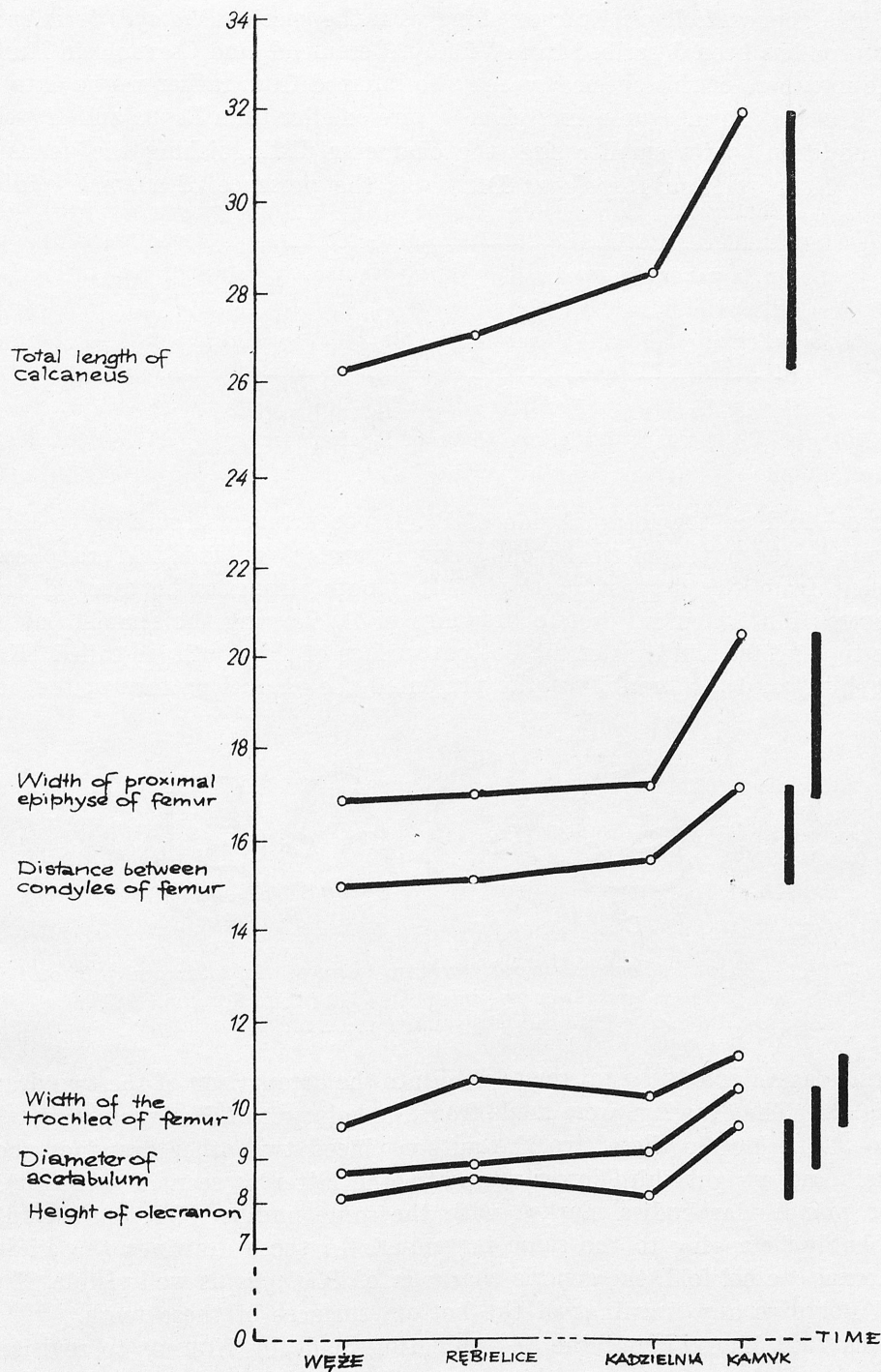


Fig. 27. Changes in measurements of some bones of the skeleton of *Hypolagus brachygnathus* from the fauna of Węże to that of Kamyk

The genus *Pliolagus* KORMOS along with the species *Pliolagus beremendensis* KORMOS has been described from Villany, Beremend, and Csarnota in Hungary. The members of this species, as may be inferred from rather vague data given by KORMOS (no measurements given), were smaller than *Lepus* and *Hypolagus*. In addition to its smaller size, the character distinguishing the genus *Pliolagus* KORMOS from *Hypolagus* DICE was the presence of a small additional

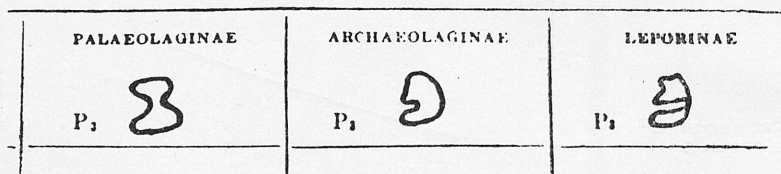


Fig. 28. Shape of P₃ after DICE

enamel fold on the internal side of P₃. Its occurrence, according to KORMOS, recurs to the phylogenetically old group *Palaeolaginae*. This fold was, however, absent from the deepest portion of the tooth, from its bottom side, which KORMOS illustrated in his two drawings of P₃ showing the enamel pattern of the top surface and that of the bottom surface of this tooth (so-called „Kauflächenbild“ and „Röhrenbild“). He presented the enamel pattern of the bottom

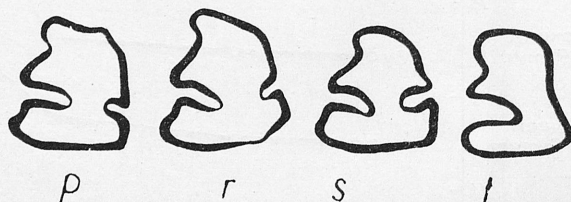


Fig. 29. s, t — P₃ of *Pliolagus beremendensis* from holotype No 3931; p, r — P₃ of *Pliolagus beremendensis* from specimen No 3692 (from KORMOS, 1934)

surface as reflected in a mirror to facilitate the comparison of the two drawings (Fig. 29). The drawings were made from the holotype of *Pliolagus beremendensis* (No 3931). Beside these two the author placed two other drawings showing a left and a right third lower premolar (the latter as seen in a mirror) from two mandibular bodies marked with the same number, Ob. 3692, and then probably belonging to the same individual. In these drawings the additional internal enamel fold, the generic character of *Pliolagus*, is well visible. KORMOS did not give any drawings of the bottom surfaces of these teeth.

In 1941 KRETZOI put the determination made by KORMOS to revision and questioned the correctness of his observation as to the existence of the internal enamel fold in P₃ of *Pliolagus beremendensis*. He offered the four above-mentioned drawings of P₃ (after the publication of 1934), all as mirror reflections

of KORMOS's drawings, preserving the details of their originals, and stated that they were the result of his faulty observation, for the internal (lingual) enamel fold described by KORMOS did not exist at all (...Das von Kormos beschriebene und abgebildete Kauflächenbild von *Pliolagus* beruht auf einem schweren Beobachtungs- und Illustrationsfehler! Die von Kormos betonte linguale Palaeolaginae-Synklinale existiert überhaupt nicht, der betreffende Zahn ist typisch archaeolagin gebaut!...)“. Nevertheless, KRETZOI recognized the validity of the species *Pliolagus beremendensis* KORMOS. Moreover, he found remains of a small hare in the Lower Pleistocene fauna from Betfia (Roumania), the specimens of P_3 of which, in his opinion, have no additional internal fold and are exactly like those of *Pliolagus beremendensis* in shape. The only character

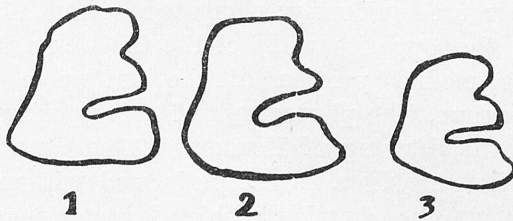


Fig. 30. *Pliolagus tothi*. P_3 after KRETZOI (1941)

distinguishing this hare from *Pliolagus beremendensis* is, according to KRETZOI, its measurements, $1\frac{1}{4}$ times as large. Like KORMOS, KRETZOI did not give any measurements. The difference in size between the two forms caused KRETZOI to describe the hare found by him as a new species, *Pliolagus tothi* KRETZOI (Fig. 30). However, he did not publish a precise diagnosis of the species, nor did he indicate the holotype except for two drawings of a specimen of P_3 (top and bottom surface) of *Pliolagus tothi*. Next to them he placed the drawing of the top surface of P_3 (Fig. 30) of the specimen of *Pliolagus beremendensis* having no additional internal fold, for comparison. It cannot, however, be inferred either from the text or from the explanations of the drawings which specimens of the original collection of KORMOS he used for this comparative drawing.

In 1958 KOWALSKI mentioned two species of fossil hares in his study on the early Pleistocene fauna of Kadzielnia in Kielce: *Hypolagus brachygnathus* KORMOS and another hare still smaller in size. On the ground of the size of its mandibles and teeth, smaller than in *Hypolagus brachygnathus*, and the traces of an additional internal fold in P_3 he decided to name it *Pliolagus* cf. *tothi* KRETZOI.

The contradictions in the observations of KORMOS and KRETZOI quoted above and the striking likeness of *Pliolagus* cf. *tothi* from Kadzielnia to *Hypolagus brachygnathus* induced me to resume the morphological analysis of both the species of *Pliolagus* and to compare them with *Hypolagus brachygnathus*.

MORPHOLOGICAL DETAILS OF *PLIOLAGUS BEREMENDENSIS* KORMOS

The present description concerns the original specimen of KORMOS („genus typus a Villany, Kalkberg, 1932. X., no 3931“).

The holotype is a fragment of a mandibular body with the complete set of cheek teeth but without incisors.

A very distinct additional internal enamel fold extending about 1/4 of the way across the tooth is to be seen on the wear surface of P_3 . The fold is filled with cement. It is not perceptible in the bottom aspect of the tooth, as it disappears at its mid-height. The shape of the lower cross-section of the tooth differs from that of the wear surface in that it is slightly narrowed mediolaterally and more evidently elongated (about 10%) anteroposteriorly. As a result, the opposite walls of the tooth are not exactly parallel to each other. The medial portion of the outline of the lower cross-section is slightly concave. The photograph of this specimen (Pl. VII, 2a, b) differs a little from the drawing of KORMOS (1934 b), probably because the latter is a freehand drawing from nature performed without using a drawing apparatus (the outer contour of rather a thick layer of enamel changes somewhat with the kind of lighting and the direction of the falling light). The accomplishment of a clear photogram of the bottom surface of P_3 from specimen No 3931 presented difficulties owing to its being partly damaged and its margins uneven. The other morphological details of the mandible of *Pliolagus beremendensis* also agree with the description given by KORMOS. The measurements of the specimens are presented in Table 20.

In view of these observations it becomes undoubtful that the additional internal enamel fold on P_3 described by KORMOS exists really and is not an error of observation or illustration. In consequence, the different observations of KRETZOI quoted above have not been confirmed.

According to the information given by KORMOS (1934, p. 71) about two specimens of *Pliolagus beremendensis* No 3692, at present missing in the collection of the Zoological Department of the National Museum in Budapest, the right and left lower premolars (Fig. 29) represent a young individual age of *Pliolagus beremendensis*, at which age the internal enamel fold in question is best visible. Even if we assume that specimens Nos 3692 and 3931 in the figures presented by KORMOS were drawn to only approximately the same scale of magnification, it seems questionable whether specimen No 3931 belonged to an adult individual, considering the fact that the neighbouring specimen, denoted as No 3692, is larger but all the same it represents, as KORMOS writes, a young age. In his opinion, the occurrence of this additional internal fold in P_3 of *Pliolagus beremendensis* is a temporary character connected with individual age.

MORPHOLOGICAL DETAILS OF *PLIOLAGUS TOTH* KRETZOI

The specimens of this species from the Lower Pleistocene of Betfia examined by me do not show any additional internal enamel fold on P_3 . The measurements of these specimens are offered in Table 20. According to KRETZOI, the specimens of his species are $1\frac{1}{4}$ times as large as those of *Pliolagus beremendensis*. It will be seen from a comparison of the measurements of *Pliolagus beremendensis* and *Pliolagus tothi* (Table 20) that the differences in size between these two species are hardly perceptible and even, in the cases of some measurements, quite absent, so they certainly cannot reach $1/4$ of their values.

In the two specimens of *Pliolagus tothi* the measurements of the bottom surface of P_3 (it was visible in both of them) were compared with those of the wear surface. The difference was considerable, it amounted to about 30%. The wear surface is thus far smaller than the bottom surface, and so the opposite walls of this tooth are not parallel. The radiogram of one of these mandibles (as in other cases, its number was not given) corroborates this observation: the tooth approximates to a pyramid in shape (Pl. VII, 3).

It has already been pointed out (p. 22) that the lack of parallelism of the walls of cheek teeth in *Hypolagus brachygnathus* is a character of the permanent dentition of young individuals. Therefore, it may be assumed that the specimens of *Pliolagus tothi* examined undoubtedly did not represent old individuals.

As for the quantitative occurrence of *Pliolagus tothi*, it formed, according to KRETZOI, hardly 3% of the remains of the *Leporidae* from Betfia, while the other specimens belonged to *Hypolagus brachygnathus* (22%) and *Lepus* sp. (75%).

CONCLUSIONS

As has been shown by a close analysis of the specimens of *Pliolagus tothi* KRETZOI and *Pliolagus beremendensis* KORMOS including their descriptive types, they represent young individuals, that is such as have atypical measurements and structure.

The measurements of both these species as well as the measurements of *Pliolagus* cf. *tothi* KRETZOI from Kadzielnia were compared with those of the third developmental stage of the young teeth of *Hypolagus brachygnathus* (p. 33). They all lie within the range of measurements of this developmental stage of *Hypolagus brachygnathus* (Table 20).

Variation in the enamel pattern of P_3 both in the deciduous and in the permanent generation presented on p. 34, 42 indicates that there were small numbers of young specimens of *Hypolagus brachygnathus* with the structure of P_3 resembling that in the two species of *Pliolagus*. These last species occurred

Table 20

Comparison of measurements of mandibles and teeth of species of the *Pliolagus* KORMOS with those of young specimens of *Hypolagus brachygnathus* KORMOS (stage II of development of permanent teeth)

	<i>Pliolagus beremendensis</i> holotyp no 3931	<i>Pliolagus tothi</i> (Betfia)		<i>Pliolagus cf. tothi</i> (Kadzielnia)				<i>Hypolagus brachygnathus</i> young			
		1	2					Rebielce Kr.	Węże		
									1	2	3
length of mandibular tooth row	13.2	—	13.5	13.7	—	—	—	—	—	—	—
thickness of mandible between P ₄ and M ₁	4.8	4.9	4.8	5.5	—	5.5	—	4.7	5.0	4.6	—
height of mandible between P ₄ and M ₁	11.4	11.7	11.6	13.3	—	13.2	—	12.0	11.8	—	—
length of diastema	—	13.5	13.4	14.0	—	—	—	—	—	—	—
P ₃ $\frac{\text{length}}{\text{width}}$	2.5 2.6	2.3 2.1	2.4 2.0	2.9 2.6	3.0 2.9	2.7 2.4	2.6 2.6	2.2—3.0 (N=9) 2.1—2.8 (N=9)	2.4 2.3	2.6 2.7	2.7 2.4
P ₄ $\frac{\text{length}}{\text{width}}$	2.2 2.9	2.0 2.6	2.2 2.8	2.7 3.5	2.6 3.5	2.6 3.5	2.6 2.9	2.1—2.8 (N=11) 2.4—3.4 (N=11)	2.4 2.9	—	2.3 2.6
M ₁ $\frac{\text{length}}{\text{width}}$	2.4 3.1	2.3 2.6	2.2 2.7	2.6 3.3	2.9 3.5	2.7 3.2	2.6 2.9	2.0—2.8 (N=7) 2.4—3.4 (N=7)	2.5 2.8	2.5 2.9	—
M ₂ $\frac{\text{length}}{\text{width}}$	2.6 2.9	2.2 2.5	2.2 2.6	2.8 3.3	3.0 3.4	2.7 3.1	2.7 2.6	—	2.7 3.0	—	—
M ₃ $\frac{\text{length}}{\text{width}}$	1.7 1.7	—	1.5 1.6	1.1 —	—	—	—	—	—	—	—

only in small numbers in the materials from Betfia and Villany, because, in my opinion, their quantity at the stage of development that they represented is, in the nature of things, small.

On the basis of observations carried out during the present study it must be stated that there are no morphological grounds to hold that *Pliolagus bere-mendensis* KORMOS and *Pliolagus tothi* KRETZOI are species distinct from *Hypolagus brachygnathus* KORMOS. There are only various juvenile stages of individual development of *Hypolagus brachygnathus* KORMOS. Consequently the genus *Pliolagus* KORMOS must be considered to be synonymous with the genus *Hypolagus* DICE, and the species *Pliolagus beremendensis* KORMOS and *Pliolagus tothi* KRETZOI synonymized with *Hypolagus brachygnathus* KORMOS.

IV. DISCUSSION

THE DYNAMICS OF VARIATION IN THE DENTITION

One of the great changes that took place in the history of the *Lagomorpha* is the transformation of their cuspidoradical type teeth into ever-growing hypsodont teeth. The permanent dentition of the late Eocene leporids shows, besides the existence of roots, also some traces of hypsodontology, which becomes still clearer in the forms from the early Oligocene, and as early as the Lower Miocene, according to DAWSON (1958), predominates over the radical structure of the dentition. It seems probable that the presence of the roots in the deciduous teeth with traces of hypsodontology described in *Hypolagus brachygnathus* (p. 34) is the partial ontogenic repetition of this very process of evolution. STACH (1904, 1910) suggests in his studies on the ontogenesis and transformation of the deciduous dentition of *Oryctolagus cuniculus* that the occurrence of one, strongly elongated, trough-shaped root in the milk teeth is caused by the necessity of their nutrition still for some time in the period when they are being ousted by the permanent teeth. The gradual prolongation of the period of nutrition of the teeth and the elongation of the roots of that type probably mark the morphological beginnings of hypsodontology.

The process of unification of the shape and partly of measurements in the teeth of the upper row of the *Leporidae* begins at the time of the appearance of hypsodontology, the molar teeth being „models“ for shape. This process, generally called molarization, consists in gradual appearance of the characters of molars in the premolars. It manifests itself, above all, in the elongation of the hypostria of the upper cheek teeth and in the increasing density of crenulation of this enamel fold. The data of DAWSON (1958) indicate that in the phylogenetically older species of the genus *Hypolagus* the crenulation of the hypostria is stronger in the premolars than in the molars. The uniformity of

crenulation occurs in the younger species of *Hypolagus* and in the modern *Leporidae*. Another feature of molarization is the anteroposterior elongation of the teeth, especially of P^3 and P^4 .

The molarization of the cheek teeth in *Hypolagus brachygnathus*, as will be noticed, advanced so far that it becomes difficult and in some cases impossible to distinguish isolated P^4 from M^1 . The crenulation of hypostria is practically the same in premolars as in molars. In this respect, therefore, *Hypolagus brachygnathus* was one of the evolutionarily advanced species of the genus *Hypolagus*.

The change in measurements of P^3 , P^4 , M^1 , and partly also of M^2 during the Weże-Kamyk interval is of this kind that the widths of anterolophid and posterolophid show parallel changes, while the crown length is in its changes quite independent of both of them (p. 40). This fact is of great importance to the process of molarization of these teeth, among others to their anteroposterior elongation. It seems that the changes in the length of crown independent of its other two measurements were a factor facilitating the molarization.

The very well developed crenulation of the upper cheek teeth of the modern *Leporidae* appears to be a good adaptation of these teeth for grinding food by characteristic of leporids transverse movements of the mandible. The occurrence of crenulation on the hypostria not only increases the grinding surface, but also prevents dentine, softer than enamel, from excessively fast wearing. This adaptation was acquired during the long process of molarization of the upper cheek teeth.

The changes that occurred in the lower cheek teeth of *Hypolagus brachygnathus* took a different direction from those discussed above. M_3 , in which, as has been shown (p. 42), the process making this tooth of simple structure similar to the other molars has started, is an exception.

The distinctness of the changes in the lower cheek tooth row is evidenced by the fact that in the case of P_4 , M_1 , and M_2 the trigonid width is the character that changes independently of the others and not, as in P^3 , P^4 , M^1 , and M^2 , the crown length. In P_4 , M_1 , and M_2 the measurements correlated with each other are the crown length and the talonid width.

The posterior external enamel fold in P_3 and the deep fold between the trigonid and the talonid of the lower cheek teeth next to it show a progressive tendency towards simplification of their shape (p. 41). On the other hand, in the evolution of various leporid species the enamel pattern exhibits a tendency to become more complicated. The occurrence of crenulation and of various kinds of waviness of the enamel fold between the trigonid and the talonid in P_3 is not an isolated case. P_3 of *Hypolagus parviplicatus* DAWSON, 1958 from the Miocene shows, as can be seen in the clear drawing on page 45 of the paper of DAWSON (1958), a distinct crenulation of the posterior wall of the posterior external enamel fold like that described from *Hypolagus brachygnathus* of Weże. The phylogenetically younger species of the genus *Hypolagus* have these folds void of crenulation, especially so in P_3 .

It is hard to establish whether the role of crenulation in the lower dentition was the same as that discussed above in connection with the upper cheek teeth. If it was similar, then the reduction in crenulation and waviness of enamel in the lower cheek teeth of *Hypolagus brachygnathus* should be regarded as a regressive tendency difficult to agree with DOLLO's rule on the irreversibility of evolutionary changes.

The appearance of primitive characters is fairly often observed in *Hypolagus brachygnathus*. Among these we can reckon the occasional additional enamel fold in P_3 , with which I dealt when discussing the systematic position of the genus *Pliolagus*. The above-mentioned reduction in crenulation in the lower cheek teeth seems to belong to the same category of characters only that it manifests itself far oftener and in the fauna from Kamyk it is to some extent a character of population. In *Hypolagus brachygnathus* the frequent occurrence of these primitive characters may have reflected the still imperfect adaptation for grinding food, which is also indicated by the results obtained from an analysis of correlations in the measurements of the lower cheek teeth (p. 46).

BIOLOGICAL SIGNIFICANCE OF CORRELATIONS IN TOOTH MEASUREMENTS

The occurrence of positive correlations between the sizes of neighbouring teeth seems to result from a need of keeping constant proportions between them, particularly so between the portions of tooth row doing different work. The mechanism enabling the maintenance of these proportions at a steady level through numerous generations is certainly founded on genetics. A reduction in correlation, as the distance between the teeth increases, is probably governed by the action of the „genetic field of growth“ determined by a set of polymeric genes. KURTÉN (1953) presented a schematic model showing the action of gene pairs on the crown size in three successive teeth. In accordance with this model, definite alleles of the genes acting on a tooth are responsible for the growth of its crown size by a certain measurable value, which decreases and increases for the neighbouring teeth depending on the possible combinations of the genes; this results in the appearance of definite correlations between the sizes of these teeth. The application of this scheme for considerations on the correlations discussed above facilitates the explanation of some problems, and yet the importance of the theory of genetic correlation fields of KURTÉN should not be overestimated, and this is not inconsistent with the very opinion of its author.

The occurrence of the highest correlations in the same tooth pairs in *Hypolagus brachygnathus*, *Lepus europaeus*, and *Oryctolagus cuniculus* gives evidence of the action of identical genes, responsible for these strong interrelations, on P_4 , M_1 , and M_2 of these species. Apart from their sizes the crowns of these teeth much resemble each other in shape (p. 22). The same likeness is observed

in a large number of both modern and fossil leporids (e. g. in phylogenetically old genera such as *Archaeolagus* DICE, 1917 or *Palaeolagus* LEIDY, 1856). The diagram illustrating the course of changes in the absolute measurements of all the teeth of *Hypolagus brachygnathus* during the Węże-Kamyk interval (p. 38) shows that the changes concerning three measurements of each tooth are uniform for P_4 , M_1 , and M_2 contrary to what has been found in the remaining teeth of the lower row. The foregoing facts indicate a close functional association of these three teeth forming a distinct unit of great phylogenetic durability within the tooth row. As regards the adaptation of teeth for grinding, I might hazard the statement that the development achieved by P_4 , M_1 , and M_2 constitutes a rather much advanced adaptation in the mandible of leporids. The only hazard results here from the fact that I do not know the correlations in the dentition of the above-mentioned fossil forms of the genera *Archaeolagus* and *Palaeolagus*, these being unavailable for me.

It will be seen from the comparison of the general degrees of correlations carried out above that *Hypolagus brachygnathus* more approaches *Lepus europaeus* than *Oryctolagus cuniculus* in this respect. This last species in general shows a lower degree of interdependence in the lengths of the tooth crowns and at the same time a tendency to expansion of correlation, though at a lower level of its value. Since the correlation fields and the course of the contour lines are very pronounced and uniform in *Hypolagus brachygnathus* and *Lepus europaeus*, it seems that the process of formation of correlations in the lower tooth row proceeds virtually in one direction in both these species, but especially so in *Lepus europaeus*. Despite a close resemblance of both the species in this respect, *Lepus europaeus* represents a higher level of development as far as the adaptation of the dentition for grinding is concerned, on account of its higher values of correlation and, what is more, their occurrence in the group of teeth constituting a functional unit (P_4 and M_1 , as shown above, differ significantly in these species).

The appearance of medium and low (not significant) correlations in the particular species is especially interesting in the case of P_3 and M_3 . Here all the three species exhibit similar low values of correlations. This proves the action of a combination of genes on P_3 different from that acting on P_4 , M_1 , and M_2 . Carrying these considerations on, we may presume that the lack of correlation expected according to „the rule of neighbourhood“ between the length of M_3 and the length of the remaining teeth, is controlled by the action of a combination of genes varying from that active in the case of the other teeth.

The lack of correlation, or its low value, should in theory afford the possibility for greater variation in the characters examined. The coefficients of variation (V) for different measurements of teeth in *Hypolagus brachygnathus* from geologically varying localities (p. 25) indicate that M_3 and partly also P_3 really differ from the remaining lower cheek teeth in their considerably higher values, and this is true not only of the length but also of other measurements.

Apart from the variation of measurements, M_3 shows a great morphological variation as well. This manifests itself particularly clearly in the material from Kamyk, in which the changes in the tooth length to width ratio and the occurrence of various patterns of the enamel between the trigonid and the talonid are observed (p. 42).

BIOMECHANIC SIGNIFICANCE OF SOME CHARACTERS OF THE SKELETON OF *HYPOLAGUS BRACHYGNATHUS*

The characters of the scapula of *Hypolagus brachygnathus* that I have already described, i. e. an increase in its surface area compared to the recent hare and wild rabbit with a simultaneous relative shortening of its neck and the less clear than in *Lepus europaeus* preponderance of the infraspinous fossa over the supraspinous fossa, refer to the analogous characters recorded by DAWSON (1958) from the Oligocene and earlier *Leporidae*, in which, according to this authoress, it is possible to trace the gradual transition from the original state of balance of both the spinous fossae to a remarkable reduction of the supraspinous fossa, which is characteristic of phylogenetically younger and recent forms.

The elongation of the scapular neck and the narrowing of the whole scapula found in the modern forms are, according to SMITH and SAVAGE (1956), a distinctive character of many mammalian species having a perfected cursorial type of locomotion. In respect of this specialization, therefore, *Hypolagus brachygnathus* was second to the recent hare, though it surpassed its Oligocene ancestors.

The widening of the scapular socket found relatively smaller in *Hypolagus brachygnathus* and the wild rabbit than in the hare, facilitates the movements of the humerus out of their principal plane, i. e., the sagittal plane. This character is associated with a slight shallowing and shortening of the bicipital groove of the humerus observed in *Hypolagus brachygnathus*. This character, peculiar to phylogenetically primitive forms, is, in addition, one of the adaptations of the fore-limb of *Hypolagus brachygnathus* for digging movements (cf. wild rabbit).

The sturdiness and elongation of the medial epicondyle of the humerus of *Hypolagus brachygnathus* and the generally less massive structure of the trochlea than in the modern hare and wild rabbit, together with its relatively low crest seem to be due to the strong development of the flexors and extensors of the forearm. The development of these muscles may have increased the efficiency of digging movements.

The articulation of the humerus with the bones of the forearm, not so tight as in the modern hare and the wild rabbit, and the looser contact of the ulna with the radial than in these species suggest that *Hypolagus brachygnathus* possessed the greater power of pronation and supination movements. The

hare has lost this property of its limbs almost completely in connection with the perfection of its cursorial type of locomotion.

The relative elongation of the olecranon process, which is the place of the insertion of the triceps, the strong muscle extending the elbow joint and retracting the forearm, observed in *Hypolagus brachygnathus*, indicates that this muscle was better developed than in the hare, resembling that in the wild rabbit. According to POPLEWSKI (1948), it plays an important role in the digging movements of the limb. The presumption that *Hypolagus brachygnathus* frequently performed such movements proves true also when considered in connection with some other above-discussed characters of its skeleton.

Most of the morphological characters of the skeleton of *Hypolagus brachygnathus* differing from the corresponding characters of the hare in respect of biomechanics concern, as will be seen, the fore-limb. Besides these characters there are still some others, specified below, which indirectly affect the motion and contribute to the formation of the general shape of body of this animal.

The following muscles having a bearing on the body shape of *Hypolagus brachygnathus* were, as may be presumed, more strongly developed than in the recent forms:

1) the supraspinatus and infraspinatus, having an increased area of attachment on the scapular blade;

2) the set of acromial muscles inserted at the greater tuberosity and in its direct vicinity, the greater growth of which is indicated by the stronger than in recent forms development of the deltoid tubercle and the deltoid crest, the presence of an additional fine tubercle above them and, finally, by the sturdiness of the greater tuberosity;

3) the triceps brachii, the properties of which have already been discussed above;

4) the rectus femoris, the remarkable development of which can be inferred from the presence of the big inferior anterior spine on the ilium;

5) the gluteus medius attached to the robust great trochanter;

6) the gastronemius, whose attachment area just above both condyles of the femur (on the posterior side) shows pronounced roughness.

Some of the muscles, being better developed, probably enabled *Hypolagus brachygnathus* to execute vigorous movements. On the other hand, the sturdiness of various elements of its skeleton, which might well be defined as „thick-bonedness“, is striking. The combination of both these properties, coinciding with the smaller absolute measurements of body than in the recent hare, suggests that the cursorial ability of this species was rather poor, as was demonstrated above.

Frequent execution of digging movements implies burrowing, which again resembles the ways of the wild rabbit.

As will be seen from the results of the analysis of the bones of limbs, *Hypolagus brachygnathus* had the musculature of the upper portions of its limbs

and partly of the shoulder and hip girdles better developed than that in the recent hare. If these characters, as may be supposed, manifested themselves in the general mould of its body, they were responsible for its being robust and stocky.

In the length ratios of the fore- and hind-limbs *Hypolagus brachygnathus*, as has been shown, resembles the recent hare.

The evidently shortened facial portion of the skull owing to the short toothless margins of the jaws (p. 17) indicates the blunt shape of the muzzle.

CHANGES IN THE BODY SIZE OF *HYPOLAGUS BRACHYGNATHUS* WITH TIME AND THEIR CLIMATIC INTERPRETATION

A comparison of the measurements of various skeletal elements of *Hypolagus brachygnathus* shows that the size of body varied in the members of this species with time. The greatest differences were found between the specimens from Weże and those from Kamyk. *Hypolagus brachygnathus* was considerably smaller in the Upper Pliocene than at the end of the first interglacial (statistically significant differences in Table 23).

Changes in body size occurring in mammals during long periods may be twofold in nature: they either reflect a general evolutionary trend to continuous change in body size of animals representing the same evolutionary lines (SIMPSON, 1955; MOODY, 1962) or are brought about by climatic changes (more strictly, changes in temperature) in accordance with the bioclimatic rule of BERGMANN (RENSCH, 1936; KURTÉN, 1960). Finally, they may as well be due to the co-action of both these factors.

The changes in the size of body of *Hypolagus brachygnathus* over the time discussed are not continuous: the differences in size of the particular parts of skeleton between the samples from Rebiełice and those from Kadzielnia are sometimes hardly visible, but they increase rapidly between the samples from Kadzielnia and from Kamyk. As can be seen from the data of WOOD (1940), the evolutionary process of growth of body measurements in the fossil *Leporidae* is hard to perceive and, if there was any, it was the most intense in the period from the middle of the Oligocene to the beginning of the Pliocene, no later changes in size being palpable. This fact, as well as the above-mentioned discontinuity of the growth of body size in *Hypolagus brachygnathus* from my material, allows the fairly probable presumption that the increase in size observed in this species over the Weże-Kamyk period was not an evolutionary process of growth in the body size.

On the other hand, the palaeoclimatic data (BROOKS, 1949; ZEUNER, 1959) indicate that the Pliocene weather was milder than later in the interglacial periods of the Pleistocene. Conclusions concerning this difference can be made on the basis of my material, for instance, comparing the colour of clay in the

particular breccias. The clay has the properties of typical *terra rosa* except for the breccia from Kamyk. The most intense red coloration is found in the breccia from Weże. The coloration is less intense in the breccias from Rębielice and Kadzielnia, while the deposits from Kamyk are only brown-yellowish. Hence it appears that, as far as temperature is concerned, the difference in climate was the greatest between the period when the fauna of Weże lived and that of the fauna of Kamyk.

The dependence of the size of body in warm-blooded animals of the same species on the temperature of the environment is, as it is well known, determined by BERGMANN'S rule. According to this rule, animals living in a cold climate have larger measurements of body than the members of the same species living in a warmer climate. This dependence is connected with a trend to achieve as advantageous a relation of the body surface area, radiating heat, to the volume (and so to the size) as possible. The ratio is more advantageous in big animals than in small ones. However, there is a large number of mammals which form exceptions, e. g., some *Mustelidae*, whose body measurements change irrespective of the fluctuations of temperature (KURTÉN, 1960).

For this reason I preceded my trials to explain the increase of absolute measurements of *Hypolagus brachygnathus* through changes in climate by checking and demonstrating that BERGMANN'S rule proves true of recent leporids. The data used for this purpose derive from two sources: 1) from the paper on bioclimatic laws by RENSCH (1936) containing, among other things, a comparison of sizes of various American subspecies of hares and rabbits having a limited range and collected at latitudes differing distinctly in climate, and 2) from my own measurements of skulls of the variable hare *Lepus timidus* L. from a few regions of Asia differing in climate. The data of RENSCH were completed with the mean annual temperatures of the geographical regions inhabited by the subspecies compared. These data were used to compile Tables 21 and 22. They permit the statement that various species of the *Leporidae* change their body measurements in accordance with BERGMANN'S rule and that the degree of these changes is proportional to the climatic differences, expressed here by the mean annual temperature. Consequently, it seems quite probable that the changes in size of *Hypolagus brachygnathus* over the period between the Upper Pliocene and the end of the Günz-Mindel interglacial were due to changes in climate.

Being in possession of the data concerning the mean changes in size of recent hares and rabbits, controlled by differences in climate according to the latitude in which they live, and knowing the magnitude of differences in size of *Hypolagus brachygnathus* between the middle Pliocene and the end of the Günz-Mindel interglacial, brought about by climatic changes of an unknown gradient, one can try to calculate the order of magnitude of this gradient. However, it should be mentioned beforehand that this kind of calculation is possible after introducing some simplifications into the initial assumptions, causing the approximate nature of the result.

Changes in measurements of body of some subspecies of leporids according to the climate of environment. (After Rensch, 1936 completed with latitudes, mean annual temperatures and percentage changes in size)

	Geographical region	Difference in latitudes	Measurements of body in mm		Difference in absolute annual temperatures of both regions	Percentage change in body size per 1° of difference in mean annual temp. of both regions
			length body + head	length of body		
<i>Sylvilagus floridanus mearnsi</i>	Kansas — Kentucky Pennsylvania	10°	457	—	7°C	2.80
<i>Sylvilagus floridanus floridanus</i>	Florida		368			
<i>Sylvilagus auduboni beileyi</i>	Montana Kansas	12°	361	—	8°C	2.10
<i>Sylvilagus auduboni minor</i>	Texas — N. Mexico		302			
<i>Sylvilagus bachmani ubericolor</i>	N. California Columbia Riv.	22°	—	368	10°C	1.3
<i>Sylvilagus bachmani cinerascens</i>	S. California			318		
<i>Lepus americanus marjani</i>	Alaska	10°	—	495	8°C	1.26
<i>Lepus americanus columbiensis</i>	Br. Columbia — Canada			445		
<i>Lepus californicus walla walla</i>	Oregon — N. California	12°	—	581	7°C	1.40
<i>Lepus californicus zanti</i>	L. California			523		

Table 22

Changes in condylobasal length of skull of *Lepus timidus* from two climatically differing regions of Arkhangel'sk and Vladivostok. N — number of specimens

	Geographical region	Difference in latitudes	Condylobasal length of skull	Difference in absolute annual temperatures of both regions	Percentage change in skull size per 1° of difference in mean annual temp. of both regions
<i>Lepus timidus</i> L.	region of Arkhangel'sk	22°	80.01 (N = 25)	5°C	1.39
	region of Vladivostok		74.80 (N = 25)		

A comparison of the measurements obtained from different parts of the skeleton of *Hypolagus brachygnathus* with these data is difficult, as we do not know the exact measurements of its body. Those obtained from the reconstructions of numerous but fragmentary long bones would not be reliable because of too great errors. It is also difficult to infer the size of the whole body from the measurements of fossil teeth, as the correlation between these values is not sufficiently high.

The only elements of the skeleton fit for such a comparison are short bones of the ankle joint, which change within very narrow limits with the changes in proportions of the long bones of limbs, as has been checked in recent hares and rabbits. Among the bones of the ankle joint theoretically fit for comparison, the calcaneus is the most abundant and least damaged in the available fossil materials. Its abundance makes it also possible to carry out the basic statistical analysis. The results of measuring and the statistical data are given in Table 23.

The general assumptions for calculation of the gradient of mean annual temperature are as follows:

1) The changes in size of *Hypolagus brachygnathus* over the period between the middle Pliocene (Weże) and the end of the first interglacial (Kamyk) were caused by the differences in the temperatures of environments according to BERGMANN'S rule.

2) The changes in size of *Hypolagus brachygnathus* caused by a gradient of temperature are proportional to the changes brought about by the same gradient in similar recent forms.

3) The measurements of the calcaneus of *Hypolagus brachygnathus* are proportional to the size of this animal.

Table 23

Mean length M of calcaneus of *Hypolagus brachygnathus* comprising statistical data: M — arithmetic mean; σ_M — standard error; s — standard deviation; t — confidence interval with Student's value t at a level of 0.05, for mean M ; N — number of specimens

	N	$M \pm \sigma$	s	$M \pm \sigma \cdot t$
Węże	18	26.33 ± 0.12	0.53	26.33 ± 0.26
Rębielice	31	27.13 ± 0.14	0.78	27.13 ± 0.29
Kadzielnia	20	28.52 ± 0.32	1.46	28.52 ± 0.68
Kamyk	34	32.04 ± 0.14	0.84	32.04 ± 0.29

4) The gradient of temperature will be determined in the form of a difference in degrees between the mean annual temperatures of environments for the faunae from Węże and Kamyk extremely remote from each other in time.

The following parameters were used for this purpose:

1) percentage difference in body size between two recent subspecies s_a and s_γ living in latitudes a and γ ;

2) difference of the mean annual temperatures t obtained from the annal isotherms I_a and I_γ of the respective regions situated in latitudes a and γ ;

3) percentage difference Δl in the total length of calcaneus between specimens of *Hypolagus brachygnathus* from Węże (l_w) and those from Kamyk (l_{ky}).

The application of percentage differences, as far as the size of body and the length of calcaneus are concerned, makes these values comparable within the limits of proportionality between them discussed above and eliminates the unknown parameter, which is the absolute size of body of the fossil species, from the calculation.

The value to be calculated is the gradient of temperature x . The following equation can be written on the basis of assumption 2:

$$\frac{\Delta l}{x} = \frac{\Delta s}{\Delta t}$$

giving

$$x = \frac{\Delta l \cdot \Delta t}{\Delta s}$$

Since

$$\Delta l = \frac{l_{ky} - l_w}{l_{ky}} \cdot 100, \quad \Delta s = \frac{s_a - s_\gamma}{s_a} \cdot 100, \quad \text{and} \quad \Delta t = I_a - I_\gamma$$

$$x = \frac{s_a(I_a - I_\gamma) \cdot (l_{ky} - l_w)}{l_{ky}(s_a - s_\gamma)}$$

Having replaced the denotations s and l by suitable arithmetic means \bar{M} , I obtain finally

$$x = \frac{\bar{M}s_a(I_a - I_\gamma)(\bar{M}l_{ky} - \bar{M}l_w)}{\bar{M}l_{ky}(\bar{M}s_a - \bar{M}s_\gamma)}$$

Substituting the suitable means from the table in the formula, I achieve the approximate difference in mean annual temperature between the environment of the middle Pliocene fauna from Weže and that of the fauna from Kamyk dated from the end of the Günz-Mindel interglacial. The mean value of this gradient obtained from the combination of the data for various species of recent leporids and for *Hypolagus brachygnathus* amounts to 10.5°. This is a very high value, approximating to the change of the Mediterranean climate (e. g., that of the Naples region) into the moderate climate (e. g., that of the Warsaw region). We should accept this figure with some reserve in view of the necessary simplifications introduced into the initial assumptions for calculation.

PROBLEM OF EXTINCTION OF *HYPOLAGUS BRACHYGNATHUS* IN THE PLEISTOCENE

The species making up the genus *Hypolagus* form an evolutionary line having origin in the middle Miocene (*Hypolagus parviplicatus* DAWSON, 1958 — North America). The last representatives of this line became extinct in the early Pleistocene in both Old and New Worlds. These forms constitute a side branch in the phylogenetic pedigree of the *Lagomorpha* (DAWSON, 1958; GUREYEV, 1964). HIBBARD'S conception (1963) is that the genus *Lepus* has a distinct genealogy and its ancestors were not related in the direct line with *Hypolagus*. As regards the place of origin of *Hypolagus*, SIMPSON (1947) believed that North America was its cradle, Asia being the cradle of *Lepus*. The dispersal of various leporid species occurred in the periods of intercontinental exchange of the fauna, which in his opinion, took place successively in the early and late Eocene, early Oligocene, late Miocene, Upper Pliocene, and Pleistocene. Thus, in the late Pliocene the Eurasian *Leporinae* are supposed to have migrated to North America, from where at the same time some members of *Hypolagus* migrated to Eurasia. On the other hand, it is known from the data given by GUREYEV (1964) that as early as the Upper Miocene *Hypolagus gromovi* GUREEV occurred in Moldavia. This fact shakes SIMPSON'S hypothesis concerning the migrations of *Hypolagus* in the late Pliocene, but it does not rule out North America being the cradle of this group of species. The majority (9) of the known species of *Hypolagus* accumulated there, the remaining ones being found in Asia (China — *Hypolagus schreuderi* TEILHARD DE CHARDIN 1940), Eastern Europe (Moldavia — *Hypolagus gromovi* GUREEV) and Central Europe (*Hypolagus brachygnathus*). Thus, Central Europe should be regarded as a periphery of the range of the genus *Hypolagus*.

If we take into consideration the fact that great variation and strong selection are most intensely active in the periphery of the range of a species, the peripheral occurrence of *Hypolagus brachygnathus* seems to have been one of

the reasons for great morphological variation in this species, reflected in the high coefficients of variation of some measurements of teeth (p. 25) and in the diversity of the shape of P^2 , P^3 , and M_3 (p. 42).

The causes of extinction of *Hypolagus* and, in general, of the whole group *Archaeolaginae* have not been elucidated so far. The fact of complete disappearance of this genus in the early Pleistocene might be explained by the effect of the cooling of climate. On the other hand, it has been found on the basis of *Hypolagus brachygnathus* that this genus showed a distinct adaptation to climatic changes in keeping with BERGMANN'S rule. Consequently, the changes in climate were not the factor leading to the continuous reduction of its particular populations.

The genus *Lepus* also appeared in the younger faunae of the Central European early Pleistocene. In KRETZOR'S opinion (1941), it is rare in the fauna of Episcopia along with dominant *Hypolagus brachygnathus*, in the fauna of Betfia it already forms about 75% of the total of leporids, while *Hypolagus brachygnathus* amounts to about 22%, it is strongly dominant in the fauna of Nagyarsanyhegy, and the only leporid species present in the youngest, early Pleistocene, fauna of Brasso.

As I have shown *Hypolagus brachygnathus* had different primitive characters. A comparative study of the correlations between the measurements of the lower teeth indicates that *Lepus europaeus* distinctly surpasses *Hypolagus brachygnathus* in the adaptation of the dentition for gnawing. The hare, as has been demonstrated by a comparison of the biomechanic properties of the skeleton, was far more efficient, in so far as locomotion and especially running are concerned, than heavy and sturdy *Hypolagus brachygnathus*.

The persistence of the two species in the common ecological niche, which was undoubtedly formed by their similar food supplies, probably led to strong competition between the hare and *Hypolagus brachygnathus*, in which the former, better adapted to the environment in many respects, was finally victorious.

The genus *Lepus*, which appeared in the Pliocene, dominated in Eurasia in a comparatively short time and came to Central Europe in the early Pleistocene. There is no reason to doubt that its expansion was equally rapid in North America, when it had reached there in one of the periods of the intercontinental exchange of the fauna. The disappearance of the species of the phylogenetic line of *Hypolagus* in the New World was also connected with the competition of the genus *Lepus*.

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STRESZCZENIE

Autor podaje szczegółową analizę morfologiczną i biometryczną licznych szczątków zającowatych z czterech różniących się wiekiem geologicznym faun z miejscowości: Weże k. Działoszyna (górny pliocen starszy), Rębielice Kró-

lewskie k. Kłobucka (górny pliocen młodszy), Kadzielnia w Kielcach (wczesny plejstocen, prawdopodobnie początek interglacjału Günz-Mindel) i Kamyk k. Częstochowy (wczesny plejstocen, prawdopodobnie schyłek interglacjału Günz-Mindel). Szczątki te we wszystkich czterech faunach należą do wymarłego w plejstocenie gatunku *Hypolagus brachygnathus* KORMOS, 1934. Poszczególne elementy jego czaszki i kości szkieletu kończyn porównano z odpowiednimi elementami u współczesnych gatunków *Oryctolagus cuniculus* LINNAEUS i *Lepus europaeus* PALLAS. W niektórych przypadkach przeprowadzono również porównanie *Hypolagus brachygnathus* z okazami tego gatunku z innych europejskich faun kopalnych oraz z pojedynczymi okazami *Hypolagus gromovi* GURJEJEV i *Hypolagus schreuderi* TEILHARD. Szczegółowo zbadano holotypy gatunków *Pliolagus beremendensis* KORMOS, 1934 i *Pliolagus tothi* KRETZOI, 1941 i porównano je z okazami *Hypolagus brachygnathus* KORMOS w różnych stadiach wieku osobniczego, co umożliwiło rewizję stanowiska systematycznego kopalnego rodzaju *Pliolagus* KORMOS, 1934. Dużo uwagi poświęcono dynamice zmienności uzębienia w okresie czasu dzielącym faunę z Węzów od fauny z Kamyka, przeprowadzając podstawową analizę statystyczną danych biometrycznych oraz porównanie korelacji wymiarów zębów u *Hypolagus brachygnathus*, *Lepus europaeus* i *Oryctolagus cuniculus*. Dzięki znacznej obfitości materiałów udało się poznać młode stadia rozwojowe zębów stałych oraz uzębienie mleczne *Hypolagus brachygnathus*.

Kości szkieletu pasa barkowego, miednicznego i kończyn zbadano pod kątem mechaniki biegu, co umożliwiło częściowo próbę odtworzenia trybu jego życia.

Wnioski

1. Okazy *Hypolagus brachygnathus* w badanych polskich faunach z górnego pliocenu i wczesnego plejstocenu nie różnią się od okazów tego gatunku z innych faun europejskich. Wymiary okazów *Hypolagus brachygnathus* z Tegelen Clay i Beremend są najbliższe wymiarom tego gatunku z Kamyka, szczątki zaś z Betfia i Villany odpowiadają wielkością szczątkom z Kadzielni.

2. Holotypy gatunków *Pliolagus beremendensis* KORMOS, 1934 i *Pliolagus tothi* KRETZOI, 1941 są młodymi okazami *Hypolagus brachygnathus* KORMOS, 1934. Do nich zaliczyć należy również okazy *Pliolagus* cf. *tothi* opisane przez KOWALSKIEGO (1958) z fauny w Kadzielni. W związku z tym nazwy *Pliolagus beremendensis* KORMOS i *Pliolagus tothi* KRETZOI uznać należy za synonimy *Hypolagus brachygnathus* KORMOS, nazwę zaś *Pliolagus* KORMOS, 1934 za synonim nazwy rodzaju *Hypolagus* DICE, 1917.

3. *Hypolagus brachygnathus* był zwierzęciem o wymiarach ciała pośrednich między dzikim królikiem *Oryctolagus cuniculus* (LINNEUS) a zającem szarakiem *Lepus europaeus* (PALLAS), bliższych jednakże temu ostatniemu. Analiza czaszki i reszty szkieletu *Hypolagus brachygnathus* pod kątem rozwoju umięśnienia wskazuje, że gatunek ten, w odróżnieniu od dzikiego królika i zająca, miał

prawdopodobnie masywną i krępą budowę ciała, pysk tępo zakończony z dość wyraźnie skróconą częścią twarzową czaszki. Masywność kości jego szkieletu i istnienie silniej rozwiniętych mięśni w różnych okolicach ciała niż u zająca i dzikiego królika skłaniają do przypuszczenia, że biegowy typ lokomocji był u *Hypolagus brachygnathus* mniej doskonały niż u zająca. Znalezienie lepiej rozwiniętych niż u zająca mięśni ułatwiających ruchy grzebiące pozwala wnioskować, że ruchy te były często przez *Hypolagus brachygnathus* wykonywane i, być może, służyły — podobnie jak u dzikiego królika — do kopania nor.

4. Stałe uzębienie *Hypolagus brachygnathus* wykazuje daleko posunięty stopień molaryzacji, zwłaszcza w górnym szeregu zębowym. Uzewnętrznia się to w silnie rozwiniętej krenulacji hypostria, co jest prawdopodobnie adaptacją do ścierania twardego pokarmu, nabytą w długim procesie molaryzacji górnych zębów policzkowych. Pod tym względem więc *Hypolagus brachygnathus* był jednym z bardziej ewolucyjnie zaawansowanych gatunków rodzaju *Hypolagus* DICE.

Natomiast znaleziona w dolnych zębach policzkowych tendencja do uproszczania fałdu szkliwa między trygonidem i talonidem pozostaje na razie bliżej niewyjaśniona.

5. Ważny taksonomicznie P_3 , pomimo istnienia różnych przypadków indywidualnej zmienności, nie wykazuje tendencji do pogłębienia tylnego zewnętrznego fałdu szkliwa wraz z upływem czasu.

6. Odróżnienie od siebie izolowanych P_4 , M_1 i M_2 u *Hypolagus brachygnathus* jest możliwe na podstawie płaszczyzn zgięcia tych zębów i kształtu talonidów. Ma to znaczenie dla wykorzystania do badań także zębów izolowanych nie tylko u *Hypolagus brachygnathus*, ale również u wielu innych zbliżonych do tego gatunku zajęcy posiadających podobny typ dolnego uzębienia.

7. Z punktu widzenia adaptacji uzębienia do gryzienia *Hypolagus brachygnathus* stoi niżej od *Lepus europaeus* ze względu na niższe wartości korelacji wymiarów zębów, w grupie stanowiącej funkcjonalną całość (P_4 , M_1 i M_2).

8. *Hypolagus brachygnathus* wykazuje cechy prymitywne: obecność niekiedy na P_3 dodatkowego wewnętrznego fałdu szkliwa i stałe istnienie tego fałdu w uzębieniu mlecznym, co nawiązuje do cech starych filogenetycznie gatunków z grupy *Palaeolaginae* DICE. Obecność na DM_4 wypuklenia ku tyłowi tylnej ścianki trygonidu nawiązuje do cech właściwych grupie *Agispelaginae* GUREEV.

9. Wymiary ciała *Hypolagus brachygnathus* powiększały się z czasem, najgwałtowniej u schyłku interejału Günz-Mindel (forma z Kamyka). Jest to prawdopodobnie wpływ ochłodzenia się klimatu zgodnie z regułą BERGMANNA, która sprawdza się z dość znaczną ścisłością na wielu podgatunkach zającowatych. Przybliżone, hipotetyczne obliczenie rzędu wielkości zmiany klimatu (średniej rocznej), która mogła spowodować zmiany wielkości ciała u *Hypolagus brachygnathus* w czasie: starszy górny pliocen (Węże) — schyłek interglacjału Günz-Mindel (Kamyk), wykazało, że różnica średniej rocznej temperatury środowiska Węzów i Kamyka mogła sięgać rzędu 10°C. Liczbę tę należy traktować

ostrożnie ze względu na konieczne uproszczenia w założeniach wyjściowych obliczenia.

10. Odnośnie wyginięcia w początkach plejstocenu *Hypolagus brachygnathus*, a także innych gatunków rodzaju *Hypolagus*, autor przypuszcza, że jedną z ważnych przyczyn była konkurencja z gatunkami z rodzaju *Lepus*, który pojawił się w pliocenie. Jak wykazało porównanie *Lepus europaeus* i *Hypolagus brachygnathus*, ten ostatni był pod wieloma względami słabszy z punktu widzenia adaptacji do środowiska.

РЕЗЮМЕ

Автор даёт подробный морфологический и биометрический анализ большого количества ископаемых остатков *Leporidae* принадлежащих к четырём, отличающимся геологической древностью фаунам из следующих местоположений: Венже возле Дзялошина (старший верхний плиоцен), Рембелице Крулевске возле Клобуцка (младший верхний плиоцен), Кадзельня в Кельцах (ранний плейстоцен, очевидно начало Гюнц-Миндельского интергласиала) и Камык возле Ченстохова (ранний плейстоцен, очевидно склон Гюнц-Миндельского интергласиала). Во всех четырёх фаунах остатки эти принадлежат к вымершему в плейстоцене виду *Hypolagus brachygnathus* KORMOS, 1934. Отдельные элементы черепа и кости скелета конечностей этого вида сравнены с соответствующими элементами современных видов *Oryctolagus cuniculus* LINNAEUS и *Lepus europaeus* PALLAS. В некоторых случаях проведено также сравнение *Hypolagus brachygnathus* с экземплярами того-же вида из иных европейских ископаемых фаун, а также с одиночными экземплярами *Hypolagus gromovi* GUREEV и *Hypolagus schreuderi* TEILHARD. Тщательно исследованы голотипы видов *Pliolagus beremendensis* KORMOS, 1934 и *Pliolagus tothi* KRETZOI, 1941 и сравнены с экземплярами *Hypolagus brachygnathus* KORMOS на разных стадиях индивидуального развития, что позволило провести ревизию систематического положения ископаемого рода *Pliolagus* KORMOS, 1934. Много внимания уделено динамике изменчивости зубов в периоде отделяющем фауну из Венже от фауны из Камыка, проводя основной статистический анализ биометрических данных и сравнение корреляции размеров зубов у *Hypolagus brachygnathus*, *Lepus europaeus* и *Oryctolagus cuniculus*. Благодаря обилию материала, удалось изучить ранние стадии развития постоянных зубов и молочные зубы *Hypolagus brachygnathus*.

Кости скелета плечевого и тазового поясов и конечностей, исследованы с точки зрения механики бега, что частично помогло сделать попытку реконструкции образа жизни этого вида.

Выводы

1. Экземпляры *Hypolagus brachygnathus* исследованных польских фаун из верхнего плиоцена и раннего плейстоцена, не отличаются от экземпляров того-же вида иных европейских фаун. Размеры экземпляров *Hypolagus brachygnathus* из

Tagelen Clay и Beremend наиболее близки размерам того-же вида из Камька, а остатки из Betfia и Villany размерами соответствуют остаткам из Кадзельни.

2. Голотипы видов *Pliolagus beremendensis* KORMOS, 1934 и *Pliolagus tothi* KRETZOI, 1941, являются молодыми экземплярами *Hypolagus brachygnathus* KORMOS. К ним зачислить следует также экземпляры *Pliolagus* cf. *tothi* описанные Ковальским (KOWALSKI, 1958) в фауне Кадзельни. В связи с этим названия *Pliolagus beremendensis* KORMOS и *Pliolagus tothi* KRETZOI следует признать синонимами, *Hypolagus brachygnathus* KORMOS, а род *Pliolagus* KORMOS, 1934 синонимом рода *Hypolagus* DICE, 1917.

3. *Hypolagus brachygnathus* по размерам тела занимает промежуточное положение между диким кроликом *Oryctolagus cuniculus* (LINNEUS) и русаком *Lepus europaeus* PALLAS, но ближе русака. Анализ черепа и остального скелета *Hypolagus brachygnathus* с точки зрения развития мускулатуры показывает, что вид этот, в отличие от дикого кролика и зайца, был очевидно массивного и крепкого телосложения, тупомордый с заметно укороченной лицевой частью черепа. Массивность его костей и более сильное, чем у русака и дикого кролика, развитие мускулатуры в разных частях тела, дают возможность предполагать, что беговой тип передвижения у *Hypolagus brachygnathus* был менее совершенный чем у зайца. Более сильное чем у зайца развитие мускулатуры способствующей гребным движениям указывает, что движения эти часто выполнялись *Hypolagus brachygnathus* и может быть служили для рытья нор, подобно как у дикого кролика.

4. Постоянные зубы *Hypolagus brachygnathus* обнаруживают сильную степень моляризации, особенно в верхней челюсти. Проявляется это в сильно развитой кренуляции hypostria, что очевидно является приспособлением к растиранию твердой пищи, приобретенным в продолжительном процессе моляризации верхнебоковых зубов. В этом отношении *Hypolagus brachygnathus* был одним из наиболее продвинувшихся в эволюции видом из рода *Hypolagus* DICE.

Отмеченная же тенденция к упрощению складки эмали между тригонидом и талонидом остается пока невыясненной.

5. Таксономически важный P_3 не проявляет склонности к углублению задней, внешней складки эмали, несмотря на наличие различных случаев индивидуальной изменчивости.

6. Отличить изолированные P_4 , M_1 и M_2 у *Hypolagus brachygnathus* можно по плоскостям изгиба зубов и по форме талонидов. Это имеет значение для использования изолированных зубов при исследовании не только *Hypolagus brachygnathus* но и других, близких ему видов *Leporidae* со сходным типом зубов в нижней челюсти.

7. С точки зрения адаптации зубов к грызению, *Hypolagus brachygnathus* стоит ниже *Lepus europaeus* ввиду более низких качеств корреляции размера зубов в группе составляющей функциональную целостность (P_4 , M_1 и M_2).

8. *Hypolagus brachygnathus* проявляет примитивные черты: наличие (иногда) на P_3 добавочной внутренней складки эмали и постоянное присутствие этой складки на молочных зубах — что указывает на филогенетическую связь древними видами

из группы *Palaeolaginae* DICE. Наличие на DM_4 , сзади на задней стенке, тригониды указывает на связь с чертами характерными группе *Algispelaginae* GUREEV.

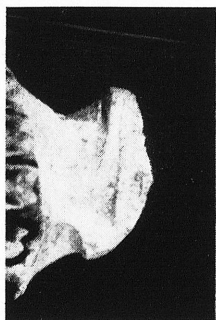
9. Размеры тела *Hypolagus brachygnathus* увеличивались постепенно, а на склоне Гюнц-Миндельского интерглатциала даже довольно резко (форма из Камыка). В этом случае очевидно повлияло охлаждение климата согласно правилу Бергмана, которое подтверждается по отношению ко многим подвидам *Leporidae*. Приблизительное, гипотетическое вычисление порядка величины изменения климата (средней годичной), которое могло вызвать изменение величины тела *Hypolagus brachygnathus* в периоде старший верхний плиоцен (Венже) — склон Гюнц-Миндельского интерглатциала (Камык) показало, что отличия средне годичной температуры в Венже и Камык могли достигать 10°C . К числу этому следует относиться осторожно, так как при его вычислении по необходимости сделаны упрощения исходных данных.

10. Относительно исчезновения *Hypolagus brachygnathus* и других видов рода *Hypolagus* в начале плейстоцена, автор предполагает, что одной из важных причин была конкуренция видов рода *Lepus*, появившегося в плиоцене. Сравнение *Lepus europaeus* с *Hypolagus brachygnathus* показало, что последний вид был во многих отношениях слабее адаптирован к среде.

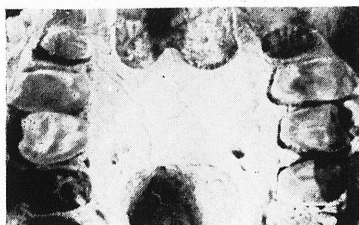
PLATES

Plate I

1. Ventral side of the anterior portion of the zygomatic arch in *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
2. Ventral side of the palatal bridge of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
3. Posterior nares of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).



1a



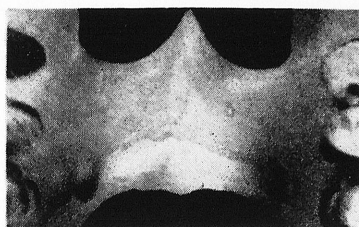
2a



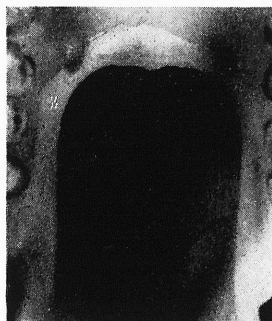
3a



1b



2b



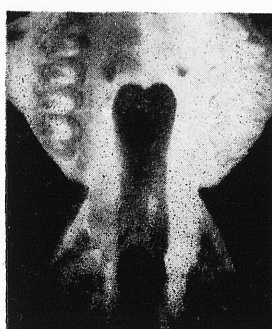
3b



1c



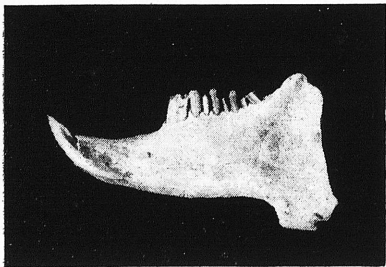
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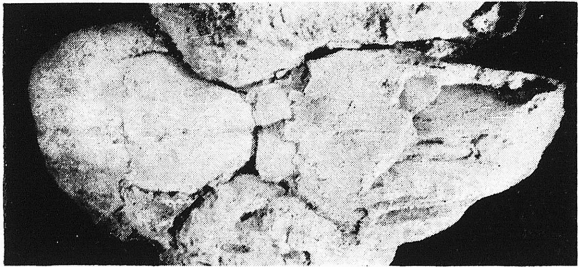
3c

Plate II

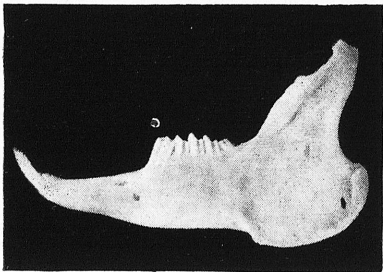
1. Shortening of mandibular diastema of *Hypolagus brachygnathus* (a) in comparison with *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
2. Fragments of skulls of *Hypolagus brachygnathus* from Weže. a — dorsal view; b — lateral view; c — ventral view.



1a



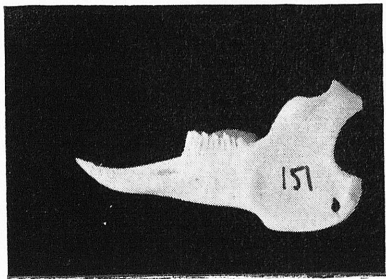
2a



1b



2b



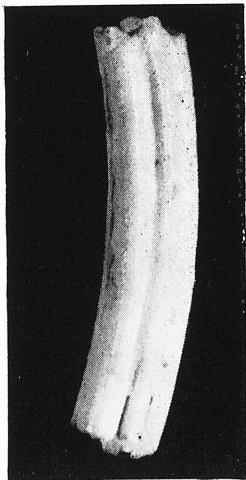
1c



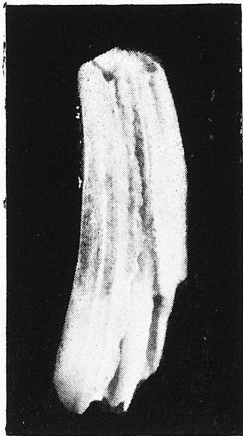
2c

Plate III

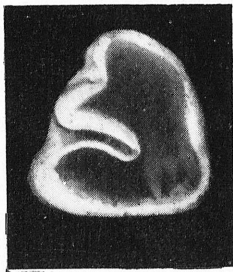
1. a — parallelism of tooth walls in adults; b — obliquity of tooth walls in young specimens.
2. Pattern of the posterior wall of the posterior external enamel fold on P_3 of *Hypolagus brachygnathus*. a — smooth line; b — irregular waviness; c — crenulation.
3. Structure of some specimens of M_3 in *Hypolagus brachygnathus* from Kamyk. Union of the trigonid with the talonid.
4. P^2 of *Hypolagus brachygnathus*. a — wear surface; b — bottom surface.



1a



1b



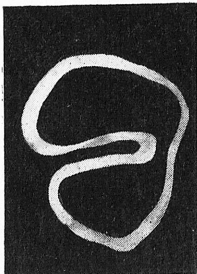
2a



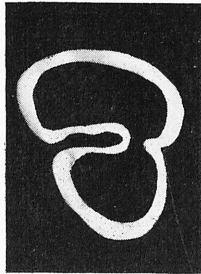
2b



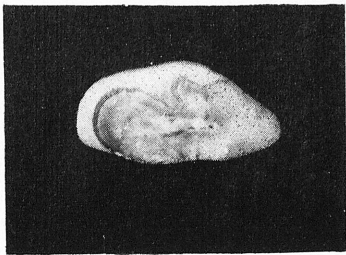
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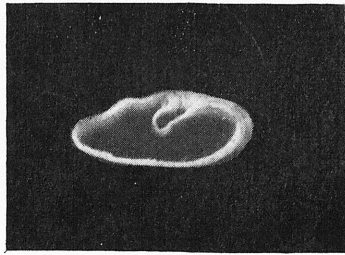
3a



3b



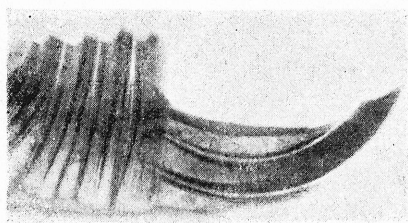
4a



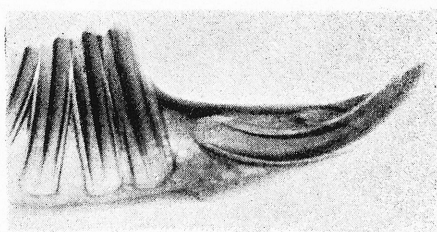
4b

Plate IV

1. Topography of lower incisors relative to the tooth row. Radiograms of mandibles a — *Hypolagus brachygnathus* from Rebielice; b — *Lepus europaeus*.
2. Cross-sections of incisors of *Hypolagus brachygnathus*. a — upper incisors of the anterior pair; b — lower incisors.
3. Wear surface of the crown of DM_1 in *Hypolagus brachygnathus* showing the trigonid bulging posterad
4. Wear surface of the crown of M^3 in *Hypolagus brachygnathus*.
5. Posterior side of the young permanent teeth (P^3) of *Hypolagus brachygnathus*. a — stage I, crown with cusps; b — stage II, crown without cusps, obliquity of walls.
6. Deciduous teeth of *Hypolagus brachygnathus*. a — DM^3 with conical roots; b — DM^2 with one trough-shaped (long) root and one conical (short) root; c — DM_3 with one trough-shaped (long) and one conical (short) root.
7. Three successive phases of wear of DM_3 of *Hypolagus brachygnathus*. a — whole internal enamel fold present; b — internal enamel fold in the form of an islet; c — no internal enamel fold as in P_3 .

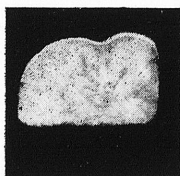


1a

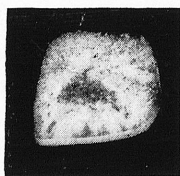


1b

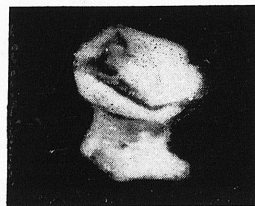
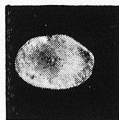
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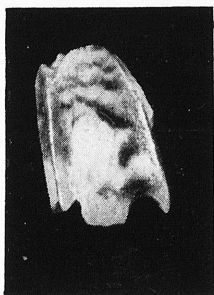
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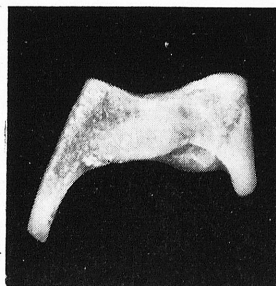
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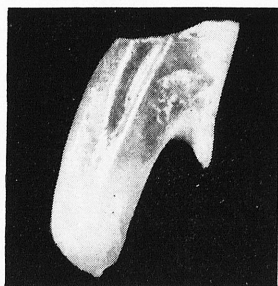
5a



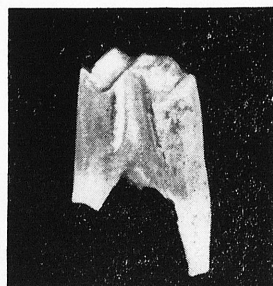
5b



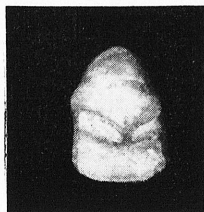
6a



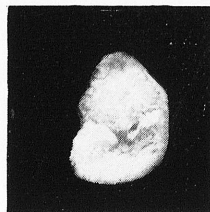
6b



6c



7a



7b

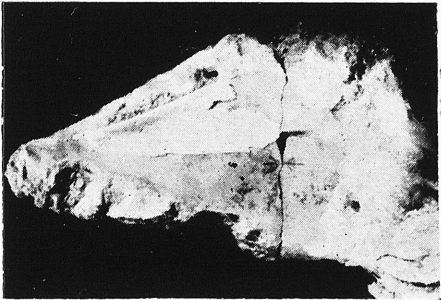


7c

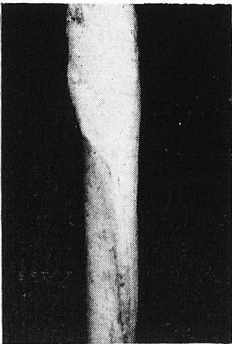
Plate V

1. Scapula of *Hypolagus brachygnathus* from Weže.
2. Deltoid tubercle and deltoid crest of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
3. Trochlea of humerus of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
4. Olecranon process of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).

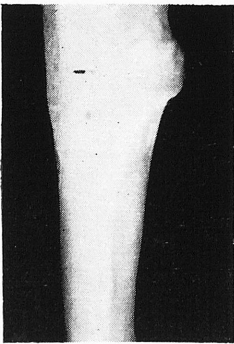
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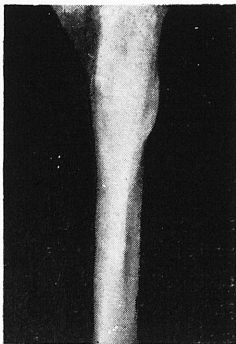
2a



2b



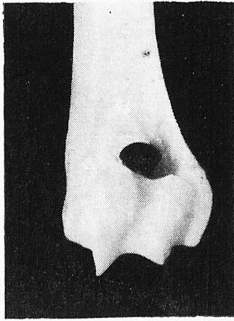
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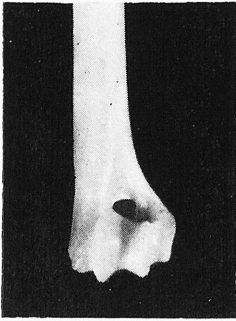
3a



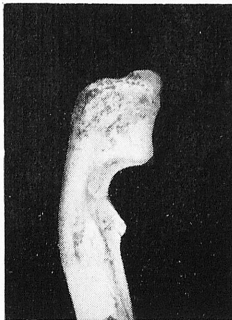
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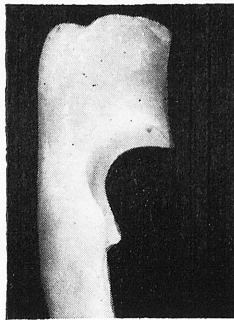
3c



4a



4b



4c

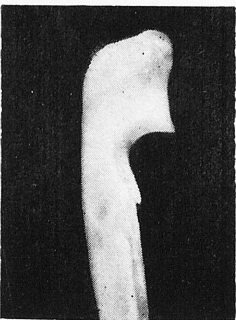
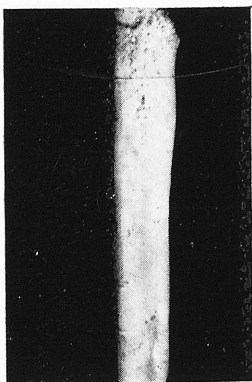
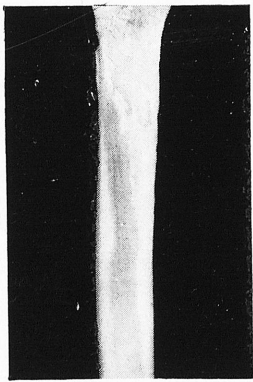


Plate VI

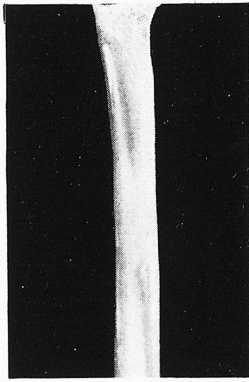
1. Anterior side of the shaft of the ulna in *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
2. Proximal epiphysis of radius of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
3. Posterior side of the distal epiphysis of the femur in *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
4. Articular facet of the proximal epiphysis of the tibia in *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).



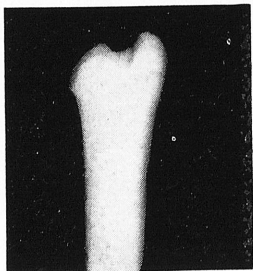
1a



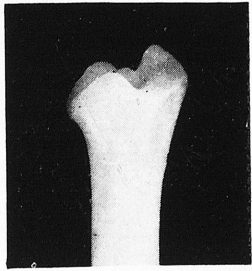
1b



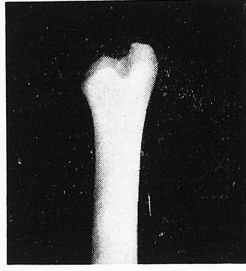
1c



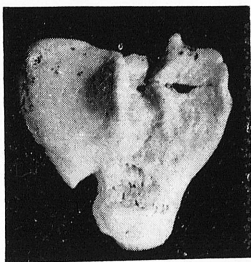
2a



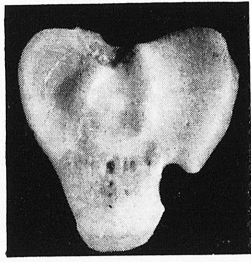
2b



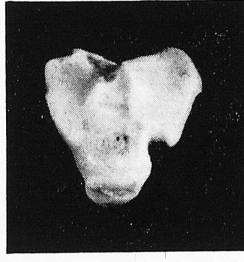
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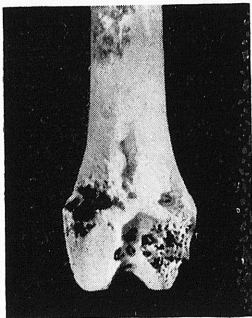
3a



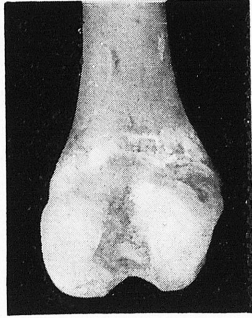
3b



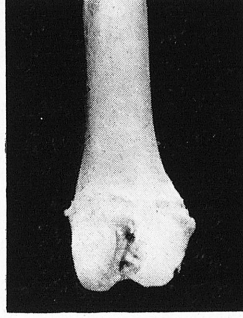
3c



4a



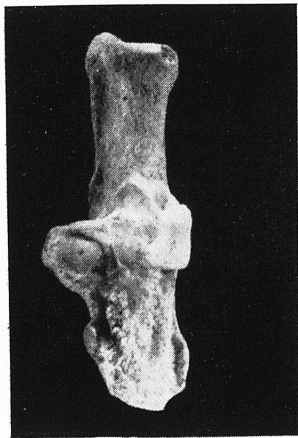
4b



4c

Plate VII

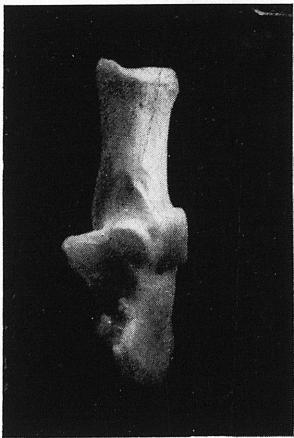
1. Calcaneus of *Hypolagus brachygnathus* (a), *Lepus europaeus* (b) and *Oryctolagus cuniculus* (c).
2. Holotype of *Pliolagus beremendensis*. Wear surface of the mandibular tooth row (a); mandible, inner surface.
3. Radiogram of a specimen of "*Pliolagus tothi*", from Betfia showing the obliquity of the walls of lower teeth.



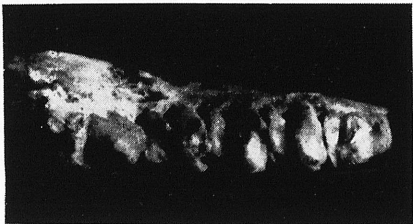
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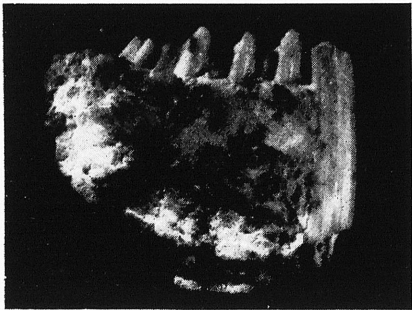
1b



1c



2a



2b



3

Redaktor zeszytu: prof. dr K. Kowalski

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