

Krystyna CABOŃ-RACZYŃSKA

Studies on the European Hare. III. Morphological Variation of the Skull

Badania nad zajęcem szarakiem. III. Zmienność morfologiczna czaszki

[With 5 Figs. & 16 Tables]

I. Introduction	250
II. Material and methods	250
1. Description of the material	250
2. Craniometrical measurements	250
3. Description of the age classes distinguished	251
III. Morphological description of the skull	254
1. <i>Os occipitale</i>	254
2. <i>Os temporale</i>	255
3. <i>Os sphenoides</i>	256
4. <i>Os parietale</i>	257
5. <i>Os interparietale</i>	257
6. <i>Os frontale</i>	258
7. <i>Os ethmoidale</i>	261
8. <i>Os nasale</i>	261
9. <i>Os lacrimale</i>	261
10. <i>Os maxillare</i>	262
11. <i>Os intermaxillare</i>	263
12. <i>Conche nasales</i>	263
13. <i>Vomer</i>	264
14. <i>Os palatinum</i>	264
15. <i>Os pterygoideum</i>	264
16. <i>Os zygomaticum</i>	265
17. <i>Mandibula</i>	266
IV. Obliteration of the skull sutures	267
V. Variation in skull measurements	268
1. Absolute values of measurements	269
2. Rate of growth of the skull	274
VI. Proportions of the skull	277
VII. Discussion	278
VIII. Summary	282
References	283
Streszczenie	285

I. INTRODUCTION

The skull of the European hare — *Lepus europaeus* Pallas, 1778 — has not as yet been given complete morphological treatment. This remark also applies to related species, which represent a similar type of skull structure to *Lagomorpha*. The relatively most abundant morphological literature is concerned with the rabbit, *Oryctolagus cuniculus* (Linnaeus, 1758) but papers on the anatomy of the skull of this species are scattered and in monographies these problems have received only general treatment (Krause, 1884; Zedenov et al., 1957). In addition the structure of the skull of *Leporidae* exhibits far-reaching specific characters which make it difficult to grasp any analogy with other species of animals of which the skull has been fully described.

Taxonomic descriptions of the characters of the hare's skull are to be found in faunistic papers (Ognev, 1940; Gaffrey, 1961; Koby, 1959; Gureev, 1963, 1964; also in the monograph by Korneev, 1960). Text-books on animal anatomy, on the other hand, with a few exceptions (Kolda, 1936; Poplewski, 1948) do not enter into a detailed description of the skull structure of *Lagomorpha*.

The present investigations are based on an extensive series composed of skulls from specimens of *L. europaeus* of different ages, taken from a relatively limited area. This material made it possible to analyse the structure of the skull from the angle of growth and age changes and formed a basis for a morphological description and definition of the scale of individual variation.

II. MATERIAL AND METHODS

1. Description of Material

The material used for the investigations consisted of hares shot in the Poznań province in monthly series, over the period from December 1958 to February 1960. Shooting was carried out chiefly in the south-eastern part of the province, according to a previously-arranged plan which ensured the random character of the samples obtained. As many of the skulls were damaged during shooting only 482 skulls were used for craniometrical purposes, and the majority of the measurements were made on these skulls.

The skulls were prepared after previously being boiled, only the undamaged mandibles being in addition subjected to maceration and later weighing.

2. Craniometrical Measurements

A total of 26 linear measurements were made on the skulls, and the value of the weight of the mandible was in addition found for 103 specimens. The measurements were made using a vernier calipers with a nonius, the result being read with accuracy to 0.1 mm. Both jaws with complete sets of teeth were weighed on a laboratory balance with accuracy to 50 mg.

The numerical material was given statistical treatment, using the Student test for comparison of differences between mean values. A large number of indices

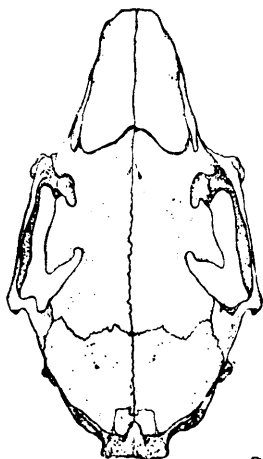
were calculated in order to grasp the proportions of the skull. Increases in measurements in different age groups were expressed in percentages in relation to age class I.

The majority of the measurements were made after Duerst (1926), but in view of the specific character of the skull structure in hares certain measurements were modified. The following measurements were made:

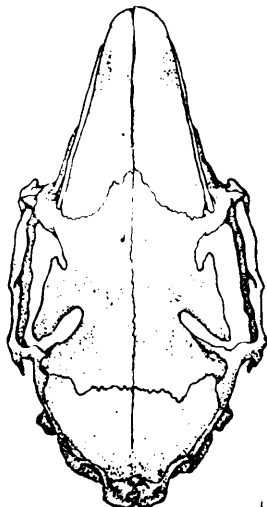
1. Basal length: *Prosthion* — *Basion*.
2. Condylbasal length: *Prosthion* — posterior plane of the occipital condyle.
3. Profile length: *Prosthion* — *Acrocranium*.
4. Length of the facial part: *Prosthion* — to a point lying on the intersection of the frontal suture with a line drawn between the anterior margins of *incisura postorbitalis*.
5. Length of brain-case: from a point lying on the intersection of the frontal suture with a line drawn between the anterior margins of the *incisura postorbitalis* — *Acrocranium*.
6. Nasal length: *Rhynion* — *Nasion*.
7. Nasal length: measured on the internasal suture
8. Maxillary tooth row: *Praemolare* — *Postdentale*.
9. Length of *margo adentalis*: from the posterior margin of alveola to the anterior margin of alveola Pm¹.
10. Sagittal length of frontal bone: *Nasion* — *Bregma*.
11. Sagittal length of parietal bone: *Bregma* — *Lambda*.
12. Mandibular tooth row.
13. Length of mandible: from a point lying nearest cranial on the mandibular symphysis — to the furthest point on the angular process of the mandible.
14. Maximum skull breadth: *Zygion* — *Zygion*.
15. Breadth of brain-case: *Euryon* — *Euryon*.
16. Occipital breadth: distance between the most laterally situated points on *exooccipitale*.
17. Minimum breadth of frontal bones: measured between the anterior margins of *inc. postorbitales*.
18. Maximum breadth of nasalia.
19. Minimum breadth of nasalia: *Nasointermaxillare* — *Nasointermaxillare*.
20. Breadth of occipital squama: measured on the nuchal ridge.
21. Breadth of *for. occipitale magnum*.
22. Height of *for. occipitale magnum*.
23. Depth of brain case: *Sphenobasion* — to a point lying in the central section of the sagittal suture.
24. Palatal height: *Staphylion* — *Nasion*.
25. Height of dental processes: measured from external margin of alveola Pm³ to upper surface of the alveolar bulla.
26. Height of *ramus mandibulae*: *conion ventrale* — *condylion medniale*.
27. Weight of jaw.

3. Description of age classes

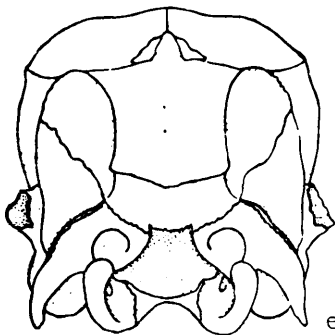
The material was divided into four age classes, according to the growth changes in the skull connected with the progressive ossification of the sutures with age, in particular of *sut. frontalis*, *sut. coronaria*, *sut. sagittalis* and *sut. parietotempo-*



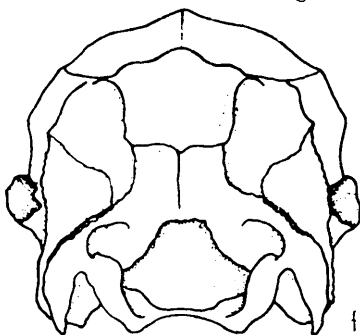
a



b



e



f

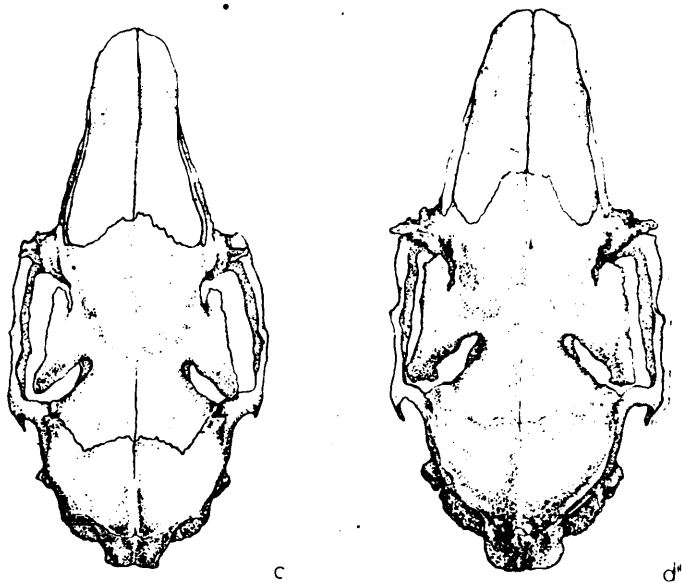


Fig. 1. Ossification of the skull sutures in consecutive age classes, a, e) Age class I, b, f) Age class II, c) Age class III, d) Age class IV.

ralis. The study made by Empel (1957) of the rabbit has been used as a guide in allocating material into age classes. On account of the possibility of making use of a large number of supplementary data on the shot hares, the date of shooting, body weight and state of the gonads were in addition taken into consideration in determination of the age classes. Comparison was also made of results with the independently classified age groups of this same material on the basis of age changes in the pelvis (Bujalska, 1964). As a result a division was obtained which grouped individuals of relatively equal absolute age in each class (Fig. 1).

Age class *I* includes individuals not over 6 months old. The skull sutures are loose without any trace of ossification, *os interparietale* is clearly distinguished and the sutures within *os occipitale* are clearly visible. The structure of the skull is delicate. During the first phase of the work all young individuals shot during the period from April to August, which came from litters born "that year" (body weight not exceeding 3 kg, gonads juvenile) were chosen. Bearing in mind that the first litters came from the end of February and beginning of March (Raczyński, 1964), none of the specimens taken as representatives exceeded the age of 6 months. Age of material from the following months was determined according to the representative standard specimens chosen. Individuals in this age class occur in the material from April to December.

Class *II* includes individuals aged from 6—8 months. *Os interparietale* is either difficult to distinguish or its margins are already completely obliterated. The sutures within *os occipitale* are either in process of obliteration or are completely obliterated. The ossification process has begun in the posterior section of *sut. sagittalis*. The skull as yet retains a fairly delicate structure. The standard examples of this age class were chosen from skulls of hares from August and September, which differed in appearance from those accepted for class *I*. This group is in addition characterised by the juvenile structure of the genital organs (in August–September), while the body weight includes values characteristic of both age class *I* and of adult individuals. Hares in this age class occur in the material from August to February.

Age class *III* includes animals aged from approximately 9—12 (13) months. The *sut. frontalis* has begun to ossify in the medial section, $\frac{1}{2}$ of the suture being already ossified (from the front) in certain individuals. *Sut. sagittalis* is ossified along $\frac{1}{2}$ of its length, counting from the posterior. The ossification process has begun in *sut. parietotemporalis*. The boundaries of *os interparietale* are completely obliterated. Age class *III* is distinctly transitional in character, since the skull does not differ greatly as regards the morphological aspect from the appearance of individuals in age class *IV*. Specimens in this class occur in all the months of the year.

Age class *IV* includes individuals over 1 year old. Complete ossification of the following sutures: *sut. frontalis*, *sut. sagittalis*, *sut. parietotemporalis* and occasionally *sut. coronaria*. Near the boundary of the juncture of sutures: *frontalis*, *sagittalis* and *coronaria* sections of these sutures not as yet ossified can often be seen. The ossification (closing) of *inc. praeorbitalis* occurring between *proc. supraorbitalis oralis* and *os frontale* can be used as a positive character in the identification of this age group. This class includes individuals shot in all the months of the year.

III. MORPHOLOGICAL DESCRIPTION OF THE SKULL

1. *Os occipitale*

The following parts can be distinguished in the occipital bone: unpaired *basioccipitale*, paired *exooccipitale* and *squama*, which in view of the fact that it differs in structure from that in other mammals is particularly worthy of notice in the hare.

Squama ossis occipitalis is composed of two principal parts (*pars nuchalis* and *pars parietalis*). *Pars nuchalis* consists of a vertical plate, the lower margin of which separates *for. occipitale magnum* from the top and terminates at the top in *crista nuchalis*. *Crista occipitalis ext.* can be seen in the middle of this part, in the vertical plane. Sutures running diagonally in relation to the vertical axis of the skull divide the squama from the lateral parts of *os occipitale*. These sutures are clearly visible in age class *I*, not infrequently in class *II*, while as from class *III* the boundaries of this part of the occiput become obliterated. The second part of the occipital squama (*pars parietalis*) is far larger in area than *pars nuchalis*. It is worthy of note that in the hare the squama directly participates in the structure of the vault of the skull. The arched part of the squama has a lacy structure but differs from that in *os maxillare*. Its structural elements are arranged very densely, the spaces between them are small, and the bone trabeculae thick. In *pars parietalis* the medial part and two lateral parts are clearly distinguishable, situated lower and adjacent to the *pars mastoideum os. temporalis*. The medial part takes the form of a narrow projection bounded by well-developed bony margins, which contrary to the medial part are very compact in structure. These margins are elongated laterally in their arched line, forming a bony ridge of compact structure. They form the anterior and partly the lateral margin of the occipital squama. In general appearance they are similar in shape to a lyre. The vaulted part of *os occipitale* borders from the front with *os. parietalia*. *Sut. lambdoides* does not ossify even in late old age in animals. From the sides the squama is bordered by *sut. occipitomastoidea*, not as yet ossified in hares from age class *III*. In older animals (from age class *IV*) it is often ossified, but is always clearly distinct in the form of a narrow, bony bridge running diagonally to the long axis of the skull.

Exooccipitale forming together with the vertical plate of *squama occipitalis* the posterior wall of the skull, borders from the front with the temporal bone (with the mastoid part and the petrous part). *Condylia occipitales* lie pericentrally, laterally bounding *for. occipitale magnum*. *Procc. jugulares*, the free ends of which protrude beyond the lower sur-

face of *bullae tympanicae*, project laterally from *condyli occipitales*. *Exooccipitalia* are joined with *basioccipitale* by means of sutures, which are clearly visible in individuals in age class I. In age class II these sutures are completely ossified and the boundary of their original course is invisible. *Fossa condyloidea ventralis* is situated between the occipital condyle and the jugular process. In this fossa, pericentrally, at the base of condyli, there is a small, usually paired *for. n. hypoglossi*. *For. lacerrum aborale*, similar in appearance to a lengthways fissure, vertical to the long axis of the skull, is situated on the boundary of the lateral occiput and the tympanic part of the temporal bone, in the condyloid fossa.

Basioccipitale is connected from the front with the sphenoid bone by means of *synchondrosis sphenoccipitalis*, and from the back is joined with the lateral parts of the occiput, with which as from age class II it forms one whole. Laterally *basioccipitale* is connected by a suture, clearly visible in old animals, with the tympanic part of the temporal bone. On the surface of the corpus of the occiput in old animals from age class IV, lengthways bony crests are often formed, which seen from the side of the occipital foramen are similar in shape to a letter Y.

2. *Os temporale*

Os temporale has a distinct squama to which the three other parts of *os temporale*: the mastoid, tympanic and petrous parts, adhere fairly loosely.

Squama os. temporalis borders from the front with the frontal bone and the temporal wing of the sphenoid, from the bottom with the pterygoid bone and from the top by parietal bone. At the back in the upper section it borders with *squama os. occipitalis*, then with the other parts of the temporal bone. The posterior margin of the squama has a lacy structure. It is possible to distinguish in the squama the orbital surface and the lateral surface which forms the lateral part of the wall of the braincase. *Proc. zygomaticus os. temporalis* is formed on the boundary of the above surfaces, running vertically to the squama and then inclining downwards. Above *proc. zygomaticus* there is a small tuberculate process, situated on the posterior extremity of the orbit, which is fairly well developed in older animals (age class IV). *Proc. squamosus* (K r a u s e, 1884), flat, relatively long, spade-shaped with a broader end runs from the posterior margin of the squama, adhering to the *pars mastoidea os. temporalis*. It strengthens the juncture of the squama with the

other parts of the temporal bone, but it is characteristic that it does not fuse permanently with the mastoid part.

Pars mastoidea is of a spongy structure. The posterior margin adheres closely to *exooccipitale*. In certain specimens from age class IV these two bones fuse. It is connected at the top with the occipital squama, from the front with the spongy margin of the temporal squama, and from the bottom with the tympanic part. *Proc. mastoideus* is faintly formed. It runs parallel to *proc. jugularis*, partly adhering to *bullae tympanicae*. On the boundary between *pars mastoidea* and *pars tympanica*, at the base of the external mastoid duct there is *for. stylomastoideum*.

Pars tympanica forms *bulla tympanica* together with *meatus acusticus ext.* *Bullae tympanicae* are relatively well developed, bullate, slightly flattened laterally. On the side of the base of the skull they adhere to *basioccipitale* by means of narrow, horizontally lying bony projection. On its margin, near the wall of the bulla, there is round opening (*for. tympanicum*). From the front of *bulla tympanica* a small *proc. muscularis* can be seen. The connection between *pars tympanica* and *basioccipitale* is strengthened by a bony process of the tympanic part, not visible from the exterior, which enters into a fairly deep sulcus situated on the lateral surface of *basioccipitale*.

Meatus acusticus ext. takes the form of a fairly short tube, directed diagonally upwards and opening in a round *porus acusticus ext.*

Pars petrosa seen from the internal side of the braincase covers *pars mastoidea*. The upper part of this bone is occupied by the extensive *fossa subarcuata*, opening into the interior of the skull by a smaller foramen. *Porus acusticus int.* is situated below *fossa subarcuata*. Towards the front from this opening there is a semilunar cavity leading to *canalis facialis*, through which the facial nerve runs, passing out through *for. stylomastoideum*. From the front *pars petrosa* passes into a well developed *crista petrosa*.

3. *Os sphenoides*

Os sphenoides is composed of three principle parts: *corpus ossis sphenoidi* and two pairs of wings: *alae orbitales* and the slightly smaller *alae temporales*.

It is possible to distinguish in *corpus os. sphenoides* the *praesphenoidium* and *basisphenoidium*. At the place where it joins the occiput the *basisphenoidium* is broader and more massive, narrowing towards the front and inclining into the middle of the braincase. Paired *procc.*

pterygoidei, which are laterally fused with the *hamuli os. pterygoidei*, run from the sides of *basisphenoideum* in downwards and slightly lateral directions. From the front they are bounded by the vertical plate of the *os palatinum*, while the posterior margin remains free. In the middle of the cranial surface of the *basisphenoideum* there is a deep *fossa hypophyseos*. On the bottom of this fossa, pericentrally there is an opening piercing in a vertical direction the middle of *corpus os. sphenoides*, this is *canalis craniopharyngeus* (Poplewski, 1948). The fact is worthy of emphasis that there is a distinct fissure separating the corpus of the two parts between *praesphenoideum* and *basisphenoideum*. Both *alae orbitales* and *alae temporales os. sphenoidalis* run from the separate *praesphenoideum*. The alae are separated by a large round *for. interorbitale* formed by the juncture of paired *foramina optica*.

Ala orbitalis borders at the top with the frontal bone, from the interior of the nasal cavity from the front with the ethmoid bone and from the bottom with the vertical plate of the palatal bone. Within the frontosphenoidal suture there is the small fissure-like *for. ethmoidale*, which is sometimes shifted slightly upwards and occurs within the orbital part of the frontal bone.

Ala temporalis borders at the top with the frontal bone, at the back with the temporal bone and at the bottom with the pterygoid bone. *Allae temporales* are slightly smaller than *alae orbitales*. There is a nodose area at the back of *ala temporalis* on the boundary of the connection with the temporal and pterygoid bones.

4. *Os parietale*

The paired *ossa parietalia* take the form of a slightly convex plate. They participate in the formation of the vault of the skull. From the front the parietal bone borders with the frontal bone, from the sides with the *squama os. temporalis* and from the back with the occipital and interparietal bones. Contrary to the rabbit, in the hare parietal bones usually have a smooth external surface.

5. *Os interparietale*

Os interparietale is visible in the skull of the hare only in age class I and takes the form of paired, small elements, which consist of two oval plates contacting each other in the sagittal plane. They are of porous structure. They do not fuse with the occipital bone even in very old animals. On the skull of adult specimens the place in which os

interparietale occurs may be defined owing to the porous structure of its surface.

6. *Os frontale*

Two principle elements can be distinguished in the paired *os frontale*: a horizontal plate, slightly convex in the centripetal part, and a vertical plate forming the upper part of the orbit. The two parts are separated by *proc. supraorbitalis*, in which *proc. supraorbitalis oralis* and *proc. supraorbitalis aboralis* (Popesco, 1961) can be distinguished. *Proc. supraorbitalis oralis* is usually separated from the vaulted part of *os frontale* by a small *incisura praeorbitalis*, *proc. supraorbitalis aboralis* is bordered laterally by the deep *incisura postorbitalis*.

The vaulted part of the frontal bone takes the form of a squama, slightly concave in the anterior part, or flat along a line connecting *incisura postorbitalis*, then becomes slightly convex, finally to decline in the direction of the parietal bones. The highest convexity of the skull lies slightly caudal from the postorbital narrowing in the sagittal plane. *Sut. coronaria* undulates symmetrically to the long axis of the skull. On both sides of *sut. frontalis* in the depression of the squama of frontal bone there are small foramina, or sometimes only a single foramen.

In the anterior part the frontal bones form the nasal processes, wedging in between the nasal bones. The shape of these processes differs, but two principal types can be distinguished: 1. processes with sharp ends together forming an isosceles triangle, the base of which is formed by a line connecting the posterior margins of the nasal bones; 2. the ends of the processes end in a line vertical to the long axis of the skull, forming a figure similar to a trapezium (Fig. 2). In cases in which the first shape occurs the processes are usually long (measuring along the frontal suture from a line connecting nasal bones), and in the case of the occurrence of the second type of shape the processes are usually short. As a rule 64% of the individuals in the material had processes of the first type described and 36% the second type.

In addition to the above nasal processes of the frontal bones well-developed lateral processes of the frontal bone occur in the hare. They lie laterally in relation to the nasal processes of the intermaxillary bone but ventrally in the anterior part in relation to the nasal processes of the intermaxillary bone. The lateral processes are very thin and fairly long — they form about $\frac{1}{2}$ of the length of the nasal processes of *os incisivum*. The base of the lateral processes is

massive, rough and forms the upper-anterior section of the orbit contiguous to *hamulus os. lacrimalis* and *proc. sphenoorbitalis* (Krause, 1884).

Procc. supraorbitales are distinguished by considerable variability of shape with age (Fig. 3). In individuals from age class I these processes have a very delicate structure, are relatively small, often similar to the analogical processes in the rabbit. With age the processes become more massive and develop. *Procc. supraorbitales post.* in certain of the individuals in age class III, and as a rule in class IV, extend to small tuberclose processes on *os temporale* and close the postorbital incisure with a cartilaginous bridge. *Procc. supraorbitales ant.* are particularly worthy of note from the systematic aspect. The shape of the processes is

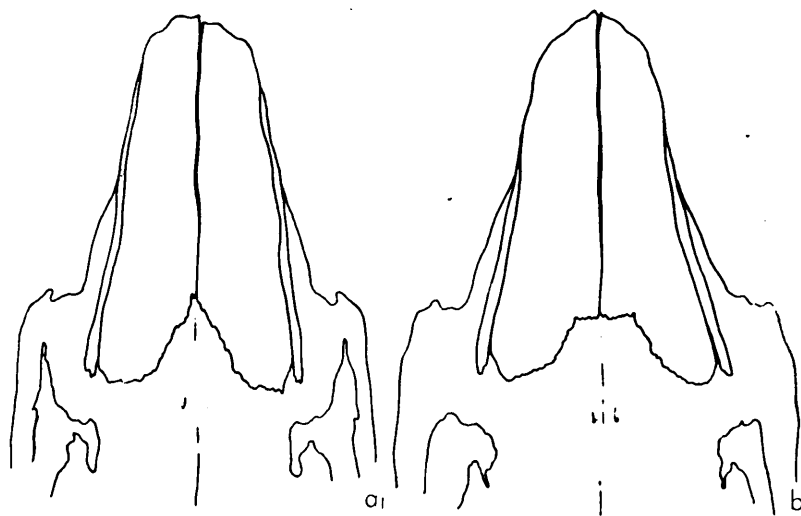


Fig. 2. Shape of nasal processes of the frontal bone. a) Type characteristic of *L. europaeus*, b) Type characteristic of *L. timidus* (after Kobay, 1959).

treated as an additional systematic character distinguishing *L. europaeus* from *L. timidus*. In *L. europaeus* these processes are described as longer and therefore the *incisura praeorbitalis* is deeper than in *L. timidus*. In the present material, in age class IV, that is, in fully-grown individuals, the process of complete closing of anterior incisure was observed. This closing of the depression occurred in 33.2% of the specimens. In the place in which the incisura had originally occurred single, small foramina in the bone plate remain in many cases. The phenomenon of the ossification of *incisura praeorbitalis* would seem to be a process connected with the age of the animals, but it does not occur

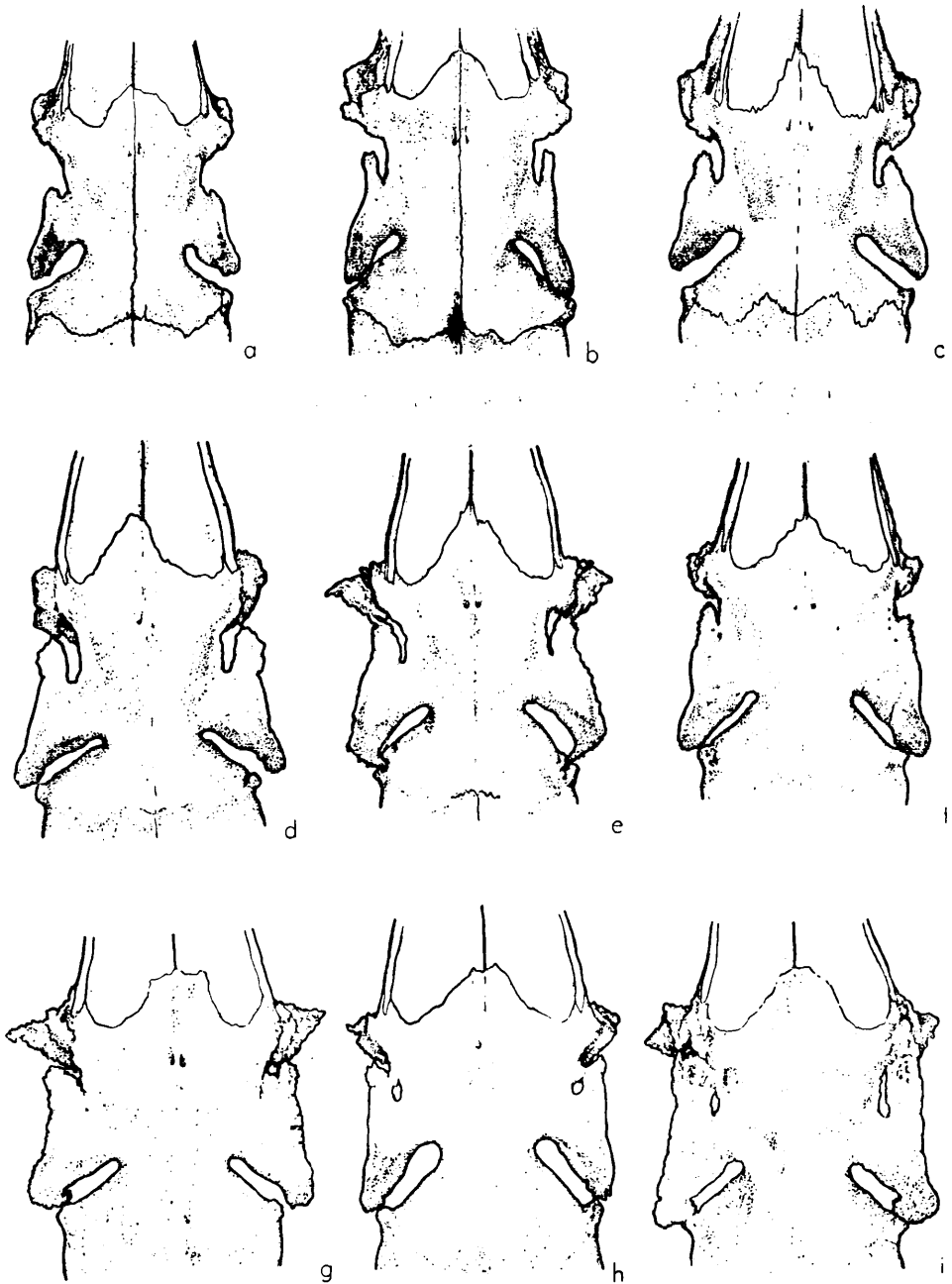


Fig. 3. Variation in the shape of supraorbital processes of the frontal bones. a) Age class I, b) Age class II, c) Age class III, d-i) Variation the shape of supraorbital processes in age class IV.

regularly. In age class *III* it was only in a few cases that the initial process of closure of *incisura praeorbitalis* was observed. This process takes place unevenly in the two *incisurae* (in right and left).

7. *Os ethmoidale*

Lamina cribrosa is divided into two parts by the narrow *crista galli*. Bony prominences can be seen on both sides of the crest, which is fairly high throughout its entire length. *Lamina cribrosa* is similar in shape to an isosceles triangle turned base upwards, and has small and large foramina scattered all over it. *Ethmoturbinalia*, in the form of rolled, thin bony plates, similar to the tube of a cigarette in shape, proceed from *lamina cribrosa* in a forwards direction.

Lamina perpendicularis together with the vomer form the posterior part of the nasal septum.

8. *Os nasale*

The nasal bones, joined medially by *sut. internasalis*, usually take the shape of a parallelogram, with diagonally directed anterior and posterior margins. They are of uniform breadth throughout their whole length, the lateral parts giving the impression of narrowing towards the front only because they decline downwards. The nasal bones border at the top with *apertura piriformis*, but their free ends do not reach to the farthest cranial point on the skull, which lies on the intermaxillary bone. —

The nasal bones border laterally with the nasal processes of the intermaxillary bones and from the back with frontal bone.

9. *Os lacrimale*

Os lacrimale in the hare takes the form of a thin, irregular bone plate situated in the anterior part of the orbit. Only *lamina orbitalis* is well shaped here, being very delicate and easily damaged during preparation. In the anterior part of *os lacrimale* there is a distinct *for. lacrimale* bordered from the front by the orbital margin of the jaw. It leads to *ductus nasolacimalis*. Immediately above *for. lacrimale* an elongate process — *hamulus os. lacimalis* — passes laterally from the plate. In the youngest specimens (age class *I*) it is delicate, while in older animals it becomes more massive and developed on the exterior. In individuals in age class *IV* spongy bony tissue is often observed to grow on its surface, which sometimes leads to the connection of the hamulus

with *proc. supraorbitalis oralis*. Lachrymal bone has a relatively loose connection with the neighbouring bones and does not fuse with them even in old animals.

10. *Os maxillare*

Os maxillare in the hare, as in other representatives of *Leporidae*, is characterised by a specific structure. *Corpus maxillae* in particular differs from the typical structural plan, possessing a delicate lacy structure, especially loosely constructed in the upper part. The corpus is, however, bordered by fairly strong bony elements — from the top by *proc. nasalis intermaxillae* and *proc. lateralis os. frontalis*. From the back strengthening is provided by the anterior margin of the orbit, formed of the compact structure of *maxilla*, shaped in the form of *proc. sphenoorbitalis* (Krause, 1884). The structure of the lower surface of the corpus (*margo adentalis*) is also strong. On the *corpus maxillae*, at the height of *Pm¹ for. infraorbitale*, opening ventral, is situated opposite the base of the zygomatic arch. *Proc. zygomaticus maxillae* connecting with the zygomatic bone, is situated at the back, behind *for. infraorbitale*. There is a well-developed *crista facialis* on the *proc. zygomaticus maxillae*.

Proc. alveolaris occupies the upper row of teeth in a straight line, almost parallel to the long axis of the skull. *Alveoli dentales* have an even internal margin and a convex, considerably higher, external margin. The external margins of the tooth crowns do not project much above the margins of the tooth sockets. Each of the tooth sockets are separated by transverse thin bony septa. The tooth sockets are closed from above by *bulla alveolaris maxillae* situated in the antero-ventral part of the orbit.

Proc. palatinus takes the form of a narrow horizontal bony plate, running vertically towards the upper premolars and is connected with the opposite process by means of *sut. palatina media*. On the boundary of the connection of the two processes they form a characteristic projection in the anterior part. The posterior margins of the processes are strongly fused with the very narrow *lamina horizontalis os. palatini* forming in the medial part, in individuals in age class I, from $\frac{1}{2}$ to $\frac{1}{3}$ of the length of the hard palate and about $\frac{1}{4}$ of the length of the hard palate in older individuals. These relations are, however, very variable and may not agree with the proportions given. At the base of the *procc. palatini maxillae* on the boundary with the *lamina horizontalis os. palatini*, there is usually one *for. palatinum*.

11. *Os intermaxillare s. os incisivum*

Os incisivum (= *intermaxillare*) in the hare has a relatively massive structure. The corpus is bordered from the side and bottom by *apertura piriformis* of the nasal cavity. From the front there is tooth socket I¹ and at the back of it the smaller tooth socket of incisor I², with a round cross-section. Inside the corpus tooth socket I¹ follows an arched course, and ends without extending to *sut. incisivomaxillaris*. *Proc. nasalis os. intermaxillaris* runs from the corpus on the dorsal side. It is a characteristic feature that it extends as far as the frontal bone, ending beyond the most caudad margin of the nasal bone or on a line with it, sometimes not extending quite as far as it. The nasal processes do not fuse with either the nasal bone or *corpus maxillae* throughout the whole life of the animal.

The palatal processes of both incisive bones run from the place at which these bones connect along a lengthways axis of the skull, ending near the hard palate. They divide along a considerable section *forr. incisiva*, which near the hard palate connect in one foramen. *Procc. palatini* fuse together only at the base and further along there is contact only between the flattened pericentral surfaces. From the dorsal side they jointly form a bony sulcus, created as the result of the upwards inclination of the external margins of the processes. The lower cartilaginous margin of the nasal septum runs along the bony sulcus, while the vomer adheres to its posterior section.

Os incisivum borders at the back with maxilla and through the nasal process with the frontal bone, from the back and top with *os nasale*, and through *procc. palatini* with the vomer.

12. *Conchae nasales*

Nasoturbinale in the hare occurs in form of a smooth, irregular lamina attached to *crista nasoturbinalis*.

Maxilloturbinale is strongly developed. The upper lamina, branching like a tree into several delicate, tube-shaped canals, passes from short basal plate attached to *crista maxilloturbinalis*. The lower lamina is smaller, far shorter and only slightly branching.

13. *Vomer*

The vomer takes the form of a thin, delicate plate bent in an arch. From the front the lower margin enters into a sulcus formed by the palatal processes of the intermaxillary bone. At the back the vomer has

a free sharp end, reaching to the level of the anterior margin of *praesphenoideum*. The upper margin of *vomer* forms the deep *sulcus vomeris*, bordered by thin lamina situated parallel to it. The two *alae vomeris*, connecting with *lamina perpendicularis os. palatini*, proceed from the posterior of the margin of sulcus. It is remarkable that *vomer* does not connect with *praesphenoideum*. As it has no connection with the hard palate it does not completely divide the internal *choanae*.

14. *Os palatinum*

Os palatinum consists of two plates situated vertically to each other. *Lamina horizontalis* is weakly developed and forms the posterior narrow margin of the hard palate, connecting by means of a suture with the *procc. palatini maxillae*.

Lamina perpendicularis, together with *basisphenoides* and *proc. pterygoideus*, form the upper and lateral walls of the nasopharyngeal cavity. In the anterior part from the bottom the *lamina perpendicularis* overlaps on the internal wall of *procc. alveolares maxillae* up to the height of the tooth sockets, then passes to the exterior of the final section of the maxilla. In its continuance caudal it forms two lateral processes, one of which, the external process, overlaps from the bottom on to hamulus of the pterygoid bone, while the second, internal process, partly overlaps on the pterygoid process of the sphenoid bone. The lower margin is free.

15. *Os pterygoideum*

Os pterygoideum in the hare is fairly distinctly separated even in adult specimens (from age class IV). It consists of two parts: of a convex squama, forming part of lateral and lower wall of the braincase, and equal in size to the *squama os. temporalis*, and of a hamulus projecting in a downwards and forwards direction.

Pars squamosa at the back, near the juncture with *pars tympanica os. temporalis*, has a characteristic lacy structure. In the front, at the place in which it is joined with the temporal pterygoid of the sphenoid bone the orbit is fairly densely tuberculate, this being visible as early as in specimens from age class I. The anterior margin of the squama is bordered from the back and bottom by the quadrilateral-shaped *for. orbitorotundum*. The base of *hamulus os. pterygoidei* is pierced by an oval *for. pterygoideum*, and laterally from this foramen two small foramina can be seen. The anterior margin of the hamulus overlaps on

to the lateral process of the palatal bone. The *hamulus os. pterygoidei* fuses with the *proc. pterygoideus os. sphenoidalis*, and both these elements jointly border the extensive *fossa pterygoidea*.

In view of the fact that a considerable part of *os pterygoideum* directly participates in the structure of the braincase, it may be considered as among the elements shaping the cranium in *Leporidae*.

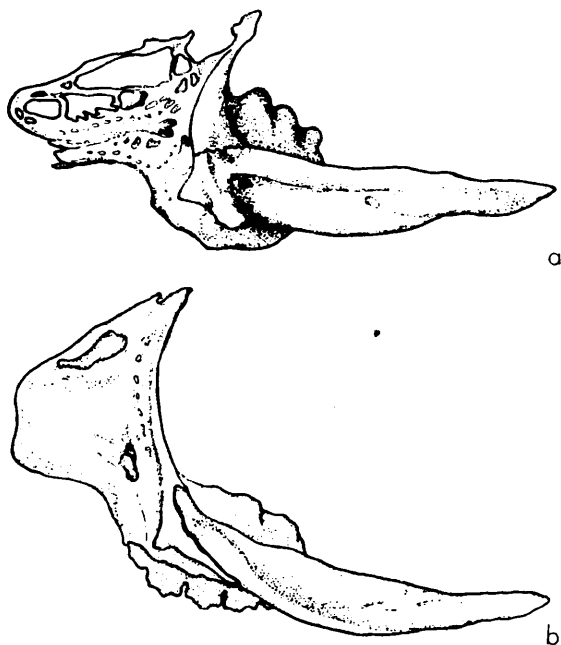


Fig. 4. Course taken by *sut. zygomaticomaxillaris*. a) In the rabbit, according to Krause (1884), b) In the hare.

16. *Os zygomaticum*

Os zygomaticum in the hare does not occur independently, since very early on it fuses completely with the maxilla by means of *proc. zygomaticus maxillae*. In the study material the *sut. zygomaticomaxillaris* was not observed, but it was present in the embryonic stage in a foetus a few days before birth. On these grounds it can be established that this suture runs above *crista maxillae*, *proc. orbitalis* forming the lower anterior angle of the orbit (Fig. 4). For the reasons given above it is more correct to use the term *arcus zygomaticus*, beginning from the front from *crista maxillae*. The arch runs caudal and inclines slightly

upward, passing into *proc. temporalis os. zygomatici*, with which *proc. zygomaticus os. temporalis* is continuous from above. The suture connecting the two processes (*sut. zygomaticotemporalis*) runs almost horizontally and does not ossify even in old animals. *Proc. temporalis os. zygomatici* has a free end which protrudes caudal beyond the suture. *Facies orbitalis* is flat, while *facies malaris* is concave, particularly in the anterior part. These relations differ from those typical of the majority of mammals. It is also characteristic of the hare that *canalis zygomaticus*, described in the rabbit (Žedenov et al., 1957) beginning with a fairly large foramen on the boundary of *proc. zygomaticus maxillae* and *os zygomaticum* either does not occur at all in the hare, or it is only in certain individuals that a very small foramen can be seen in this place.

Os zygomaticum is neighboured by two bones only — from the back by means of *proc. zygomaticus* by *os temporalis* and from the front by the *maxilla*.

17. Mandibula

The symmetrical mandibles are joined by a non-ossifying *symphysis mandibularis*. The symphysis on the ventral side extends almost to the extreme edge of the row of teeth, while from the top it occupies less than half the diastem.

Corpus mandibulae has a *margo adentalis* behind the incisor, forming half the length of the corpus and situated almost parallel to the long axis of the skull, and a part bearing teeth, declining outwards. Within the diastem, $\frac{1}{3}$ of the length from the side of the tooth row, on the lateral wall of the corpus, usually one, but sometimes two, *forr. mentalia* occur. When two occur, the second foramen is situated at the back and lower in relation to the first. This region is in addition pitted with small, numerous foramina. The external surface of the corpus is smooth, while the internal surface within the row of teeth has prominences corresponding to the tooth sockets of the malar teeth.

Ramus mandibulae is formed like a thin, broad plate. The lower margin, edged by a bony ridge, begins with *inc. varosum*, passes in an arch caudal, then inclines upwards and ends in *proc. angularis*. *Proc. articularis* is the most strongly developed process of the jaw, and ends in a distinct capitulum. Its anterior margin is fairly thick and runs from capitulum to the corpus mandibulae on the internal side of *ramus mandibulae*. *Proc. muscularis mandibulae*, which takes the form of a narrow plate curled inwards, is situated on the external side. The anterior margin of *proc. articularis*, together with *proc. muscularis*,

form a very characteristic sulcus, beginning at the base of the capitulum of *proc. articularis* and ending by the final molar tooth. Near the final molar the sulcus is pierced by an oval foramen. On the internal side of *ramus mandibulae*, below this foramen, there is *for. mandibulare*.

IV. OBLITERATION OF THE SKULL SUTURES

The degree of obliteration of the boundaries of the sutures, leading in extreme cases to the fusing of the two bony elements without any trace of connection, expresses the stages of ossification of the sutures. The defined succession of ossification of the sutures on the skull and the time taken by this process made it possible to use these observations for age classification.

One of the sutures to disappear earliest is *sut. parietointerparietalis*. In specimens from age class *I* this suture had not infrequently reached the initial phase of obliteration. In the youngest individuals it is clearly visible throughout its whole course. In age class *II* in a small number of individuals the outline of the interparietal bones is still visible, but in the majority of cases the suture becomes completely obliterated. The suture between the paired interparietal bones disappears simultaneously.

During this time the sutures within the occiput exhibit ossification — particularly the suture between *exooccipitale* and *basioccipitale*. The suture between *exooccipitale* and *squama occipitalis* becomes obliterated somewhat later, and it can still be seen, although very indistinctly, in specimens from age class *II*. The other sutures mentioned above are completely obliterated on the skulls of specimens from age class *III*.

Sut. sagittalis begins to ossify in principle in age class *III*, although in certain individuals the most posterior section immediately in front of *os interparietale*, which is no longer separate, is ossified as early as in age class *II*. In age class *III* the ossification of this suture occupies more or less $\frac{1}{3}$ of its length, counting from the posterior. Skulls in age class *IV* are characterised by elongation of the ossified section cranial and even complete ossification of the suture.

Sut. frontalis begins to ossify most often in the medial section, or sometimes in the anterior section. This process can be observed as from age class *III*, but individuals are also encountered in which the obliteration of this suture has not yet begun. In age class *IV* it is possible to find a posterior section, occupying $\frac{1}{3}$ of the length of the suture, not as yet ossified. In some of the specimens from this class the suture was observed to be ossified throughout its entire length.

Sut. parietotemporalis partly ossifies in age class *III*, but its full obliteration as a rule occurs in specimens from age class *IV*.

Sut. coronaria sometimes begins to ossify in age class *III*, but this invariably applies only to the most lateral of its sections. In adult specimens in age class *IV* ossification is the rule, although in the majority of cases the pericentral sections of the suture continue to remain unossified. Complete ossification of *sut. coronaria* probably takes place in hares several years old. Of the 5 specimens of known age having lived at least 4 years, it was only in one that the pericentral sections of the suture had not yet been obliterated.

It is worthy of note that of the sutures of the braincase hitherto mentioned, only *sut. parietointerparietalis*, the suture joining the interparietal bones and the sutures visible in young specimens within the *os occipitale*, disappear in old animals to an extent which makes it impossible to find them on the skull. In the case of the remainder of the sutures discussed, although subject to a greater or lesser degree to ossification, the boundaries of the bones are not completely obliterated and the lines of the sutures generally continue to be distinct.

In the structure of the braincase of the hare the different relations in the connection of the anterior part of the braincase with the rear part, formed by the occipital bone and parts of the temporal bone, are particularly noteworthy. The posterior part, generally of a thickened structure owing to the spongy structure of the upper occipital bone and mastoid part of the temporal bone and to the compact structure of the petrous portion and the thickness of the basioccipital, constitutes a certain complex element. It is true that functionally it forms one with the skull as a whole, but remains loosely connected with it. This is due to the fact that neither the sutures: *sut. parietooccipitalis* from the top, then from the side the suture connecting the *squama os. temporalis* with *pars mastoidea*, nor the juncture of *os pterygoideum* with *pars tympanica os. temporalis* and finally *synchondrosis sphenoccipitalis*, ossify throughout the whole life of the hare.

The sutures within the facial part of the skull were discussed in describing each of the bones. Generally speaking they undergo ossification to a slight degree only, and they usually remain clearly visible on the skulls of adult animals. The sutures of this part of the skull do not express the changes progressing with age to an extent which would make them of any use in age classification.

V. VARIATION IN SKULL MEASUREMENTS

Skull measurements were analysed in each age class, taking individual variations into consideration. In work on this material it was decided not to split it up according to the sex of the hare, in view of

the negative results obtained from attempts at grasping dimorphic differences, in either the whole of the material taken jointly or in each age class.

1. Absolute Values of Measurements

The maximum age variation is revealed by measurements made of the facial part and by measurements of the length of the whole skull. The three principal measurements of length made of the skulls: condylobasal length, basal length and profile length are subject to very similar age variations. They exhibit the greatest growth differences between age class *I* and *IV*. The relatively smallest differences occur between age classes *III* and *IV* (although they are statistically significant). This points to the fact that the skull gradually increases in length throughout the animal's life. As an example the relations discussed are illustrated by Table 1, giving the variations in condylobasal length. The occurrence of considerable individual variation in this measurement within age classes *III* and *IV* is worthy of emphasis. In the case of class *IV* the range of variation is from 81.3 — 96.2 mm.

Table 1.
Age variation in condylobasal length.

Age class	70.0	71.5	73.0	74.5	76.0	77.5	79.0	80.5	82.0	83.5	85.0	86.5	88.0	89.5	91.0	92.5	94.0	95.5	n	\bar{x}	%	
I	2	5			3	2	1	3											16	75.06	100	
II							1	4	12	12	8	6							43	81.89	109.1	
III							1	4	5	10	21	30	23	29	16	4			143	85.71	114.2	
IV										3	7	18	37	51	61	39	12	1	1	230	88.51	117.9

In comparison with the condylobasal length, the length of the facial part exhibits greater age variation, expressed in the higher percentage of increase in each age class. The increase in this measurement in age class *II* is of the same order as the increase in condylobasal length in age class *IV* (Table 2). There is a real, although slow, increase here between age class *III* and *IV*.

Only age class *I* is distinctly different in respect of the measurement of length of diastem (Table 3), the other classes have similar ranges of variation. Differences in the mean values between classes *III* and *IV* are, however, statistically significant, which indicates that this measurement increases in adult animals.

The length of the maxillary teeth row (Table 4) is subject to variation similar to that in the length of the diastema. A more even increase in

each age class and considerable individual variation in age classes *III* and *IV*, in which the range is from 16.8 — 21.7 mm, is observed in this dimension.

Among measurements of length made on the facial part the length of the nasal bones (Table 5) and length of the internasal suture are subject to the greatest changes with age. Relatively large differences

Table 2.
Age variation in rostral length.

Age class	52.5	54.0	55.5	57.0	58.5	60.0	61.5	63.0	64.5	66.0	67.5	69.0	70.5	72.0	73.5	75.0	n	\bar{x}	%
I	2	4	4			3	2	2	1	1							19	58.66	100
II						2	2	10	13	10	6	1					44	64.67	110.24
III									3	11	33	44	23	8	1		123	68.73	117.16
IV									1	2	21	43	72	62	24	3	228	70.66	120.46

Table 3.
Age variation in length of the diastem.

Age class	21.0	22.5	24.0	25.5	27.0	28.5	30.0	31.5	33.0	34.5	n	\bar{x}	%
I	3	11	3	19	14	1					51	24.97	100
II				11	20	34	1	1			67	27.63	110.65
III				3	13	49	36	5			106	28.88	115.65
IV				1	16	89	114	35	2	1	258	29.52	118.22

Table 4.
Age variation in length of the maxillary tooth row.

Age class	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	19.5	20.0	20.5	21.0	21.5	n	\bar{x}	%
I	3	3	10	3	5	3										27	15.74	100
II			2	1	9	11	17	7	4	2						53	17.32	110.03
III					1	13	26	33	34	24	11	2		1		145	18.26	116.01
IV						6	15	45	62	53	30	19	4	2	1	237	18.73	119.00

are observed here, both in the ranges of variation for each class and in the mean values. It is a characteristic feature here that differences between classes *III* and *IV* are relatively greatest in comparison with all the other measurements. This points to the constant, intensive growth of the elements of the skull, which is possible owing to the loose connection of the nasal bones with the frontal bones, by means of a suture which does not ossify even in late old age.

Measurements of breadth and height made of the facial part were also characterised by considerable variation, both age and individual. Among these measurements are: breadth of nasal bone and palatal height (Tables 6—7). The occurrence of considerable individual variation in the breadth of the nasal bone in age classes *III* and *IV* is remarkable.

Table 5.

Age variation in nasal length.

Age class	30.0	31.5	33.0	34.5	36.0	37.5	39.0	40.5	42.0	43.5	45.0	46.5	48.0	49.5	n	X̄	%
I	1	2	1	3	1										8	33.19	100
II				2	4	4	10	10	6	3					39	39.50	119.0
III							5	11	25	32	17	11	2		103	43.25	130.0
IV								9	23	51	55	51	28	3	220	44.95	135.4

Table 6.

Age variation in maximum breadth of both nasals together.

Age class	16.5	17.0	17.5	18.0	18.5	19.0	19.5	20.0	20.5	21.0	21.5	22.0	22.5	23.0	23.5	24.0	24.5	25.0	25.5	26.0	26.5	n	X̄	%	
I	1		3	2	3	2	1	1	1					1									15	19.20	100
II					1	2	7	5	11	8	5	1	1	4									45	20.68	107.70
III						2	3	5	3	12	12	20	23	17	10	3	5	2	3	1			121	22.30	116.14
IV						1	1	5	3	12	17	26	28	32	24	23	20	16	10	7	4		229	23.16	120.60

Table 7.

Age variation in palatine height.

Age class	18.0	18.9	19.8	20.7	21.6	22.5	23.4	24.3	25.2	26.1	27.0	27.9	28.8	n	X̄	%
I	1	2	5	8	11	8	11	2	2					50	21.89	100
II					1	3	21	19	15	6	1			66	24.30	110.01
III						2	6	21	36	29	11	2		107	25.35	115.81
IV						1	8	29	66	85	50	12	5	256	25.89	118.27

The group of measurements made of the brain-case is characterised by the generally small age variation found. A typical measurement here is the length of the cerebral part (Table 8), the increase of which in age class *IV* in relation to class *I* is half that of the increase in the facial part, although it is statistically significant. Occipital breadth was subject to similar variation.

The three next measurements: zygomatic breadth, depth and breadth of brain-case represent a common type of age variation. It is characteristic here that the total percentage of increase is about 7% for these measurements, the minimum values, beginning with age class *II*, being maintained on a constant level and differences in mean values being slight. No statistically significant differences between age classes *III*

Table 8.
Age variation in length of the brain-case.

Age class	38.0	39.5	41.0	42.5	44.0	45.5	47.0	48.5	50.0	51.5	n	\bar{X}	%
I	1	3	5	3	4	3					19	42.18	100
II			2	6	14	15	5	1			43	44.63	105.81
III					11	42	38	23	7		121	46.66	110.62
IV				2	7	36	74	77	29	5	230	47.61	112.67

Table 9.
Age variation in zygomatic breadth.

Age class	40.0	40.7	41.4	42.1	42.8	43.5	44.2	44.9	45.6	46.3	47.0	47.7	48.4	49.1	49.8	n	\bar{X}	%
I	4	2	4	2	4	11	7	5	5	1	1					46	43.39	100
II						6	10	13	15	9	6	3				62	45.36	104.54
III						5	8	11	16	29	20	7	4	1		101	46.08	106.20
IV							13	24	34	65	29	39	10	4	1	219	46.42	106.98

Table 10.
Age variation in depth of brain-case.

Age class	24.0	24.7	25.4	26.1	26.8	27.5	28.2	28.9	29.6	30.3	31.0	31.7	32.4	n	\bar{X}	%
I	1	2	6	8	10	13	3	2	3					48	26.90	100
II					3	9	15	14	12	5	4			62	28.10	104.46
III					2	5	20	25	26	16	4	2	1	101	28.53	106.05
IV					2	10	33	61	62	39	26	9	1	244	28.79	107.03

and *IV* were found in the zygomatic breadth. Real differences occur between the three first classes (Table 9). No statistically significant differences between age classes *II* and *III*, and between *III* and *IV* were found in the depth of the brain-case (Table 10), but the real differences occurring between classes *II* and *IV* are evidence of the increase in this measurement with age. Significant differences in the breadth of the braincase were found to occur only between age classes *I* and *II*.

The two principle measurements made of the jaw: length and height of the mandible (Tables 11 and 12) are subject to slight variation with age, expressed by a total increase of 12 and 13%.

There are some measurements among those made which do not reveal any age variation. A typical example here is formed by distributions of the values of the minimum breadth of the frontal bone (Table

Table 11.
Age variation in length of mandible.

Age class	51.5	53.0	54.5	56.0	57.5	59.0	60.5	62.0	63.5	65.0	66.5	68.0	69.5	71.0	72.5	74.0	n	X̄	%	
I	4	1	4	3	4	5	10	10	1	1	1						44	58.86	100	
II				1		2	8	11	16	16	6	1						61	63.33	107.59
III									7	13	19	25	14	5	1	1		85	65.08	110.56
IV							2	6	14	57	43	59	33	9	1			224	66.80	113.48

Table 12.
Age variation in height of *ramus mandibule*.

Age class	32.0	33.5	35.0	36.5	38.0	39.5	41.0	42.5	44.0	45.5	47.0	n	X̄	%
I	1	2	3	6	7	12	11	5				47	38.86	100
II						6	14	25	24	3		72	42.58	109.57
III					1	4	13	42	28	9	2	99	42.92	110.45
IV						3	19	67	88	44	9	230	43.66	112.35

Table 13.
Age variation in minimum breadth of frontal bones.

Age class	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	n	X̄	%
I				1	3	2	4	3	2			2				17	13.59	100
II						5	5	11	9	4	8	1		1		44	13.91	102.35
III	1			2	5	9	17	20	21	20	13	8	8	4		128	14.01	103.09
IV			3	8	6	16	27	36	43	43	25	12	5	2	3	229	13.91	102.35

13). A relatively small range of individual variation in young animals (from classes I and II) and relatively wide range in class IV, is observed here. Height and breadth of *for. occipitale magnum* are subject to similar variation.

The data given show that the various measurements, on account of the different character of variation, are distributed in three principle groups: 1. group of measurements with considerable age variation

(profile length, condylobasal length, basal length, length of facial part, nasal length, breadth of nasal bones and palatal height); 2. measurements with relatively slight age variation (length of brain-case, length and height of mandible, zygomatic breadth and depth and breadth of brain-case); 3. group of measurements exhibiting individual variation only, irrespective of age (minimum breadth of frontal bone and height and breadth of *for. occipitale magnum*).

2. Rate of Growth of Skull

The age variation discussed above in the various measurements of the skull constitute a reflection of the process of formation with age of the final form of the skull. The growth in different elements of the skull characterised by chosen linear measurements takes place with equal intensity in time and is expressed in the form of different increases. Fig. 5 shows the course taken by curves of increase in the majority of the skull measurements subject to variation with age. Four groups of measurements with a similar rate of growth are clearly distinguished on the diagram.

1. Two measurements: nasal length and length of *sut. internasalis* exhibit the highest percentage of increase. The most intensive growth in nasal length takes place between class I and II (19%). A rapid rate of growth is maintained in class III (11%), and in age class IV (5.4%). No other measurement is characterised by so high a percentage of increase in age class IV.

2. The second group of measurements is characterised by a very evenly maintained rate of growth, total increase coming within limits of 17.9% — 20.5%. The maximum increases are observed between classes I and II, the only exception here being the maximum nasal breadth, which exhibits maximum increase between age classes II and III (8.4%).

3. The third group of measurements has an even total increase (11 — 13%), but the various measurements are subject to uneven rate of growth in different age classes. The length of the brain-case exhibits, for instance, a similar increase in classes II and III (5.8% and 4.8%), and does not alter distinctly until class IV (2.2%). The height of *ramus mandibulae* exhibits very considerable increase in age class II (9.6%) and only negligible increase in class III (0.8%) and class IV (1.9%). Increase in length of the mandible decreases gradually in consecutive age classes.

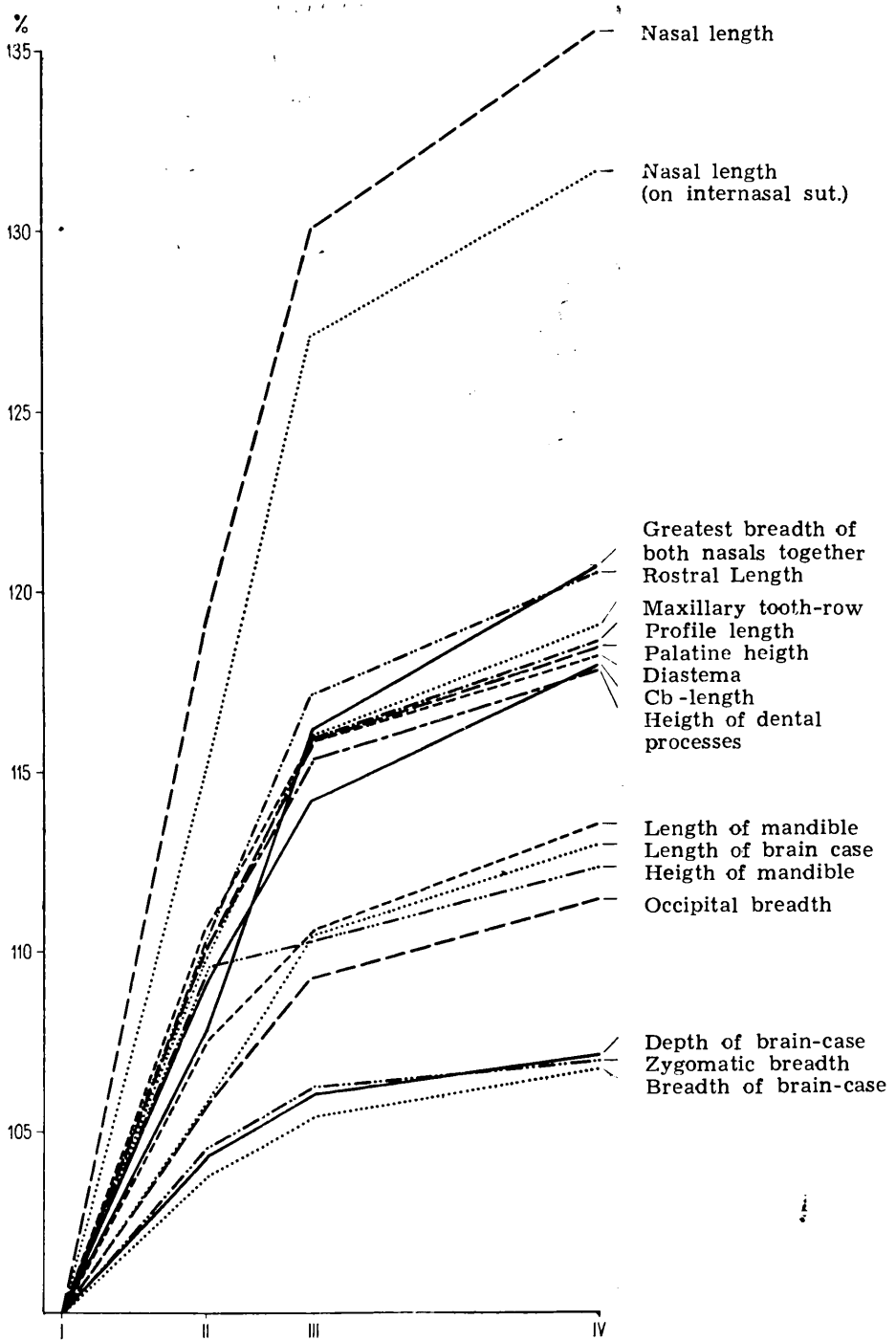


Fig. 5. Rate of growth of the skull in age classes.

The above three groups of measurements, with different rates of growth, are characterised by a common feature, that in all measurements between classes *III* and *IV* growth continues to be statistically significant.

4. Contrary to the three foregoing groups, the fourth group of measurements exhibits a real increase between classes *I* and *II* (for height and breadth of the brain-case) and it is only in the case of zygomatic breadth that statistically significant growth differences occur between classes *II* and *III*. A general feature of these measurements is the slight total increase from class *I* to *IV* (6.7—7.0%) which takes place primarily between age classes *I* and *II*. Bearing in mind the fact that these measurements are subject only to slight age variation, the ranges of measurements obtained may be treated as individual variations as from age class *II*.

Analysis of increase in the various measurements reveals a non-uniform rate of growth of different parts of the skull. The elements relatively loosely connected with the skull, that is, the nasal bones, which can freely increase in length, are subject to the greatest and most intensive growth. This process probably does not cease with the halting of the growth of the other elements of the skull.

The facial part of the skull is characterised by considerable growth — this applies equally to measurements of length, breadth and height. This is most probably connected with the development of the function of the jaws as an apparatus active throughout the whole of the animal's life. In the group of measurements made of the facial part the maximum increases are exhibited by: length of diastem and length of maxillary and mandibular teeth-rows. The condylobasal length, varies chiefly as a result of the growth of the facial part, forming about half the total length of this measurement. The fact is characteristic of the measurements given here that their rate of growth is most intensive up to the time the animals attain the age of 8—12 months. Later growth, although considerably weaker, is, however, perceptible between classes *III* and *IV* and is statistically significant.

Measurements of the brain-case reveal that it is subject to considerably less growth. The increase in length of the brain-case is relatively the greatest, increasing intensively between classes *II* and *III*. The other measurements of the skull are subject to real growth up to age class *II*,

VI. PROPORTIONS OF THE SKULL

Several indices were calculated in order to grasp age variation in the proportions of the skull. In calculating indices comparison was made of measurements subject to small growth changes with those which exhibit considerable increase with age.

Index of $\frac{\text{breadth of brain-case}}{\text{length of facial part}} \times 100$ has values decreasing in successive age classes (Table 14). In classes *III* and *IV* the ranges of this index are uniform (41.6 — 51.5), but differences occur in the mean values of this index, which may provide evidence that the proportions of these measurements are established only in age class *IV*.

Table 14.

Age variation in index of $\frac{\text{breadth of brain-case}}{\text{rostral length}} \times 100$

Age class	42.0	43.0	44.0	45.0	46.0	47.0	48.0	49.0	50.0	51.0	52.0	53.0	54.0	55.0	56.0	57.0	N	X
I					1			5	2	2	2	2	2	1	1	1	19	51.53
II					2	11	12	5	9	3	1	1					44	48.59
III	2		7	15	42	29	23	10	6	1							135	46.72
IV	3	8	29	35	53	46	32	10	4	2							222	46.17

Index $\frac{\text{zygomatic breadth}}{\text{profile length}} \times 100$ exhibits fairly considerable differences between the three first age classes, and a slight difference in class *IV* in relation to class *III*. The range of variation of this index is wide, particularly in class *IV* (43.8 — 49.7). The differences which are evident between classes *III* and *IV* in the mean values of the index are statistically significant, although small. This points to the establishment of this proportion only in class *IV*.

Index $\frac{\text{length of cranial part}}{\text{profile length}} \times 100$ exhibits slight differences as from age class *II*. In age classes *III* and *IV* the fact of the occurrence of considerable variation in this index, from 44 — 52, is worth of attention, as is also the absence of significant differences between these classes in the mean values of the index (Table 15). Proportion is therefore established, in this case, in age class *III*.

Index $\frac{\text{height of brain-case}}{\text{weight of mandible}} \times 100$ was introduced by Rossoli-

mo (1959) as a character making it possible to define age in nutria. The relatively small amount of jaw material did not permit of finding whether this index may also form a reliable age character in relation to the hare. The fact of the occurrence of wide differences between the mean values for each class, indicating real age variation in this index is, however, worth emphasising. However in this case also, the ranges of classes III and IV are common from 30.0 to 46.5, while differences in mean values are real (Table 16).

Table 15.

Age variation in index of $\frac{\text{length of the brain-case}}{\text{profile length}} \times 100.$

Age class	44.0	44.5	45.0	45.5	46.0	46.5	47.0	47.5	48.0	48.5	49.0	49.5	50.0	50.5	51.0	51.5	52.0	52.5	53.0	N	X
I								1	1		3	3	4	2	1		2	2	2	21	50.38
II				1	1	4	3	2	8	9	2	6	4	1	1	2				44	48.49
III	1	1	1	7	9	14	11	26	19	21	13	11	3	5	2	1	1			146	47.88
IV		2	1	7	12	24	37	44	44	24	20	8	10	3	3	2				241	47.75

Table 16.

Age variation in index of $\frac{\text{depth of brain-case}}{\text{weight of mandible}} \times 100.$

Age class	30.0	33.0	36.0	39.0	42.0	45.0	48.0	51.0	54.0	57.0	60.0	63.0	66.0	69.0	72.0	75.0	N	X
I								1	3	1		1				1	7	53.28
II					1	4	3	1				1					10	43.00
III	1	2	8	7	6	1											25	33.16
IV	4	7	20	18	4	4											57	37.21

VII. DISCUSSION

An essential condition for work on variations in the skull structure of the species examined is that sufficiently abundant material, providing the fullest possible range of morphological variation in individuals in the population, should be available. This condition was complied with in the present study thanks to the comprehensive series of skulls used for study purposes, and to the availability of random samples from the population. Fortuitous selection of material due to damage to skulls during shooting did not affect in principle the material from the aspect of quality.

The problem of the correct classification of age groups is of fundamental importance to the study as a whole. On account of the lack of standard model skulls of hares of known age, as a criterion of the markings on the skull, use was made of the results of investigations of the ossification of the pelvis (B u j a l s k a, 1964) and the state of sexual activity (R a c z y ń s k i, 1964), based on the same material. Estimation of the absolute age of young hares was made possible by the fact that the material contained monthly series. R a c z y ń s k i (1964) found the first litter to occur in February-March in 1959, and the last (in a small number of females only) at the end of September. A knowledge of the breeding period and data on body weight (C a b o ń - R a c z y ń s k a, 1964 b) enabled the young hares to be divided into classes (from class *I* to *III*). Only age class *IV* is non-uniform from the aspect of absolute age, since in addition to specimens beginning their second year of life it also contains animals several years old. These latter are, of course, few in number, judging from the observations made by R i e c k (1956) on the age structure of a population of marked hares under the conditions prevailing in a area used for organised game shooting. Confirmation of the correctness of the division made in relation to classes *I* and *II* is their regular distribution in monthly samples over the course of a year: age class *I* occurs in the material up to December, and age class *II* up to February of the next year. The survival of young hares from the final litter is not very probable under field conditions (R i e c k, 1956). It must therefore be assumed that only the last young hares born in July and August are represented in the material.

The plan accepted for dividing the age groups made it possible to trace the rate of growth of the skull as a whole on the basis of analysis of measurements made. The fact that between age classes *III* and *IV* real increase takes place in the majority of measurements suggests that the skull of the hare is subject to constant although slow growth to a late age. Similar results were obtained by D a l q u e s t (1942) for the related American species *Lepus americanus* E r x l e b e n, 1777 and by E m p e l (1957) for the rabbit *Oryctolagus cuniculus* L i n n a e u s, 1758. The phenomenon of growth of the skull in old individuals was also observed in certain rodents such as, e.g. *Clethrionomys glareolus* S c h r e b e r, 1780 (W a s i l e w s k i, 1952), *Microtus arvalis* (P a l l a s, 1778) (S t e i n, 1958) and *Microtus agrestis* L i n n a e u s, 1761 (G ę b c z y ń s k a, 1964).

The final proportions of the hare's skull are not in principle reached until age class *IV*. The establishment of this fact was possible owing

to comparison of measurements and indices of the skull from successive age classes set out together with observations on correlative connections between different measurements. Percentages of increase in skull measurements (Fig. 4) indicate that differences are small between age classes III and IV, but reveal a distinct growth in relation to young animals (age classes I and II). Comparison of correlative connections in the skull of the hare made in an earlier study (Caboń-Raczyńska, 1964 a) permitted of explaining the phenomenon of formation of the final form of the skull. It was shown that the high coefficient of correlation characterise reciprocal connections of the majority of skull measurements in young hares. This correlation is the result of the process of growth of the skull, which takes place very intensively in all its elements during this period. In age class IV, on the other hand, a high degree of correlation is found only in the group of measurements very similar to each other (Cb. length, profile length and basal length). The remaining measurements exhibit connections far smaller and even statistically insignificant, despite the fact that rate of growth may be very similar. A situation of this sort arises as the result of individual differences in the rate of growth of different elements of the skull, leading to differentiation of individual morphological types. Variation in measurements observed in age class IV, i.e. in hares over one year old, therefore express true individual variation within the species and may provide a basis for studies of a systematic character.

Ranges of the basic measurements of the skull of *L. europaeus*, given by different authors in studies of a taxonomic character, differ from each other to a certain extent. An example of this is given below in a table of Cb. lengths:

Miller (1912)	Ognev (1940)	Gureev (1962, 1964)	Caboń-Raczyńska
85.2 — 92.2	84 — 95	80 — 96.3 (68 — 83?)	81.3 — 96.2

These differences may result from the use of too small an amount of material (e.g. Ognev had only 4 skulls of *L. e. europaeus*), or from not adhering to age criteria in determining the ranges of variation of measurements. The limits of Cb.-length determined for the present material include in principle ranges of variation given by other authors with the exception of Gureev (1964), which are most certainly erroneous.

The problem of the subspecific appurtenance of the hare inhabiting Poland is not clear. The majority of authors state that a nom-

inative subspecies occurs in West Poland (Ognev, 1940; Gaffrey, 1961; Gureev, 1964. Poland, according to Ognev (1940) forming *terra typica* for *L. europaeus*. Lubicz-Niezabitoski (1933) writes that the occurrence of subspecies of *L. europaeus* and their distribution in Poland is unknown. Ellerman & Morroson-Scott (1951), in addition to the western part of the Soviet Union and the Lithuanian Socialist Republic, give Germany as an area settled by *L. e. hybridus* Desmarest, 1822, which would form evidence of the occurrence of this particular subspecies in Western Poland. This subspecies, according to other authors, occurs only to the East of the Vistula (Gaffrey, 1961), or in the Soviet Union (Ognev, 1940). Differences between the above-mentioned subspecies are expressed chiefly in the shade of their coloration. On the basis of a description of the coloration of the same series of hares (Borowski, 1964) it may be concluded that it is typical of the nominative subspecies. Differences in the skull consist only in the slightly larger dimensions in the form *L. e. hybridus* Desm. (Ognev, 1940). Ranges of variation in a series of measurements given in the present study include, however, ranges of both the subspecific forms discussed here. In view of the fact that the colour plays a decisive part here I am of the opinion that the nominative subspecies — *L. europaeus europaeus* Pallas, 1778, inhabits the Poznań province.

In the species systematics of the genus *Lepus*, in addition to the dimensional characters of the skull, anatomic data, constituting descriptive taxonomic characters, are of importance. The shape of *procc. supraorbitales* is given, inter alia, as characteristic of many of the species of the genus *Lepus* (Gureev, 1964). An analysis was made in the present material of the shape of these processes in specimens in age class IV. It was found that within series of adult hares the shape of the supraorbital processes varies greatly and almost all types can be found here, described as characteristic of various species of the genus *Lepus*.

Ossification of *incisura praeorbitalis* in a large number of individuals in age class IV (33,2%) is a phenomenon connected with age, but it did not characterise all the adult specimens. This is borne out by the fact that of 5 marked hares living under natural conditions and killed when at least 4 years old, it was only in one specimen that complete closure of *incisura praeorbitalis* occurred. Simultaneously among hares from age class III 3 cases were found of closure of *incisura praeorbitalis*. This character is therefore subject to considerable individual variation and cannot be taken as a criterion of age, although as a rule

it is characteristic of the group of older hares. It must be emphasised that the kind of formation of *proc. supraorbitalis oralis* is treated as characteristic of species of *L. europaeus* and *L. timidus* (Siivonen, 1956; Gaffrey, 1961). The observations given above prove that this character, in view of the considerable variability in *L. europaeus*, cannot be treated as being a completely certain one.

Koby (1959) emphasises the differences in shape of nasal processes of frontal bones supposedly making it possible to distinguish *L. europaeus* from *L. timidus*. It was found in the present material that the shape typical of the European hare occurred in 64%, while the shape of these processes typical of *L. timidus* occurred in 36% of the specimens (Fig. 2). This is evidence that the character described comes within the range of individual variation of *L. europaeus*.

The questions of systematics and taxonomic characters of the skull constitute an important problem in relation to *Leporidae*, which cannot be dealt with in greater detail in the present study, on account of the lack of comparative material. The present study permitted, however, of formulating the postulate, that research of this type must be based on comprehensive collections including material of varying ages and sufficiently numerous series of adult specimens.

VIII. SUMMARY

A morphological description of the skull of the European hare (*Lepus europaeus* Pallas, 1778) and an analysis of variation in 27 craniological measurements from the age and individual aspects were made on material ($n = 482$) obtained from the Poznań province (West Poland). Four age classes were distinguished on the basis of the degree of ossification of the skull sutures.

1. It was established that *sut. zygomaticomaxillaris* runs immediately behind the *proc. zygomaticus maxillae*, diagonally to the long axis of the skull (Fig. 4).

2. *Os interparietale* occurs in young individuals up to approximately 6 months old and takes the form of small paired plates. This character made it possible to distinguish the skull of a young hare from a rabbit, which has a single *os interparietale*.

3. *Canalis zygomaticus*, beginning in the rabbit with an oval foramen in the anterior part of the zygomatic arch, is in process of disappearance in the hare or does not occur at all.

4. In addition to a small hamulus, a well formed wide squama, participating in the structure of the braincase, occurs in the pterygoid bone of the hare. This points to the greater functional connection of *os pterygoideum* with the braincase then with the facial part of the skull.

5. *Procc. supraorbitales* exhibit variation in size and shape with age (Fig. 3). In age class IV it is possible to distinguish all the types of these processes given as characteristic of different species of the genus *Lepus*. In 33.2% of specimens in age class IV ossification by means of bony tissue of *incisura preorbitalis* was observed.

6. It was found that the nasal processes of the frontal bone occur in the form typical of *L. europaeus* in 64% and of *L. timidus* in 36%, which throws doubt on the taxonomic value of this character.

7. Analysis made of measurements in the facial part of the skull, that is, length, breadth and height and measurements of the total length of the skull reveal a constant increase, particularly intensive up to age class III, i.e. about 8—12 months old. A real increase in measurements takes place between age classes III and IV, which leads to the assumption that the skull of the hare is subject to a constant, although slow, growth until the end of the animal's life.

8. Measurements of the brain-case reveal a slight increase, real up to about 8 months of life (age class II).

9. The different measurements of the skull reveal a different rate of growth. Four groups of measurements were distinguished (Fig. 5).

10. Analysis of indices made it possible to establish that the true proportions of the skull are not established until age class IV, i.e. in individuals in the second year of their life.

11. Using a description of the coloration of this same series of hares (Borowski, 1964), it was found that it is typical of the nominative subspecies. The range of the craniological measurements analysed includes both the values given for the nominative subspecies and for *L. e. hybridus*. The authoress is of the opinion that the nominative subspecies — *L. e. europaeus* — occurs in the Poznań province.

Acknowledgments: My thanks are in particular due to W. Jeziorski, M. Sc., of the Scientific Research Station of the Polish Hunting Union, Czempin, for sending me 5 specimens of marked hares.

REFERENCES

1. Borowski, S., 1964: Studies on the European hare. I. Moulting and coloration. *Acta theriol.*, 9, 15: 217—231.
2. Bujalska, G., 1964: Studies on the European hare. IV. Variations in the pelvis and sacrum. *Acta theriol.*, 9, 18: 287—304.
3. Caboń-Raczyńska, K., 1964: Correlations of skull measurements of *Lepus europaeus* Pallas, 1778. *Acta theriol.*, 8, 13: 207—216.
4. Caboń-Raczyńska, K., 1964: Studies on the European hare. II. Variations in the weight and dimensions of the body and the weight of certain internal organs. *Acta theriol.*, 9, 16: 233—248.
5. Dalquest, W. W., 1942: Geographic variation in northwestern snowshoe hare. *J. Mamm.*, 23, 2: 166—183.
6. Duerst, J. U., 1926: Vergleichende Untersuchungsmethoden am Skelett bei Säugern. *Handbuch d. biol. Arbeitsmethoden* 7, 2: 126—530. Berlin.
7. Ellerman, J. R., & Morrison-Scott, T. C. S., 1951: Checklist of palaeartic and Indian mammals 1758 to 1946. *Brit. Mus.*, 1—810. London.
8. Empel, W., 1957: Zmiany w morfologii czaszki królika dzikiego (*Oryctolagus cuniculus* L.) związane z wiekiem i rozmieszczeniem na terenie Polski. *Folia Morph.* 8 (16), 3: 169—194. Warszawa.
9. Gaffrey, G., 1961: Merkmale der Wildlebenden Säugetiere Mitteleuropas. *Geest & Portig K.—G.*, 1—284. Leipzig.

10. Gębczyńska, Z., 1964: Morphological changes occurring in laboratory *Microtus agrestis* with age. *Acta theriol.*, 9, 6: 67—80. Białowieża.
11. Gureev, A. A., 1963: *Lagomorpha* [Sokolov, I. I., (Ed.): „Mlekovpitajuščie fauny SSSR”]. AN SSSR: 218—243. Moskva — Leningrad.
12. Gureev, A. A., 1964: Fauna SSSR. Mlekovpitajuščije. Zajceobraznyje (*Lagomorpha*) Izd. “Nauka”, 3, 10: 3—275. Moskva — Leningrad.
13. Koby, F. E., 1959: Contribution au diagnostic osteologique différentiel de *Lepus timidus* Linné et *Lepus europaeus* Pallas. *Verh. Naturf. Ges. Basel.* 70, 1: 19—44. Basel.
14. Kolda, J., 1936: Srovnávací anatomie zvířat domácích se zřetlem k anatomii člověka. II. Nauka o kostech a thrupavkách. Nakladem vlastním — Tiskla Novina v Brne. 1—914. Brno.
15. Korneev, O. P., 1960: Zaec — rusak na Ukraini. Izd. Kijevskogo Univ., 3—107. Kijev.
16. Krause, W., 1884: Die Anatomie des Kaninchen in Topographischer und Operativer Rücksicht. Verlag V. W. Engelmann. 3—383. Leipzig.
17. Lubicz-Niezabitowski, E., 1933: Klucz do oznaczania zwierząt ssących Polski. Nakł. Koła Przyr. Uczniów Univ. Jagiellońskiego 3—124. Kraków.
18. Miller, G. S., 1912: Catalogue of the mammals of Western Europe. *Brit. Mus.*, 1—1019. London.
19. Ognev, S. I., 1940: Zveri SSSR i priležaščih stran. Gryzuny. Izd. AN SSSR, 4: 6—615. Moskva — Leningrad.
20. Popesco, P., 1961: Atlas anatomii topograficnej zwierząt gospodarskich. Głowa i szyja. Państw. Wyd. Rolnicze i Leśne: 5—215. Warszawa.
21. Poplewski, R., 1948: Anatomia Ssaków. Tom. II. Układ Kostnostawowy. Spółdzielnia Wydaw. “Czytelnik”: 1—690. Stockholm.
22. Raczyński, J., 1964: Studies on the European hare. V. Reproduction. *Acta theriol.*, 9, 19: 305—352.
23. Rieck, W., 1956: Untersuchungen über die Vermehrung des Feldhasen Z. *Jagdwiss.* 2, 11: 49—90.
24. Rossolimo, O. L., 1958: Vozrastnaja izmjenčivost čerepa nutrii. Uč. zap. Mos. gos. pied. inst. im W. P. Potemkina. 84: 83—136.
25. Siivonen, L., 1956: Suuri Nisäkäskirja. Suomen Luonto 5—800. Helsinki.
26. Stein, G. W., 1958: Die Feldmaus (*Microtus arvalis* Pallas). Die Neue Brehm Bücherei. Zinsen Verlg. Wittenberg Lutherstadt. 5—76.
27. Wasilewski, W., 1952: Morphologische Untersuchungen über *Clethrionomys glareolus glareolus* Schreb. *Ann. Univ. M. Curie-Skłodowska C.* 7, 3: 119—211. Lublin.
28. Žedenov, W. N., Bigdan, S. S., Lukjanova, V. P., Samborskaja, E. P., Udovin, G. M., Janšin, K. I., 1957: Anatomija kroljika. Gosud. Izd. “Sovetskaja Nauka”. 3—309. Moskva.

Polish Academy of Sciences,
Mammals Research Institute,
Białowieża, Poland.

STRESZCZENIE

Dokonano opisu morfologicznego czaszki zająca szaraka (*Lepus europeus* Pallas, 1778) oraz przeprowadzono analizę zmienności 27 pomiarów kraniologicznych w aspekcie wiekowym i osobniczym na materiale (n = 482) pochodzącym z województwa poznańskiego. Na podstawie stopnia skostnienia szwów czaszki wydzielono 4 klasy wiekowe.

1. Ustalono, że szew jarzmowoszczękowy (*sut. zygomaticomaxillaris*) przebiega bezpośrednio za wyrostkiem jarzmowym szczęki, skośnie do osi długiej czaszki (Ryc. 4).

2. Kość międzyciemieniowa (*os interparietale*) występuje u osobników młodych do ca 6 miesięcy życia i jest wykształcona w postaci niewielkich parzystych blaszek. Cecha ta pozwala odróżnić czaszkę młodego zająca od królika, posiadającego pojedynczą kość międzyciemieniową.

3. Kanał jarzmowy, rozpoczynający się u królika owalnym otworem w przedniej części łuku jarzmowego, jest u zająca w zaniku lub w ogóle nie występuje.

4. W kości skrzydłowej zająca występuje obok niewielkiego haczyka (*hamulus*) dobrze wykształcona obszerna łuska, biorąca udział w budowie puszkii mózgowej. Wskazuje to na większe funkcjonalne powiązanie kości skrzydłowej z mózgowczaszką niż z twarzoczaszką.

5. Wyrostki nadoczodołowe (*procc. supraorbitales*) wykazują z wiekiem zmienność wielkości i kształtu (Ryc. 3). W IV klasie wieku można wyróżnić prawie wszystkie typy tych wyrostków, podawane jako charakterystyczne dla różnych gatunków rodzaju *Lepus*. U 33,2% okazów z IV klasy wieku stwierdzono zarastanie tkanką kostną wcięcia przedoczodołowego (*incisura praeorbitalis*).

6. Stwierdzono, że wyrostki nosowe kości czołowych występują w postaci typowej dla *L. europaeus* u 64% a dla *L. timidus* u 36% okazów co podważa taksonomiczną wartość tej cechy.

7. Analizowane pomiary przeprowadzone w części twarzowej czaszki, zarówno długościowe, szerokościowe jak i wysokościowe oraz pomiary całej długości czaszki wykazują stały wzrost, szczególnie intensywny do III klasy wieku tj. ca 8—12 miesięcy życia. Realny wzrost pomiarów odbywa się między III i IV klasą wieku, co pozwala przypuszczać, że czaszka zająca podlega stałemu, choć powolnemu wzrostowi do końca życia.

8. Wymiary mózgowczaszki wykazują niewielki wzrost, realny do ca 8 miesięcy życia (II klasa wieku).

9. Poszczególne pomiary czaszki wykazują różne tempo wzrostu. Wyróżniono cztery grupy pomiarów (Ryc. 5).

10. Analiza wskaźników pozwoliła stwierdzić, że właściwe proporcje czaszki ustalają się dopiero w IV klasie wieku tj. u osobników w drugim roku życia.

11. W oparciu o opis ubarwienia tej samej serii zajęcy (Borowski, 1964), stwierdzono, że jest ono typowe dla podgatunku nominatywnego. Zakres analizowanych pomiarów kraniologicznych obejmuje zarówno wartości podawane dla podgatunku nominatywnego jak i dla *L.e. hybridus*. Autorka sądzi, że w województwie poznańskim występuje podgatunek nominatywny — *L. e. europaeus* Pallas, 1778.

