The hind limb skeleton and cursorial adaptations of the Plio-Pleistocene rabbit *Hypolagus beremendensis*

ŁUCJA FOSTOWICZ-FRELIK

Fostowicz-Frelik, Ł. 2007. The hind limb skeleton and cursorial adaptations of the Plio-Pleistocene rabbit *Hypolagus beremendensis*. *Acta Palaeontologica Polonica* 52 (3): 447–476.

Hypolagus beremendensis, a representative of the Archaeolaginae, was one of the most abundant and widespread leporids in the Plio-Pleistocene of Europe. The vast accumulations of skeletal remains from the Polish Pliocene sites (Węże 1, Rębielice Królewskie 1 and 2, and Kadzielnia 1) yielded thousands of bones representing almost all skeletal regions. The detailed hind limb morphology of *Hypolagus beremendensis* is presented in comparison with five extant leporids (*Lepus europaeus*, *Oryctolagus cuniculus*, *Pentalagus furnessi*, *Sylvilagus floridanus*, and *S. brasiliensis*), which represent a wide range of locomotor adaptations. The UPGMA analysis of 98 metric characters places *Hypolagus beremendensis* next to the leporine rabbits. *Hypolagus beremendensis* has the os coxae, femur, and talus most similar to *P. furnessi*, tibia and calcaneus to the leporine rabbits, and the structure of foot to *Lepus*. The elongation of the foot and tibiofibular segment in relation to the femur indicates an advanced cursorial adaptation and a relatively steep jump. The similarities in the proximal segments (os coxae and femur) between *Hypolagus* and *Pentalagus* highlight the conservative morphology of this region in the Leporidae.

Key words: Lagomorpha, Leporidae, *Hypolagus beremendensis*, hind limb, functional morphology, cursorial adaptations, Neogene.

Łucja Fostowicz-Frelik [lfost@twarda.pan.pl], Institute of Paleobiology Polish Academy of Sciences, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Hypolagus Dice, 1917, one of the most speciose genera within Archaeolaginae, currently includes 24 species of rabbits and is known from the early Miocene to early Pleistocene in North America and from the latest Miocene (Turolian) to middle Pleistocene in Eurasia. The majority of species, however, are known from dental and cranial remains (Dawson 1958; White 1984; Voorhies and Timperley 1997; Fostowicz-Frelik 2003). The European record includes at present four species, with *Hypolagus beremendensis* (Kormos, 1930) being the most abundant and widespread. The species is known from the early Pliocene (MN 15) to early Pleistocene (earliest Biharian) period in Central Europe (Kormos 1934; Sych 1965; Fladerer and Reiner 1996; Fostowicz-Frelik 2003, 2007). The richest findings of this species come from Poland in the form of the vast accumulations of calcified bone breccia in Węże 1 site, clay-bone deposits in Rębielice Królewskie 1 and 2 (all three sites located in the Cracow-Wieluń Upland), and Kadzielnia 1 in the Holy Cross Mountains (Sulimski 1964; Sych 1965; Nadachowski 1990).

The extremely abundant collections that include well-preserved fragments of virtually all bones enable detailed study of the skeleton. The subject is relatively poorly researched and the European *Hypolagus* has not been examined in terms of functional morphology (apart from the forelimb, covered in some aspects by Fladerer 1984). Cursorial adptations of the appendicular skeleton of some North American extinct leporids (*Hypolagus* aff. *vetus* (Kellogg, 1910) and *Pratilepus* Hibbard, 1939) were analysed by Campbell (1969). The initial work of Sych (1965) based on the Polish material included only general description of the bone morphology. Sych (1965) and other authors (Fladerer 1984, Fladerer and Fiore 2003) suggested that *Hypolagus beremendensis* was intermediate in morphology between fossorial *Oryctolagus cuniculus* and highly cursorial *Lepus*. Fostowicz-Frelik (2001) noticed that it rather resembled some species of *Sylvilagus*, like the North American representatives of *Hypolagus* mentioned by White (1984).

In this paper the comprehensive morphology of the hind limb skeleton of *Hypolagus beremendensis* is provided, along with quantitative and qualitative comparisons (including phenetic analysis) with four species of rabbits: *Oryctolagus cuniculus* (Linnaeus, 1758), *Pentalagus furnessi* (Stone, 1900), *Sylvilagus brasiliensis* (Linnaeus, 1758), and *S. floridanus* (Allen, 1890), and the European hare, *Lepus europaeus* Pallas, 1778.

The general leporid morphotype (distinguished from the ochotonid type by the significant elongation of hind legs, particularly shank and foot) is very uniform, conservative, and recognisable already in the Oligocene *Palaeolagus haydeni* Leidy, 1856 (Wood 1940). As a result of this shared skeletal morphology the motion and biomechanics is generally similar in all representatives of the group (López-Martinez 1985). All leporids display cursorial adaptation but there is some variation in running ability within the group. The type of locomotion observed in leporids is referred to as a "leaping gallop" because of the extended phase when the whole body is in the air and no limb touches the ground (Maynard Smith and Savage 1956). In contrast to a so-called "horse gallop", the leaping gallop (observed in some other mammals such as cheetahs and small antelopes) involves flexion and extension of the backbone. In leporids the main bending point is at the eleventh (known as anticlinal) thoracic vertebra (Craigie 1948).

The basic morphological hallmarks of fast runners are the elongation of the distal segments of limbs (forearm and shank) as well as the proximal and medial phalanges, and simultaneously shortening of the proximal segments (humerus and femur; Gambaryan 1974; Hildebrand 1974). The bones are slim with delicate and elongated shafts. The main mass of musculature concentrates around the proximal part of the limb, with elongated ligaments animating distal parts of the limb (Hildebrand 1974).

The whole locomotor apparatus in mammals performing a leaping gallop is specialised to fast limb movements but with relatively small forces (Maynard Smith and Savage 1956). However, running endurance varies in different taxa and is correlated with their top speed. According to Camp and Borel (1937), in hares the muscles are adapted to endurance and their muscle attachments are positioned to produce maximal speed. In rabbits and pikas the muscles support quicker movements, but their endurance is much lower and the muscle attachments are not especially adjusted to maximize top speed.

In the study of cursorial adaptations, the hind limb bone morphology, proportions, and muscle attachments are the most important features, because in the type of locomotion employed by leporids they provide most of the propulsive force (Camp and Borel 1937; Gambaryan 1974). The forelegs play a supportive role on landing, while the momentum translates the body forward. They also absorb the shock of hitting the ground (Gambaryan 1974). Thus, the flexors and extensors of the hind limb, especially of the hip and femur are the primary generators of horizontal movement (Alexander 2002).

Closer consideration of this "leaping gallop" type of locomotion reveals that it is possible to split it into two sub-types. The first of them is less cursorial, sometimes associated with some degree of fossorial adaptation. It is found in the majority of fossil and modern genera, described under common name of rabbits and cottontails and in this contribution it is referred to as the "rabbit type". The second type is highly cursorial, adapted to fast running and long leaps. It seems to be restricted to the members of the genus *Lepus*, which includes hares and jackrabbits, so it will be named the "hare type". However, there is at least one species in this genus, *Lepus americanus*, which employs the rabbit type of locomotion (Averianov 1995).

In this study, the structure of hind limb in *Hypolagus beremendensis* was compared with extant leporids, exhibiting the entire range of rabbit and hare locomotor adaptations. On the one hand, the European hare (*Lepus europaeus*) exhibits typical hare type locomotion, on the other, cottontails (*Sylvilagus floridanus* and *S. brasiliensis*) and the wild rabbit (*Oryctolagus cuniculus*) are typical rabbits of the New and Old Worlds, respectively. Moreover, *Oryctolagus* is the most fossorially adapted of all leporids. The Amami or Ryukyu rabbit (*Pentalagus furnessi*) is a stocky species with rather low cursorial ability, inhabiting dense subtropical forests. This rabbit is occasionally a digger. Its phylogenetic position within Leporidae is close to *Caprolagus* and *Bunolagus* (Robinson and Mathee 2005). The Amami rabbit, although more specialised than *Nesolagus* (Alexander O. Averianov, personal communication 2007; Robinson and Mathee 2005), has a relatively long evolutionary history after the middle Miocene leporid radiation (Yamada et al. 2002) and is one of the least cursorial species within Leporidae (Gureev 1964).

Institutional abbreviations.—BMNH, Natural History Museum, London, United Kingdom; FM, Finnish Museum of Natural History, Helsinki, Finland; HNHM, Hungarian Natural History Museum, Department of Zoology, Budapest, Hungary; ISEZ, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland; NSM, National Science Museum, Tokyo, Japan; SGGW, Warsaw Agricultural University, Warsaw, Poland; SM, Senckenberg Museum, Frankfurt am Main, Germany; ZBS, Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland; ZMB, Natural History Museum of Humboldt University, Berlin, Germany.

Material and methods

Specimens examined.—The fossil material of *Hypolagus beremendensis* studied here is housed at ISEZ. The specimens of extant leporids used for comparison: *Lepus europaeus* (HNHM 3258/a, 4432, 58.15.13, 83.90.1, 83.91.1, 83.92.1, 83.93.1, 83.94.1, 83.95.1, 83.96.1; ZBS 1102 sad.), *Oryctolagus cuniculus* (SGGW 2090, 2103; ZBS 88480/27184; ZMB 3241, 82102; SM 44042, 55787, 42234, 1420, 1421, 1422), *Pentalagus furnessi* (NSM 31591, NSM-PO133, BMNH 76.1366, 76.1367), *Sylvilagus brasiliensis* (SM 41104), and *Sylvilagus floridanus* (SM 13381, 13448, 15091; FM 1499, 1501). Additionally, for purposes of this study the hind limbs of *Lepus europaeus* and *Oryctolagus cuniculus* were dissected to examine the morphology and topography of soft tissues.

Measurements.—The measurements were taken with a Sylvac electronic caliper with an accuracy of 0.1 mm. The 111 measurements (Fig. 1, Table 1) and 49 indices (Table 2) are either standard ones, based on maximal dimensions of bones and particular structures or believed to be of functional relevance to the study. The detailed measurements of the bones for *Hypolagus beremendensis* and comparative taxa are placed in Table 3 (Appendix 1). All quantitative data were subjected to

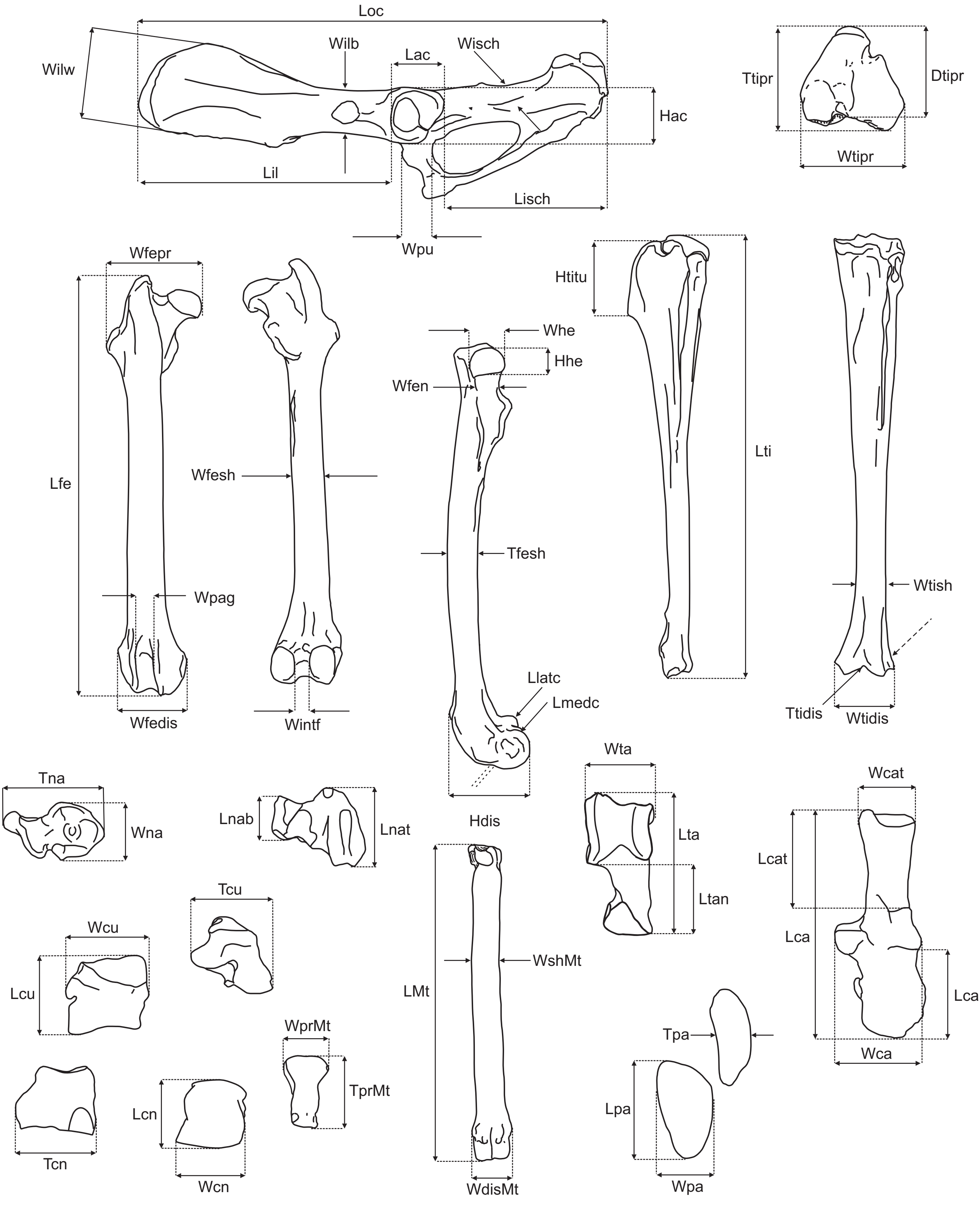

Fig. 1. Scheme of hind limb measurements (see Table 1 for descriptions and abbreviations). Measurements for phalanges (not figured) are the same as for metatarsals.

Table 1. Meaurements of hind limb (see Fig. 1 for illustration).

	Measurement	Description
Os coxae	Length (Loc)	maximal cranio-caudal length of os coxae
	Length of ilium (Lil)	from most cranial part of wing of ilium to most cranial point of acetabulum
	Length of ischium (Lisch)	from most caudal point of ischial tuberosity to most caudal point of acetabulum
	Width of wing of ilium (Wilw)	dorsal-most point of tuber sacrale to ventral-most point of tuber coxae
	Width of body of ilium (Wilb)	dorso-ventral dimension at attachment of rectus femoris muscle
	Length of acetabulum (Lac)	cranio-caudal dimension of acetabulum
	Height of acetabulum (Hac)	dorso-ventral dimension of acetabulum
	Width of ischium (Wisch)	medio-lateral dimension of body of ischium
	Width of pubis (Wpu)	width of body of pubis near acetabulum
Femur	Length (Lfe)	maximal length of femur
	Proximal width (Wfepr)	distance from medial-most point of head to lateral-most point of third trochanter
	Distal width (Wfedis)	maximal width of distal end of femur
	Width of intercond fossa (Wintf)	medio-lateral dimension of intercondyloid fossa at its widest part
	Width of patellar groove (Wpag)	medio-lateral dimension of patellar groove
	Diameter of distal extremity (Hdis)	from cranial point of medial ridge of trochlea to caudal point of medial condyle
	Width of the neck of femur (Wfen)	cranial-caudal width of femoral neck
	Width of the head (Whe)	cranial-caudal width of femoral head
	Height of the head of femur (Hhe)	proximal-distal dimension of femoral head
	Width of the shaft (Wfesh)	medio-lateral dimension at distal point of trochanter minor
	Thickness of the shaft (Tfesh)	cranial-caudal thickness of shaft
	Length of the med. cond. (Lmedc)	cranial-caudal dimension of medial condyle
	Length of the lat. cond. (Llatc)	cranial-caudal dimension of lateral condyle
Patella	Length (Lpa)	maximal length of patella
	Width (Wpa)	maximal medio-lateral dimension of patella
	Thickness (Tpa)	distance from facies articularis to facies cranialis, in mid-shaft of femur
Tibia	Length (Lti)	maximal length of tibia
	Proximal width (Wtipr)	maximal medio-lateral dimension of proximal end
	Proximal thickness (Dtipr)	distance from cranial point of tibial tuberosity to caudal point of popliteal notch
	Proximal diameter(Ttipr)	maximal cranio-caudal dimension of proximal end
	Distal width (Wtidis)	maximal medio-lateral dimension of distal end
	Distal thickness (Ttidis)	cranio-caudal dimension measured along lateral groove of cochlea tibiae
	Height of tibial tuberosity (Htitu)	proximal-distal dimension of tibial tuberosity
	Width of shaft (Wtish)	medio-lateral dimension at the thinnest point near distal end
Talus	Length (Lta)	maximal length of talus
	Width of trochlea tali (Wta)	medio-lateral dimension of trochlea
	Length of neck (Ltan)	distance from the distal-most point of neck to its contact with trochlea tali
Calcaneus	Length (Lca)	maximal length of calcaneus
	Width (Wca)	distance from medial point of sustentaculum tali to lateral point of body of calcaneus
	Length of calcaneal tuber (Lcat)	distance from proximal point of trochlea peronealis to proximal tip of calcaneal tuber
	Length of calcaneal body (Lcab)	distance from distal point of trochlea peronealis to distal-most point of body
	Width of calcaneal tuber (Wcat)	medio-lateral dimension of proximal end of calcaneal tuber
Naviculare	Length of navicular body (Lnab)	length along dorsal wall of navicular body
	Width of navicular body (Wna)	maximal medio-lateral dimension
	Thickness of naviculare (Tna)	from dorsal-most point of navicular body to plantar-most point of the tuberosity
	Length of the tuberosity (Lnat)	distance from the posterior-most point of the tuberosity to most distal point
Cuboid	Length (Lcu)	maximal length of bone
	Width (Wcu)	maximal medio-lateral dimension of cuboid
	Thickness (Tcu)	maximal dimension from dorsal wall to plantar-most point of tuberosity
Cuneiforme laterale	Length (Lcn)	maximal length along dorsal margin
	Width (Wcn)	medio-lateral dimension at widest point
	Thickness (Tcn)	maximal dorso-plantar dimension
Metatarsals (MtII–V), phalanges proximal (PhpII–V), medial (PhmII–V)	Length (L)	maximal length of bone
	Proximal width (Wpr)	maximal medio-lateral dimension
	Proximal thickness (Tpr)	maximal dorso-plantar dimension
	Width of shaft (Wsh)	medio-lateral dimension of shaft in its mid-width
	Distal width (Wdis)	maximal medio-lateral dimension of the distal extremity

Table 2. Indices.

Index	Description
General	Ico-fe (coxo-femoral) – Loc/Lfe Icru (crural) – Lfe/Lti Ifoot1 (foot index 1) – Lfoot /Lti, where: Lfoot = Lca+LMtIII+LPhpIII+LPhmIII Ifoot2 (foot index 2) – Lca/Lti
Coxal	Ico1 – Lil/Loc Ico2 – Lil/Wilw Ico3 – Lac/Hac Ico4 – Lisch/Loc Ico5 – Lac/Wilb Ico6 – Wpu/Wilb
Femoral	Ife1 – Wfepr/Lfe Ife2 – Wfedis/Lfe Ife3 – Wintf/Wfedis Ife4 – Wpag/Wfedis Ife5 – Wfedis/Hdis Ife6 – Wfen/Whe
Tibial	Iti1 – Ttipr/Wtipr Iti2 – Wtipr/Lti Iti3 – Htitu/Lti Iti4 – Ttidis/Wtidis Iti5 – Wtidis/Lti Iti6 – Wtish/Lti
Tarsal	*Calcaneal indices* Ica1 – Wca/Lca Ica2 – Lcat/Lca Ica3 – Lcab/Lca Ica4 – Wcat/Lcat
	Talar indices Ita1 – Wta/Lta Ita2 – Ltan/Lta
	Navicular indices Ina1 – Lnab/Lnat Ina2 – Wna/Tna Ina3 – Lnab/Wna
	Cuboid indices Icu1 – Lcu/Wcu Icu2 – Wcu/Tcu
Metatarsal and phalangeal	*MtII–MtV* Iprox (index for proximal articular surface) – Wpr/Tpr
	MtII–PhmV Is (index of slenderness) – Wprox + Wdis/L

statistical analyses using StatView 5.0.1. The homogeneity (monospecificity) of material of *Hypolagus beremendensis* from the Polish localities was confirmed by ANOVA and PLSD Fisher's tests, which have shown no statistically significant differences between the samples (Fostowicz-Frelik 2006). In this study, some of the statistical tests (parametric tests) could not be used because of the disparities between the sample size of *Hypolagus* and the other species. To estimate the interspecific differences, box plots were used instead. Each box plot displays the 10th, 25th, 50th (the median), 75th and 90th percentiles of variable. The shaded box covers the central 50% of the data (the interquartile range). The box plots are especially useful for displaying outliers, as all values above the 90th and below the 10th percentile are plotted separately. In the presence of outliers, the median and interquartile range are appropriate measures of central tendency and variability, respectively.

Cluster analyses (UPGMA) based on measured variables of all skeletal elements except the patella, naviculare, cuboid and cuneiforme laterale (because of scarcity of comparative material) were performed using the PHYLIP package version 3.65 (Felsenstein 1989). The results are presented as trees with Euclidean distances. The anatomical nomenclature follows Nomina Anatomica Veterinaria (I.C.V.G.A.N. 2005).

Osteological description

Os coxae.—The complete os coxae of *Hypolagus beremendensis* was not found. Thus, the reconstruction was performed on the basis of the ischial and ilial parts preserving at least part of the acetabulum. The total length of os coxae was estimated at ca. 78 mm, with possible range of 73–86 mm. This value places *H. beremendensis* between the ranges of size typical for representatives of *Oryctolagus cuniculus* and *Pentalagus furnessi* (Table 3 in Appendix 1).

The relative length of the ilium does not differ significantly among leporids. The coxal index 1 (Ico1) is lowest for *Hypolagus* (reconstructed value 45.5%) and *Lepus* (46%) which possess the shortest ilium in proportion to the length of pelvis. In other rabbits, it varies ca. 50%.

The relative length of ischium (Ico4) in *Hypolagus* (42%) does not differ from that in other leporines (*Oryctolagus* 41%, *Sylvilagus* 41%, and *Lepus* 43%), except from *Pentalagus* which displays a slightly shorter ischium (38.5%).

The exact shape of the wing of the ilium in *H. beremendensis* is not known; however, a few fragments may indicate that the cranial part of the wing had a more extended flare than *Oryctolagus*. It is also more robust than in *Sylvilagus* and *Oryctolagus*, with a significant caudo-dorsal portion of the iliac spine, forming a strong iliac tuberosity on the medial side. The auricular surface on the medial side in *H. beremendensis* is distinct and wide, forming an irregular semi-lunar shape of relatively high thickness resembling that in *Lepus*. In *Oryctolagus* and *Sylvilagus*, the auricular surface is shaped like a thin, strongly curved semicircle.

The os coxae of *H. beremendensis* is relatively more robustly built in comparison with those of *Sylvilagus* and *Oryctolagus*. The width of the body of the ilium in comparison with the length of the acetabulum (Ico5) is relatively high (Fig. 3B), exceeding the average value for a wild rabbit and approaching the values observed in *Pentalagus furnessi*.

The shape of the acetabulum in leporids is generally uniform and the length to height ratio (Ico3) is very similar in all studied genera (Fig. 3A). In rabbits it is slightly more round than in *Lepus* and the acetabular notch (*incisura acetabuli*) is

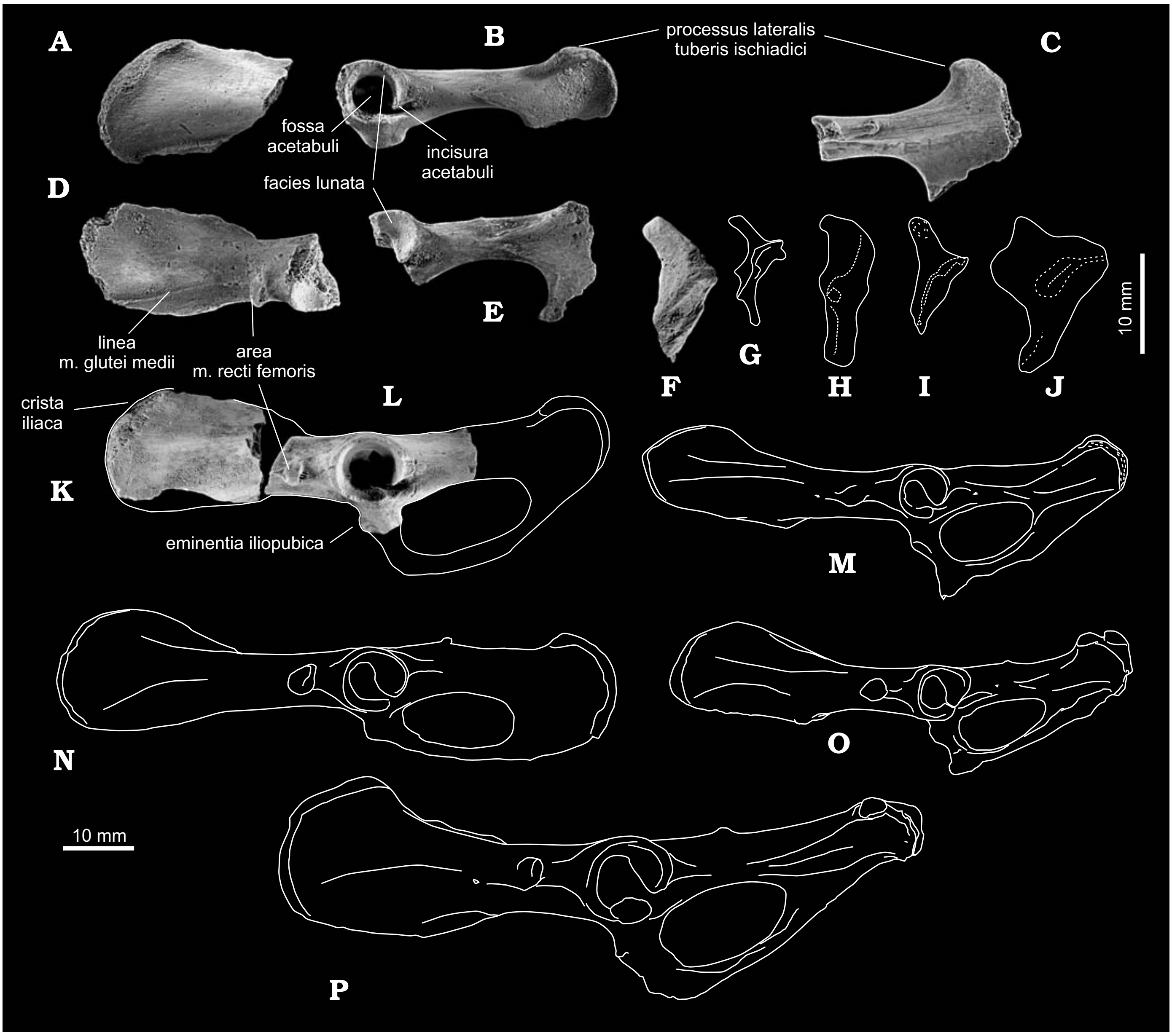

Fig. 2. Morphology of os coxae of *Hypolagus beremendensis* (Kormos, 1930) (**A**–**F**, **K**, **L**) from the Pliocene of Poland and extant Leporidae (**G**–**J**, **M**–**P**). **A**. Anterior part of left ilium, ISEZ MF/2220/oc/147, Węże 1, in lateral view. **B**. Right ischium with acetabulum, ISEZ MF/2224/oc/9, Rębielice Królewskie 1, in lateral view (mirror image). **C**. Lateral process of right ischial tuberosity, ISEZ MF/2220/oc/74, Węże 1, in ventro-lateral view. **D**. Left ilium with part of acetabulum, ISEZ MF/2220/oc/61, Węże 1, in lateral view. **E**. Left ischium with fragment of acetabulum, ISEZ MF/2220/oc/131, Węże 1, in lateral view. **F**. Ischial tuberosity, ISEZ MF/2225/oc/28, Rębielice Królewskie 2, in caudal view. **G**–**J**. Outlines of ischial tuberosity in caudal views: *Oryctolagus cuniculus* (Linnaeus, 1758) (**G**), *Pentalagus furnessi* (Stone, 1900) (**H**), *Sylvilagus floridanus* (Allen, 1890) (**I**), and *Lepus europaeus* Pallas, 1778 (**J**). **K**. Cranial part of left ilium, ISEZ MF/2220/oc/158, Węże 1, in lateral view. **L**. Acetabulum with fragments of bodies of ilium, ischium and pubis, ISEZ MF/2220/oc/20, Węże 1, in lateral view. **M**–**P**. Outlines of os coxae: *Sylvilagus floridanus* (**M**), *Pentalagus furnessi* (**N**), *Oryctolagus cuniculus* (**O**), and *Lepus europaeus* (**P**).

very narrow or almost fused. As a result, the *facies lunata* seems to be almost continuous (especially in *Oryctolagus* and *Sylvilagus brasiliensis*). In *Lepus* the cranial and caudal parts of *facies lunata* are more extended than in rabbits, and the acetabular notch in *Lepus* is always well-developed and wide. In *Hypolagus beremendensis* the acetabulum is more round than in *Lepus* but less than in *Oryctolagus* (Fig. 3A) and the acetabular notch is always present and wide (Fig. 2B, L).

The ischial tuberosity (*tuber ischiadicum*), one of the most characteristic structures of the leporid coxal bone, expresses significant intergeneric differences. In *Hypolagus beremendensis* its caudal surface is notably wider than in *Oryctolagus* and *Sylvilagus* and narrower than in *Lepus*, with a less marked crest and a generally more oblong outline and smooth surface, more closely resembling the condition found in *Pentalagus* (Fig. 2F–J). The lateral process of the ischial

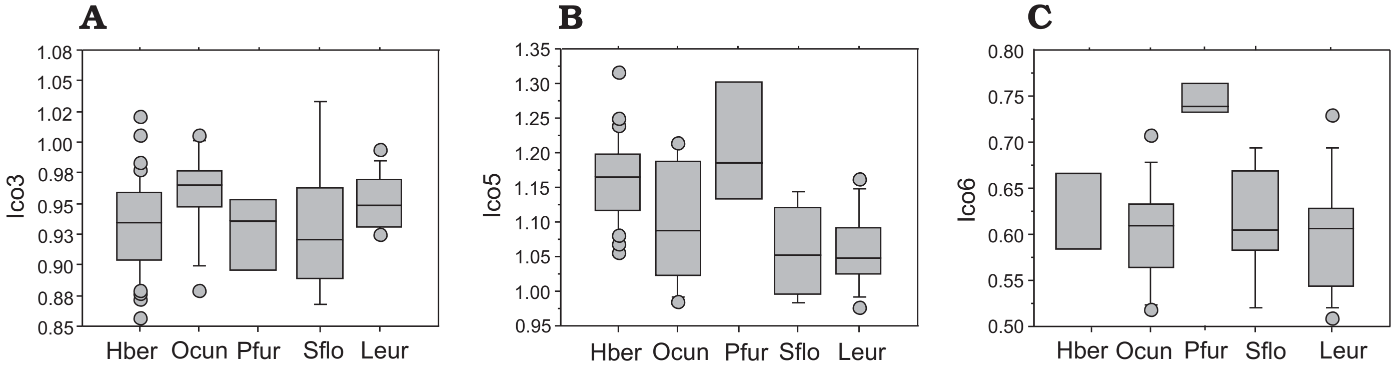

Fig. 3. Box plots of selected coxal indices. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

tuberosity (*processus lateralis tuberis ischiadici*) in *Hypolagus beremendensis* is blunter and more massive than in *Oryctolagus*. It is hooked cranially more strongly than in *Sylvilagus floridanus*, *S. brasiliensis*, and *Pentalagus furnessi* and sharper than in *Lepus*.

The os pubis of *H. beremendensis* is not preserved in the material except for its most dorsal part, the body of pubis. It is relatively wide and strong (Figs. 2, 3C) with a significant iliopubic eminence (*eminentia iliopubica*, see Fig. 2L) resembling in this respect the bones of *P. furnessi* and *L. europaeus*.

Femur.—The shape and proportions of *H. beremendensis* femur show an overall rabbit-like type of morphology; however it is slenderer than the femora of both *Oryctolagus cuniculus* and *S. floridanus*, with a shaft that is more round in cross-section. The approximate length for the femur of *H. beremendensis* was estimated at ca. 94 mm, on the basis of preserved complete proximal and distal extremities with large fragments of the shaft. The dimensions of the femur in *H. beremendensis* are generally larger than in *Oryctolagus* and *Sylvilagus*, but smaller than in *Lepus*. They partially overlap with values for *P. furnessi*, but the femur in that species is much more robust and has higher values for the width of the proximal and distal extremities, and the shaft (Table 3 in Appendix 1).

The proximal extremity of the femur in *H. beremendensis* is relatively less medio-laterally expanded than in *Lepus europaeus*. The trochanters (minor and third) are grouped closer to the proximal end of the bone than in *O. cuniculus*, *S. brasiliensis*, and *P. furnessi*, resembling in that respect the bones of *L. europaeus* and *S. floridanus* (Fig. 4G, H). The most cranial part of the greater trochanter (*trochanter major*) is not as strongly medially bent as in *Lepus*. Its condition closely resembles that found in *S. floridanus* (Fig. 4G). The surface of the first trochanter for the attachment of the gluteal muscles is inclined more medially in *L. europaeus* and *S. floridanus*. The third trochanter (*trochanter tertius*) is not significantly extended and shaped like an isosceles triangle with its upper tip pointing laterally as in *L. europaeus*, *P. furnessi*, and *S. floridanus*, but not caudo-laterally as in *Oryctolagus* and *S. brasiliensis*. The second trochanter (*trochanter minor*) in *H. beremendensis* is strongly marked and forms an eminent tubercle, placed closer to the femoral head than in *Oryctolagus* and *S. brasiliensis*.

The neck of the femur in *H. beremendensis* is a little shorter and wider than in *S. brasiliensis* and *P. furnessi*, similar to the condition found in *L. europaeus*, *O. cuniculus*, and *S. floridanus*. The incision between the first trochanter and the neck is not as deep as in *Oryctolagus* and *S. brasiliensis*. Thus, the neck of the femur in *H. beremendensis* is more robust and less distinct, similar to the condition observed in *L. europaeus* and *S. floridanus* (Fig. 4G, H).

On the caudal side distally, from the trochanteric fossa and the lesser trochanter, the oval surface surrounded on the medio-caudal side with a roughened margin creates the attachment for the quadratus femoris muscle (Fig. 4C). This surface in *H. beremendesis* is round and prominent, resembling the condition found in *Lepus*. The deep imprints of the vastus medialis and pectineus muscles are located distally to this structure, at the medial side of the shaft.

The distal extremity of the femur in *H. beremendensis* resembles in proportions that of *Oryctolagus* and *Sylvilagus* but is slightly more extended medio-laterally in relation to the width of the shaft and the total bone length than in these two rabbit genera (Fig. 5B, Table 3 in Appendix 1). Also, *H. beremendensis* has a significantly wider intercondylar fossa (*fossa intercondylaris*), resembling that found in *L. europaeus* (Fig. 5C). On the other hand, the patellar groove (*facies patellaris*) is relatively narrower in *H. beremendensis*, in comparison to the width of distal extremity, expressing the lowest values for all compared taxa (Fig. 5D). The diameter of the distal epiphysis of the femur (Hdis) is distinctly high, exceeding the width of the distal extremity (Wfedis) in *H. beremendensis*. This feature distinguishes the species from all other studied taxa. The femoral index Ife5 is the lowest for *H. beremendensis*, whereas for other leporids it is uniform and close to 100% (Fig. 5E).

The structure of the condyles in *Hypolagus* does not differ significantly from that in other leporids. The lateral condyle at the anterior side has deep *fossa extensoria* for the extensor digitorum longus muscle and significant *fossa musculi poplitei*, strongly marked in *Hypolagus beremendensis* (Fig. 4B).

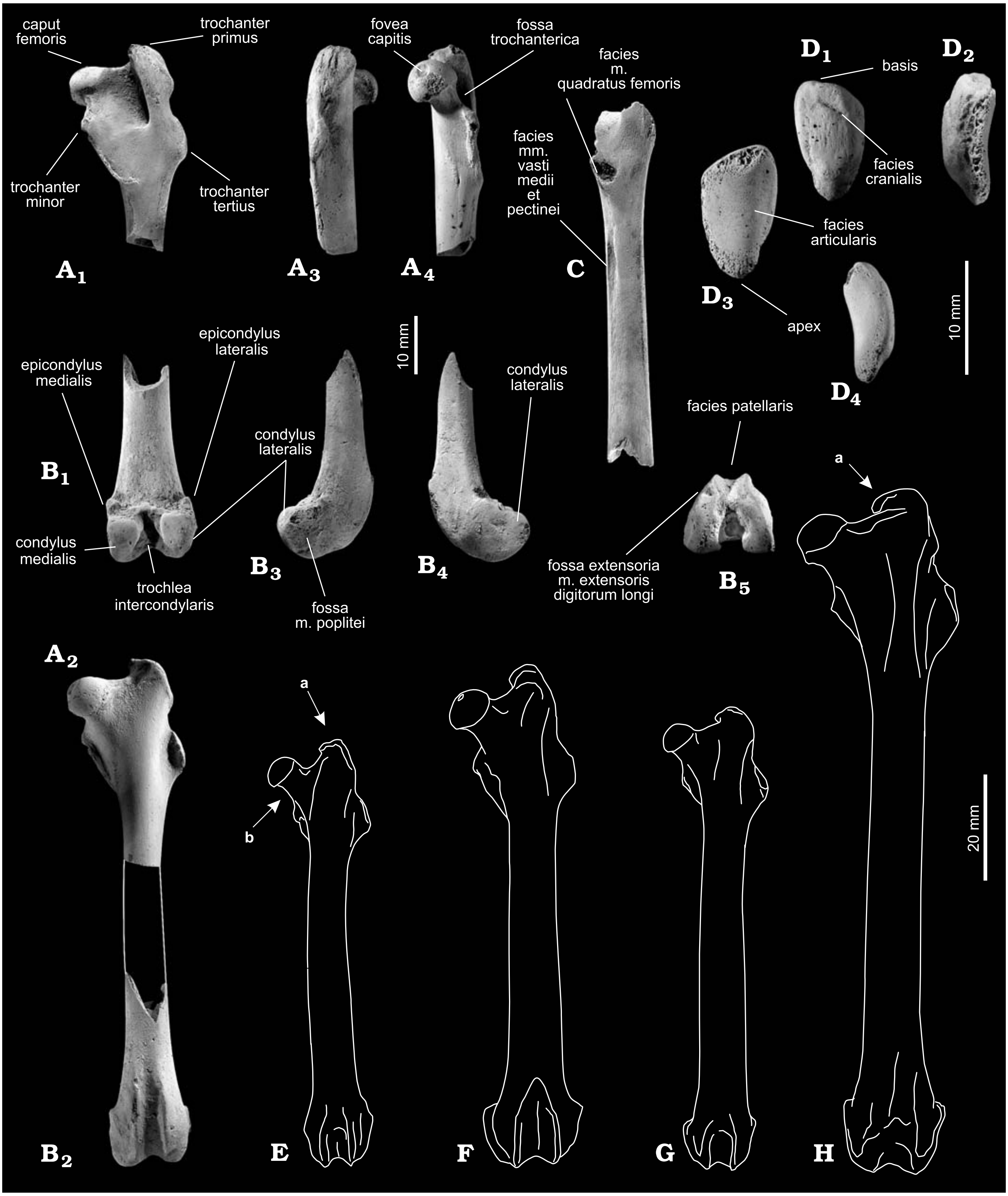

Fig. 4. Morphology of femur and patella of *Hypolagus beremendensis* (Kormos, 1930) from the Pliocene of Poland (**A**–**D**) and femur of extant Leporidae (**E**–**H**). **A**. Proximal extremity of left femur, ISEZ MF/2220/fe/69, Węże 1, in caudal (A_1) cranial (A_2), lateral (A_3), medial (A_4) views. **B**. Distal extremity of right femur, ISEZ MF/2220/fe/15, Węże 1, in caudal (B_1), cranial (B_2), lateral (B_3), medial (B_4), distal (B_5) views. **C**. Shaft of right femur, ISEZ MF/2224/fe/9, Rębielice Królewskie 1, in caudal view. **D**. Left patella, ISEZ MF/2220/pa/1, Węże 1, in cranial (D_1), lateral (D_2), caudal (D_3), and medial (D_4) views. Outline of left femur for *Oryctolagus cuniculus* (**E**), *Pentalagus furnessi* (**F**), *Sylvilagus floridanus* (**G**), and *Lepus europaeus* (**H**). Note morphology of the first trochanter (arrow a) and femoral neck (arrow b).

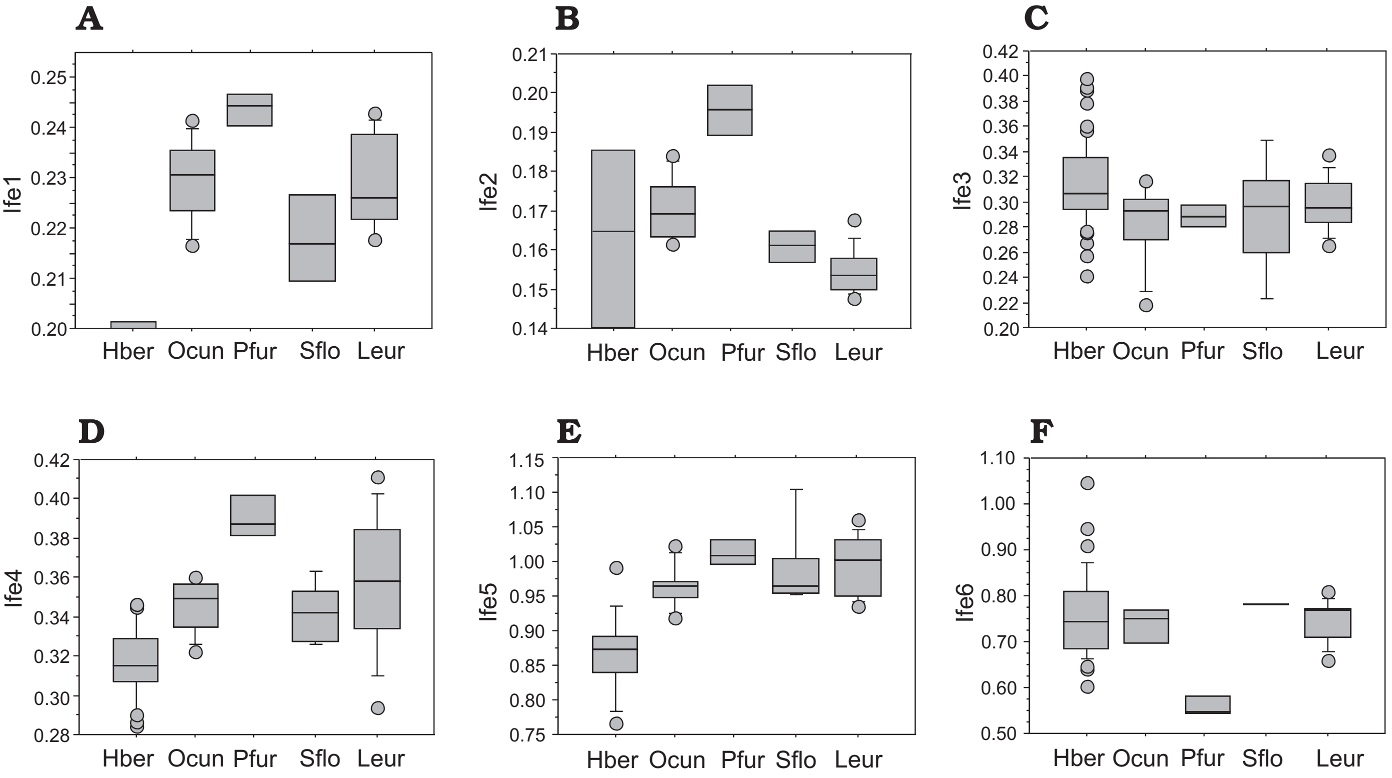

Fig. 5. Box plots of femoral indices. Note the low value of Ife2 (**A**), Ife5 (**E**), and Ife6 (**F**) for *Hypolagus beremendensis*. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

Patella.—The patella in leporids is tear-shaped with the cranial external surface (*facies libera*) rough and convex and the caudal surface (*facies articularis*) forming a smooth plane for the femoral articulation at the patellar groove. The patella in *Hypolagus beremendensis* is more slender and elongated than that of *Lepus europaeus* (Table 3 in Appendix 1).

The base of the patella (*basis patellae*), the point of attachment for the tendon of the quadriceps femoris muscle, is gently flattened and its proximal edge is inclined laterally (Fig. 4D). The tendon of the quadriceps femoris continues on the distal side of the patella (*apex*) as a patellar ligament connecting to the tuberosity of the tibia.

The pointy, elongated apex is directed distally, creating the place of attachment for the middle and lateral patellar ligaments.

Tibiofibula.—The zeugopodial part of the lagomorph hind limb consists of two distally fused bones, the tibia and the fibula, forming one bony element. The two bones are joined for roughly half of their length, forming a common distal articular surface for the tarsal elements. The extent of this fusion varies among leporid genera. The highest degree of fusion occurs in *L. europaeus* with 62% of the length of tibia being fused. The lowest proportion of fusion can be found in *Pentalagus furnessi*, with 48% of the tibial length fused to the fibula. In *H. beremendensis* this ratio is 59%, higher than in all other included rabbit species (*Sylvilagus brasiliensis* 52%, *S. floridanus* 55%, and *Oryctolagus cuniculus* 57%).

The tibia of *H. beremendensis* is slender and delicate with a relatively slender shaft. Its total length, assessed from the well-preserved proximal and distal extremities with large portions of the shaft (Fig. 6), is 111.4 mm. The slenderness of the bone is expressed by the relatively low width of the proximal and distal extremities and the shaft in relation to the total bone length (Figs. 6, 7B, E, F). The ends of the tibiofibula are significantly narrower than in *O. cuniculus* and *P. furnessi*, resembling in the proportions the tibiae of *S. floridanus* and *L. europaeus* (Fig. 7D). The tuberosity of the tibia in *H. beremendensis* is significantly shorter in relation to total tibia length (Iti3) than in *O. cuniculus*, both species of *Sylvilagus*, and *P. furnessi*. Iti3 in *H. beremendensis* most closely resembles the proportions observed in *L. europaeus* (Fig. 7C). The tuberosity of the tibia has a well-developed crest, which extends parallel to the shaft and terminates in a prominent tubercle, the attachment for the semitendinous muscle. This tubercle is slightly smaller in *H. beremendensis* than in *O. cuniculus* and *S. brasiliensis*, but more distinct than in *S. floridanus*. The ratio of the length-to-width of the tibial head (Iti1) is closest to that of *S. floridanus* and *O. cuniculus*, being slightly smaller than in *Lepus europaeus* (Fig. 7). At the plantar side of the shaft, just below the proximal extremity, an s-shaped linear muscle attachment (*linea musculi poplitei*) for the popliteus muscle is marked (Fig. 6A). This line is well pronounced, significantly longer and more distinct in *H. beremendensis* than in *Oryctolagus* and *Sylvilagus*. Its most

Fig. 6. Morphology of tibia of *Hypolagus beremendensis* (Kormos, 1930) from Kadzielnia 1, late Pliocene of Poland. **A**. Proximal extremity with shaft of right tibia, ISEZ MF/2226/ti/1, in medial (A_1), lateral (A_2), cranial (A_3), and caudal (A_4) views. **B**. Distal extremity with shaft of right tibia, ISEZ MF/2226/ti/5, in medial (B_1), lateral (B_2), and caudal (B_3) views. Note point of fusion with fibula (arrow a).

noticeable part is placed more distally in contrast with the condition found in *Lepus*, where the proximal part of the *linea m. poplitei* is more twisted.

The distal extremity of the tibiofibula in *Hypolagus beremendensis* is relatively thicker than in *Oryctolagus* and *Pentalagus*, and resembles the shape of the distal end of the tibiofibula in *Lepus* and *Sylvilagus* (Fig. 7D). The lateral malleolus (*malleolus lateralis*) that forms the fibular part of the articular surface for the calcaneus is significantly more prominent distally in *H. beremendensis* than in any of the four studied rabbit species. It resembles the condition found in *Lepus*. The *sulcus malleolaris lateralis* for the tendon of the peroneus longus muscle, is significantly deeper and directed more laterally than in the studied rabbits, similar to that of *Lepus*.

The medial malleolus (*malleolus medialis*) shows a large, deep *sulcus malleolaris medialis* for the tibialis posterior muscle and a shallower, more medially placed sulcus for the extensor hallucis longus muscle. The depth of *sulcus malleolaris medialis* is comparable with that found in *Lepus*, deeper than in all rabbit species.

The relative thickness of the articular surface of the tibiofibula (Iti4) is relatively high in *H. beremendensis*, exceeding that in *Oryctolagus* and *Pentalagus* and lower than in *Lepus* (Fig. 7D).

On the cranial side of the tibiofibula, near the distal extremity, two small ridges are marked, being the points of attachment of the proximal extensor retinaculum, the suspensory ligament framing the ligaments of the tibialis cranialis muscle and of the extensor digitorum longus muscle. The first of these ridges is placed close to the distal end of the tibiofibula on the lateral side, just above lateral malleolus. The second ridge is positioned higher on the shaft on the medial side. Both are strongly developed in *Hypolagus beremendensis*.

The shaft of the tibiofibula of *H. beremendensis* is more flattened cranio-caudally in its distal portion than that of *Lepus* but the compression of the shaft is less than in *Oryctolagus*, resembling that of *S. floridanus*. Moreover, the minimal width of the shaft in relation to total bone length (Iti6), resembles in this respect the bones of leporine rabbits (Fig. 7F).

Skeleton of the ankle joint.—The tarsus of leporids consists of six elements (Fig. 8), the anklebones, arranged in two rows: proximal and distal. The only exception is the navicular bone (*os naviculare*) which is placed centrally. The proximal row contains two elements, the talus, the medial element, and the calcaneus, the lateral element. The talus is the tibial tarsal bone, while the calcaneus creates the articular surface for the fibular portion of the tibiofibula, a unique feature within mammals, observed only in ungulates and lagomorphs (López Martinez 1985). The distal ankle row contains the second (*os cuneiforme intermedium*), third (*os cuneiforme laterale*), and fourth (*os cuboideum*) tarsal bones (Fig. 8). The first tarsal bone (*os cuneiforme mediale*) in lagomorphs is fused with the second metatarsal bone (*os metatarsale II*) and totally merged with the metatarsal segment.

Talus.—The talus of *H. beremendensis* is longer than in other rabbits, but shorter than in the hare (Table 3 in Appendix 1). The bone is also relatively more slender in *H. beremendensis*, as expressed by the greater length of the bone in relation to the width of the trochlea (*trochlea tali*). The ratio of trochlear width to the length of the talus (Ita1) is relatively low in *Hypolagus beremendensis* and closest to the value for *Lepus* (Fig. 9A).

The length of the neck of the talus (*collum tali*) in comparison with entire bone length (Ita2) is generally similar in all examined species (Fig. 9B).

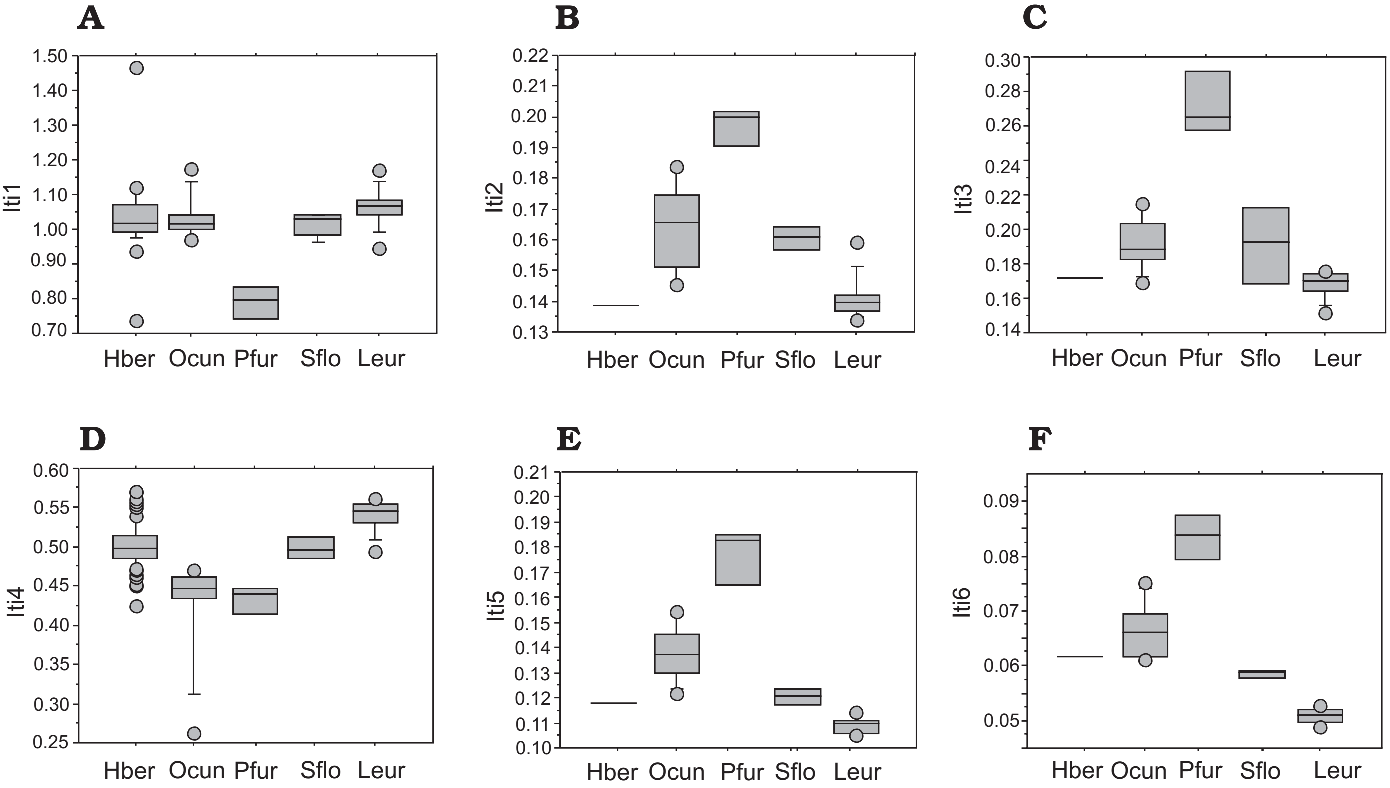

Fig. 7. Box plots of tibial indices. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

The trochlea of the talus in *Hypolagus beremendensis* has a smaller radius of curvature than *Lepus*. The talus contacts the calcaneus on three surfaces (Fig. 10). The first of them, the posterior one (*facies articularis calcanea posterior*) is composed of two rounded irregular spots located in the concavity at the plantar side of the trochlea. The medial articular surface (*facies articularis media*) is located at the plantar side of the trochlea/collum border. It is a flat, elongated oval, connecting with the articular surface of the talus head by a thin isthmus. The third, distal-most and the smallest articular surface (*facies articularis calcanea anterior*) lies at the medial side of the talus head. Its shape varies in *H. beremendensis* from planto-dorsally elongated to nearly round.

The surface of articulation with the navicular bone (*facies articularis navicularis*) occupies the head of the talus. In *H. beremendensis* its outline varies from oval to nearly round, frequently being wider than in *Lepus europaeus*.

Calcaneus.—The calcaneus of *H. beremendensis* is longer than in *Oryctolagus* and *Sylvilagus*. It is almost equal in length to that of *P. furnessi* but more slender and gracile (Table 3 in Appendix 1). The maximal width of calcaneus in relation to the total length of the bone (Ica1) is smaller in *H. beremendensis* than in *Pentalagus furnessi* (Fig. 11A). The length of the tuber calcanei in relation to the total bone length (Ica2) is slightly lower than in *Pentalagus*, *Oryctolagus*, and *Lepus* but greater than in *Sylvilagus* (Fig. 11B).

On the other hand, the body of the calcaneus in *H. beremendensis* is longer in relation to the total bone length (Ica3) than in *Oryctolagus*, *Pentalagus*, and even *Lepus* (Fig. 11C).

The trochlea (*trochlea peronealis*) for the articulation with the fibular part of the tibiofibula in *H. beremendensis* does not differ noticeably from the morphology in other leporids, but the two crests are of similar size, in contrast with those observed in *Lepus*, in which the lateral crest is more prominent. The crests are also more parallel to each other and to the sagittal axis of the bone than these of *Lepus*. The curvature of the trochlea is greater and in lateral view it is more similar to the trochlea of *Lepus* than to that of *Pentalagus*, which has a more flattened, massive trochlea.

On the medial side of the calcaneal body there are three oval surfaces for the connection with talus (Fig. 12). The posterior one (*facies articularis talaris posterior*) is placed at the medio-proximal side of the trochlea and is isolated from anterior talus surface (*facies articularis talaris media*) by the prominent ridge of the medial trochlear crest. The anterior face is more rounded and extended in *Lepus* than in *Hypolagus*. The third, surface for the attachment with the talus is formed by the *sustentaculum tali*, the most medial extension of the bone. It is a planar, round bony shelf inclined plantarly, slightly concave on the dorsal side where the surface for the talus is located. In *Hypolagus beremendensis* this surface is less inclined than in *Lepus*, where the angle between horizontal plane and the surface of attachments reaches ca 40°.

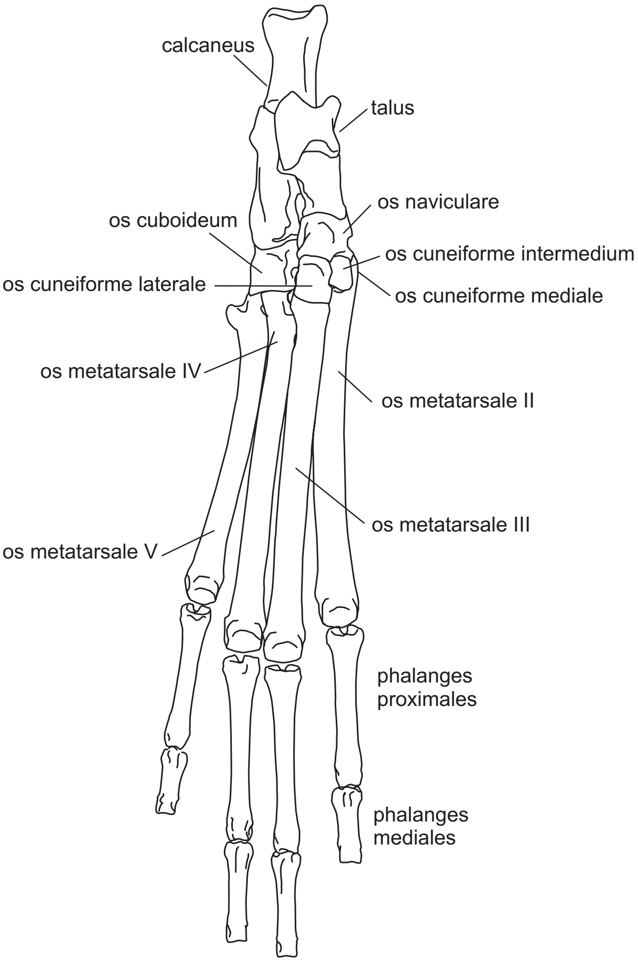

Fig. 8. Schematic drawing of pes structure in leporids, showing the arrangement of tarsal bones. Distal phalanges not shown.

At the medial side anteriorward from the *sustentaculum tali* there is a small surface, *facies articularis talaris anterior*, for the attachment of the head of the talus. It is the small rounded surface positioned on the narrow, obliquely elongated eminence and connected by it with the slightly larger area for the navicular bone (Fig. 12). These two surfaces could be either merged or separated in leporids. In *Hypolagus beremendensis* they are frequently joined, whereas in *Lepus* they are clearly separated. The distal surface of the calcaneus is obliquely oriented with its longer edge placed dorsally. Its lateral part serves as a surface for the articulation of the cuboid. It is a semilunar surface, occupying the dorso-lateral part of the distal surface of calcaneus. It is slightly narrower and less extended dorso-plantary in *H. beremendensis* than in *Lepus europaeus*. However, in the outline, the proximal articular surface of the cuboid in *H. beremendensis* resembles more that of *L. europaeus* than that of *Pentalagus furnessi*. In the latter species it is more square with medial margin almost as long as the dorsal one, while in both *Hypolagus* and *Lepus* the dorsal margin is distinctly longer.

Naviculare.—The navicular bone is situated medially between the talus on the proximal side and the cuneiform bones on the distal side (Fig. 8). It consists of the body and extended plantar process (*processus plantaris ossis navicularis*). The body is an irregular cube, flattened proximo-distally and deeply concave on the proximal face where the single, oval surface for the articulation of the head of the talus occurs (Fig. 13). This surface is almost circular in *H. beremendensis* and *P. furnessi*, while it is significantly constricted medio-laterally in *L. europaeus* and *Sylvilagus floridanus*.

The plantar process is flattened on the plantar side and has a shallow longitudinal groove oriented planto-medially. In *H. beremendensis* the plantar process is shorter in relation to body length (Ina1) than in *P. furnessi*, *Oryctolagus cuniculus*, and *L. europaeus* (Fig.14A). In *H. beremendensis* it broadens distally, forming a shovel-like structure (Fig. 13B), while in each of the comparative species it is much narrower. It is also somewhat plantarly directed, while in *Lepus* and *Sylvilagus* it is oriented more along the longitudinal axis and parallel to the dorsal surface of the body.

In *H. beremendensis* the body of the naviculare is significantly shorter in relation to the body width (Ina3) than in *L. europaeus* and *S. floridanus*, but it is longer than in *O. cuniculus* and *P. furnessi* (Fig. 14C).

The navicular bone contacts with the three cuneiform bones at its distal side (Fig. 13). The most medial bone (*os cuneiforme mediale*) is a part of the second metatarsal bone and contacts the navicular bone in a minute oval area at the medio-distal side of the navicular body, near the base of the plantar process.

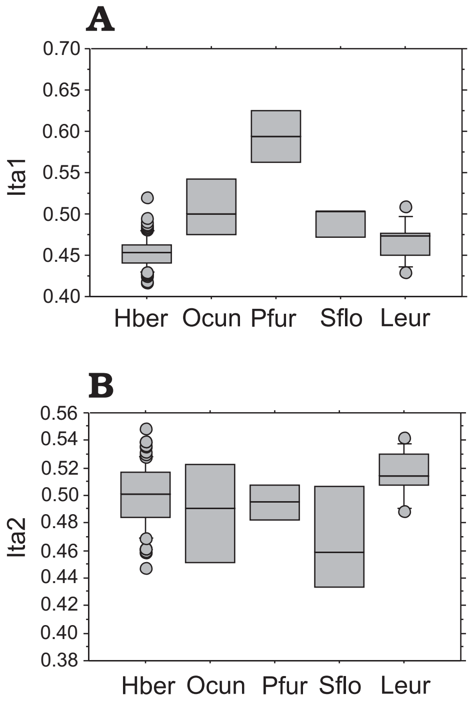

Fig. 9. Box plots of talar indices. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

The second tarsal bone (*os cuneiforme intermedium*) is placed lateral to the first tarsal bone, and contacts the navicular bone in a small area positioned planto-medially at the distal surface of the navicular body. The third tarsal bone (*os cuneiforme laterale*) is largest and contacts the navicular bone in a rounded and partly convex articular surface that occupies the majority of the distal surface of the navicular body.

The navicular bone contacts the cuboid laterally (Figs. 8, 13) at the deeply incised articular surface. In *Hypolagus beremendensis* it forms a deep groove opening toward the distal surface of the navicular body. The smaller surface for the connection with the calcaneus is located near the dorsal side of the articulation with the cuboid. In *Lepus* it is relatively small and oval or rounded in shape, while in *H. beremendensis* it forms a triangle with its apex directed proximally.

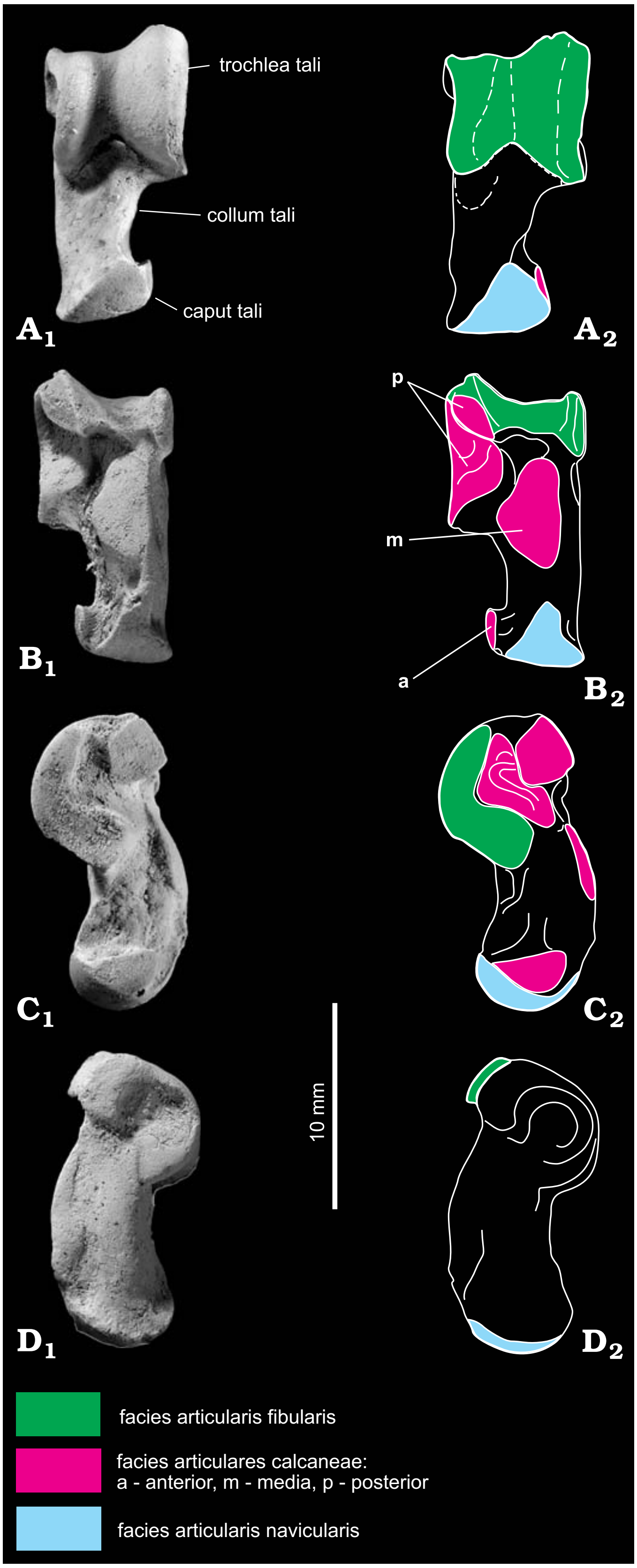

Fig. 10. Morphology of left talus of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2224/ta/12, Rębielice Królewskie 1, late Pliocene, Poland, in dorsal (**A**), plantar (**B**), lateral (**C**), and medial (**D**) views, and explanatory drawings with articular surfaces marked (A_2–D_2).

Cuboid.—The cuboid bone is the most lateral element of the distal ankle row (Fig. 8). The cuboid in leporids actually resembles a rhombohedron. It has a distinct plantar tuberosity, forming transverse ridge crossing the plantar side of the bone (Fig. 15). In *H. beremendensis* the elongation (Icu1) of the bone resembles that of *Lepus*, while it is less elongate than in *Sylvilagus*, and more than in *Oryctolagus* (Fig. 16; the measurements for *Pentalagus* were unavailable).

The proximal surface of the cuboid forms a large and convex surface for the calcaneus, which extends onto the dorsal side of the bone. The surface is almost square in *Lepus europaeus*, while in rabbits it is generally oval and gently bent, forming two rounded horns that project plantarly. In *H. beremendensis* the bending is more pronounced and the whole surface, in proximal view, is more triangular, with a flat medial margin and a curved dorsal margin. It is also more strongly sloped and extends more dorsally than in *Lepus*, *Sylvilagus*, and *Oryctolagus*.

The surface for the contact with navicular bone (*facies articularis navicularis*) is tripartite (Fig. 15C). In *H. beremendensis* its shape resembles that of *Sylvilagus floridanus*, forming a more consistent triangle in medial view and a deeper depression above the plantar tuberosity.

The cuboid connects distally with the fourth and fifth metatarsal bones. The articular surface for the metatarsals is pear-shaped with its broader part, the articulation with the fourth metatarsal bone, placed medially. It has relatively more rounded margins and is slightly narrower than the articular surface in *Lepus*. The distinct elongated prominence of the cuboid tuberosity (*tuberositas ossis cuboidei*) is situated on the plantar side of the cuboid. In *H. beremendensis* the tuberosity is thinner and has uniform thickness. Its plantar surface is wavy in some specimens. At its lateral edge the tuberosity in *H. beremendensis* is thickened, producing a small tubercle, which is significantly enlarged in *L. europaeus* and *S. floridanus*.

Third tarsal bone.—The second and third tarsal bones or *os cuneiforme intermedium* and *os cuneiforme laterale* are small, pyramid-like bones rarely found in the fossil deposit because of their size and inconspicuous shape. The second tarsal bone

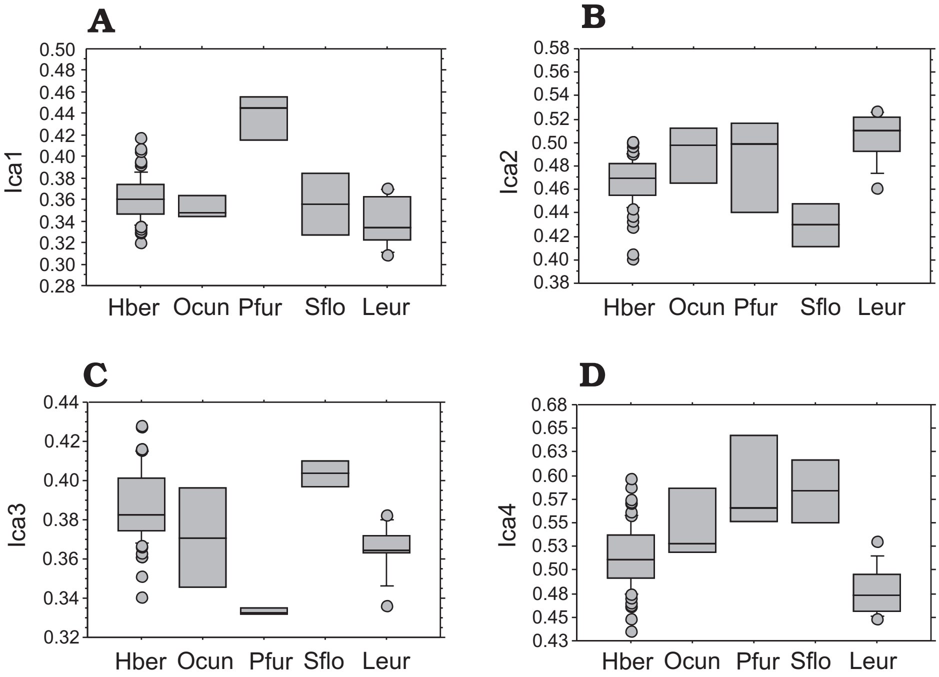

Fig. 11. Box plots of calcaneal indices. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

was not found within the studied fossil material, while seven *ossa cuneiformia laterales* were yielded by the material from Węże 1.

The third tarsal bone is shorter in *Hypolagus* than in *Lepus europaeus*, and less extended dorso-plantarly (Table 3 in Appendix 1). Thus, its articular surfaces for the naviculare (proximal) and metatarsal bone III (distal) are relatively broader medio-laterally and shorter dorso-plantarly. The proximal articular surface of the third tarsal bone of *Hypolagus beremendensis* is slightly concave and almost round, the distal surface is flat and triangular in outline, with the tip, formed by plantar tuberosity (Fig. 17). The dorso-plantar extension of the third tarsal bone and the relative breadth of the distal surface, for attachment with metatarsal bones, differ between the studied genera. The third tarsal bone in *H. beremendensis* is smaller than in *L. europaeus* and larger than in *Sylvilagus floridanus*. The third tarsal bone of *H. beremendensis* is also significantly broader at its dorsal margin and has an enlarged medial tubercle, forming the articulation for metatarsal bone II. In all studied leporins the third tarsal bone has a narrower dorsal margin and the tuberosity is not so extended.

Metatarsals.—The metatarsal bones (*ossa metatarsalia* II–V) are built according to the same plan. Their proximal extremities create a base (*basis*) which articulates with the tarsals (the proximal articular surfaces) and join the metatarsals together in a row (medial and lateral articular surfaces). The shaft or body (*corpus*) is elongated and the distal extremities of metatarsals form a head (*caput*), creating trochlea for the connection with phalanges (Figs. 8, 18, 19).

The metatarsals of *H. beremendensis* are relatively long and slender (Figs. 20, 21). Their general morphology does not differ significantly from that of other species, with the exception for *P. furnessi* which has distinctively short, robust bones (Fig. 21). The indices of slenderness (Fig. 20) calculated for metatarsal bones of all studied species reveal that *H. beremendensis* has similar proportions to *O. cuniculus* (Fig. 20). Interestingly enough, the second metatarsal bone of *H. beremendensis* shows more similarity to *Lepus* than to *Oryctolagus* in overall proportions, being more slender than in *Oryctolagus* and both *Sylvilagus* species (Fig. 20). The proximal articular surfaces of metatarsal II and metatarsal III for the tarsal bones are somewhat deeper (dorso-plantarly) in *Hypolagus* than in *Sylvilagus* and *Oryctolagus*, resembling the proportions of *Lepus* (Table 4 in Appendix 1). The fourth and fifth metatarsals of *H. beremendensis* are relatively wider, approaching the proportions found in rabbits (*Oryctolagus* and *Sylvilagus*). Moreover, the fifth metatarsal in *H. beremendensis* possesses a relatively large, laterally-projecting tubercle, where the tendon of the peroneus brevis muscle is attached (Fig. 19E–H). The tubercle for the peroneus brevis tendon in *H. beremendensis* is more laterally extended than in *Sylvilagus* and *Oryctolagus* but less so than in *Lepus*. It is also positioned perpendicular to the long axis of the corpus of metatarsal V (as in *Lepus*), while in *Oryctolagus* and *Sylvilagus* it is gently inclined proximally.

Phalanges.—The proximal and medial phalanges in leporids are delicate and elongated, differing between the taxa in their slenderness indices and length (Tables 3, 4 in Appendix 1). They consist of a gently broadened and proximally concave

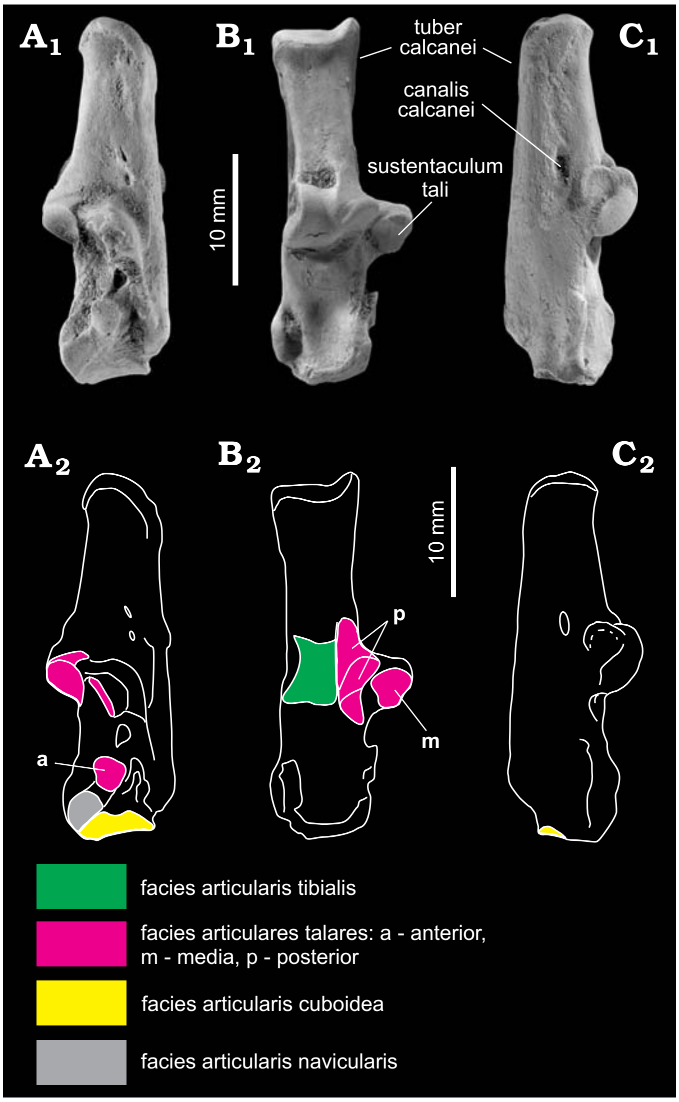

Fig. 12. Morphology of right calcaneus of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2220/ca/77, Węże 1, Pliocene, Poland, in medial (**A**), dorsal (**B**), and lateral (**C**) views, and explanatory drawings highlighting articular surfaces (A_2, B_2, C_2).

base, an elongated body that is round in cross-section, and a head that forms a crestless trochlea (Fig. 8).

The distal phalanges form the bony cores for claws and have only a proximal articular surface, which is a simple shallow concavity. Their distal ends taper, forming sharp, highly porous tips.

The proximal phalanges in *Hypolagus beremendensis* are significantly longer in relation to the metatarsal segment than in leporines. The medial phalanges show similar elongation but to a lesser extent (Fig. 21, Tables 3, 4 in Appendix 1).

The general proportions of the proximal and medial phalanges in *H. beremendensis* are as in *Oryctolagus*, *Sylvilagus*, and *Lepus*, which share a similar, gracile pattern of phalanx morphology. The slenderness of the proximal phalanges in *H. beremendensis* is in most cases greater than or at least equal to that of *Lepus* (Table 4 in Appendix 1). The slenderness of the medial phalanges shows the highest value of the slenderness index for phalanges III and IV. The medial phalanges of the second and fifth toes in *H. beremendensis* are more slender than those of *Oryctolagus cuniculus*, *Sylvilagus floridanus*, and *L. europaeus* (Table 4 in Appendix 1).

The intra-membral indices and proportions of the foot.—Proportions of the hind limb bones in *H. beremendensis* show relative elongation of the tibial and metatarsal segments. The ratio of os coxae length to the femur length (Ico-fe) is lower in *H. beremendensis* than in *Oryctolagus* and *Sylvilagus*, approaching the value for *Lepus* (Fig. 22A). The low index value in *H. beremendensis* is caused by a notably longer femur in relation to the innominate bone. A similar pattern is expressed in the crural ratio (Icru), which in *H. beremendensis* is close to *Oryctolagus*, *Sylvilagus*, and *Lepus*, but lower than in *Pentalagus* (Fig. 22B). On the other hand, *H. beremendensis* has a relatively longer foot (Ifoot1). This index has a significantly lower value only in *P. furnessi*, possessing a short and robust feet (Fig. 22C). The proportion of the calcaneus to the tibiofibula length (Ifoot2) is similar in *H. beremendensis*, *L. europaeus*, and *S. floridanus*, that have the relatively longer tibiofibulae than *P. furnessi* (Fig. 22D).

Results of phenetic analysis

The cluster analysis employing UPGMA method of distance examination was performed for 98 of the bone measurements (Table 1). The UPGMA analyses of the proximal segments including the pelvis, femur (Fig. 23A, B), and talus (Fig. 23E) group *H. beremendensis* with *P. furnessi*. On the other hand, the analysis of the tibiofibula places it just outside the *O. cuniculus*–*S. floridanus* (Fig. 23C) cluster and that of the calcaneus joins links *Hypolagus* with *Oryctolagus* (Fig. 23D). Furthermore, the analyses of the metatarsal and phalangeal segments link *H. beremendensis* to *Lepus* (Fig. 23F, G) because of the elongation of toes in both species (Fig. 21).

The general cluster for the hind limb places *H. beremendensis* just outside the cluster of typical leporine rabbits formed by *Oryctolagus* and *Sylvilagus* (Fig. 23H). Outside the branch with *H. beremendensis* is *P. furnessi*, while *L. europaeus* is the most divergent species. The position of *H. beremendensis* between leporine rabbits and *Pentalagus*, points to the specific and unique adaptations possibly typical for Archaeolaginae. The clustering of *Hypolagus* and *Pentalagus* in the case of the os coxae and femur parameters may suggest the conservative features retained in these structures in Leporidae.

Functional interpretation

Hip.—The relative increase in width of the iliac wing is one of the hallmarks of cursoriality or the ability to performing powerful leaps, observed in many terrestrial mammals (Taylor 1975; Sargis 2002). The wide iliac wing creates the expanded

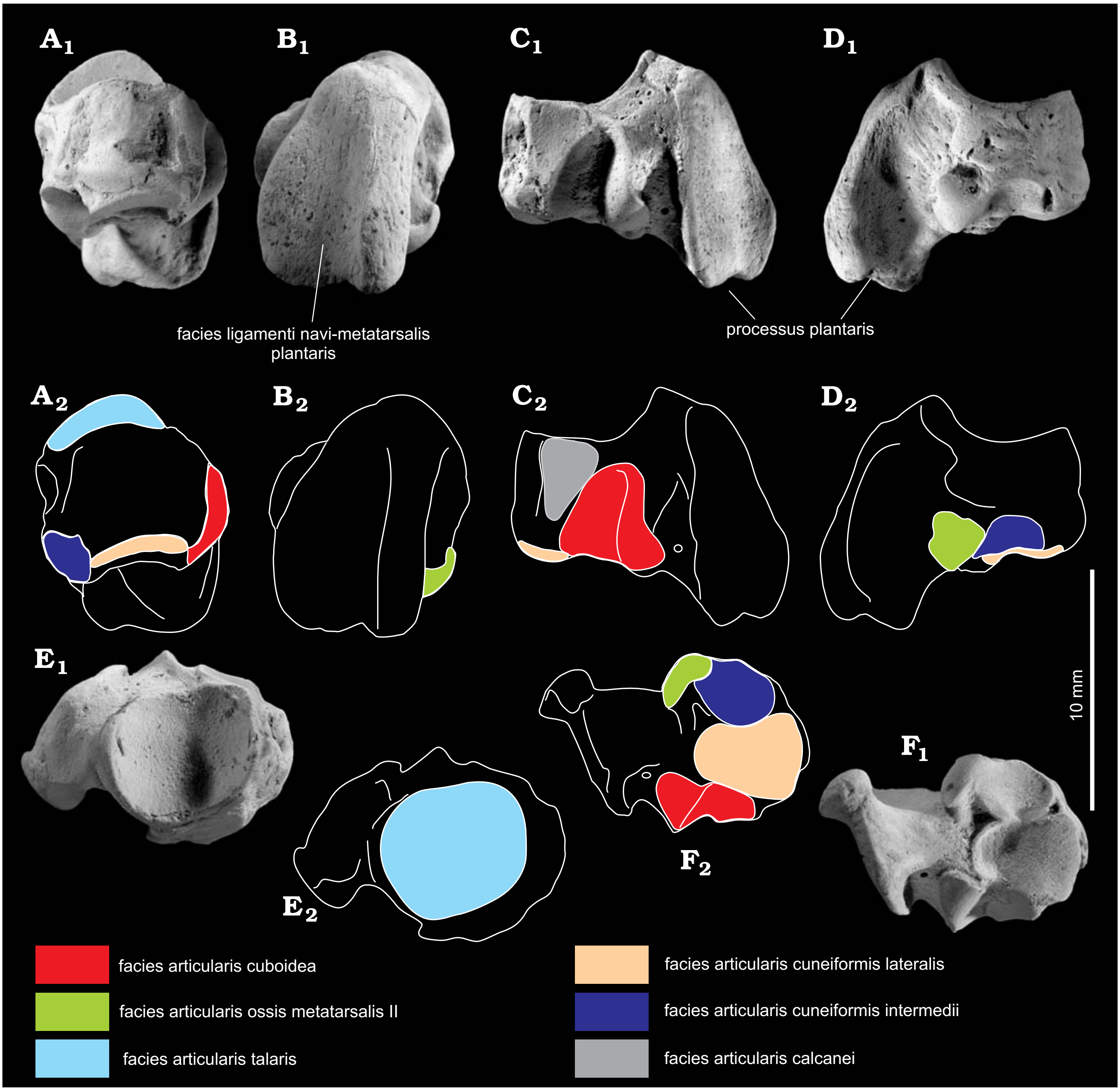

Fig. 13. Morphology of left naviculare of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2224/na/2, Rębielice Królewskie 1, late Pliocene, Poland, in dorsal (**A**), plantar (**B**), lateral (**C**), medial (**D**), proximal (**E**), and distal (**F**) views, and explanatory drawings with articular surfaces marked (A_2–F_2).

surface for the attachment of the gluteus medius muscle, one of the most powerful thigh extensors; the iliac crest is the attachment for the gluteus superficialis muscle, also a hind limb extensor (Young 1975; Taylor 1976; Argot 2002). Among analysed taxa *Lepus europaeus* has the relatively widest ilium (Ico2 = 62.5%). The other extant species express lower values of Ico2 (44% in *Oryctolagus cuniculus* and *Sylvilagus floridanus*, and 47% in *Pentalagus furnessi*). Thus, the action of the glutei muscles in rabbits is weaker. The complete iliac wing of *Hypolagus beremendensis* is not known, however the morphology of some larger fragments indicates that it was most similar to that of *S. floridanus* (Fostowicz-Frelik personal observation). It has well-developed *tuber coxae* (particularly caudal dorsal iliac spine), the strong iliac crest, and distinct *linea musculi glutei medii* (Fig. 2).

The second set of extensors of the thigh are hamstrings, large and long muscles adjusted primarily for excursion but also able to generate large forces (Lieber and Blevins 1989). The hamstrings include the semitendinosus, semimembranosus, and biceps femoris (caudal portion) muscles, attached

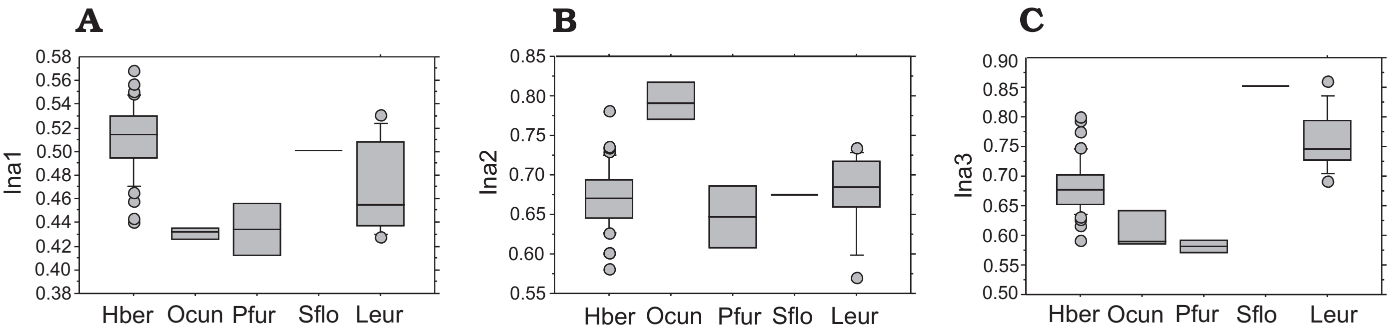

Fig. 14. Box plots of navicular indices. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

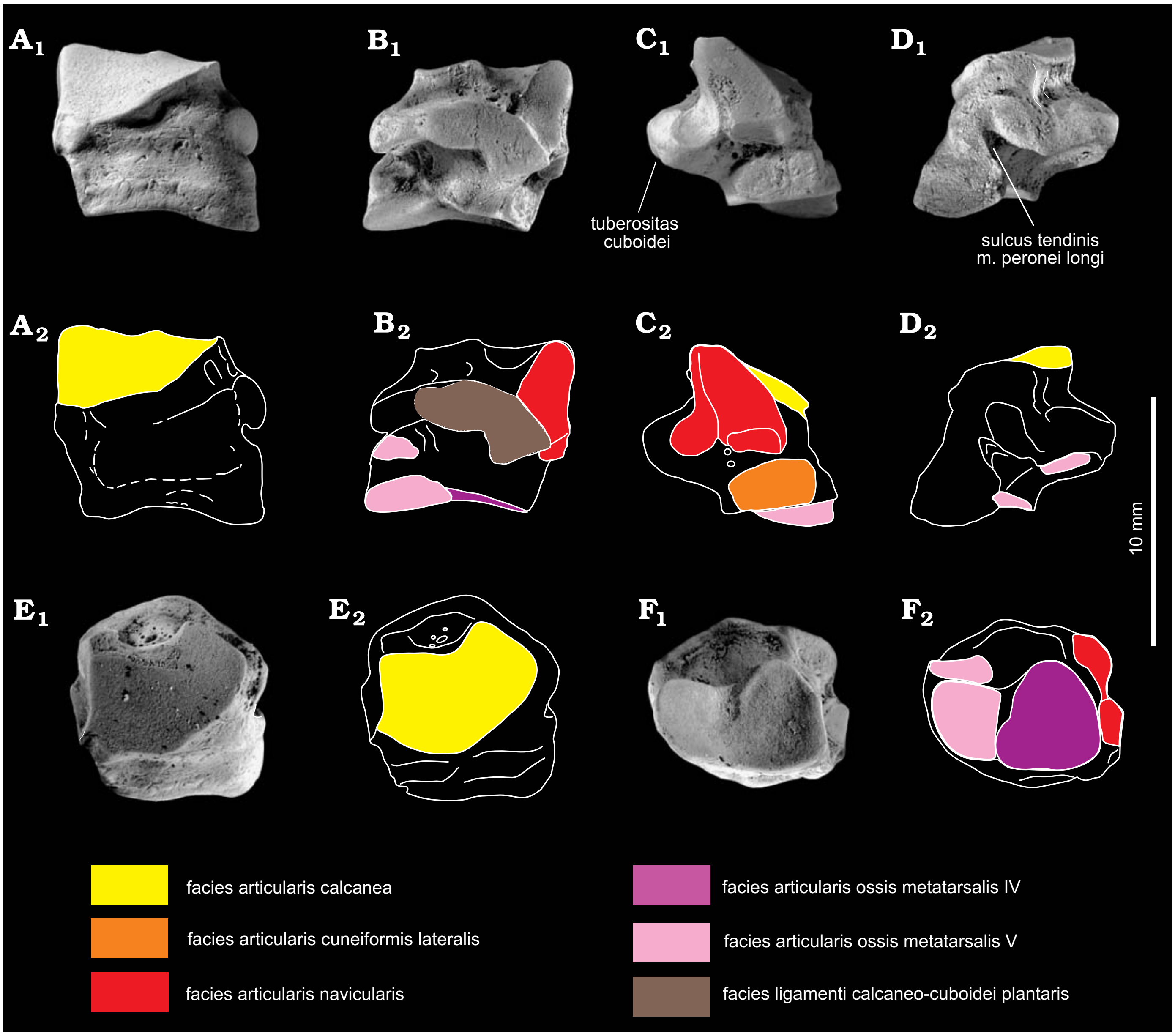

Fig. 15. Morphology of left cuboid of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2220/cu/1, Węże 1, Pliocene, Poland, in dorsal (**A**), plantar (**B**), medial (**C**), lateral (**D**), proximal (**E**), and distal (**F**) views, and explanatory drawings with articular surfaces marked (A_2–F_2).

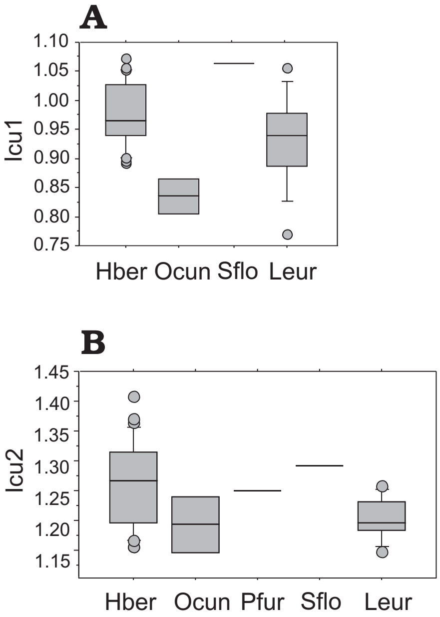

Fig. 16. Box plots of cuboidal indices. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

to the ischial tuberosity and the lateral process of the ischium (Camp and Borell 1937; Klebanova et al. 1971). The size and shape of the ischial tuberosity is variable in Leporidae. In *Lepus* the ischial tuberosity is very large and robust. The surface for the muscle attachments is more expanded and more isometric, while in rabbits its surface is much more limited, compressed medio-laterally, and crescent-like in caudal view (Fig. 2F–J). The more isometric areas of muscle attachments indicate the relatively greater area of the cross-section of the muscles which results in relatively greater strength of contraction. Thus, the muscles attached to the ischial tuberosity in *Lepus* are the strongest among all leporid taxa. In that respect *Hypolagus beremendensis* expresses general rabbit morphotype, although it is among the more cursorial species. On the other hand, the lateral process in *Oryctolagus* and *H. beremendensis* is distinctly enlarged dorso-laterally, creating a larger space between its cranio-dorsal margin and the body of the ischium. This, in all probability, reflects the strong action of the sacrotuberous ligament, which attaches to the tip of the ischium and is the insertion for the biceps femoris and abductor cruris caudalis muscles. It also can indicate a powerful quadratus femoris muscle (attaching cranially from the lateral process of ischium to the body of ischium), that extends the thigh and rotates the femur outward at the hip joint (Young 1975; Evans 1993). The rotation and abduction functions of the quadratus femoris, as well as the strong action of sacrotuberous ligament, can be related in *Oryctolagus* with digging. While burrowing, a wild rabbit suspends the main body mass on hind limbs and shifts its weight back and forth like a pendulum, digging with the forelegs. This position generates the stretching forces applied to the muscles of the caudal side of the thigh and demands the strong action of the muscles of the cranial side of thigh suspending the body (e. g. biceps femoris muscle). Also, during burrowing there is flexion and extension of the vertebral spine, which enables a strong sacrotuberous ligament to act as a spring, giving additional momentum to the pendulum-like movements. The morphology of the lateral process of the ischial tuberosity in *Hypolagus beremendensis* could, to some extent, indicate adaptation to digging. On the other hand, the hook-like extension of the lateral process is not observed in *Pentalagus furnessi*.

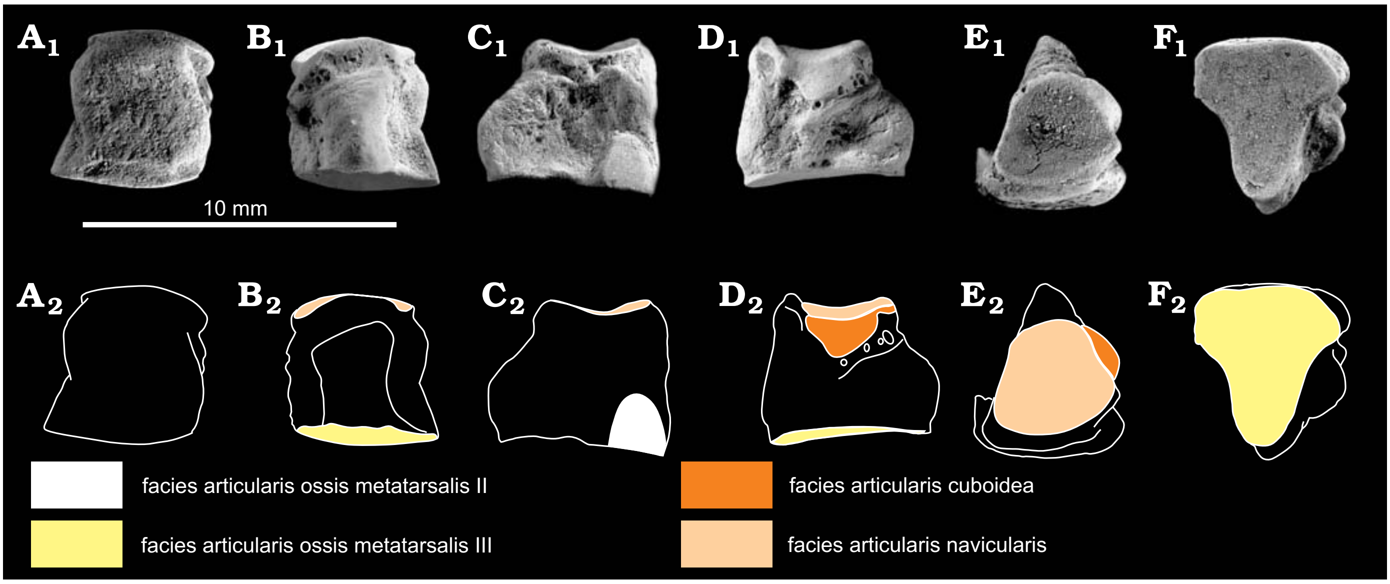

Fig. 17. Morphology of right lateral cuneiform of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2220/cn/1, Węże 1, Pliocene, Poland, in dorsal (**A**), plantar (**B**), medial (**C**), lateral (**D**), proximal (**E**), and distal (**F**) views, and explanatory drawings with articular surfaces marked (A_2–F_2).

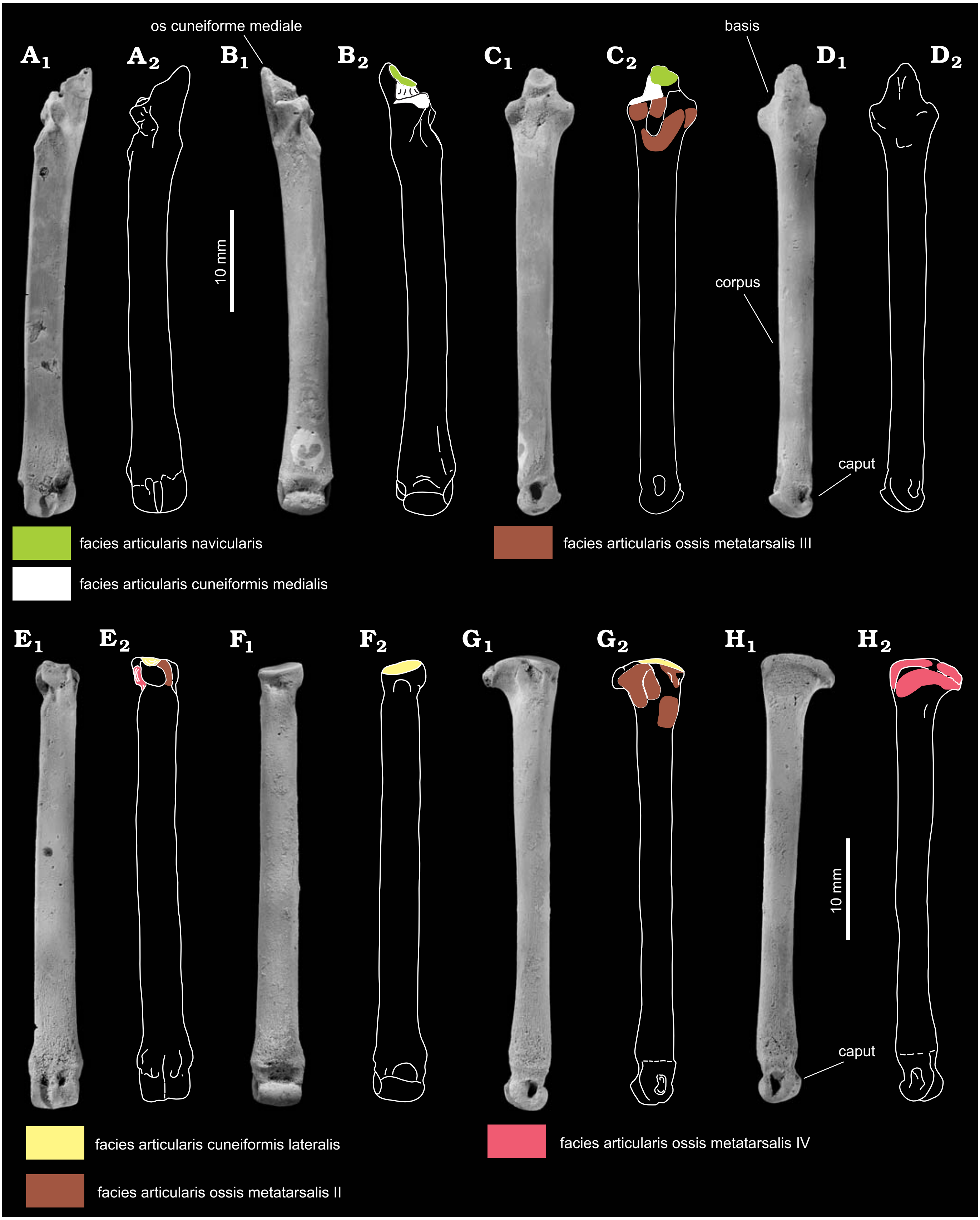

Fig. 18. Morphology of right metatarsal II (**A**–**D**) and left metatarsal III (**E**–**H**) of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2220/mt2/9, Węże 1, ISEZ MF/2224/mt3/10, Rębielice Królewskie 1, late Pliocene, Poland, in plantar (**A**, **E**), dorsal (**B**, **F**), lateral (**C**, **H**), and medial (**D**, **G**) views, and explanatory drawings with articular surfaces marked (A_2–H_2).

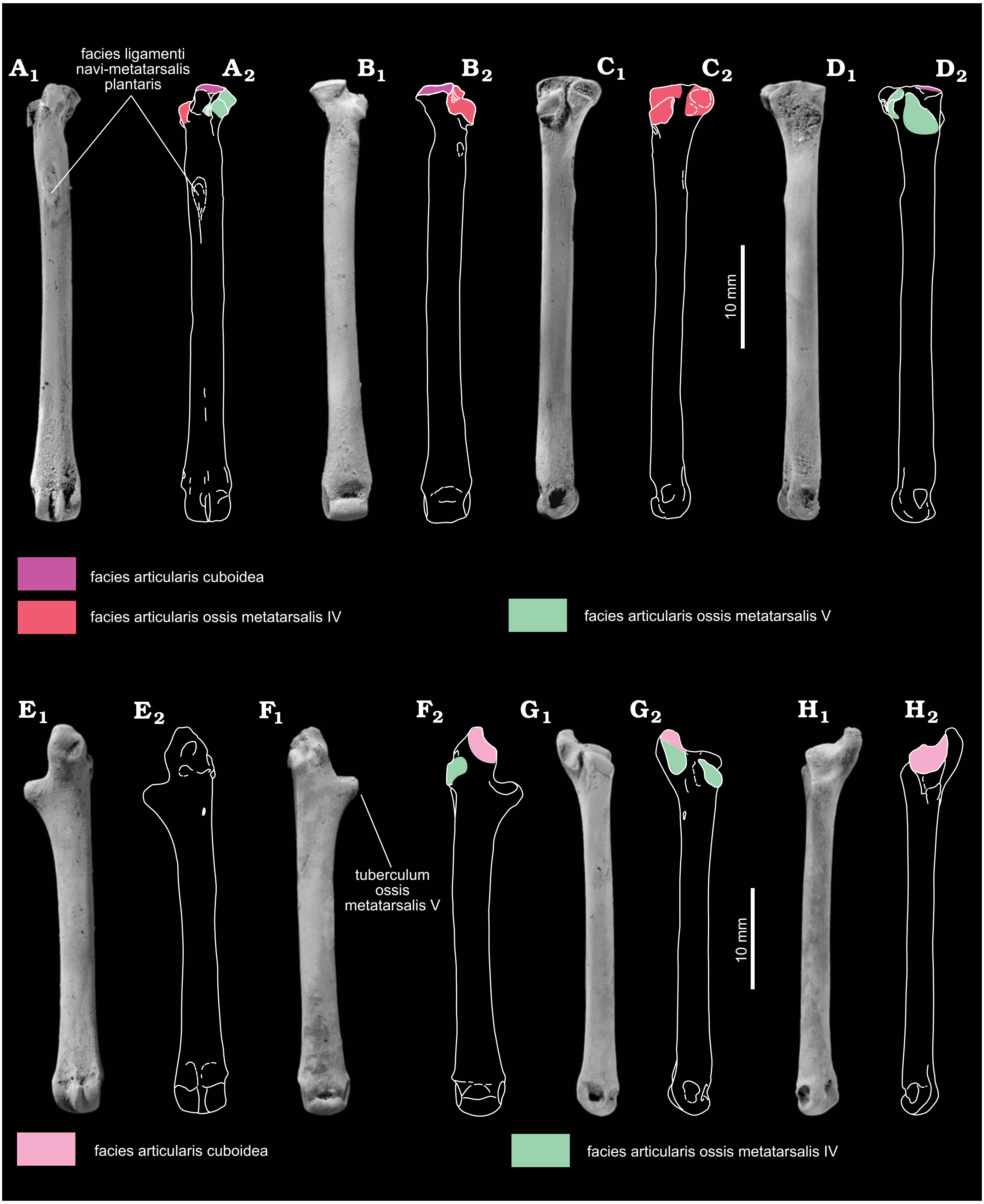

Fig. 19. Morphology of right metatarsal IV (**A**–**D**) and left metatarsal V (**E**–**H**) of *Hypolagus beremendensis* (Kormos, 1930), ISEZ MF/2224/mt4/1, Rębielice Królewskie 1 and ISEZ MF/2225/mt5/12, Rębielice Królewskie 2, late Pliocene, Poland, in plantar (**A**, **E**), dorsal (**B**, **F**), medial (**C**, **G**), and lateral (**D**, **H**) views, and explanatory drawings with articular surfaces marked (A_2–H_2).

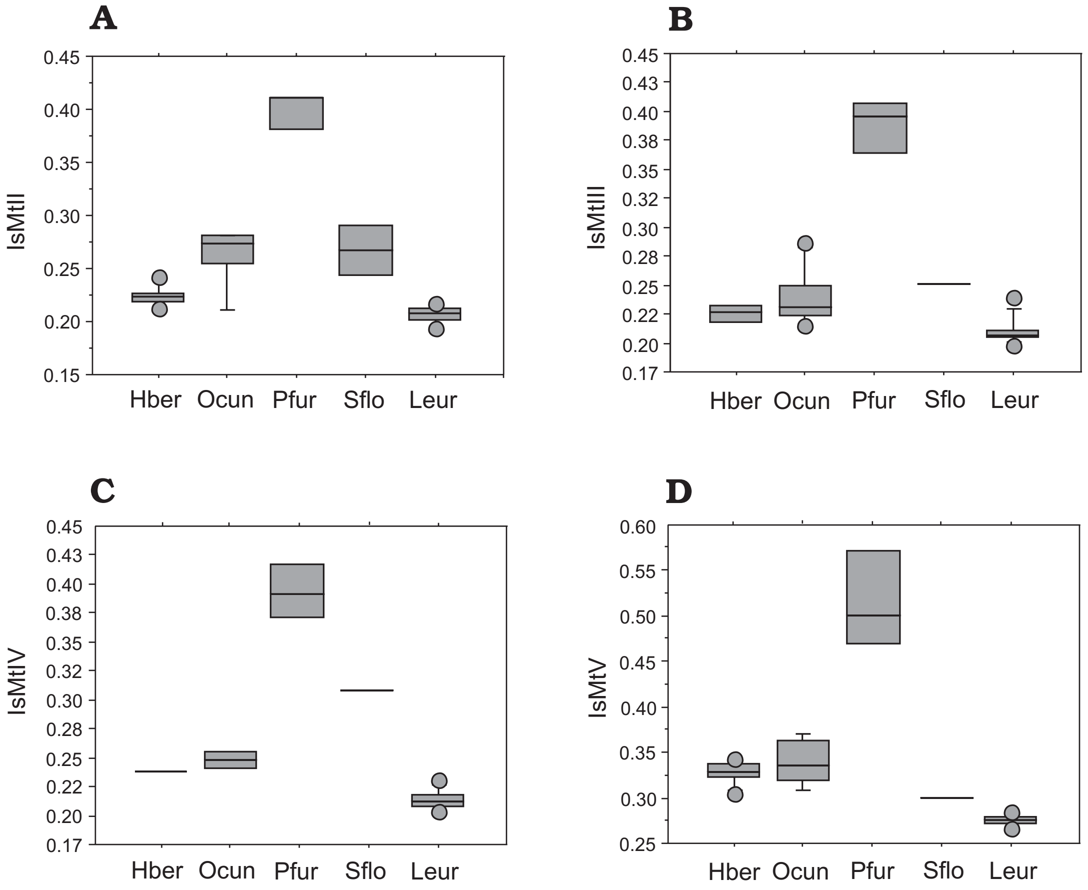

Fig. 20. Box plots of the indices of slenderness for metatarsal bones. Note the low index of slenderness of metatarsal II for *Hypolagus beremendensis* (**A**). Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

Thigh.—In highly cursorial and saltatorial mammals, the femur is generally slim and the trochanters are concentrated closer to the proximal end of the bone. It shortens the lever arms over which muscle forces acts and produces swifter responses to the contraction of muscles, yielding quicker but less powerful flexion (the iliopsoas muscle) and extension (the gluteus superficialis, tensor fasciae femoris and gluteus medius muscles) of the thigh at the hip joint (Hildebrand 1974; Anemone and Covert 2000). This particular morphology is best-developed in *Lepus*. *Hypolagus beremendensis* expresses an intermediate development of this feature between *Lepus* and *Oryctolagus*, implying a relatively high degree of cursoriality.

The proximally extended greater trochanter is interpreted in small carnivores as an adaptation to the terrestrial locomotion, because it restricts the action of the gluteus medius in abduction of the femur at the hip joint and makes the parasagittal action of the limb more efficient (Taylor 1976). In leporids however, which all have the greater trochanters relatively extended posteriorly, the most erect trochanters are observed in slower runners. The medial bending of the greater trochanter increases the area of attachment for the gluteus medius muscle (see discussion of the pelvis, above), thus strengthening the force with which it extends the hip joint. The strongest bending of the greater trochanter is observed in *Lepus*. In *Oryctolagus* and *Pentalagus* the structure is generally erected proximally and pointy (Fig. 4). In *Sylvilagus floridanus* and *H. beremendensis* the bending of the greater trochanter is markedly weaker than in *Lepus*.

In leporids the articular surface of the head of the femur intrudes into the dorsal part of the femoral neck. This feature is frequently observed in arboreal marsupials and some carnivorans, which stand with the thighs in a more abducted position (Argot 2002; Heinrich and Houde 2006). The extension of this surface is quite significant in leporids and it is directed slightly caudally. It seems to be connected with the orientation of the pelvis, which is inclined backward and the caudal margin of the semilunar surface braces the caudo-dorsal part of the femoral head. Thus, the greater abduction of the thigh can be related with digging behaviour. The abduction of the hind limbs allows an animal pushing the soil backward with the forelegs between the hind legs (Taylor 1976) and easily shifts the position of the trunk during burrowing. Among the studied taxa, *Oryctolagus cuniculus* shows the most extended and defined articular surface of the femoral head with sharp, pronounced margins. The femoral neck in *O. cuniculus* seems to be also the longest and best developed, allowing for greater mobility in a transverse plane. In *H. beremendensis* the shape

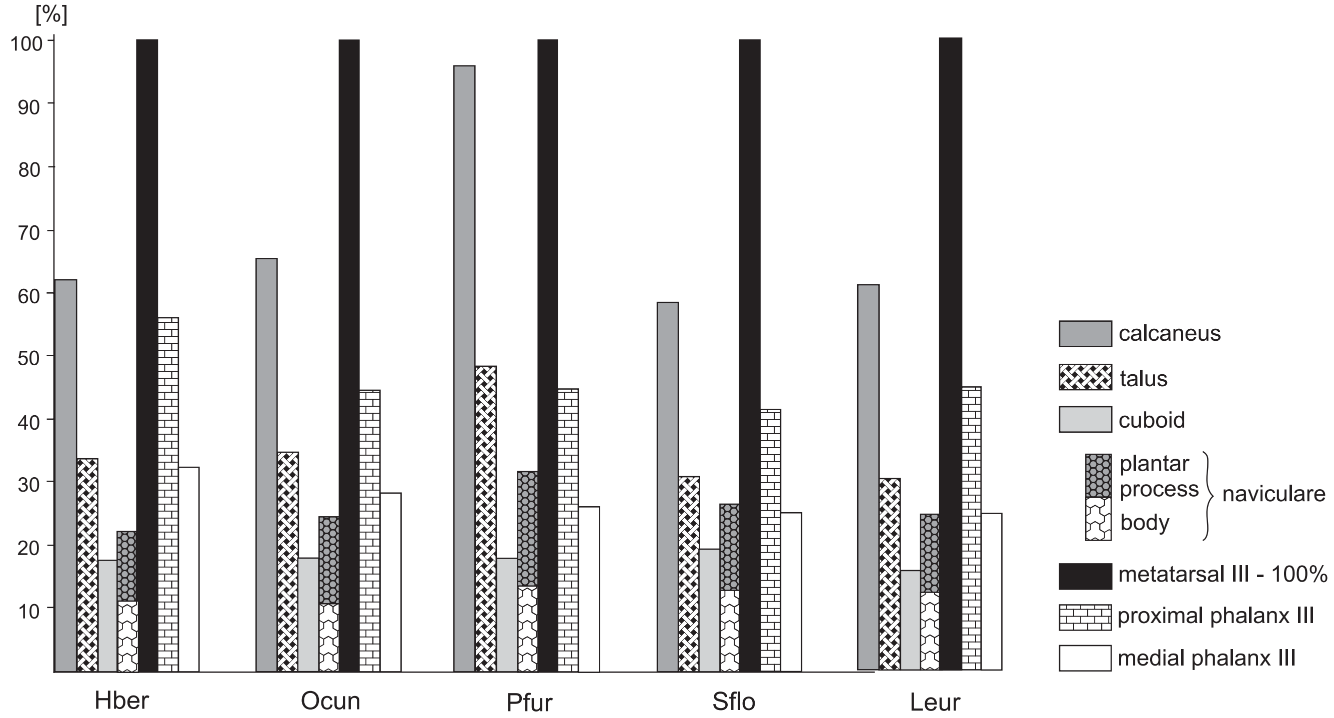

Fig. 21. Proportions of bones of the foot of Leporidae, metatarsal bone III (black bar), used as 100% for each species. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

and extent of the articular surface of the head are more similar to those observed in *Lepus*. Therefore *Hypolagus* was probably not able to abduct the hip joint to such an extent as *O. cuniculus*. It may indicate weaker burrowing ability, if *H. beremendensis* was at all capable of burrowing.

The relatively high cursorial ability of *H. beremendensis* is emphasised also by the relatively high cranio-caudal thickness (Hdis) of the distal extremity of the femur, even exceeding its width (Wfedis), and a distinctly narrow patellar groove (Fig. 5D, E). The deeper condyles, one of hallmarks of cursoriality, allow more powerful extension of the knee by the action of the quadriceps femoris (Anemone and Covert 2000).

Shank.—The tibiofibula, the sole bone of the zeugopodial segment in the hind limb of leporids is the main bone responsible for the elongation of the leg in highly cursorial species (Gambaryan 1974; Hildebrand 1974), apart from the metatarsal segment. It is also the most distal bone having large muscle attachments in leporids. The most powerful hind limb musculature occupies the upper regions of the leg, reaching about one third of the proximal part of the tibiofibula, while the distal end of the bone and the foot forms the attachments for ligaments. This general plan is expressed more strongly in cursorial taxa, as the shortening of the muscle arms quickens the responses of the limb bones to their action (Camp and Borell 1937; Hildebrand 1974). The most prominent and important structure within the tibiofibula is the tibial tuberosity. It serves as the attachment area for shank flexors such as the biceps femoris and semitendinosus muscles and the patellar ligament of the quadriceps femoris complex. The sartorius muscle, which acts as an adductor and rotator of the thigh and extensor of the shank, and the gracilis muscle, which adducts the shank, are attached to the medial condyle of the tibia (Camp and Borell 1937; Craigie 1948; Evans 1993; Wingerd 1985). The relative length of the tibial tuberosity to the overall tibiofibular length (Iti3) in studied taxa is lowest for *L. europaeus* and *H. beremendensis* (Fig. 7C). This index implies that the most cursorial leporids, such as *Lepus*, possess the relatively shortest tibial tuberosity. This agrees with the tendency to group the muscle attachments near the bone ends in highly cursorial mammals (Hildebrand 1974) as is also observed in the femur. The proportions of the proximal and distal extremities of the tibiofibula in the studied taxa reflect the tibial aspect of "deepening of the knee" (observed also in the distal end of the femur) by increasing relative cranio-caudal depth of the proximal extremity. In *Lepus*, *Sylvilagus*, and *Oryctolagus*, as well as in *H. beremendensis*, the maximum cranio-caudal dimension of the proximal end of the tibiofibula exceeds its maximum width (Fig. 7A), while *Pentalagus furnessi* displays significantly greater width. The distal end deepens similarly to the proximal one in *Lepus* (Fig. 7D) as well as in *Sylvilagus floridanus* and *H. beremendensis*, differentiating them from *O. cuniculus* and *P. furnessi*. These last two taxa have tibiofibulae with more medio-laterally extended distal ends.

In general, the slenderness of the tibiofibula of *Hypolagus beremendensis* and the relative deepening of the surface of the stifle joint, the shortening of the tuberosity and the more square distal articular surface show similarities to the tibiofibula of *Lepus*.

Pes.—The foot in terrestrial mammals is another anatomical region (along with the shank) of the hind limb in which signifi-

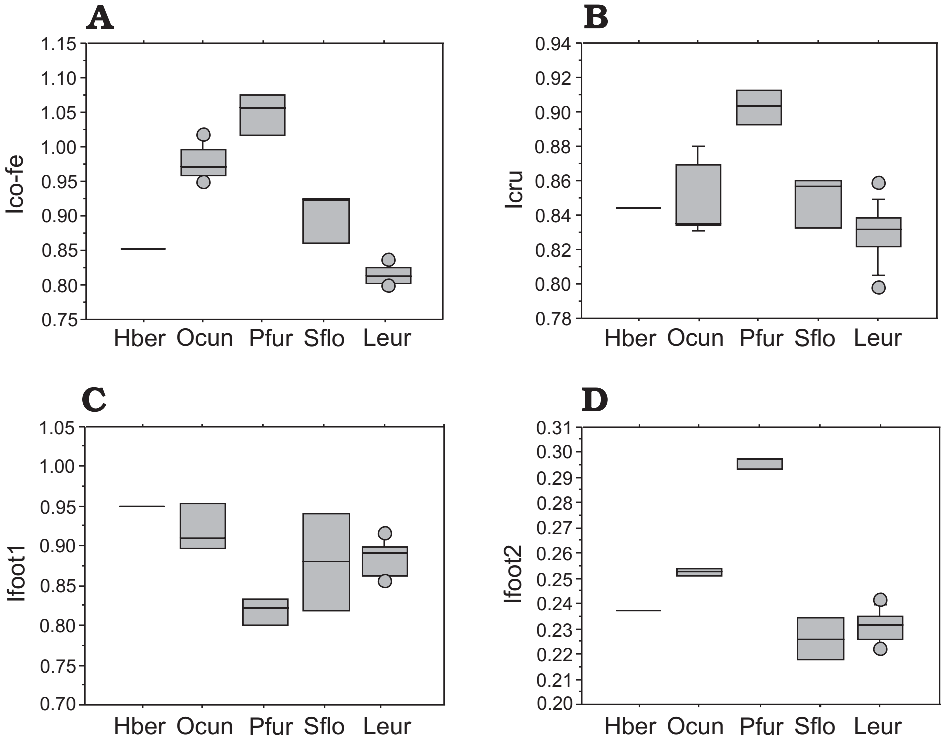

Fig. 22. Box plots of the intramembral indices. Note the relatively low values of coxo-femoral index (**A**) and Ifoot2 index (**D**), as well as the relatively high Ifoot1 index (**C**) for *Hypolagus beremendensis*. Median, range and 50%-segment of values are given. Values above the 90th and below the 10th percentile are plotted as points. Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

cant cursorial and saltatorial adaptations are apparent (Gambaryan 1974; Hildebrand 1974). The metatarsals are the bones that most fully reflect cursoriality, being relatively elongated in fast-running mammals (Hildebrand 1974). On the other hand, the tarsal elements in cursorial animals serve to stabilise the ankle joint by creating large and deep surfaces for the articulation with the tibia and fibula. Therefore they generally are not elongated. However, in some small arboreal primates, such as tarsiers and galagos, probably the best leapers among the mammals, they can be lengthened significantly, reflecting some particular saltatorial adaptations (Hildebrand 1974; Anemone and Covert 2000).

In leporids the basic ankle joint structure is very uniform (Lyon 1904; Dawson 1958; Averianov 1995), although some differences in the proportions of the tarsal bones can be recognised. The main differences in the foot morphology can be seen in elongation of the metatarsals and phalanges

In more cursorial genera, the talus is slender and the index value (Ita1) for *Hypolagus* is closest to that of *Lepus* (Fig. 9A). However, the length of the neck of the talus (Ita2) varies only slightly among all studied genera and is relatively longer in *Lepus* than in the other species (Fig. 9B). The head of the talus is placed posteriorly in relation to the distal end of the calcaneus (Fig. 8), strengthening and stabilising the ankle joint and limiting the mobility of the foot only to flexion and extension (Taylor 1976). This feature is enhanced by the elongation of the neck of the talus in leporids.

The most powerful muscle attachment in the distal part of the hind limb (the gastrocnemius muscle, the ankle plantar flexor; Lieber and Blevins 1989) is located on the tuber of calcaneus. The analysis of the proportions of the calcaneus revealed that the values of Ica2 are within a narrow range except for *Sylvilagus*, which has the shortest calcaneal tuber (Fig. 11B).

On the other hand, the elongation of the body of the calcaneus (Fig. 11C) seems to be closely related to saltatorial adaptation. The lowest values of Ica3 are found in *Pentalagus furnessi*, which is one of the stockiest and most heavily-built rabbits and has weakly developed cursoriality. The other studied species exhibit higher ratios (Fig. 11C) with *Sylvilagus floridanus* attaining the highest value. Remarkably, the value for *Lepus* is second lowest. It suggests that the feature is affected by body mass (*S. floridanus* ca. 1.3 kg, *Pentalagus* and *Oryctolagus* ca 2.0 kg and *Lepus* ca. 5.0 kg; Chapman and Flux 1990). This could be expected, as the strength of the gastrocnemius muscle must act against the force of gravity (Hildebrand 1974; Alexander 2003).

The cuboid and navicular bones are relatively elongated in species with greater cursorial adaptations (Fig. 16). On the other hand, the length of the plantar tuberosity of the navicular in relation to the length of its body (Ina1) is highest in less cursorial species, *O. cuniculus* and *P. furnessi* (Fig. 14).

The relative proportions of particular bones within the foot in the studied species (Fig. 21) are generally similar in all studied species save *P. furnessi*, which has significantly

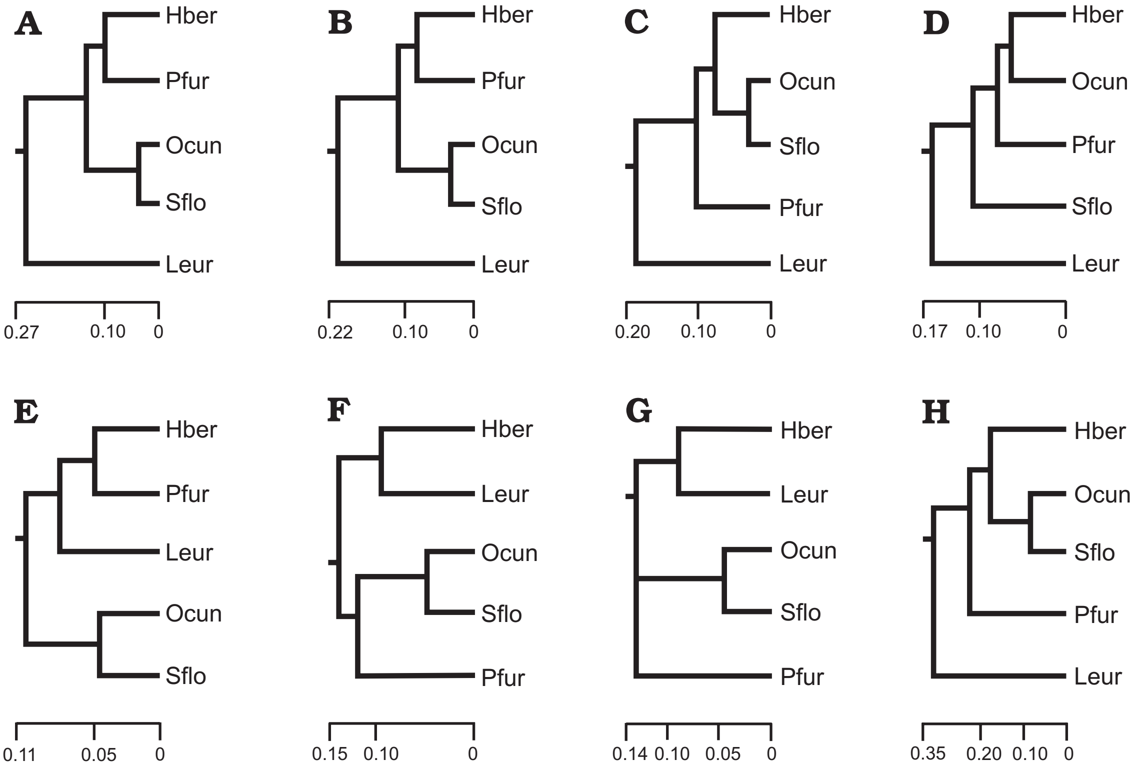

Fig. 23. Cluster analyses of 98 variables measured on leporid hind limb. Cluster for os coxae (**A**), femur (**B**), tibia (**C**), calcaneus (**D**), talus (**E**), metatarsals (**F**), pes, tarsus excluded (**G**) and general cluster for all variables used in the analyses (**H**). Species abbreviations: Hber, *Hypolagus beremendensis*; Ocun, *Oryctolagus cuniculus*; Pfur, *Pentalagus furnessi*; Sflo, *Sylvilagus floridanus*; Leur, *Lepus europaeus*.

shorter metatarsal and phalangeal segments. The characteristic feature found in *Hypolagus beremendensis* is the greatest elongation of the proximal and medial phalanges relative to the metatarsal segment (Fig. 21). This feature, observed also in *H. brachygnathus* (Petényi, 1864) probably contributes to the increase in cursoriality of both species (Fostowicz-Frelik 2007).

The bones of the ankle joint in all species apart from *P. furnessi* are relatively short in comparison with the third metatarsal bone used there as an internal reference (100%) for the foot bones (Fig. 21). The relative length of the ankle bones is lowest in *Lepus europaeus*, implying that it possesses the most elongated metatarsals of all included species.

The elongation of the foot relative to the rest of the limb is observed in all efficient runners (Gambaryan 1974; Hildebrand 1974). Hildebrand (1974) uses a “gear ratio” concept to illustrate, among others, the dependence of the speed and the general foot proportions higher gear ratios are indicative of greater running ability. The gear ratio for the gastrocnemius was calculated herein. It is defined as the proportion of the length of the portion of the foot placed prior to the point of support for tibia (*trochlea peronealis*) to the length of the portion of the foot skeleton placed caudally to the tibia junction (here identical with the length of the calcaneal tuber).

Among all studied species the gear ratio is lowest for *Pentalagus furnessi* (5.3), while it varies slightly among the rest of the taxa, being higher for *Sylvilagus floridanus* (8.6) and *H. beremendensis* (8.2), and lower for *Oryctolagus cuniculus* (7.05) and *L. europaeus* (7.0). The low gear ratio for *Lepus* is most probably the result of noticeably greater weight. Thus, the gear ratio is most informative when it is used for a group of species exhibiting similar locomotor adaptations (as in the case of leporids) and body weight, or when the compared taxa differ greatly in the structure, that is to say in the mode of locomotion (e.g., kangaroo and wombat).

Paleobiological implications

The measurements of the bones of *Hypolagus beremendensis* point to a size intermediate between *Oryctolagus cuniculus* and *Pentalagus furnessi*. The latter species, however, is robustly built, what is not observed in the skeleton of *H. beremendensis*. This is in contrast with the interpretation of Sych (1965) made on the basis of specimens from Kamyk (early Pleistocene of Poland), which were also assigned to *H. beremendensis* by that author. These specimens are now regarded as *H. brachygnathus*, a significantly larger and more heavily-built species (Fostowicz-Frelik 2007).

The morphological analysis of the skeleton of *H. beremendensis* allowed recognition of particular adaptations and estimation of the possible style of locomotion. The increase in width of the ischiac tuberosity, strongly built ilium with a moderately wide iliac wing and the marked closer grouping of the femoral trochanters near the proximal extremity of the femur imply that the animal possessed the relatively well-developed flexor-extensors muscle set adapted to relatively quick movements (reaction). These features along with the relative elongation of the shank and foot (the metatarsal region in particular) indicate that *Hypolagus beremendensis* exhibited well-developed cursorial ability with high jumping potential. According to Gambaryan (1974) the foot proportions are influenced by habitat, and the relatively longer feet are found in forest species (e.g., in *Lepus timidus* contra *L. europaeus*). That condition is to enhance the jumping potential i.e., the ability to perform powerful jumps of high steepness. Animals, living in more closed, bushy habitat, are characterised by the greater angle of jump departure (Gambaryan 1974). However, the problem needs further investigation, because, for example, some highly saltatorial Pliocene group of marsupials (Argyrolagidae) from Argentina developed in more open savannah-like environments (Christine Argot, personal communication 2007).

The plausibility of good jumping ability in *H. beremendensis* is strengthened by the morphology of the calcaneus, which has an elongated body, a feature connected with high jumping performance in some small mammals (Hildebrand 1974; Anemone and Covert 2000).

The paleoecological analysis of fossil assemblages from Węże 1, which yielded the majority of *H. beremendensis* material, indicates a mixed habitat with typical forest inhabitants such as cervids, flying and tree squirrels, glirids, and some species closer related with more open habitats, such as extinct representatives of Seleviniidae and Spalacidae (Sulimski 1964; Nadachowski 1990). Thus, the environment type, as inferred from the fossil assemblage and floristic studies, is the forest-steppe habitat, with more or less dense patches of vegetation (Sulimski 1964). According to White (1984) the North American *Hypolagus* was paleoecomorph of extant *Sylvilagus*, while Campbell (1969) analysing the cursorial ability of *Hypolagus* aff. *vetus* based on crural and inter-membral indices stated its intermediate position between *Lepus californicus* Gray, 1837 (one of the most cursorially-adapted leporids) and *Sylvilagus floridanus*. Moreover, the ratios calculated for *Hypolagus* aff. *vetus* are close to those of *L. europaeus* (Campbell 1969). On the other hand, the recently described *Hypolagus peregrinus* Fladerer and Fiore, 2003 from Sicily seems to be a relatively slow-running rabbit adapted to an insular habitat with diversified landscape morphology and scarce predatory threat (Fladerer and Fiore 2003). Thus, the genus *Hypolagus* exhibits a certain extent of variability in cursorial adaptations among the representatives.

Acknowledgements

The project was supported by grant P04 C 090 26 from the Ministry of Education and Sciences (Poland). The access to the collections of the Museum für Naturkunde was possible by the European Commission's Research Infrastructure Action via the SYNTHESYS (Project at DE-TAF). Thanks are addressed to Daphne Hills (Natural History Museum, London, UK), Robert Asher (University of Cambridge, UK), Renate Angermann and Irene Thomas (Museum für Naturkunde, Berlin, Germany), Gerhard Storch and Katrin Krohman (Senckenberg Forschunginstitut, Frankfurt a. Main, Germany), Naoki Kohno and Shin-ichiro Kawada (National Science Museum, Tokyo, Japan) for access to the specimens and valuable discussions. The author would like to express the warmest gratitude to Christine Argot (Muséum national d'Histoire naturelle, Paris, France) and Alexander O. Averianov (Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia) for critically reading the manuscript and many valuable comments. Also, the author is indebted to Magdalena Borsuk-Białynicka (Institute of Paleobiology, Warsaw, Poland) for helpful suggestions at the earlier stage of this work and to Samantha Hopkins (National Evolutionary Synthesis Center, Durham, USA) for the careful linguistic corrections and incisive remarks. Thanks are also directed to Grzegorz Frelik (University of Oxford, UK) for help with UPGMA analysis. The photos were made by Grażyna Dziewińska, whereas photo editing was performed by Aleksandra Hołda-Michalska and Agnieszka Kapuścińska to whom the author would like to express her gratitude.

References

Alexander, R.McN. 2003. *Principles of Animal Locomotion*. 371 pp. Princeton University Press, Princeton.

Anemone, R.L. and Covert, H.H. 2000. New skeletal remains of *Omomys* (Primates, Omomyidae): functional morphology of the hindlimb and locomotor behavior of a Middle Eocene primate. *Journal of Human Evolution* 38: 607–633.

Argot, C. 2002. Functional-adaptive analysis of the hindlimb anatomy of extant marsupials ans the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andius*. *Journal of Morphology* 253: 76–108.

Averianov, A.O. 1995. Osteology and adaptations of the early Pliocene rabbit *Trischizolagus dumitrescuae* (Lagomorpha: Leporidae). *Journal of Vertebrate Paleontology* 15: 375–386.

Camp, C.L. and Borel, A.E. 1937. Skeletal and muscular differences in the hind limbs of *Lepus*, *Sylvilagus*, and *Ochotona*. *Journal of Mammalogy* 18: 315–326.

Chapman, J.A. and Flux, J.E.C. 1990. *Rabbits, Hares and Pikas. Status Survey and Conservation Action Plan*. 168 pp. IUCN, Gland, Switzerland.

Craigie, E.H. 1948. *Bensley's Practical Anatomy of the Rabbit*. xiv + 391 pp. University of Toronto Press, Toronto.

Dawson, M.R. 1958. Later Tertiary Leporidae of North America. *University of Kansas Paleontological Contributions, Vertebrata* 6: 1–75.

Dice, L.R. 1917. Systematic position of several American Tertiary lagomorphs. *University of California Publications, Bulletin of the Department of Geology* 10 (12): 179–183.

Evans, H.E. 1993. *Miller's Anatomy of the Dog. Third edition*. 1113 pp. Saunders, Philadelphia.

Felsenstein, J. 1989. PHYLIP—Phylogeny Inference Package (Version 3.2). *Cladistics* 5: 164–166.

Fladerer, F.A. 1984. Das Vordergliedmaßenskelett von *Hypolagus beremendensis* und von *Lepus* sp. (Lagomorpha, Mammalia) aus dem Altpleistozän von Deutsch-Altenburg. *Beiträge zur Paläontologie von Österreich* 11: 71–148.

Fladerer, F.A. and Fiore, M. 2003. The Early Pleistocene insular hare *Hypolagus peregrinus* sp. nov. from Northern Sicily. *Palaeontographia Italica* 89: 37–63.

Fladerer, F.A. and Reiner, G. 1996. Evolutionary shifts in the first premolar pattern of *Hypolagus beremendensis* (Petényi, 1864) (Lagomorpha, Mammalia) in the Plio-Pleistocene of Central Europe. *Acta zoologica cracoviensia* 39: 147–160.

Fostowicz-Frelik, Ł. 2001. Limb biomechanics of the Plio-Pleistocene lagomorph *Hypolagus beremendensis* and its behavioral implications. In: Abstracts of Sixth International Congress of Vertebrate Morphology—Jena, Germany, July 21–26, 2001. *Journal of Morphology* 248: 230.

Fostowicz-Frelik, Ł. 2003. Species distribution and differentiation of Eurasian *Hypolagus* (Lagomorpha: Leporidae). *In*: J.W.F. Reumer and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia. A volume in Honour of Hans de Bruijn. *Deinsea* 10: 197–216.

Fostowicz-Frelik, Ł. 2006. *Fossil lagomorphs of Poland*. 525 pp. Unpublished Ph.D. thesis. Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Fostowicz-Frelik, Ł. 2007. Revision of *Hypolagus* (Mammalia: Lagomorpha) from the Plio-Pleistocene of Poland: qualitative and quantitative study. *Annales Zoologici* 57 (3): 541–590.

Gambaryan, P.P. 1974. *How Mammals Run. Anatomical Adaptations*. xiv + 368 pp. Keter Publishing House, Jerusalem.

Gray, J.E. 1837. Description of some new or little known Mammalia, principally in the British Museum Collection. *Annals of Natural History* 1: 577–587.

Gureev, A.A. 1964. *Zajceobraznye (Lagomorpha). Fauna SSSR, III (10)*. 276 pp. Nauka, Moskva.

Heinrich, R.E. and Houde, P. 2006. Postcranial anatomy of *Viverravus* (Mammalia, Carnivora) and implications for substrate use in basal Carnivora. *Journal of Vertebrate Paleontology* 26: 422–435.

Hibbard, C.W. 1939. Four new rabbits from the upper Pliocene of Kansas. American Midland Naturalist 21: 506–513.

Hildebrand, M. 1974. *Analysis of Vertebrate Structure*. 710 pp. John Wiley and Sons, New York.

I.C.V.G.A.N. 2005. *Nomina Anatomica Veterinaria. Fifth Edition*. Editorial Committee, Hannover. Available online at: http://www.wava-amav.org/nav_nev.htm.

Kellogg, L. 1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. *University California Publications, Bulletin of the Department of Geology* 5 (29): 421–437.

Klebanova, E.A., Polakova [Polâkova] , R.S., and Sokolov, A.S. 1971. Morfo-functional characteristics of organs of movement in lagomorphs [in Russian]. *In*: E.A. Klebanova (ed.), Morfo-funkcional'nye osobennosti organov opory i dviženiâ zajceobraznyh. Morfologiâ i ekologiâ pozvonočnyh. *Trudy Zoologičeskogo Instituta* 48: 58–120.

Kormos, T. 1930. Beiträge zur Präglazialfauna des Somlyóberges bei Püspökfürdo. *Allatani Közlemények* 27: 40–62.

Kormos, T. 1934. Zur Frage der Abstammung eurasiatischer Hasen. *Allattani Közlemények* 31: 65–78.

Leidy, J. 1856. Notices of remains of extinct Mammalia, discovered by Dr. F.V. Hayden in Nebraska Territory. *Proceedings of the Academy of Natural Sciences* 8: 88–90.

Lieber, R.L. and Blevins, F.T. 1989. Skeletal muscle architecture of the rabbit hindlimb: functional implications of muscle design. *Journal of Morphology* 199: 93–101.

López Martínez, N. 1985. Reconstruction of ancestral cranioskeletal features in the order Lagomorpha. *In*: W.P. Luckett and J.-L. Hartenberger (eds.), Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis. *NATO ASI Series A* 92: 227–276. Plenum Press, New York.

Lyon, M.W. 1904. Classification of the hares and their allies. *Smithsonian Miscellaneous Collections* 45: 321–447.

Maynard Smith, J. and Savage, J.G. 1956. Some locomotory adaptations in mammals. *Journal of the Linnean Society* (*Zoology*) 42: 603–622.

Nadachowski, A. 1990. Review of fossil Rodentia from Poland. *Senckenbergiana Biologica* 70 (for 1989): 229–250.

Petényi, S.J. 1864. A Beremendi mészkőbánya természetrajz-és őslénytanilag Petényi Salamon által leírva. *In*: F. Kubinyi (ed.). *Petényi S. János Hátrahagyott munkái*, 35-81. Magyar Tudományos Akademia, Pest.

Robinson, T.J. and Mathee, C.A. 2005. Phylogeny and evolutionary origins of the Leporidae: a review of cytogenetics, molecular analyses and supermatrix analysis. *Mammal Review* 35: 231–247.

Sargis, E.J. 2002. Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *Journal of Morphology* 254: 149–185.

Stat View 5.0.1. for Macintosh and Windows. 2001. SAS Institute Inc., Cary, USA.

Sulimski, A. 1964. Pliocene Lagomorpha and Rodentia from Węże 1 (Poland). *Acta Palaeontologica Polonica* 9: 149–244.

Sych, L. 1965. Fossil Leporidae from the Pliocene and Pleistocene of Poland. *Acta zoologica cracoviensia* 10: 1–88.

Taylor, M.E. 1976. Functional anatomy of the hindlimb of some African Viverridae (Carnivora). *Journal of Morphology* 148: 227–254.

Virchow, H. von 1928. Anatomie und Mechanik des Hasenfußes. *Zeitschrift für Säugetierkunde* 3: 98–171.

Voorhies, M.R. and Timperley, C.L. 1997. A new *Pronotolagus* (Lagomorpha: Leporidae) and other leporids from the Valentine Railway Quarries (Barstovian, Nebraska), and the Archaeolaginae–Leporinae transition. *Journal of Vertebrate Paleontology* 17: 725–737.

White, J.A. 1984. Late Cenozoic Leporidae (Mammalia, Lagomorpha) from the Anza-Borrego Desert, Southern California. *In*: R.M. Mengel (ed.), Papers in Vertebrate Paleontology Honoring Robert Warren Wilson. *Carnegie Museum of Natural History Special Publication* 9: 41–57.

Wingerd, B.D. 1985. *Rabbit Dissection Manual*. 70 + X pp. The Johns Hopkins University Press, Baltimore.

Wood, A.E. 1940. The mammalian fauna of the White River Oligocene. Part III, Lagomorpha. *Transactions of the American Philosophical Society, New Series* 28: 269–362.

Yamada, F., Takaki, M., and Suzuki, H. 2002. Molecular phylogeny of Japanese Leporidae, the Amami rabbit *Pentalagus furnessi*, the Japanese hare *Lepus brachyurus*, and the mountain hare *Lepus timidus*, inferred from mitochondrial DNA sequences. *Genes and Genetic Systems* 77: 107–116.

Young, J.Z. 1975. *The Life of Mammals. Their Anatomy and Physiology. Second Edition*. 528 pp. Oxford University Press, Oxford.

Appendix 1

Table 3. Measurements of hind limb. N, number of specimens, M, arithmetic mean, SD, standard deviation, reconstructed values italicised.

Measurement		*Hypolagus beremendensis*	*Oryctolagus cuniculus*	*Pentalagus furnessi*	*Sylvilagus floridanus*	*Lepus europaeus*
Os coxae						
Loc	N M±SD	 *78.0*	9 74.2±3.2	4 86.4	5 69.7±8.0	10 101.1±2.5
Lil	N M±SD	1 35.5	1 35.9	2 40.9	1 38.6	2 46.7
Lisch	N M±SD	4 32.6	1 29.2	2 31.5	1 31.5	2 43.0
Wilw	N M±SD	11 15.7±0.8	9 16.4±1.4	4 21.5	5 16.5±2.2	10 27.5±1.8
Wilb	N M±SD	65 8.5±0.4	9 7.6±0.6	4 8.9	5 7.4±0.8	10 11.8±0.5
Lac	N M±SD	41 9.7±0.5	9 8.3±0.3	4 10.7	5 7.8±0.7	10 12.4±0.5
Hac	N M±SD	41 9.1±0.4	9 7.9±0.3	4 9.9	5 7.2±0.5	10 11.9±0.4
Wisch	N M±SD	11 7.2±0.6	9 6.9±0.5	4 7.5	5 5.7±1.7	10 9.9±0.3
Wpu	N M±SD	4 5.8	9 4.6±0.3	4 6.6	5 4.5±0.4	10 7.1±0.7
Femur						
Lfe	N M±SD	 *94.0*	8 82.6±3.4	4 89.5	4 81.8	10 132.4±2.2
Wfepr	N M±SD	5 18.5±1.2	8 18.9±0.6	4 21.8	5 18.3±2.2	10 30.4±1.5
Wfedis	N M±SD	60 15.6±0.8	8 14.0±0.5	4 17.5	5 13.4±1.4	10 20.4±0.8
Wintf	N M±SD	62 4.0±0.5	7 4.0±0.4	3 5.0	5 3.8±0.7	10 6.1±0.5
Wpag	N M±SD	27 5.0±0.4	8 4.8±0.2	4 6.8	5 4.5±0.5	10 7.3±0.7
Hdis	N M±SD	13 17.9±1.2	7 14.7±0.5	4 17.2	5 13.6±1.4	10 20.6±1.2
Wfen	N M±SD	42 5.7±0.7	6 5.0±0.4	4 4.8	4 5.0	10 7.7±0.6
Whe	N M±SD	33 7.6±0.4	3 6.6	4 8.6	1 6.3	10 10.3±0.4
Hhe	N M±SD	40 7.0±0.7	7 6.3±0.5	4 8.2	4 5.8	10 8.9±0.4
Wfesh	N M±SD	20 7.7±0.6	8 7.0±0.5	4 8.0	5 7.0±0.7	10 9.7±0.6
Tfesh	N M±SD	20 7.1±0.5	8 6.7±0.25	4 7.6	5 6.5±0.2	10 8.9±0.5
Lmedc	N M±SD	57 10.2±0.5	6 9.0±0.3	3 11.4	4 8.5	10 13.2±0.4
Llatc	N M±SD	56 10.2±0.5	6 9.2±0.2	3 10.5	4 9.3	10 13.6±0.5
Patella						
Lpa	N M±SD	19 9.0±0.5	1 11.9	1 10.6	–	1 12.39
Wpa	N M±SD	19 5.4±0.3	1 7.13	1 6.8	–	1 6.87
Tpa	N M±SD	19 3.5±0.3	–	1 4.0	–	1 4.26
Tibia						
Lti	N M±SD	 *111.4*	7 90.4±3.8	3 91.5	4 92.7	10 148.2±4.4
Wtipr	N M±SD	27 15.5±1.3	8 14.7±0.8	3 17.9	5 14.4±1.6	10 21.0±1.4
Dtipr	N M±SD	28 14.4±1.0	8 13.0±0.5	3 12.8	5 12.7±1.1	10 19.7±0.8
Ttipr	N M±SD	25 16.0±1.2	8 15.1±0.5	3 14.2	5 14.5±1.3	10 22.3±1.0
Wtidis	N M±SD	70 13.1±0.6	8 12.4±0.6	3 15.9	4 11.2	10 16.4±0.5

Measurement		*Hypolagus beremendensis*	*Oryctolagus cuniculus*	*Pentalagus furnessi*	*Sylvilagus floridanus*	*Lepus europaeus*
Ttidis	N	70	8	3	4	10
	M±SD	6.6±0.4	5.3±0.8	6.8	5.5	8.8±0.4
Htitu	N	5	8	3	3	10
	M±SD	19.1±1.4	17.2±0.7	25.0	18.2	24.8±1.5
Wtish	N	13	8	3	5	10
	M±SD	6.8±0.5	5.9±0.3	7.6	5.3±0.3	7.6±0.2
Talus						
Lta	N	80	4	2	3	10
	M±SD	14.1±0.6	11.9	13.7	10.8	17.3±0.5
Wta	N	80	4	2	3	10
	M±SD	6.4±0.3	6.0	8.1	5.3	8.1±0.4
Ltan	N	80	4	2	3	10
	M±SD	7.0±0.4	5.8	6.8	5.1	8.9±0.4
Calcaneus						
Lca	N	69	4	3	2	10
	M±SD	26.4±1.0	23.0	27.0	20.4	34.5±0.8
Wca	N	63	4	3	2	10
	M±SD	9.5±0.6	8.1	11.8	7.2	11.7±0.8
Lcat	N	69	4	3	2	10
	M±SD	12.4±0.8	11.2	13.0	8.8	17.4±1.0
Lcab	N	69	4	3	2	10
	M±SD	10.2±0.5	8.5	9.0	8.2	12.6±0.5
Wcat	N	66	4	3	2	10
	M±SD	6.3±0.3	6.2	7.6	5.1	8.3±0.4
Naviculare						
Lnab	N	41	3	2	1	10
	M±SD	4.6±0.3	4.9	3.8	4.5	6.4±0.2
Wna	N	41	3	2	1	10
	M±SD	6.8±0.4	8.1	6.6	5.4	8.5±0.5
Tna	N	42	3	2	1	10
	M±SD	10.2±0.6	10.2	10.2	8.0	12.5±0.4
Lnat	N	42	3	2	1	10
	M±SD	9.1±0.6	11.5	8.8	9.1	13.7±0.9
Cuboid						
Lcu	N	27	2	–	1	10
	M±SD	7.8±0.5	7.4		7.1	9.3±0.7
Wcu	N	28	2	1	1	10
	M±SD	8.0±0.3	8.9	8.7	6.7	10.0±0.3
Tcu	N	29	2	1	1	10
	M±SD	6.4±0.3	7.4	7.0	5.2	8.3±0.2
Third tarsal bone (lateral cuneiforme)						
Lcn	N	7	–	–	1	1
	M±SD	4.4±0.2			4.1	6.2
Wcn	N	7	–	–	1	1
	M±SD	4.4±0.3			3.8	5.0
Tcn	N	6	–	–	1	1
	M±SD	5.3±0.3			4.2	6.6
Metatarsal II						
LMtII	N	6	7	3	4	10
	M±SD	43.9±1.7	34.8±1.0	29.6	33.4	55.6±1.8
WprMtII	N	62	5	3	2	10
	M±SD	4.4±0.2	4.7±1.0	5.6	4.6	5.2±0.2
TprMtII	N	63	5	2	2	10
	M±SD	6.9±0.4	5.2±0.8	6.8	4.1	8.7±0.4
WshMtII	N	41	5	3	1	10
	M±SD	3.8±0.2	3.5±0.3	4.4	2.8	4.35±0.2
WdisMtII	N	10	7	3	2	10
	M±SD	5.5±0.3	4.6±0.2	6.2	4.6	6.3±0.3
Metatarsal III						
LMtIII	N	5	7	3	4	10
	M±SD	42.1±2.6	35.0±2.8	27.9	34.4	56.6±2.8
WprMtIII	N	74	6	3	1	10
	M±SD	4.2±0.2	4.0±0.4	5.4	4.5	5.7±0.2
TprMtIII	N	73	2	1	1	10
	M±SD	7.0±0.3	5.1	7.2	6.0	9.1±0.3
WshMtIII	N	43	7	3	3	10
	M±SD	3.5±0.2	3.2±0.3	3.7	2.9	4.1±0.2
WdisMtIII	N	11	7	3	3	10
	M±SD	5.2±0.3	4.4±0.3	5.3	4.2	6.2±0.2

Measurement		*Hypolagus beremendensis*	*Oryctolagus cuniculus*	*Pentalagus furnessi*	*Sylvilagus floridanus*	*Lepus europaeus*
Metatarsal IV						
LMtIV	N M±SD	1 42.8	7 32.5±1.4	3 26.5	3 33.3	10 55.1±1.8
WprMtIV	N M±SD	22 5.1±0.3	4 4.1	3 4.9	2 3.6	10 5.9±0.3
TprMtIV	N M±SD	22 6.2±0.3	2 5.5	1 6.9	1 5.5	10 8.1±0.4
WshMtIV	N M±SD	21 3.3±0.3	6 3.1±0.5	3 3.7	2 3.0	10 3.9±0.2
WdisMtIV	N M±SD	12 4.6±0.5	5 4.2±0.1	3 5.5	2 4.9	10 5.9±0.2
Metatarsal V						
LMtV	N M±SD	10 37.6±0.8	6 28.1±1.6	3 21.9	3 28.1	10 48.6±1.5
WprMtV	N M±SD	35 7.4±0.4	6 5.6±0.5	3 6.7	1 5.2	10 8.1±0.3
TprMtV	N M±SD	36 5.4±0.3	5 4.0±0.9	3 6.3	1 4.3	10 7.4±0.1
WshMtV	N M±SD	23 3.3±0.2	5 2.6±0.3	3 3.5	1 2.4	10 3.5±0.2
WdisMtV	N M±SD	15 5.0±0.3	5 3.9±0.3	3 5.1	1 3.5	10 5.3±0.2
Proximal phalanx II						
LPhpII	N M±SD	12 19.74±1.6	7 15.1±0.6	3 12.8	4 14.7	10 21.2±0.7
WprPhpII	N M±SD	12 5.0±0.2	7 4.6±0.3	3 6.2	1 4.8	10 5.9±0.1
TprPhpII	N M±SD	12 4.1±0.1	7 3.6±0.1	1 4.8	1 3.5	10 5.1±0.1
WshPhpII	N M±SD	12 3.0±0.1	7 2.8±0.3	3 4.0	3 2.4	10 3.4±0.1
WdisPhpII	N M±SD	12 3.7±0.1	7 3.4±0.2	3 4.3	4 3.1	10 4.5±0.1
Proximal phalanx III						
LPhpIII	N M±SD	11 23.7±0.8	7 15.4±0.9	3 12.7	4 14.5	10 25.2±1.0
WprPhpIII	N M±SD	11 5.3±0.2	7 4.5±0.4	3 5.7	2 4.2	10 6.2±0.2
TprPhpIII	N M±SD	11 4.1±0.1	6 3.5±0.2	1 4.2	1 3.2	10 5.1±0.2
WshPhpIII	N M±SD	11 3.0±0.1	7 2.7±0.3	3 3.8	3 2.5	10 3.4±0.2
WdisPhpIII	N M±SD	11 3.8±0.1	7 3.3±0.3	3 4.3	4 3.0	10 4.4±0.2
Proximal phalanx IV						
LPhpIV	N M±SD	9 22.7±1.3	7 15.7±0.5	3 12.4	4 15.2	10 25.2±1.0
WprPhpIV	N M±SD	9 5.0±0.1	7 4.3±0.3	3 5.3	2 4.0	10 5.8±0.2
TprPhpIV	N M±SD	9 4.0±0.2	6 3.5±0.3	1 4.3	1 4.1	10 4.9±0.2
WshPhpIV	N M±SD	9 2.7±0.2	7 2.7±0.1	3 3.6	3 2.4	10 3.3±0.1
WdisPhpIV	N M±SD	8 3.5±0.1	7 3.2±0.5	3 4.1	3 3.1	10 4.3±0.2
Proximal phalanx V						
LPhpV	N M±SD	8 16.7±0.4	7 12.2±0.5	3 9.7	4 10.9	10 19.0±0.9
WprPhpV	N M±SD	8 4.5±0.1	7 3.8±0.2	3 5.1	1 3.3	10 5.0±0.2
TprPhpV	N M±SD	8 3.6±0.1	6 3.3±0.4	1 3.9	1 2.8	10 4.5±0.2
WshPhpV	N M±SD	8 2.7±0.1	7 2.2±0.2	3 3.3	3 1.9	10 2.8±0.1
WdisPhpV	N M±SD	8 3.4±0.1	7 3.0±0.1	3 3.4	3 2.6	10 4.0±0.2
Medial phalanx II						
LPhmII	N M±SD	20 10.3±0.4	6 8.5±0.6	3 7.0	4 8.7	9 10.8±0.7

Measurement		*Hypolagus beremendensis*	*Oryctolagus cuniculus*	*Pentalagus furnessi*	*Sylvilagus floridanus*	*Lepus europaeus*
WprPhmII	N M±SD	20 4.9±0.5	6 3.7±0.3	3 4.7	2 3.5	9 4.9±0.2
TprPhmII	N M±SD	20 3.9±0.2	6 3.6±0.3	3 4.4	2 3.3	9 4.4±0.2
WshPhmII	N M±SD	20 2.8±0.1	6 2.7±0.2	2 3.9	3 2.5	9 3.7±0.3
WdisPhmII	N M±SD	20 3.1±0.1	6 2.9±0.2	3 3.8	4 2.7	9 3.8±0.2
Medial phalanx III						
LPhmIII	N M±SD	21 13.6±0.4	7 9.7±0.6	3 7.3	4 8.5	9 14.0±0.7
WprPhmIII	N M±SD	21 4.1±0.1	7 3.5±0.2	3 4.7	3 3.4	9 5.0±0.3
TprPhmIII	N M±SD	21 4.1±0.2	7 3.5±0.3	2 4.2	2 3.5	9 4.7±0.2
WshPhmIII	N M±SD	21 2.7±0.1	7 2.5±0.2	3 3.8	3 2.5	9 3.5±0.3
WdisPhmIII	N M±SD	21 3.0±0.1	7 2.7±0.2	3 3.8	4 2.7	10 3.7±0.2
Medial phalanx IV						
LPhmIV	N M±SD	22 12.8±0.6	6 10.0±0.5	3 7.4	4 9.3	10 13.5±0.8
WprPhmIV	N M±SD	22 3.9±0.2	6 3.5±0.3	3 4.6	3 3.3	10 4.7±0.2
TprPhmIV	N M±SD	22 3.8±0.2	6 3.4±0.2	2 4.3	2 3.4	10 4.5±0.2
WshPhmIV	N M±SD	22 2.5±0.1	6 2.5±0.2	2 3.9	3 2.4	10 3.2±0.2
WdisPhmIV	N M±SD	22 2.9±0.1	6 2.7±0.2	3 3.7	4 2.7	10 3.6±0.3
Medial phalanx V						
LPhmV	N M±SD	22 9.1±0.6	6 6.9±0.5	3 5.1	4 5.8	6 9.1±0.7
WprPhmV	N M±SD	22 3.8±0.2	6 3.1±0.2	3 4.4	1 2.9	6 4.3±0.1
TprPhmV	N M±SD	22 3.6±0.2	6 3.1±0.3	2 4.0	1 2.5	6 3.7±0.1
WshPhmV	N M±SD	22 2.7±0.1	6 2.3±0.2	1 3.6	1 2.3	6 3.3±0.2
WdisPhmV	N M±SD	22 3.0±0.2	6 2.5±0.2	3 3.5	4 2.4	6 3.4±0.1

Table 4. Indices of metatarsal bones and phalanges in percentages. N, number of specimens, M, arithmetic mean, SD, standard deviation, reconstructed values italicised.

Index		*Hypolagus beremendensis*	*Oryctolagus cuniculus*	*Pentalagus furnessi*	*Sylvilagus floridanus*	*Lepus europaeus*
IproxMtII	N M±SD	62 63.6±5.4	4 98.1	2 82.1	1 66.9	10 59.5±2.1
IproxMtIII	N M±SD	73 59.5±2.8	2 73.6	1 73.4	1 74.4	10 62.2±2.4
IproxMtIV	N M±SD	22 81.7±4.0	2 75.2	1 72.6	1 84.1	10 72.9±3.8
IproxMtV	N M±SD	35 137.4±9.0	5 144.7±34.2	3 98.6	1 121.1	10 109±5.4
IsPhpII	N M±SD	12 44.4±2.4	7 53.3±3.1	3 82.6	1 56.1	10 49.5±1.9
IsPhpIII	N M±SD	11 38.2±1.2	7 51.3±5.1	3 79.0	2 50.2	10 42.2±1.4
IsPhpIV	N M±SD	8 37.8±2.2	7 48.2±4.6	3 76.3	2 47.8	10 40.4±1.5
IsPhpV	N M±SD	8 47.6±1.5	7 56.0±3.8	3 88.6	1 52.4	10 47.1±1.7
IsPhmII	N M±SD	20 69.1±2.8	6 77.3±5.1	3 122.1	2 71.3	9 81.5±7.0
IsPhmIII	N M±SD	21 52.9±1.9	7 64.4±6.4	3 117.5	3 73.0	10 62.3±2.5
IsPhmIV	N M±SD	26 53.7±3.0	6 61.9±3.6	3 113.6	3 65.8	10 62.1±4.3
IsPhmV	N M±SD	22 75.3±4.7	6 81.7±9.1	3 155.5	2 101.3	6 85.0±7.3