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Morphological Variability of the Skull and Body Weight of the Red Deer

[With 20 Figs. & 13 Tables]

The material used for the investigations consisted of 483 skulls. An anatomical description was made of the skull, taking into consideration sex dimorphism and age, and also the characters distinguishing the skull of the red deer from other ruminants. The process of obliteration of the sutures takes place more rapidly in males than in females. The variability and rate of increase in 34 craniometric measurements and measurements of body weight are given. Sex dimorphism in the red deer is best illustrated by: zygomatic breadth, breadth on facial tubers, condylo-occipital breadth, maximum length of skull, length of mandibula, height of *pars rostralis*, height of neurocranium and index of *pars rostralis*×100/length of mandibulary tooth-row. The capacity of the cranial cavity is greater in males than in females. Skull length in Polish red deer is greater than in Norwegian, and less than in Hungarian red deer. Most intensive growth of the skull takes place in females between the first and second, and in males during the second and third, years of life. The viscerocranium grows more intensively in females than the neurocranium, while in males the neurocranium and viscerocranium grow at an even rate. All the measurements can be divided into three groups: (1) those which increase with age more in females than in males, (2) increasing equally in both sexes and, (3) increasing more rapidly in males. The only measurements which decrease with age are the length of maxillary and mandibulary tooth-rows. Red deer in Poland are distinguished by greater body weight and larger skull dimensions than red deer from Western Europe, but they are smaller than red deer from Eastern Europe.

I. INTRODUCTION

The majority of studies of red deer are primarily concerned with the antlers, which have formed a valuable hunting trophy in great demand for many centuries. Such studies often include mention of body weight which, in the opinion of most authors (Botezat, 1904; Beninde, 1940; Mager, 1941), is strictly connected with the size of the antlers. Only a few studies (Ingebrigtsen, 1927; Geptner & Calkin, 1947; Flerov, 1952; Szunyoghy, 1963) give craniometric measurements and these are usually made on small amounts of material. In none of the papers to which I had access did I find a morphological description of the skull, and only in certain of them data on the capacity of the cranial cavity (Ingebrigtsen, 1927; Szunyoghy, 1963).

Red deer have occurred in Polish forests since extremely ancient times, as is evidenced by the excavations made in different regions of Poland which have revealed many fragments of the skeleton or antlers (Krysiak, 1959; Kubasiewicz, 1959). Examination of accounts e. g. fees paid for animals shot and for skins and also records of red deer caught alive, shows that in the 16th and 17th centuries the red deer was to be found in great abundance in all the forests (Mager, 1941). With the passage of time the living area of the red deer in Poland has shrunk and the density of the game decreased in the shoots in different areas, while at the same time the quality of the antlers has deteriorated and the weight of the carcass decreased. In order to correct this state of affairs red deer possessing desirable characters were moved to areas in which either this game had been exterminated, or the local population was extremely poor (as regards quality of the antlers and weight of carcass). The greater part of such operations were carried out at the end of the 19th century and beginning of the 20th (Mager, 1941; Cenk i e r, 1957), although as early as the 16th century mention is made of the introduction into Poland of three stags and three hinds (M a g e r, 1941).

The Carpathian red deer *Cervus elaphus montanus* B e t e z a t, 1903, from the Hungarian parts of the Carpathian Mts. were most often introduced into Polish hunting grounds, chiefly on account of their good body structure (body weight as much as 300 kg) and powerful antlers. They were introduced to the hunting grounds in the area forming the present-day Olsztyn province (Sorkwity), the Białystok province (Białowieża Primaeval Forest), Łódź province (Spała), Katowice province (Pszczyna), the Opole province (Tułowieckie forests) and the Wrocław province (Siedlisko and Kliczkowo) (C e n k i e r, 1957).

Cervus elaphus canadensis E r x l e b e n, 1777, which is distinguished by considerable body weight and fine mass of antlers, the shape of which differs from that characteristic of the European red deer, was also introduced, primarly into Silesia in the hunting areas in the Katowice province (Pszczyna), Opole province (Tułowieckie forests and Zyglinek) and the Wrocław province (Siedlisko, Kliczkowo) (B e n i n d e, 1940; C e n k i e r, 1957).

Cervus elaphus sibiricus S e v e r z o v, 1878, was introduced into the Białowieża Primaeval Forest (C e n k i e r, 1957).

Red deer from German breeding areas at Potsdam and Schorfheide were also introduced into Poland. The deer from Potsdam formed material consisting of a mixture of the local population with importations from the Carpathians (B e n i d e, 1940; C e n k i e r, 1957).

Apart from the above, red deer were moved about in Poland itself, chiefly from the shoots at Spała and Pszczyna to other areas (C e n k i e r, 1957).

The Niepołomice Forest occupies a special position among Polish hunting grounds as it was there that a local form of red deer was preserved, always allowing for the possibility, of course, that the deer might crossbreed with individuals migrating from other areas during the rutting season (C e n k i e r, 1957).

None of these operations consisting in the introduction of breeding material more valuable from the game point of view, as a rule produced the results anticipated. The first generation of hybrids with the local stock was very good and always surpassed the local population as to body weight and antlers, but after a few generations the good points of the imported race disappeared and the whole population returned to its original state (B e n i n d e, 1940). The hunting grounds at Pszczyna may serve as an example of this. After the Canadian red deer had been introduced there the crossbred animals were very good[1]), although the body weight never equalled that of the wapiti bucks. The mean weight of the carcass was maintained within limits of 170 kg, but the weight of the largest individuals reached as much as 200 kg. After eleven years the mean body weight had fallen to 135 kg, that is, it had returned to the local level (B e n i n d e, 1940).

It is a fact that only a few specimens of alien animals were introduced into different hunting grounds, and the effect of their introduction was effacted after a lapse of some years, but at the same time it must be emphasised that operations connected with transfer of individuals from a better population to areas inhabited by a poorer population were in effect completed by 1914. The rare cases of later transfers apply only to transfers of red deer within Poland itself. This justifies the

[1]) By the term "good" and "poor" antlers is meant the attainment of certain height and weight dimensions, the formation of a certain number of points, size of the transverse section of the antler and its weight.

statement that for 46 years all the characters of the individuals introduced have been thoroughly mixed with the local ones and that no significant influence has been left on the present population of red deer in Poland, which can therefore be considered as homogeneous, formed by the influence of local conditions.

The aim of the present study is to present the individual and age morphological variability in the skull, its rate of growth and also variability in the body weight of the red deer, *Cervus elaphus* Linnaeus, 1758 in Poland. This leads us nearer to grasping the morphological characteristics of the red deer, about which so little knowledge has so far been obtained.

II. MATERIAL AND METHODS

The material was collected over the period from 1960 to 1962, and thus comes from three shooting seasons. It was obtained in the majority of cases (in relation to males) from exhibitions of hunting trophies organised by the Polish Hunting Union. In addition I had access to the collections in the Forest Research Institute, and also I made use of private material to some extent. The greater part of the skulls of hinds which I measured belonged to the collections of the Mammals Research Institute, Polish Academy of Sciences at Białowieża.

Table 1.
Comparison of material.

Palatinate	♂♂					♀♀				
	I	II	III	IV	Total	I	II	III	IV	Total
Olsztyn	15	32	27	19	93	49	38	29	8	124
Poznań	11	22	30	10	73	21	18	8	1	48
Koszalin	6	16	11	18	51	15	16	13	2	46
Szczecin	1	5	6	4	16	–	–	–	–	–
Bydgoszcz	1	2	3	1	7	–	1	–	–	1
Białystok	–	1	3	1	5	–	1	–	1	2
Kraków	–	2	–	1	3	–	–	–	–	–
Katowice	1	1	3	–	5	–	–	–	1	1
Zielona Góra	1	1	2	–	4	–	–	1	–	1
Opole	–	–	1	–	1	–	–	–	–	–
Łódź	–	–	1	1	2	–	–	–	–	–
Total	36	82	87	55	260	85	74	51	13	223

A total of 223 skulls of hinds and 260 skulls of stags were measured (Table 1). It did not prove possible to make all of the 34 measurements given below on the whole of the material, as some of the skulls were damaged in the region of *os occipitale* and *os sphenoides*.

The material examined was obtained primarily from the Olsztyn, Poznań and Koszalin provinces. There are fewer individuals from other provinces but the whole represents the almost complete range of the red deer's occurrence in Poland.

The stag material, as previously mentioned, came from exhibitions of hunting trophies, so that it was to a certain extent selected. The skulls measured came either from so-called "selective" individuals, or from those included in the group of der deer "trohpy stag". Selection was based primarily on the antlers. It might seem that stag material obtained in this way does not represent the whole of the Polish red deer population, but antlers constitute a factor so variable that an individual which is "selected" in one year, may in the following year, with a change of conditions for the better, develop antlers which if not "good" are at any rate average for the given hunting ground.

When considering material from this aspect it must be mentioned that red deer from different regions of Poland and from different hunting grounds are equal as regards body weight and massiveness of antlers. An individual with large body weight and considerable antler mass in relation to the general level of the local individuals in one hunting area (Poznań province) will be less than average in a different area (Olsztyn province). The criteria of selection therefore differ in different regions of Poland, these criteria being stricter in hunting areas when planned reduction shooting had been carried out.

The material was collected over a period of three years, which eliminated the possible effect of one unfavourable year as regards food and climatic conditions. In addition to stags correctly shot according to selection principles a high percentage (about 20%) of my material was formed by individuals shot in error in the given hunting area. These are individuals with a good future, that is deer which will probably develop better antlers than their present ones in succeeding years, or which currently come up to the level of the local population as regards quality of antlers and body weight, or even exceed it.

Taking the above into consideration I have permitted myself to treat the material as a whole representing the range of occurrence of the red deer in Poland.

In the case of hinds the sample from the population is of a random character.

The age of individuals was determined on the basis of the degree of wear of the teeth (Raesfeld, 1957), according to the method generally used in studies on red deer. The whole material was divided into four age groups: group I — individuals from 1 to 3 years; group II — 4 to 7 years; group III — 8 to 11 years; group IV — 12 to 16 years.

Biome (1957) divides his material into 5 age groups, but a division of this sort into smaller classes seemed pointless to me, on account of the lack of a method enabling the age of individuals below 3 years to be accurately determined. The dividing lines between the ages of 4—5 and 6—7 years are difficult to grasp. The division of material into smaller groups reduces the possibility of error to a minimum. In view of the lack of a sufficient number of skulls of older hinds in group III, and particularly in group IV, I combined these two groups in certain cases, which does not produce any great changes in the mean values, absolute measurements or indices.

The skulls were measured with a vernier calipers and zoometric compasses with sharp and closely filed points. Measurements made with the compasses were transferred to a linear measure.

A total of 34 measurements were made. All the measuring points were established after Duerst (1926) while for the few modified measurements I have described the way in which they were made. Measurements were made in the following order:

1. *Cb* — length of skull from the posterior plane of the occipital condyles to point *P* — Prosthion.
2. *P-B* — Prosthion — Basion, length of base of skull.

3. *P-Op* — Prosthion — Opisthokranion, maximum length of skull.
4. *Zl-P* — Zygolacrimale — Prosthion, lateral length of viscerocranium.
5. *Zl-Op* — Zygolacrimale — Opisthokranion.
6. *Op-Br* — Opisthokranion — Bregma.
7. *Br-N* — Bregma — Nasion, length of frontal bones.
8. *P-Br* — Prosthion — Bregma.
9. *N-Nsi* — Nasion — central point on a line connecting *Ni* with *Ni* (Nasiointermaxillare), length of nasal bones.
10. *St-B* — Staphylion — Basion, length of base of skull from end of posterior hard palate to anterior margin of *for. occipitale magnum.*
11. *St-P* — Staphylion — Prosthion, length of palate.
12. *Mol-P* — Molare — Prosthion.
13. *Pm-P* — Praemolare — Prosthion.
14. *Pm-Mo-Mo* — Praemolare — centre of line connecting *Mo* with *Mo* (Maxilloorale) length of *margo adentalis* of maxilla.
15. *Pm-Pd* — Praemolare — Postdentale — length of maxillary tooth-row, P_1—M_3.
16. *Mo-Mo* — Maxilloorale — Maxilloorale, breadth of incisive bones.
17. *Ni-Ni* — Nasointermaxillare — Nasointermaxillare, minimum breadth of nasal bones.
18. *Nm-Nm* — Nasomaxillare — Nasomaxillare, maximum breadth of nasal bones.
19. *M-M* — Molare — Molare, breadth of facial part of skull measured on facial tubers.
20. *Zy-Zy* — Zygion — Zygion, breadth of skull on lower edge of orbit.
21. *Ect-Ect* — Ectoorbitale — Ectoorbitale, breadth on posterior edge of orbit.
22. *Da-Da* — Dacryon — Dacryon, minimum breadth of frontal bones on margin of eye sockets.
23. *fs-fs* — frontostenion — frontostenion, minimum breadth of bases of antlers.
24. *eu-eu* — euryon — euryon, maximum breadth of cranium.
25. *Ot-Ot* — Otion — Otion, breadth of occipital bones.
26. *Con-Con* — breadth between external edges of occipital condyles.
27. *Nsi-margo adentalis* — measurement of height, made by sliding scale from *Nsi* vertically to *margo adentalis.*
28. *St-N* — Staphylion — Nasion, height of viscerocranium.
29. *Sph-Br* — Sphenobasion — Bregma, height of cranium.
30. *Op-O* — Opisthokranion — Opistion, maximum height of occipital.
31. *if-goc* — infradentale — gonioncaudale, length of mandibula.
32. Length of *margo adentalis mandibulae*, measured from the edge of tooth socket of final incisor to edge of tooth socket of first praemolar.
33. Length of mandibulary tooth-row, measured from the edge of tooth socket of first praemolar to edge of tooth socket of final molar.
34. *gov-cr* — gonion ventrale — coronion, height of *ramus mandibulae.*

All the measuring points are indicated on fig. 1 a-d.

Calculation was made of the confidence interval for the mean $\bar{x}$ on the level of significance $\alpha=0.01$. The limits of this interval are the values $\bar{x}-s\bar{x}\cdot t$ and $\bar{x}+s\bar{x}\cdot t$. Values t were obtained from tables of the normal distribution for mean values estimated on the basis of at least 30 element samples ($n\geqslant30$), while for the mean values estimated from smaller samples ($n\leqslant30$) *t*-Student tables were used.

The following indices were used in the study:

1. $\frac{Zy-Zy\times100}{P-Op}$
2. $\frac{Zy-Zy\times100}{P-Br}$
3. $\frac{St-N\times100}{P-Op}$
4. $\frac{St-P\times100}{P-Op}$
5. $\frac{Nsi-margo\ ad.\times100}{Pm-Pd}$
6. $\frac{Mo-Mo\times100}{Pm-P}$
7. $\frac{Pm-MoMo\times100}{St-P}$
8. $\frac{N-Nsi\times100}{M-M}$

9. $\frac{Br - N \times 100}{Ect - Ect}$

10. $\frac{Op - O \times 100}{con - con}$

11. $\frac{M - M \times 100}{St - P}$

12. $\frac{eu - eu \times 100}{St - B}$

13. $\frac{\text{length of } \textit{margo ad. mandib.} \times 100}{if - goc}$

14. $\frac{\text{length of mandibulary tooth-row} \times 100}{if - goc}$

The capacity of the cranial cavity was measured using 4.25 mm diameter shot and was expressed in cm^3.

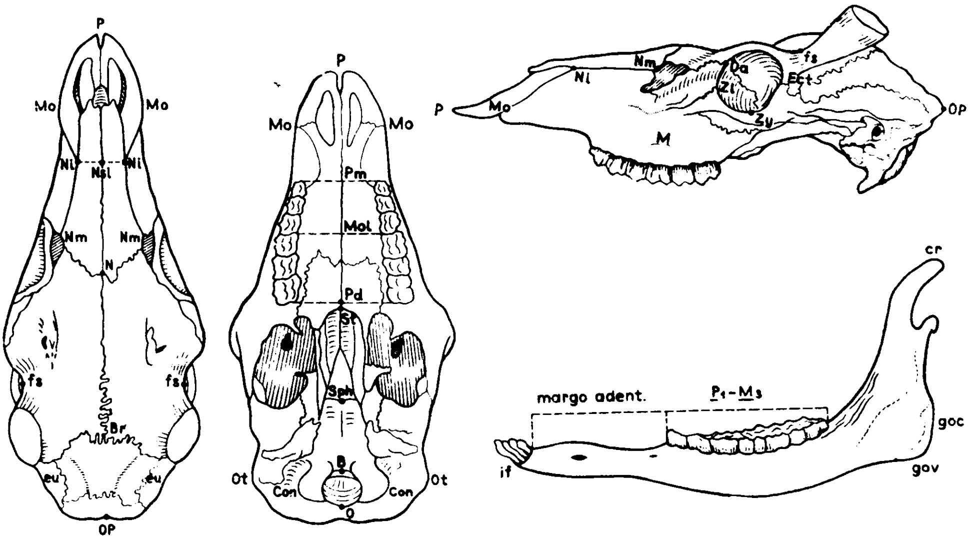

Fig. 1 (a—d). Marking of measuring points.

The body weight[2]) of stags is given according to the data of the Polish Hunting Union, the material used in this section not completely covering the material measured osteometrically. Data on the body weight of hinds were obtained from the collections of the Forest Research Institute and the Mammals Research Institute.

III. MORPHOLOGICAL DESCRIPTION OF THE SKULL

1. *Os occipitale*

The squama of the bone is oval in shape and has a clearly distinct *linea nuchalis superior,* which separates the *pars nuchalis* from *pars parietalis.* In *pars parietalis ossis occipitalis* in hinds there is a *crista sagittalis ext.* which reaches to the above-mentioned *linea nuchalis.* In the majority of stags the crista is completely invisible, although there are

[2]) The term body weight in relation to wild animals means the whole animal, only gralloched, with or without the head.

a very few cases in which it occurs. Underdevelopment of the crista in stags is compensated for by the more extensive and deep *fossa temporalis*, which is the place of insertion of *m. temporalis;* this forms a remarkable exception to the rule that the degree of development of *crista sagittalis ext.* indicates the degree of development of *m. temporalis*. In the case of red deer, despite the fact that *m. temporalis* is more strongly formed in stags than in hinds, yet, the presence of *crista sagittalis* is not always manifested.

In *pars nuchalis* in both sexes the *protuberantia occipitalis ext.* can be clearly seen, similar in shape to a triangle, the base of which is formed by *linea nuchalis*. In hinds *protuberantia occipitalis ext.* is more elongated ventral, and *crista occipitalis ext.* runs in the direction of *for. occipitale magnum*. In stags *crista occipitalis ext.* is less distinctly marked. Under *protuberantia occipitalis ext.* there is a distinct *fossa ligamentosa* divided into two parts by *crista occipitalis ext.* This fossa is more distinct in stags than in hinds. On the sides of *squama occipitalis* there are two

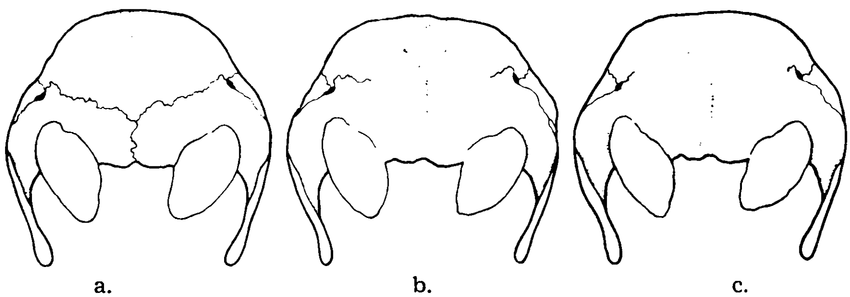

Fig. 2 (a—c). Ossification of *sut. interparietalis*.
a) ♂ aged 2—3 years, b) ♂ aged 4—5 years, c) ♂ aged 8 years.

forr. supramastoidea, which are situated either above the suture or within the trace of coalescence between exooccipitale and supraoccipitale and *pars mastoidea oss. temporalis*. The trace of fusion between the supraoccipitale and exooccipitale runs above *for. occipitale magnum* through the squama of *os occipitale*, and can be clearly seen in individuals from 2—4 years old (Fig. 2a). As from the age of 4 years the line of fusion is obliterated in the middle above *for. occipitale magnum*, to the right and left from *crista occipitalis ext.* Sections of it are still visible at this age running centripetally from *forr. supramastoidea*, the length of which is about $^{1}/_{5}$ the length of the lamina (Fig. 2b). The obliteration of this line progresses with the passage of years. At 7 years old only very small lateral sections are visible (Fig. 2c), and as from 11 years of age this fusion is completely obliterated.

The external surface of *pars nuchalis squamae occipitalis* is flatter in older stags than it is in hinds, only the part contiguous to *condyles occipitalis* being convex in the former. *For. occipitale magnum* is round in shape. Two openings occur at the base of *condyles occipitalis: for. condyloideum* and *for. nervi hypoglossi.* The greatly elongated *procc. jugulares* are situated laterally from *condyles occipitalis*, and about $^1/_3$ of their total length reaches below *condyles occipitalis*. The free ends of *procc. jugulares* are bent in bowshape towards the centre and forwards.

The basal part of *os occipitale* is elongated, narrowing in the direction of its juncture with *os sphenoides*. In the place in which it connects with *os temporale* the symmetrical *for. lacerum* occurs in the form of a gap lying parallel to the long axis of the skull. *For. lacerum aborale* is rounded, *for. lacerum orale* narrows in the direction of *os sphenoides*.

2. *Os temporale*

The suture connecting *os temporale* with *os parietale* — *sut. parietotemporalis s. squamosa* runs diagonally in an arch across the skull forwards and downards as far as *os sphenoides*. This suture can be clearly seen in all the age groups.

Proc. zygomaticus oss. temporalis runs forward and away from the centre. The upper surface of *proc. jugularis* is sharp. Near the base *geniculum proc. zygomatici* occurs, beginning at the base and running along *proc. zygomaticus* to its end. *Proc. zygomaticus* is flattened laterally: its shape, or rather the shape of the cross-section, may be compared to a triangle with one longer side. In its final part *proc. zygomaticus oss. temporalis* overlaps *proc. temporalis os. zygomaticus* and connects with it over a space equal to half the whole length of the process. The suture runs diagonally downwards from the margin of *annulus orbitalis*. This process does not contact with *proc. postoribitalis os. frontalis*. The anterior part of the process participates in the formation of the orbit from the lower and medial sides over a very small area. As in other ruminants a wide foramen leading to the temporal duct occurs on the upper surface of *lamina zygomatica*. Not infrequently it is double, or it may be completely absent. *Fossa mandibularis* is faintly marked and shallow. *Proc. postglenoidalis* is high, lamelliform and bent outwards and backwards. *Tuberculum articulare* is shaped in the form of a small prominence. At the back and towards the centre from *proc. postglenoidalis* there is a large *for. postglenoideum*. In *Cervidae* this foramen is equal in size to *porus acusticus ext. Proc. muscularis* is fairly long. pointed and directed forwards. *Crista temporalis* is well formed and caudal passes without any distinct boundary into *crista nuchalis*.

Pars mastoidea oss. temporalis takes the form of a narrow band widening slightly ventral. It is thrust between *squama oss. temporalis* and the nuchal plate of *oss. occipitalis* and the *pars tympanica oss. temporalis*. The lower part overlaps on to *proc. jugularis*, forming the lateral part of its base.

The cross-section of *pars petrosa oss. temporalis* is quadrilateral in shape with a rounded lower side. Two sides, the upper and lateral of this geometrical figure participate in forming the bottom of the skull cavity. The medial surface together with the upper surface forms a sharp edge, the *crista petrosa*, which is directed backwards and in a direction from the centre to the side. The medial surface is folded and there is a wide and deep depression *(porus acusticus int.)* in its central part, divided into two parts by the high, well-defined *crista transversa*.

Looking backwards and upwards from this opening a gap can be seen bounded on the lateral side by a bony process — this is *apertura ext. aqueductus vestibuli*. Immediately above *for. lacerum aborale* there is a similarly well defined *apertura ext. aqueductus cochlae. Incisura nervi trigemini* is faintly marked.

Beyond the posterior margin of *pars petrosa* a wide foramen opens on *os occipitale* connected by a canal with *for. supramastoideum* described simultaneously with *os occipitale*.

3. *Os sphenoides*

Two parts of the shaft of *os. sphenoides*, i. e. *praesphenoideum* and *besisphenoideum*, are connected by *synchondrosis intersphenoidalis*. Caudad the shaft of *os sphenoides* is joined with *basioccipitale* by means of *synchondrosis sphenooccipitalis*, on which normal *tubercula muscularia* are situated.

Allae orbitales ossis sphenoides are larger than *alae temporales*. They are similar to an elongated plate in shape, lying in the lower part of the orbit, forming two processes, one running upwards and thrusting into *pars orbitalis oss. frontalis* and the other running forwards, bounded from the top by *pars orbitalis ossis frontalis* and from the bottom by *lamina perpendicularis oss. palatini*. In the posterior part of *alae orbitales*, just below the suture with the frontal bone there is *foramen opticum*, and further backwards and downwards between *alae orbitales* and *alae temporales* there is the large *for. orbitorotundum* quadrilateral in shape. *Ala temporalis* runs towards the back of the skull bordering the lateral margin of *for. orbitorotundum*, then forms in its anterior part a process directed upwards and thrusting between *os temporale, os parietale, os frontale* and *alae orbitales ossis sphenoiles*. There is a large *for. ovale* in the posterior part of this process. *Alae* *temporales ossis sphenoides* are bounded from the front by *for. lacerum orale.*

4. *Os ethmoidale*

Lamina cribrosa is divided into two parts by the low *crista galli*, which is fairly narrow at the base and broadens upwards. Both parts of *lamina cribrosa* i. e. *fossa olfactoria* are a regular oval in shape and each of them is situated diagonally from bottom upwards and away from the centre.

Lamina perpendicularis together with vomer form the posterior part of the *septum cavi nasi.*

Labirynthus *oss. ethmoidalis* is formed by a group of very thin bony laminae rolled in the shape of cylinders — *ethmoturbinalia*, situated in the posterior upper region of *cavum nasi.*

5. *Os parietale*

Partes parietales of the paired *ossa parietalia* are rectangular in shape, bent in the shape of a bow in the central part. *Partes temporales* on the other hand form a narrow band running diagonally downwards, surrounding the anterior part of the braincase from the sides. They thrust between *os temporale* and *os frontale*, and in males bound the base of the antlers from the back. The measuring point *eu* is situated on *os parietale* in older individuals or on *sut. squamosa* in younger animals. In females this point lies on *os parietale* or on *os temporale. Crista parietalis ext.* can be seen only in the form of a slight eminence taking the form of a bony line.

6. *Os frontale*

The vaulted parts — squamae of the paired *ossa frontalia* take the form as a whole of a slightly convex lamina between *margines orbitales.* In its posterior part this lamina broadens considerably and forms antlers in males. The posterior part of the lamina is raised upwards and at times point *Br.* is the highest point of the skull. *Sut. coronaria* is situated horizontally in females, along an almost straight line (similarly to that in goats): in males it surrounds the bases of the antlers and enters between them in a forwards direction. *Sut. interfrontale* is clearly visible in individuals of both sexes up to 8 years of age (and in females is not obliterated up to the end of their lives. Obliteration of the suture begins from point *Br* in a forwards direction. A bony crest occurs on this suture starting at a distance of $1/3$ the length of the frontal bone going from front to back. This crest is clearer in females and is most distinct in the highest point of the skull. It begins in both females and males in the depression on the front of the squama between the *margines orbitales*. Central from *margines supraorbitales* there are extensive *for. supraorbitale* on both sides, usually single ones, although a larger number of additional foramina may occur here occasionally. *Sulci supraorbitales ant. et post.* begin from these foramina. The medial margin of these sulci is sharp and high. *Margo supraorbitalis* is slightly inclined upwards and semi-circular in its central part. *Proc. postorbitalis s. proc. zygomaticus oss. frontalis,* situated almost vertically to *arcus zygomaticus,* is connected with *proc. postorbitalis oss. zygomatici,* forming the posterior margin of *annulus orbitalis. Crista frontalis ext.* is clearly defined in females only. This crest does not occur in males on account of the presence of the antlers. This character distinguishes male stags from other ruminants. The bases of the antlers are surrounded with *sut. coronalis* from the back and exterior.

The antlers of males of *C. elaphus* take very varied forms, depending on age, endocrine secretion, components of their food, heredity and the possibility cannot be excluded that other factors may play a part in shaping the antlers in one and not another form (Vogt, 1947; Frankenberger, 1955; Bališ, 1959). Taking into consideration only the lowland males it can be stated that in the material examined the best heads were those of males in the Olsztyn province, the poorest males from the Poznań and Opole provinces.

Margo supraorbitalis is situated diagonally in relation to the long axis of the skull and in its anterior part the left and right sides of the margin run diagonally and central in the direction of *os lacrimale*.

Sut. nasofrontalis takes very varied forms (Fig. 3a-l) and is clearly visible throughout the whole life of the animal. *Procc. nasale oss. frontalis* are bounded from the sides by *ossa nasalia* which in their central part thrust far between *ossa frontalia*. The above processes partly separate the *os nasale* from *hiatus lacrimalis:* cases occur in which *os frontale* reaches to *os maxillare* (Fig. 3 d, f, l). Such cases are in general rare; more often the *os frontale* does not contact the *os maxillare* and is separated from it by processes of *ossis nasalis*.

Pars orbitalis oss. frontalis takes the form of a lamina running downwards from the vaulted part and participates in the formation of the greater part of the orbit. The suture between *os frontale (pars orbitalis)* and *os lacrimale, os sphenoides* and *os temporale* is clearly visible in all age groups. In the upper part of the *lamina orbitalis* there is *for. supraorbitale inf. For. ethmoidale laterale* is situated in the lower part of *lamina orbitalis,* immediately above the suture with *os sphenoides*.

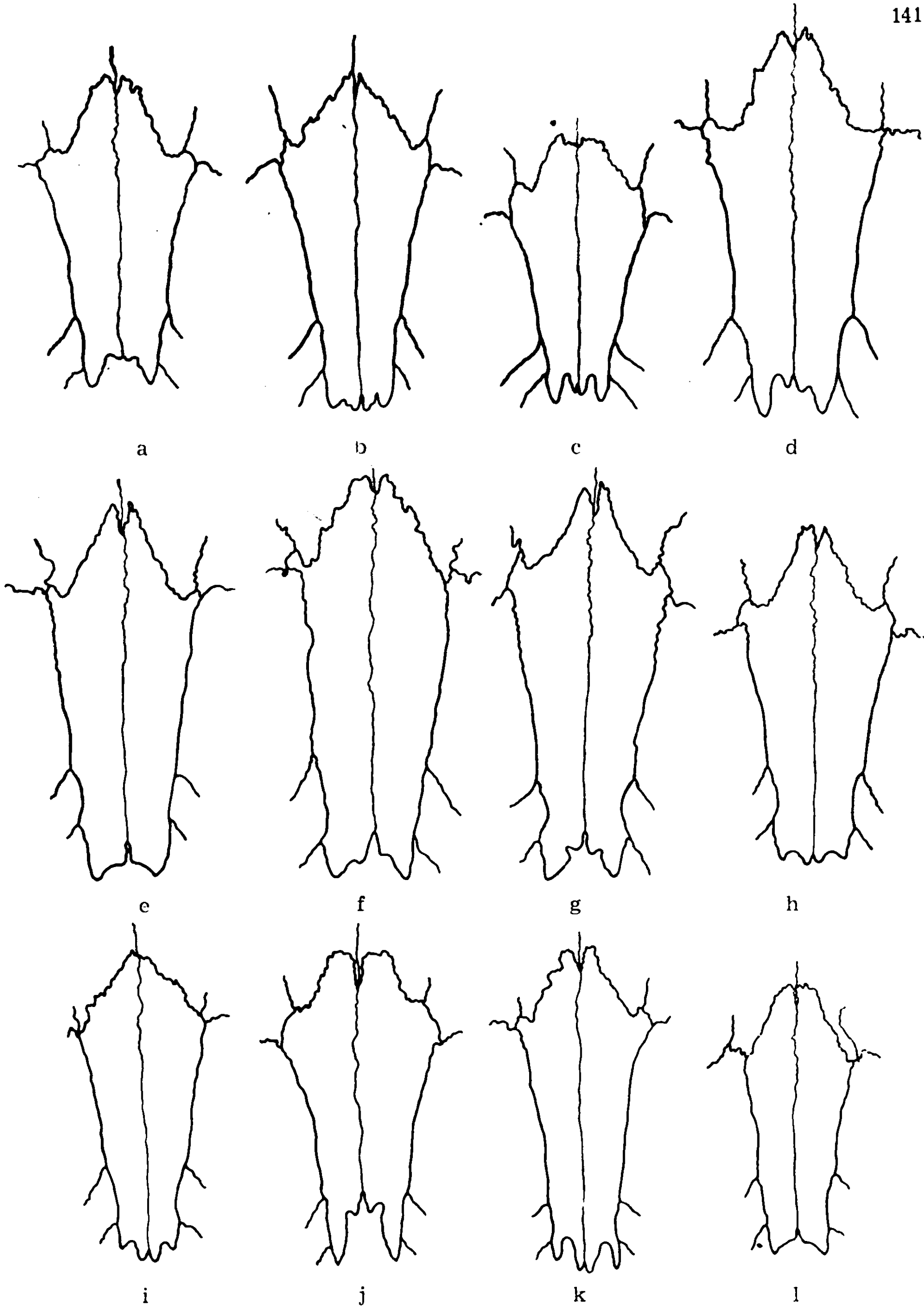

Fig. 3 (a—l). Structure of nasal bones.
a) ♂ — 2 years; b) ♂ — 3 years; c) ♂ — 5 years — Poznań province; d) ♂ — 8 years — Bydgoszcz province; e) ♂ — 10 years — Olsztyn province; f) ♂ — 10—11 years — Olsztyn province; g) ♂ — 11 years, Poznań province; h) ♂ — 12 years — Koszalin province; i) ♀ — 6 years, Olsztyn province; j) ♀ — 8 years, Olsztyn province; k) ♀ — 9 years, Olsztyn province; l) ♀ — 12 years, Koszalin province.

7. *Os nasale*

Ossa nasalia are formed in the shape of elongated, arched *laminae. Sut. internasalis* is clearly marked throughout the whole of the animal's life. In the posterior part *ossa nasalia* thrust deep in between *ossa frontalia.* From the side, on the boundary with *hiatus lacrimalis,* there are processes separating *os frontale* from *os maxillare.* These processes take different shapes, considerable individual variation occurring here (Fig. 3a-1). They may be either broad or very narrow. Occasionally they do not occur at all and then *os frontale* is directly connected with *os maxillare,* as mentioned above. In the anterior part *ossa nasalia* protrude beyond *os intermaxillare* for a distance of 5—10 mm, and sometimes even more. *Margo liber* is formed in the shape of a letter W, the sides of which are formed by the exterior part of the bone reaching to *os intermaxillare.* This margin takes the form of two *procc. nasale* — pericentral and lateral. The lateral processes on both sides are usually longer, but this is not invariable (Fig. 3).

8. *Os lacrimale*

Pars facialis is similar in shape to a triangle, the base of which is formed by *margo orbitalis.* A large, irregular opening, termed *hiatus lacrimalis,* occurs between this part of *os lacrimale* and the following bones: *os frontale, os nasale* and *os maxillare.* An extensive depression, often with numerous foramina, situated lengthways and diagonally forwards and downwards in relation to the long axis of the skull, can be seen on the facial part of *os lacrimale.* This is *fossa lacrimalis ext.* A similar *fossa lacrimalis* occurs in sheep. On *margo orbitalis oss. lacrimalis* there are two *forr. lacrimalia,* situated on the *margo orbitalis* itself. One of them may also lie in the facial part. *Sut. lacrimo-zygomatica* is clearly visible throughout the whole life of the animals. The suture between *os lacrimale* and *os frontale* is loose in age group one, ossifying in higher age groups, but always distinct. There is a deep incision on this suture on *margo orbitalis,* between *os frontale* and *os lacrimale,* on which the measurement point Dacryon — *Da* is situated. The incision is deeper and most distinct in the skulls of older animals.

Pars orbitalis is somewhat similar in shape to an acute-angled triangle. There is a depression in the form of a funnel — *fossa sacci lacrimalis* — in this lamina above the suture with *os maxillare.* A well formed *bulla lacrimalis* is situated in the anterioro-lateral part of the orbit.

9. *Vomer*

The vomer takes the form of a thin lamina, decreasing in height from back to front. Vomer begins slightly to the fore from *synchondrosis* *intersphenoidalis*. In its central part it forms, together with *lamina perpendicularis oss. ethmoidalis, septum nasi osseum.*

Sulcus vomeris forms a fairly deep groove which reaches to *procc. palatinus oss. intermaxillaris,* overlapping them on their posterior part for a distance of approx. 1.5 to 2 cm.

10. *Os maxillare*

The external surface of the shaft may be compared to a trapezium with one side markedly elongated. It is convex in the shape of a roof, this convexity increasing caudad, and beginning in the region of *for. infraorbitale,* which lies at the level of the P_1. The convexity then runs backward and downward in the direction of *tuber faciale.* This tuber is faintly marked in young individuals (age group I), in which it is situated in the plane of the M_1. In the second age group it shifts to the boundary between the M_1 and M_2. In the third and fourth age group *tuber faciale* lies in the plane of the M_2 or M_3. *Tuber maxillae* lies in the extension backwards of the edge of the tooth socket and ends in a sharp process bent central. *For. maxillare* is situated in the posterior part of the shaft and is also formed by *lamina perpendicularis oss. palatini.*

As in all ruminants the premolars and molars are separated from the canine teeth by *margo adentalis.* In the anterior part of *proc. alveolaris* there is *alveolus caninus,* also partly formed by *os intermaxillare.*

Proc. palatinus is similar to an elongated lamina in shape. From the front it is bounded by *proc. palatinus oss. intermaxillaris,* thus participating in the formation of the lateral and posterior part of *fissura palatina.* In the medial and anterior part of the two *procc. palatini* there is a triangular incision on *sut. palatina media,* into which the posterior parts of *procc. palatini oss. intermaxillaris* enter. *Forr. palatina majora* described in detail in connection with *os palatinum,* occur on the suture between *procc. palatini oss. maxillaris* and *laminae horizontales ossa palatini.* The left and right *sulci palatini,* which are relatively short (since they scarcely reach the height of the first molar), run from these foramina along *procc. palatini oss. maxillaris* to the front. *Sut. palatina media* between the left and right *proc. palatinus* is clearly visible throughout the whole of the animals' life.

Proc. zygomaticus is faintly marked, and thrusts between *proc. zygomaticus oss. temporalis* and *proc. temporalis oss. zygomatici,* participating to a minimum extent in the formation of the medial part of *arcus zygomaticus.*

11. *Os intermaxillare*

Ossa intermaxillaria protrude very strongly forwards and form *hilus nasalis* at the entrance to *cavum nasi.*

Fissura incisiva is visible on *corpus oss. intermaxillaris,* and is similar in shape to that in sheep. In the posterior part of the corpus where it connects with *os maxillare* there is a small depression, which is part of *alveolus caninus.* The greater part of this alveolus is however formed by *os maxillare. Proc. nasalis,* shaped like an elongated and convex plate reaches to *ossa nasalia* and is connected with them by a suture which does not ossify throughout the animals' entire lifetime. The suture between *proc. nasalis* and *os maxillare* does not ossify at any time. *Procc. palatini* are very thin and long and form the medial margin and the edge of *fissura palatina.*

12. *Os palatinum*

Laminae horizontales of both bones are similar in shape to a letter U with the base directed to the front. The anterior edge of these laminae, bounded by the *procc. palatini oss. maxillaris,* is ragged. The suture between the right and left *laminae horizontales* has slightly raised edges which form a characteristic bony crest. The measurement point *St.* lies on the posterior margin of this suture. In young individuals (age group I) *St.* lies in the convexity between *oss. palatina* in front of the measurement point *Pd.* This point is situated in the centre of a line connecting the edges, the posterior margins of the alveoli of the final molars M_3 on the left and right sides. In older individuals (age groups II, III and IV) *St.* is situated at the back of *Pd.* This is connected with the change in the length of the tooth row with the animal's age.

For. palatinum majus is situated on the suture between *lamina horizontalis* and *proc. palatinus oss. maxillaris.* This foramen forms a sort of kink, a depression between the two bones, its lower ventral wall being formed by *lamina palatina* and upper dorsal wall by *proc. palatinus oss. maxillaris. For. palatinum aborale* is situated on the lateral surface of *lamina perpendicularis oss. palatini. For maxillare* can be seen in the place where *lamina perpendicularis oss. palatini* joins *os maxillare.*

Proc. pterygoideus is large and irregular in shape.

13. *Os pterygoideum*

Os pterygoideum on the left and right side takes the form of a thin lamina shaped like an acute-angled triangle. The acute angle of this triangle is directed forwards and downwards. It is elongated in its apical part, forming a thin plate ending in a hamulus. *Margo inf.* of this complicated geometrical figure is arched downards.

14. *Os zygomaticum*

Pars facialis is rectangular in shape. A bony crest runs through its whole length (similarly to that in cattle and goats, except that in cattle it is extended on to *os maxillare*, and in goats surrounds *margo orbitalis* and runs upwards). In the stag this crest begins from the suture between *os zygomaticum* and *os maxillare* and runs along the bone below *annulus orbitalis* as far as *proc. temporalis oss. zygomatici.* It next runs to the suture with *proc. zygomaticus oss. temporale* on *arcus zygomaticus,* then passes on the lateral side of this process and ends at its base. A depression like a long groove, which is clearly visible in older individuals (as from age group II) can be seen under this crest in the region of the anterior part of the orbit.

Proc. temporalis is elongated and overlaps in its posterior part on to the lateral and lower side of *proc. zygomaticus oss. temporalis.*

Proc. postorbitalis oss. zygomatici forms the posterior and lower edge of *annulus orbitalis.* It is situated almost perpendicularly to *arcus zygomaticus* and is connected by a suture with *proc. postorbitalis oss. frontalis.* This suture ossifies in age groups III and IV and is more difficult to see than in age groups I and II.

Pars orbitalis oss. zygomatici is shaped like an elongated, rectangular plate bounding the lower lateral part of the orbit, and where it connects with *pars facialis* it forms the *margo inf. annuli orbitalis.*

15. *Conchae nasales*

Conchae nasales are similar in shape to those in other ruminants.

Concha nasalis sup., or *nasoturbinale,* is faintly developed. It occurs in the form of a long, porous bony lamina attached to the *crista nasoturbinalis.*

Conache nasalis inf. or *maxilloturbinale,* far larger than the preceding, can be distinguished by the two rolled bony laminae running from a common basic lamina attached to *crista maxilloturbinalis. Lamina sup. maxilloturbinale* rolls upwards and forms four twists, *lamina inf.* forms only one twist and is rolled downards.

16. *Mandibula*

Both *ossa mandibularia* are set in *symphysis mandibularis* which does not ossify throughout the animals' life. The inferior surface of *corpus mandibulae* is bent in a bow shape upwards. There is a clearly visible *incisura praemasseterica. Margo adentalis mandibulae,* with a sharp edge, occurs on the upper margin of the corpus between the alveolus of the final "incisor" and the first premolar. A fairly large oval *for. mentale* occurs on the external surface of the corpus in its *pars incisiva.* At the back of this opening there is a second opening of varying size but usually smaller, characteristic only of *Cervidae,* although it does not occur in all individuals.

Ramus mandibulae takes the shape of a rectangular lamina broadening towards the base. The angle between *corpus* and *ramus mandibulae* is almost a right angle.

Proc. articularis is shaped similarly to that in other ruminants. *Proc. temporalis* takes the form of a long lamina arched upwards and backwards. *Fossa masseterica*, shaped like rectangular triangle, is situated on the external surface of *ramus mandibulae*, below *incisura mandibulae*. A long and convex bony crest, characteristic of red deer, occurs in the posterior and lower part of *angulus mandibulae*. It begins in the lower part of *angulus mandibulae*, at the back of *incisura praemasseterica*, and runs in a bow along the angle upwards ending approximately halfway along the ramus in fairly large protuberantia inclined forwards and sideways. This crest is more distinct and larger in older individuals, and only faintly marked in females.

On the medial surface about halfway along *ramus mandibulae* there is the fairly large horseshoe-shaped *for. mandibulare*.

IV. OBLITERATION OF SUTURES

I should like to draw attention in this section to certain differences in the rate of obliteration of some sutures in the skulls of males and females, connected with sex dimorphism. This may prove of some assistance in identifying the age of different individuals, or at least in defining the age group of, e. g. fossil remains, when only a fragment of the skull, deprived of teeth, is preserved.

Males and females must be considered separately, since the rate at which the sutures become obliterated is not uniform in the two sexes. (Tables 2, 3). All the sutures in males ossify far earlier than in females, which agrees with the observations made of the European bison (Empel, 1962). Such sutures as *sut. coronaria, sut. frontalis, sut. frontalis, sut. lambdoidea* do not ossify in females throughout their lifetime. Only occasionally, in rare cases, does their obliteration begin in a certain place in very old females. *Sut. interparietalis* and *sut. sphenooccipitalis* undergo obliteration earliest. In males 4 years old these sutures are already obliterated, in females the first is obliterated at the age of 7 and in the second at the age of 4 years. The fact is remarkable that *sut. coronaria*, which begins to obliterate fairly early in males (as early as the 4th year of life), in females remains unobliterated up to the animals' death. This is probably connected with the considerable burden placed on the skull of the male by the antlers, which may often weigh up to nearly 12 kg. The same explanation applies to the earlier

Table 2.

Description of skull suteres in ♂♂

Age in years	*Sut. coronaria*	*Sut. lambdoidea*	*Sut. interparietale* (Trace of adhesion between *oss. occipit.*)	*Sut. squamosa*	*Sut. frontalis*	*Synch. spheno-occipitalis*	*Synch. inter-sphenoidalis*
1	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct
2							
3			Obliterating in medial part				
4	Obliterating in medial part between bases of antlers		Obliterated in medial part above *for occip. magnum.* Lateral parts visible $^1/_5$ length of squama			Obliterated in medial part, lateral parts distinctly obliterating	
5		Obliterating in medial part to left and right of *crista ocip. ext.*					
6							
7			Obliterated for approx. $^3/_4$ length of suture. Very small lateral sections visible,			Obliterated	
8		Obliterated or obliterating in medial part. Lateral parts reaching *linea partietal. ext.* obliterating			Obliterating in posterior part beginning from *Br* forwards		
9	Obliterated in medial part, obliteration of further part behind antlers				$^1/_5$ length oblitd. app. $^1/_5$ obliterating (forwards) $^3/_5$ distinct		
10							Obliterating or obliterated
11			Obliterated		$^1/_3$ suture oblitd. remainder obliterating. Small section distinct from front		Obliterated
12	Obliterated at back of antler bases obliterated or obliterating from sides	Obliterated in medial part, obliterating on sides.			$^1/_2$ suture obltd. remainder oblitg. cases occur when at 14 years of age suture is still in obltg. stage		
over 12							

Table 3.

Description of skull sutures in ♀♀

Age in years	*Sut. coronaria*	*Sut. lambdoidea*	*Sut. interparietale* (Trace of adhesion between *oss. occipitalia*)	*Sut. squamosa*	*Sut. frontalis*	*Synch. spheno-occipitalis*	*Synch. intersphenoidalis*
1			Distinct			Distinct	
2			Medial part obliterating, visible. Lateral parts. length app. 1/5 of whole distinct			Obliterated but small side parts sometimes visible	
3			Medial part obliterating or obliterated. Lateral parts still distinct				Distinct
4			Obliterated in medial part. Lateral parts app. 1/7 of total length of suture still distinct				
5		Distinct					
6	Distinct		Almost whole obliterated. Side parts distinct, are very short		Distinct		
7			Obliterated but cases occur in which side parts are still visible	Distinct			Obliteration beginning in medial part
8						Obliterated	Obliteration in medial part. Cases occur in which suture allready obliterated
9							
10		Distinct or obliteration beginning in medial part of suture above *protuberantia occipitalis*	Obliterated				
11							
12							Obliteratad
over 12	Distinct in majority of cases, but obliteration beginning at Bregma				In majority of cases suture is distinct but obliteration is beginning at Bregma		

obliteration in males of *sut. lambdoidea*. *Sut. frontalis* and *sut. intersphenoidalis* remain unobliterated for a very long time.

V. VARIATIONS IN SKULL MEASUREMENTS AND INDICES

Thirty-four measurements were made on the skulls, and the results are given in tables 4 and 5. The calculated values of 14 indices are given in table 6, retaining the division into the same age groups.

Discussion in this section has been limited to the most interesting measurements, which throw some light on the question of sex dimorphism in the red deer.

Table 4.
Variations in skull measurements of males (in mm).

No.	Measurement	I group			II group			III group			IV group		
		n	$\bar{x}$	$\pm S_{\bar{x}} \cdot t$	n	$\bar{x}$	$\pm S_{\bar{x}} \cdot t$	n	$\bar{x}$	$\pm S_{\bar{x}} \cdot t$	n	$\bar{x}$	$\pm S_{\bar{x}} \cdot t$
1	CB	20	370.1	±12.0	44	386.3	±7.0	40	405.1	±12.6	26	396.8	±8.6
2	P - B	20	348.0	±12.3	44	363.9	±7.5	57	374.6	± 6.2	24	376.4	±9.0
3	P - Op	36	386.7	±12.6	86	406.8	±5.4	101	418.5	± 4.9	57	419.3	±5.7
4	Zl - P	36	220.2	± 6.7	86	232.7	±4.4	78	241.8	± 3.9	57	239.7	±4.6
5	Zl - Op	37	188.4	± 4.4	86	197.3	±2.3	103	203.0	±1.8	57	205.2	±2.1
6	Op - Br	37	86.2	± 1.8	85	88.9	±3.4	103	89.5	±1.3	55	90.9	±2.1
7	Br - N	37	122.7	± 3.9	85	128.4	±3.1	103	131.6	±2.8	57	132.6	±3.1
8	P - Br	23	321.0	± 8.8	85	343.1	±5.9	101	352.5	±5.2	56	356.6	±5.9
9	Nsi - N	37	95.7	± 6.7	86	103.3	±3.4	102	106.4	±2.6	56	107.1	±2.6
10	St - B	20	129.7	± 6.3	43	130.2	±13.7	59	138.1	±4.1	23	143.6	±3.9
11	St - P	36	218.2	± 5.9	81	231.0	±4.4	95	238.3	±3.6	53	237.1	±4.4
12	Mol - P	36	159.9	± 4.1	85	165.7	±2.3	101	168.1	±2.6	55	169.1	±3.4
13	Pm - P	36	117.0	± 3.6	86	125.2	±3.4	100	128.7	±2.3	56	130.2	±2.6
14	Pm - Mo -Mo	37	75.9	± 5.2	85	78.4	±2.1	99	81.2	±2.1	54	82.4	±2.3
15	Pm - Pd	-	-		86	107.4	±2.3	102	105.6	±1.3	53	101.3	±1.5
16	Mo - Mo	36	60.0	± 2.1	85	65.0	±0.8	100	68.5	±1.3	56	69.7	±1.3
17	Ni - Ni	33	29.4	± 1.8	66	32.4	±1.5	84	35.2	±1.0	52	35.8	±1.5
18	Nm - Nm	37	46.7	± 2.3	83	50.3	±1.5	102	51.9	±1.5	57	57.4	±2.1
19	M - M	37	117.8	± 2.3	82	127.0	±1.8	103	131.2	±2.3	57	133.2	±2.3
20	Zy - Zy	37	158.4	± 2.8	85	169.1	±2.1	103	175.3	±2.1	57	177.1	±2.3
21	Ect - Ect	37	162.5	± 3.1	86	173.4	±2.1	103	179.3	±2.1	56	181.4	±2.3
22	Da - Da	37	114.5	± 8.3	86	115.5	±1.8	102	120.5	±1.3	57	121.1	±2.3
23	fy - fs	37	116.4	± 2.1	85	119.3	±1.8	102	123.3	±1.5	54	126.3	±2.3
24	eu - eu	36	96.0	± 1.8	86	100.9	±1.3	103	104.8	±1.8	57	105.9	±2.1
25	Ot - Ot	34	117.7	± 3.4	75	127.3	±2.1	88	133.5	±1.8	50	134.7	±2.1
26	Con - Con	21	71.4	± 1.4	44	71.5	±1.5	58	73.9	±1.8	26	72.2	±1.7
27	Nsi-margo ad	37	57.1	± 1.8	86	60.2	±0	103	62.8	±1.0	56	63.3	±1.3
28	St - N	37	87.4	± 2.6	82	93.3	±1.8	97	96.1	±1.3	53	96.1	±1.3
29	Sph - Br	35	87.7	± 1.8	79	92.4	±1.3	89	96.9	±1.3	46	99.2	±1.8
30	Op - O	21	53.6	± 2.0	43	56.1	±6.2	57	55.0	±1.3	29	53.8	±1.9
31	if - goo	32	294.2	± 7.5	56	310.6	±8.3	77	313.3	±6.2	44	320.9	±5.2
32	Length m. ad. mand.	32	90.1	± 4.4	68	96.6	±2.6	78	100.6	±2.3	47	103.5	±3.1
33	Length P_1-M_3	-	-		66	120.7	±1.0	79	119.7	±1.5	47	117.1	±1.8
34	gov - cr	32	145.6	+ 3.9	54	·50.2	+2.3	76	154.3	+2.1	42	156.5	+2.6

Table 5.
Variations in skull measurements of females (in mm).

No.	Measurement	I group			II group			III group			IV group		
		n	$\bar{x}$	$\pm S_{\bar{x}}t$	n	$\bar{x}$	$\pm S_{\bar{x}}t$	n	$\bar{x}$	$\pm S_{\bar{x}}t$	n	$\bar{x}$	$\pm S_{\bar{x}}t$
1	CB	81	301.3	±9.5	65	351.8	±4.4	45	360.7	±6.2	13	362.9	±17.1
2	P - B	81	279.9	±9.3	63	329.7	±4.6	45	338.5	±5.9	13	339.8	±15.0
3	P - Op	87	312.3	±9.3	73	363.5	±4.9	52	372.6	±5.4	13	375.4	±15.3
4	Zl - P	85	174.5	±6.7	73	211.1	±3.4	52	219.5	±3.6	13	220.8	±36.7
5	Zl - Op	87	156.0	±3.6	73	172.0	±2.1	52	173.6	±2.3	13	175.1	± 5.8
6	Op - Br	86	76.5	±0.8	72	79.9	±1.5	52	80.1	±1.0	13	80.3	± 3.4
7	Br - N	87	94.2	±2.6	73	106.6	±2.1	51	107.6	±2.1	13	110.7	± 5.2
8	P - Br	87	255.6	±8.5	73	303.2	±4.1	52	312.2	±4.6	13	314.6	± 5.0
9	Nsi - N	85	77.3	±3.6	72	95.6	±0.8	52	100.2	±2.8	13	97.1	±17.7
10	St - B	75	103.3	±3.1	59	117.1	±2.3	39	119.3	±2.3	10	123.0	± 6.2
11	St - P	82	179.6	±9.3	65	212.6	±7.5	45	218.8	±4.9	10	217.7	±15.0
12	Mol - P	87	138.9	±3.1	72	153.5	±2.3	52	157.9	±3.4	13	160.6	± 9.5
13	Pm - P	87	96.4	±3.4	72	112.9	±2.1	52	118.1	±2.8	13	121.5	± 6.4
14	Pm-Mo-Mo	87	61.9	±2.6	71	72.7	±1.5	52	77.1	±2.1	13	78.9	± 6.7
15	Pm - Pd	-	-		71	106.8	±1.5	52	104.7	±1.5	13	99.1	± 3.4
16	Mo - Mo	87	47.6	±1.3	72	55.8	±1.8	52	58.1	±1.0	13	60.6	± 4.6
17	Ni - Ni	69	22.9	±1.3	69	27.1	±1.3	51	28.1	±1.0	13	28.0	± 1.8
18	Nm - Nm	68	38.9	±1.3	70	43.1	±1.3	51	44.8	±1.5	13	43.7	± 4.3
19	M - M	85	98.0	±2.6	73	112.8	±1.8	52	117.5	±1.8	12	120.1	± 3.4
20	Zy - Zy	86	129.7	±2.8	71	145.3	±3.4	51	147.8	±2.1	13	150.4	± 4.3
21	Ect - Ect	85	132.1	±2.6	70	146.4	±3.4	51	149.7	±2.1	11	151.5	± 6.7
22	Da - Da	86	87.2	±2.3	71	99.1	±2.6	52	102.3	±1.5	13	104.7	± 4.0
23	fs - fs	-	-		-	-		-	-		-	-	
24	eu - eu	86	86.8	±1.3	73	90.1	±1.3	52	90.8	±1.0	13	91.9	± 3.4
25	Ot - Ot	83	95.0	±0.3	67	104.8	±2.8	46	106.5	±1.8	12	106.1	± 5.0
26	Con - Con	80	62.9	±1.3	62	65.3	±1.3	44	65.9	±1.0	13	65.2	± 3.4
27	Nsi-margo ad.	73	47.3	±1.5	70	53.6	±0.5	50	54.6	±1.3	13	54.1	± 3.1
28	St - N	81	71.2	±1.8	66	79.1	±1.0	46	80.5	±1.8	12	80.3	± 4.3
29	Sph - Br	77	74.7	±2.6	58	79.0	±1.3	43	79.2	±1.5	10	81.3	± 2.6
30	Op - O	82	43.5	±1.3	63	46.7	±0.8	46	47.6	±1.3	12	46.8	± 2.2
31	if - goc	85	239.3	±8.0	67	284.2	±2.6	49	291.3	±4.6	12	296.6	± 9.9
32	Length m.ad.mand.	85	71.4	±2.3	68	84.6	±1.7	49	90.1	±1.6	12	92.6	± 6.8
33	Length P_1-M_3	-	-		68	121.9	±2.1	49	118.8	±1.3	12	116.3	± 3.7
34	gov - or	84	123.1	±3.8	68	140.4	±2.1	49	142.9	±2.6	12	143.6	± 5.9

A choice was made of 13 of the 34 measurements, and calculation was made by means of the *t*-Student statistics of the significance of differences between their values in males and females. These differences are significant at the level of $\alpha = 0.01$ with $(n_1 + n_2 - 2)$ degrees of freedom for all 13 measurements. The mean values of these measurements are given in table 7 for males and females, also t-empirical values and number of degrees of freedom.

When considering the measurement of maximum length of the skull (*P — Op*) it will be noticed that sex dimorphism in the red deer is very distinct here. The greatest differences between males and females occur

Table 6.
Variations in skull indices of males and females.

Index	Age class	♂♂ n	♂♂ Min.	♂♂ Avg.	♂♂ Max.	♀♀ n	♀♀ Min.	♀♀ Avg.	♀♀ Max.
Zy-Zy x 100 / P-Op	I	37	37.8	41.4	48.0	86	37.6	41.7	46.9
	II	85	37.9	41.6	45.6	72	37.2	39.9	47.8
	III	101	38.5	41.9	48.0	51	37.0	39.7	42.5
	IV	57	39.1	42.3	46.0	13	38.4	40.1	42.4
Zy-Zy x 100 / P-Br	I	35	45.4	49.3	55.7	86	45.2	51.1	58.2
	II	84	44.9	49.6	61.3	72	43.8	47.7	52.3
	III	101	44.6	49.4	55.9	51	44.0	47.4	51.4
	IV	56	45.8	49.7	54.1	13	44.9	47.9	51.3
St-N x 100 / P-Op	I	36	21.0	22.7	24.8	81	20.2	23.0	28.2
	II	82	20.4	23.0	27.5	65	19.9	21.8	24.7
	III	94	21.1	23.0	25.2	46	19.9	21.6	23.6
	IV	52	20.9	22.8	24.5	12	19.9	21.3	22.2
St-P x 100 / P-Op	I	36	53.0	56.6	64.0	82	51.0	56.7	62.6
	II	81	53.5	57.1	61.3	66	54.7	58.3	62.8
	III	95	53.5	57.0	59.9	45	55.5	58.8	60.9
	IV	53	54.0	56.5	59.8	10	55.7	57.8	60.0
Nsi-margo adent x 100 / Pm-Pd	I								
	II	85	39.9	55.8	67.0	68	42.7	50.5	61.8
	III	102	51.6	59.5	74.7	50	43.6	52.2	60.0
	IV	52	55.2	62.8	76.1	13	50.1	54.7	62.0
Mo-Mo x 100 / Pm-P	I	33	45.7	51.6	59.5	87	43.7	49.7	57.9
	II	84	45.5	52.4	59.0	72	45.5	49.4	55.7
	III	94	47.6	53.5	60.2	52	44.8	49.3	57.8
	IV	55	47.5	53.7	62.1	13	43.2	50.0	55.4
Pm-Mo Mo x 100 / St-P	I	34	29.3	33.7	42.3	81	27.7	35.1	44.6
	II	78	29.6	33.5	39.6	64	30.7	34.4	38.7
	III	90	29.6	34.0	39.3	45	31.6	35.3	39.0
	IV	52	31.7	34.7	40.0	10	33.3	36.2	41.4
N-Nsi x 100 / M-M	I	36	66.0	79.5	93.0	85	57.1	78.7	96.7
	II	83	64.9	81.4	100.7	72	69.7	84.8	100.5
	III	101	60.5	80.8	97.9	52	67.6	85.3	100.5
	IV	57	64.3	80.4	98.4	12	67.4	82.3	96.0
Br-N x 100 / Ect-Ect	I	37	66.0	75.6	89.6	85	63.8	71.5	80.4
	II	84	62.0	73.8	87.3	71	60.4	73.3	83.0
	III	102	62.8	73.6	90.0	48	61.9	71.9	81.0
	IV	56	58.5	72.6	84.1	11	64.8	72.3	80.5
Op-O x 100 / Con-Con	I	24	71.0	75.5	82.1	80	53.6	69.2	79.7
	II	42	67.1	75.1	82.0	62	57.0	71.1	82.3
	III	55	51.8	73.9	82.2	44	61.5	72.3	86.1
	IV	26	59.2	74.1	84.0	12	66.1	71.7	77.8
M-M x 100 / St-P	I	36	49.2	54.1	62.3	79	48.2	55.3	65.3
	II	75	48.8	54.7	63.0	66	47.6	53.2	58.3
	III	94	50.8	55.4	63.5	45	49.5	53.7	59.3
	IV	54	49.8	56.3	62.1	9	52.5	55.3	61.6
Eu-Eu x 100 / St-B	I	20	68.0	74.2	81.9	74	72.2	84.6	98.1
	II	43	67.4	74.8	89.8	58	67.2	77.0	89.5
	III	56	63.2	74.7	82.2	39	71.3	76.2	83.1
	IV	23	65.4	74.2	91.7	10	69.1	75.6	85.1
Margo ad.mand. x 100 / If-goc	I	32	26.4	30.6	40.7	85	27.4	29.8	33.7
	II	67	27.6	31.3	35.2	67	27.5	29.7	32.5
	III	77	27.9	31.8	34.5	49	28.0	30.9	33.1
	IV	44	28.3	32.3	35.3	12	29.0	31.2	33.9
Mandib. tooth-row x 100 / If-goo	I								
	II	64	33.3	39.4	49.8	67	39.0	43.1	48.0
	III	77	34.2	37.9	41.1	49	37.2	40.8	47.6
	IV	44	32.0	36.5	42.3	12	36.8	39.2	42.7

in age group I. The difference between mean values attains a value of 74.4 mm. This difference decreases with increasing age of the individuals, attaining a value of 43.9 mm in age group IV. The differences between the mean values are statistically significant in all groups.

In order to find the measurement corresponding to the maximum skull breadth the skull was measured in two places, i. e. on the lower (*zy—zy*) and posterior (*Ect—Ect*) walls of the orbits. Figures show that the zygomatic breadth is usually slightly smaller and only in certain cases is equal to the breadth on the posterior walls of the orbits. It is, however, never greater. The values of these two measuerements increase up to age group IV in both males and females. The differences between the mean values of the two measurements in females and males are statistically significant. Confidence intervals of average for the oldest

Table 7.
Degree of significance of differences between values of selected skull measurements in males and females.

Measure-ment	$\bar{x}$♀	$\bar{y}$♂	t_{emp}	$t_{0.01}$	Degree of freedom	$\bar{x}$♀	$\bar{y}$♂	t_{emp}	$t_{0.01}$	Degree of freedom
	Age class I					Age class II				
P-Op	312.3	386.7	112.34	2.617	121	363.5	406.8	148.00	2.576	157
Zl-P	174.5	220.2	103.28	2.615	119	211.1	232.7	98.70	2.576	157
Br-N	94.2	122.7	159.60	2.614	122	106.6	128.4	140.39	2.576	156
St-B	103.3	129.7	97.15	2.637	93	117.1	130.2	28.03	2.631	100
St-P	179.6	218.2	69.09	2.615	118	212.6	231.0	57.04	2.576	144
Zl-Op	156.0	188.4	135.43	2.614	122	172.0	197.3	197.34	2.576	157
P-Br	255.6	321.0	113.14	2.617	120	303.2	343.1	136.45	2.576	156
Pm-P	96.4	117.0	93.52	2.617	121	112.9	125.2	76.64	2.576	156
Zy-Zy	129.7	158.4	156.41	2.617	121	145.3	169.1	157.32	2.576	154
Ect-Ect	132.1	162.5	177.53	2.617	120	146.4	173.4	184.41	2.576	154
Ot-Ot	95.0	117.7	242.20	2.628	115	104.8	127.3	85.29	2.576	140
Sph-Br	74.7	87.7	189.67	2.624	110	79.0	92.4	188.54	2.576	135
if-goc	239.3	294.2	101.01	2.629	117	284.2	310.6	78.94	2.617	121
	Age class III					Age class IV				
P-Op	372.6	418.5	150.55	2.576	151	375.4	419.3	269.54	2.654	68
Zl-P	219.5	241.8	100.79	2.576	128	220.8	239.7	88.45	2.654	68
Br-N	107.6	131.6	148.08	2.576	152	110.7	132.6	255.35	2.654	68
St-B	119.3	138.1	89.30	2.634	96	123.0	143.6	82.81	2.750	31
St-P	218.8	238.3	80.92	2.576	138	217.7	237.1	44.23	2.659	61
Zl-Op	173.6	203.0	235.79	2.576	153	175.1	205.2	507.18	2.654	68
P-Br	312.2	352.5	128.56	2.576	151	314.6	356.6	78.12	2.655	67
Pm-P	118.1	128.7	66.67	2.576	150	121.5	130.2	35.84	2.655	67
Zy-Zy	147.8	175.3	219.45	2.576	152	150.4	177.1	415.18	2.654	68
Ect-Ect	149.7	179.3	231.18	2.576	152	151.5	181.4	126.47	2.657	65
Ot-Ot	106.5	133.5	235.71	2.576	132	106.1	134.7	163.87	2.660	60
Sph-Br	79.2	96.9	211.51	2.576	130	81.3	99.2	115.45	2.674	54
if-goc	291.3	313.2	64.24	2.576	124	296.6	320.9	56.86	2.674	54

females do not overlap on to the intervals of averages for the youngest males: the interval for females in age group IV is 146.1—154.7 mm, and for males in age group I 155.6—161.2 mm, when zygomatic breadth is measured.

The differences in the shape of the skull in males and females are best illustrated by the index: $zy—zy \times 100/P—Op$ (Fig. 4). This index increases in males from age group I to IV from 41.4—42.2, and in females decreases from 41.6—40.0. This is probably connected with the slower increase in females of skull breadth in relation to its maximum length. The shape of the skull is the same in both sexes in age group I, but differences

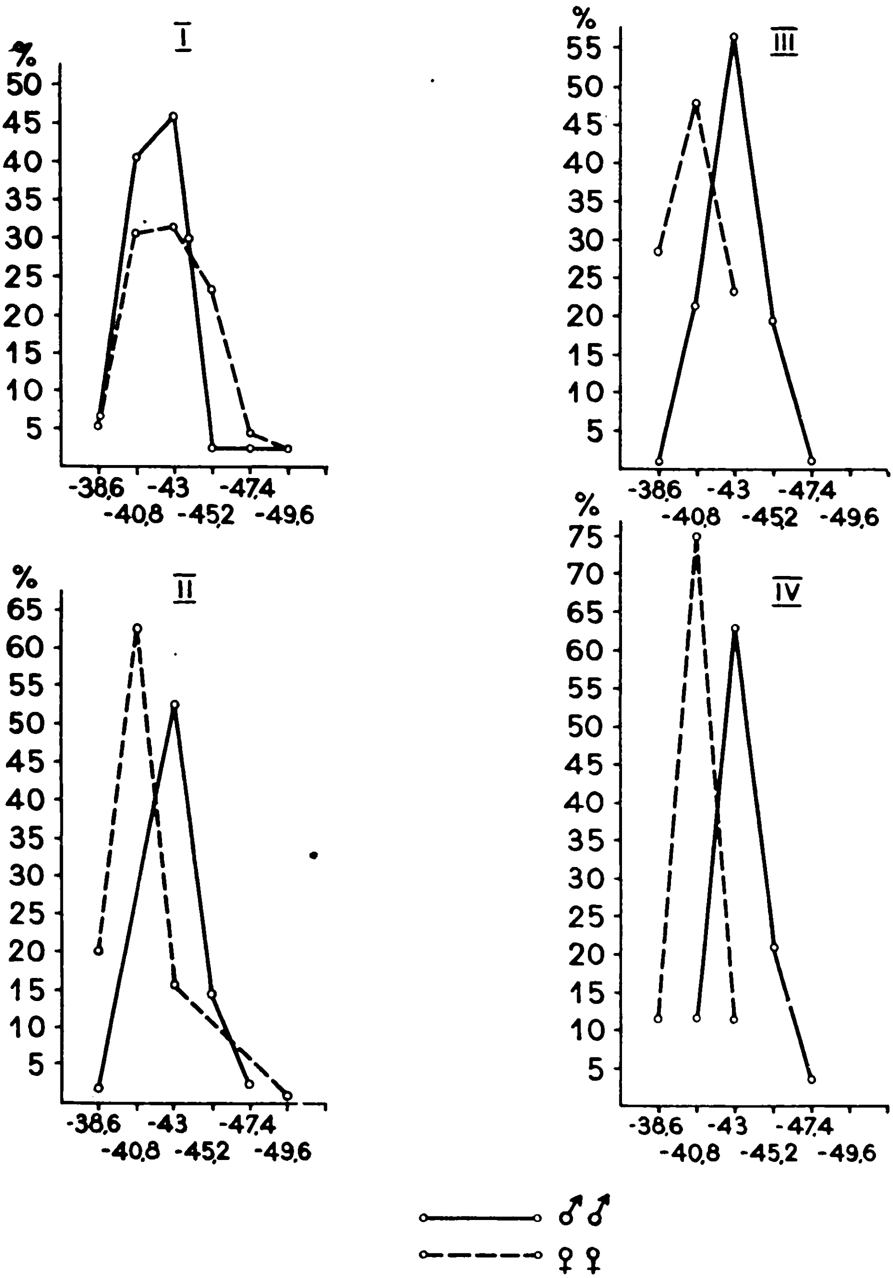

Fig. 4. Changes in index $\frac{zy—zy \times 100}{P—Op}$ with age in males and females (Roman numerals indicate age groups).

occur in the latter. In age group I the two curves overlap. As from age group II the apices of the two curves are shifted in relation to each other, this being most distinct in group IV[4]).

Statistically significant difference is also revealed between the skulls of males and females in the value of measure *P—Br*. The difference between the mean values is 65.4 mm in age group I, 39.9 mm in group II, then increases progressively up to group IV, in which it reaches the figure of 42.0 mm.

Index $zy—zy \times 100/P—Br$ illustrates the differences between males and females in relation to this length. In age group I the two curves on the diagram of this index (Fig. 5) almost completely coincide, and it is not until group II that the apices of the curves are shifted in relation to each other. It must be emphasised that the mean value of the index in males is almost the same in all age groups, varying within limits of 49.2 (group I) to 49.6 (group IV), whereas in females the index is higher (mean 51.1) in age group I and decreases in the following groups to 47.8 (group IV). This is evidence of the disproportionate increase in zygomatic breadth to *P—Br* length in females. The length measurement increases more rapidly. The skull of adult females is slightly narrower in relation to *P—Br* length than in males.

The length of the viscerocranium in red deer is best described by the palatine length measurement *St—P*. The size of this measurement differs fairly considerably in males and females. In age group I the difference between the mean values is 38.6 mm, as from group II decreases to 18.4 mm, to increase to a minimum extent to 19.5 mm in group III. In all age groups the differences between averages are statistically significant.

The proportions between length of viscerocranium and maximum skull length — (index $St—Px \times 100/P—Op$) are distributed similarly in males and females in age groups I and II. The mean value of the index in group I is 56.6 in both cases. In diagram (Fig. 6) of this index the two curves can be seen to coincide in age groups I and II. As from group III the apices of the curves are shifted in relation to each other. In group III the mean value of the index is 56.9 for males and 58.7 for females, which is reflected in the diagram and is evidence that length of viscerocranium in relation to total length of the skull is greater in females than in males.

Breadth of viscerocranium, *M—M* for Polish male red deer in age group III is on an average 131.2 mm, and in females 117.5 mm. The difference between males and females in the size of this measurement

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[4]) When making diagrams the ranges of values of the given index were set out on the axis of abscissae, and the frequency of individuals in a given range on the axis of ordinates. Continuous line indicates males, broken line, females.

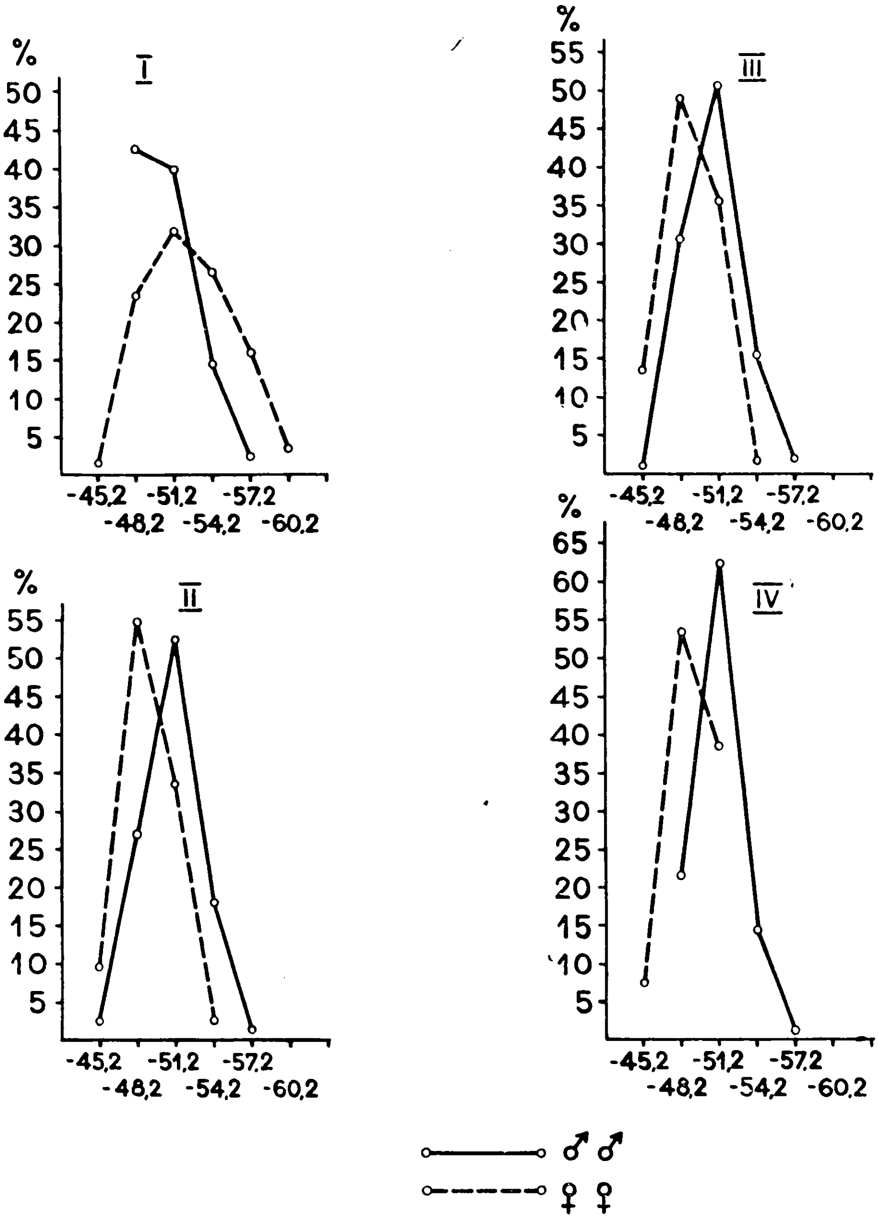


Fig. 5. Changes in index $\frac{zy—zy \times 100}{P—Br}$ with age in males and females (Roman numerals indicate age groups).

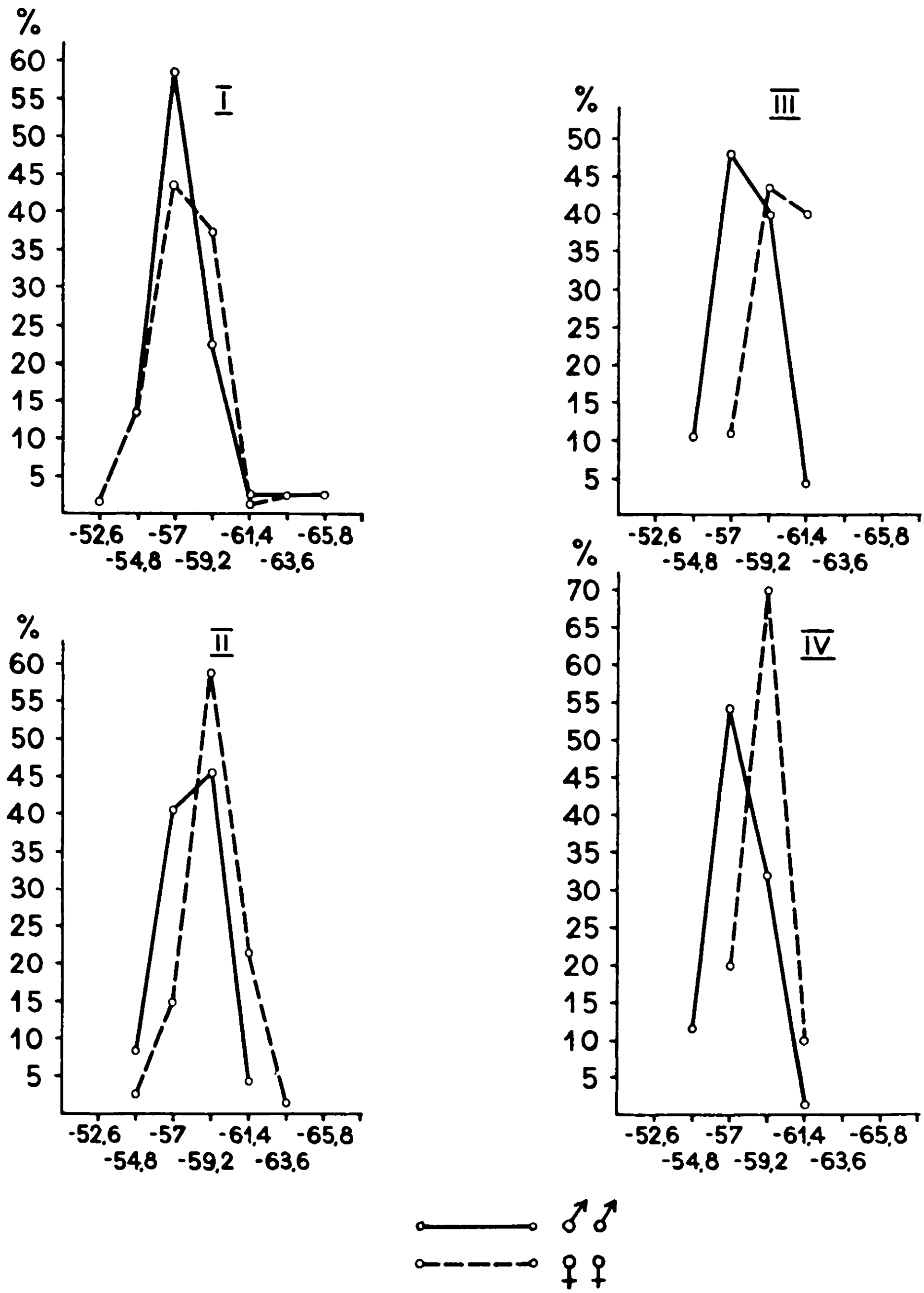


Fig. 6. Changes in index $\frac{St—P\times100}{P—Op}$ with age in males and females (Roman numerals indicate age groups).

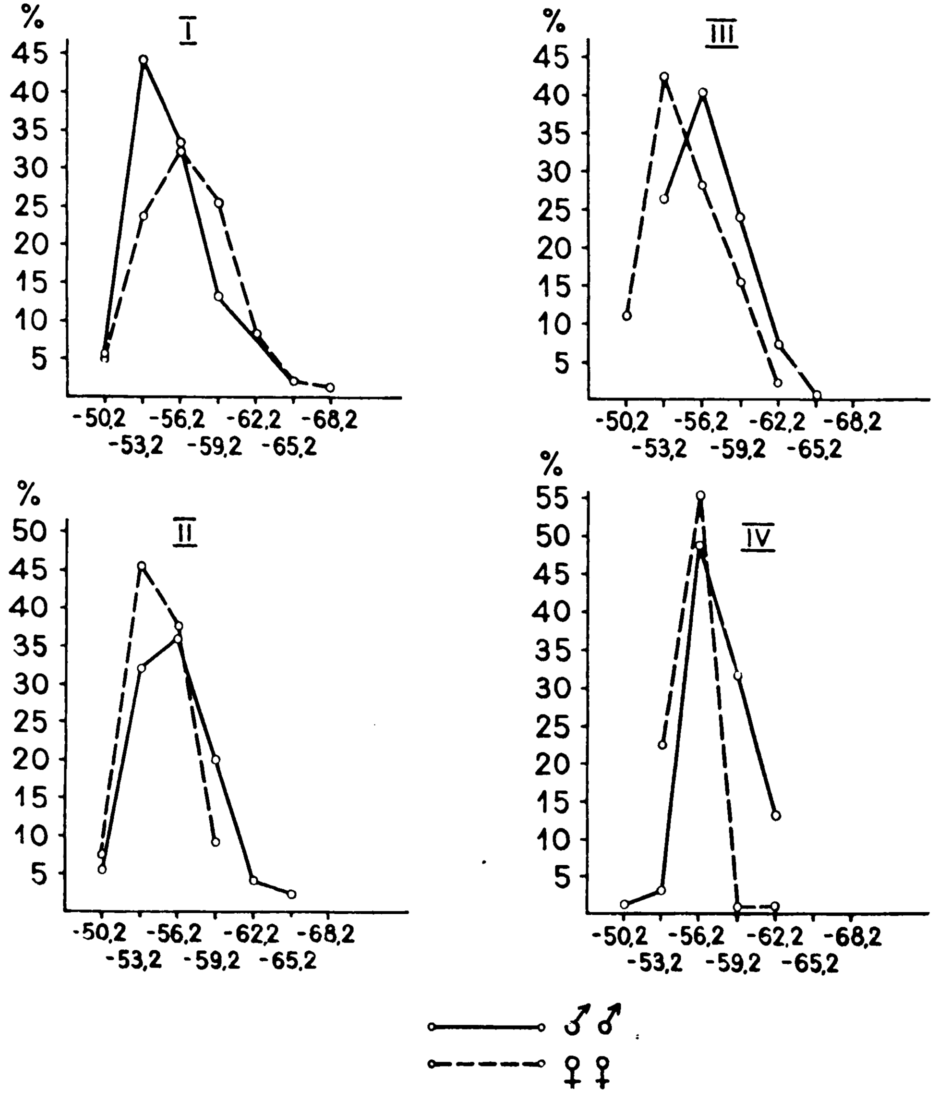


Fig. 7. Changes in index $\frac{M—M \times 100}{St—P}$ with age in males and females (Roman numerals indicate age groups).

is smaller than in previous measurements, being 19.8 mm for age group I, and decreases with age, reaching 13.7 mm in age group III.

Measurement of breadth of the viscerocranium above the canine teeth, *Mo—Mo*, is similar in this respect. The differences between the skulls of males and females in relation to this measurement is greatest in age group I (difference between means 12.4 mm), and decreases to 9.1 mm in later groups.

Differences in breadth of the viscerocranium connected with sex dimorphism are described by the index $M—M \times 100/St—P$. In age group I this index is lower for males than for females (males average 54.1 mm, females, average 55.3). The apex of the curve for males occupies the left side of the diagram. In later groups the index for females decreases to the value 53.7 — group III and in males increases to 55.4. This is shown on the diagram of this index (Fig. 7): the apices of the two curves are shifted in relation to each other, the curve for males shifting towards greater values. This is connected with the more rapid growth in females than in males of the palatine length between age groups I and II and the minimum increase in $M—M$. The differences are clearest in the values of the index between males and females in age group III. The apices of the surves are shifted farthest from each other. This is confirmation of the conclusion previously reached as to the greater breadth of viscerocranium in males than in females.

The index $Mo—Mo \times 100/Pm—P$ (Fig. 8) illustrates the changes in breadth of the rostral part in relation to $Pm—P$ length in the skulls of males and females within different age groups. In group I differences in the value of this index between males and females are slight (males 49.7, females 51.6). The value of index alters in older individuals, increasing for males of 53.7 (group IV), and decreasing slightly in females to 49.3 in group III, to increase in group IV to 50.0. It must be added that measurement $Pm—P$ is fairly constant and not greatly influenced by sex and age. The greatest difference between males and females is in group I, where it attains a value of 20.6 mm. In later groups it decreases to 8.07 mm (group IV). Differences within the index $Mo—Mo \times 100/Pm—P$ may therefore be attributed primarily to the difference in breadth of the rostral part, which is wider in males than in females. The most distinct shifts in apices of the curves can be seen in age group III.

The length of the maxillary tooth-row, $Pm—Pd$, decreases with age in both males and females. When examining this measurement only those individuals in which eruption of the teeth is complete, i. e. 3 years old (the final molar erupts in the third year of life), can be taken into consideration. In males the measurement of this length decreases from 107.4 mm in group II to 101.3 mm in group IV. In females this difference is better expressed: the mean value of the measurement decreases from 106.8 mm in group II to 99.1 mm in group IV. There are no great differences connected with sex dimorphism in the size of this measurement. Differences in the value of this measurement between skulls of males and females are very slight and attain 2.2 mm in age group IV (0.6 mm in group II, and 0.9 mm in group III).

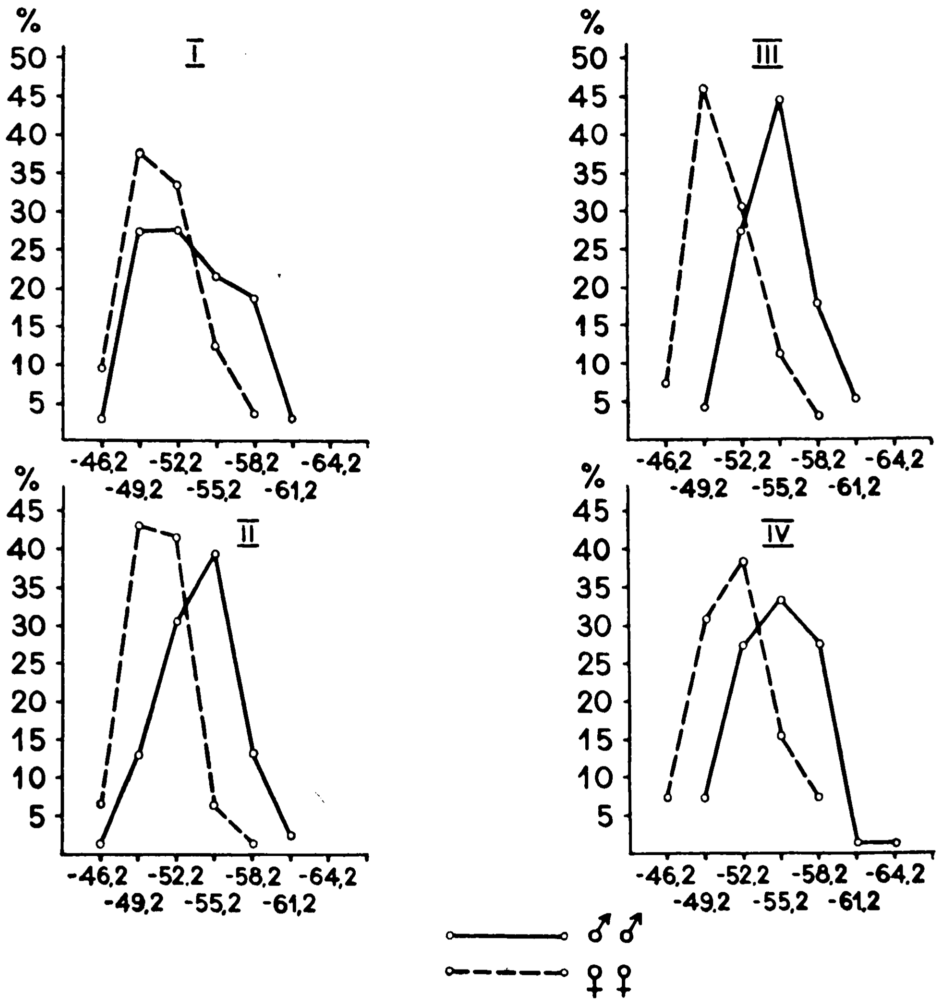


Fig. 8. Changes in index $\frac{Mo—Mo \times 100}{Pm—P}$ with age in males and females (Roman numerals indicate age groups).

Index *Nsi—Margo adent.* × 100/*Pm—Pd* (Fig. 9) is influenced by age. An increase in its value with increasing age of the individual can be seen in both males and females, from 55.8 (group II) to 62.8 (group IV) for males and from 50.5 (group II) to 54.7 (group IV) for females. The measurement of the height of the rostral part *Nsi—margo adentalis* is fairly stable and increases very slightly with age: from 60.2 mm to 63.3 mm in males and from 53.6 mm to 54.1 mm in females (these are mean values for age classes II and IV). Increase in the value of the

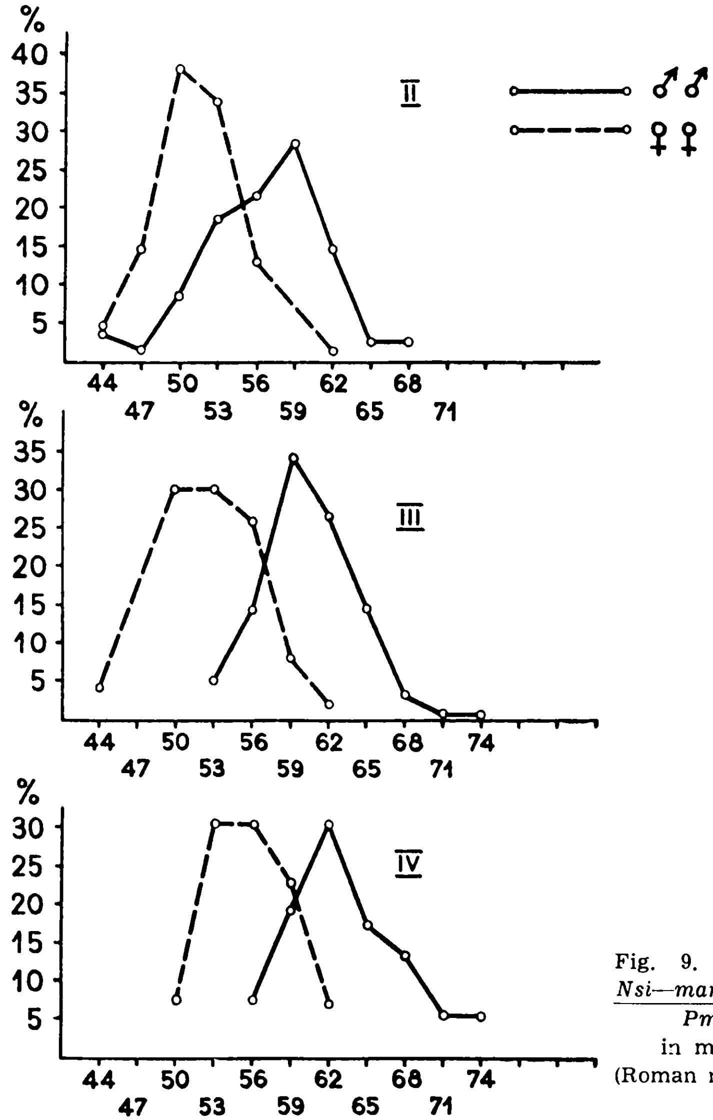


Fig. 9. Changes in index $\frac{Nsi\text{—}margo\ ad. \times 100}{Pm\text{—}Pd}$ with age in males and females (Roman numerals indicate age groups).

index may therefore be attributed primarily to changes in the length of the tooth row. These changes in the index, connected with the age and sex of the individuals, are illustrated by a diagram. The apices of the two curves can be seen to have shifted towards the right side of the diagram. Differences connected with sex dimorphism become more distinct with age. The most marked shift of the apices of curves in relation to each other are observed in groups III and IV. These distinct dimorphic differences can be connected with differences in the height between the averages of this measurement for males and females is 6.6 mm in group II, and in the following groups increases to 8.2 mm,

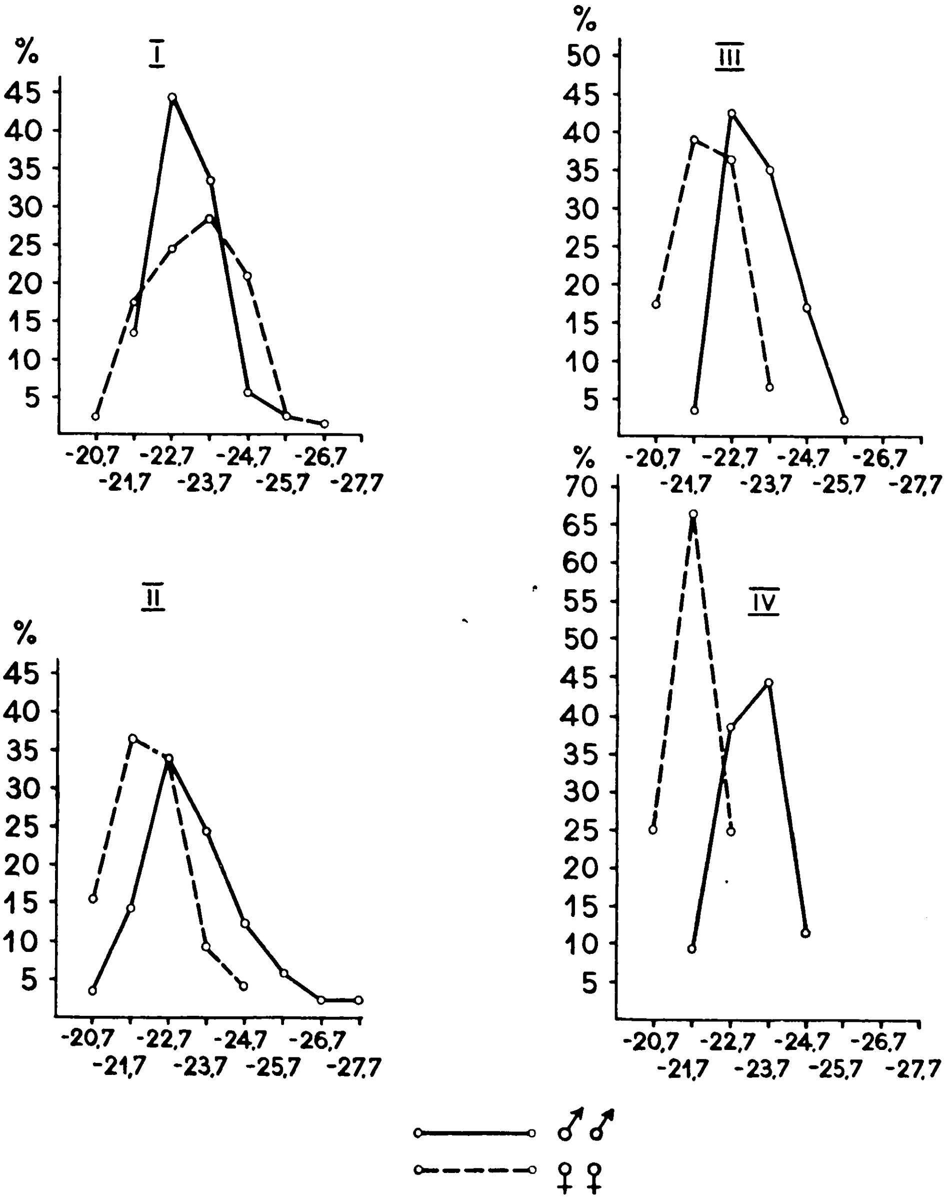


Fig. 10. Changes in index $\frac{St—N \times 100}{P—Op}$ with age in males and females (Roman numerals indicate age groups).

with a fairly similar value of the measurement *Pm—Pd* in both cases. This index best illustrates sex dimorphism in red deer.

The height of the viscerocranium in Polish red deer, *St—N*, varies in males within limits of 87.4 mm to 113.6 mm, and in females from

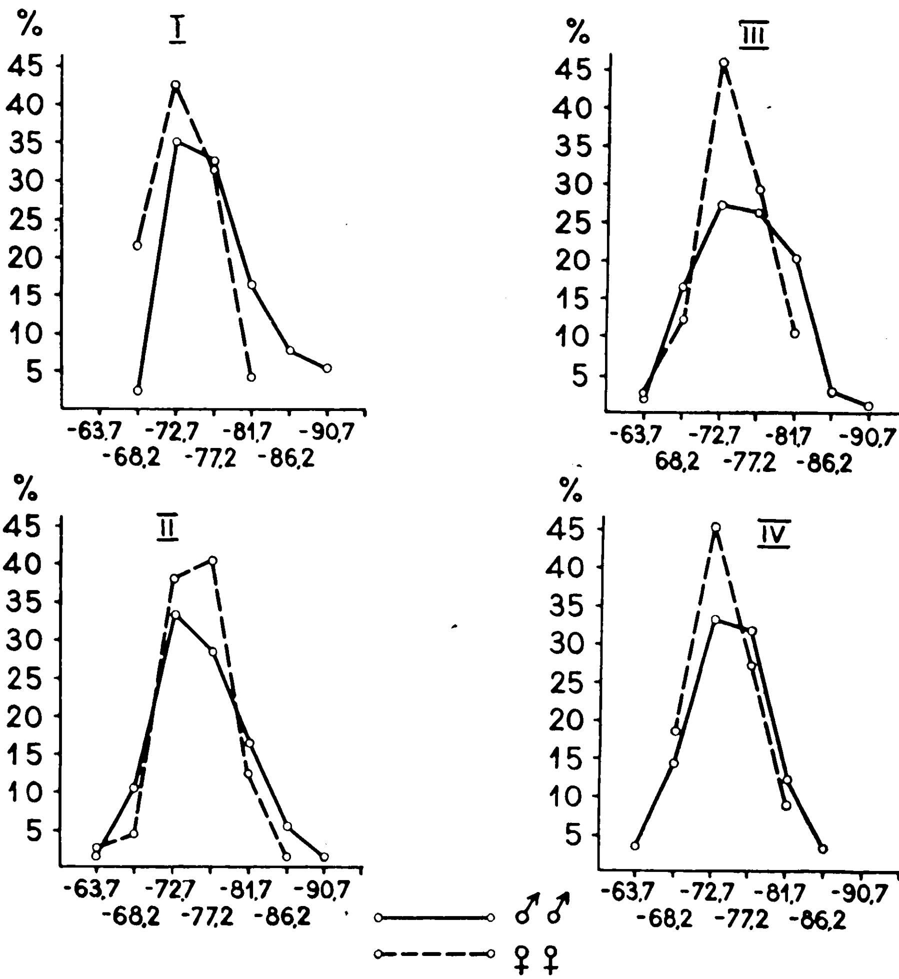


Fig. 11. Changes in index $\frac{Br—N\times100}{Ect—Ect}$ with age in males and females (Roman numerals indicate age groups).

71.2 mm to 80.3 mm (mean values of this measurement in groups I and IV). Dimorphic differences are most distinct in age groups III and IV. The curves of the diagram *St—N*$\times$100/*P—Op* (Fig. 10) illustrate the proportions between the height of the viscerocranium and total skull length. The greatest shift in apices of the two curves in relation to each other can be seen in groups III and IV.

The skulls of males and females differ as to length and breadth of *os frontale (Br—N* and *Da—Da)* most markedly in age class I. In the case of the length measurement the difference in this group is 28.5 mm, and breadth 27.3 mm. The difference decreases in older animals.

The value of the index *Br—N*$\times$100/*Ect—Ect* (Fig. 11) in males decreases with age, from 75.5 to 72.6 (mean values in age groups I and IV), which may be explained by the fairly rapid increase in skull breadth on the posterior walls of the orbits. This same index increases in females up to the group II (average in group I, 71.4; in group II, 73.2) and decreases in older individuals in age group III (71.9). This is connected with the change in rapidity of growth of these two measurements depending on age. This is an index which is not influenced by sex. The two curves and their apices coincide in the diagram.

Increase in length and breadth of *ossa nasalia (Nsi—N, Nm—Nm* and *Ni—Ni*) ends in age group III. The greatest differences between averages of measurement of nasal bone length in males and females occur in age group I, i. e. 18.4 mm decreasing in later groups to 6.2 mm (group III). Conversely, in the case of measurements of breadth the greatest difference is in group IV, being 13.7 mm for maximum breadth, and 7.8 mm for minimum breadth.

Index *Nsi—N*$\times$100/*M—M* which illustrates the proportions between nasal bone length and breadth on *tuber faciale* exhibits the most marked shift in apices of curves in age group I (Fig. 12). This is connected with the existence of the maximum dimorphic differences within measurements *Nsi—N* in age group I. In older individuals the differences between males and females are smaller, yet despite this the apices of curves are still shifted in relation to each other in age groups II and III. In age group IV the two curves coincide completely.

A shift in the curve for females from left to right side of the diagram within groups I and III, with simultaneous shift of the second curve from right to left side, can be seen in this same diagram. With continued development between groups II and III, we observe an increase in the index in females and its reduction in males. These changes in the index with age should be related to the difference in breadth of the viscerocranium between males and females.

Differences in the measurement of length of neurocranium connected with sex dimorphism are greatest in age group I (26.4 mm). In the next group the difference is smaller ($\bar{x}$=13.1 mm) which is caused by the more rapid increase in this length in females between groups I and II. In later age groups this difference increases, reaching 20.6 mm in group IV.

The value of measurement of neurocranium height *Sph—Br* increases throughout the whole life time of the animal, up to age group IV (from 87.7 mm to 99.2 mm in males and from 74.7 mm to 81.3 mm in females — averages in groups I and IV). The interval of the mean value of the measurement for the group of oldest females does not coincide with the interval of mean value for the group of youngest males. The difference between averages in age class I for males and females is 13.0 mm and increases to 17.9 mm in group IV. It is therefore one of the measurements which aptly characterises sex dimorphism in red deer.

Condylar breadth, *con—con*, is one of the measurements which give a good illustration of sex dimorphism, particularly in young individuals. In group I in my material the difference in the averages of this

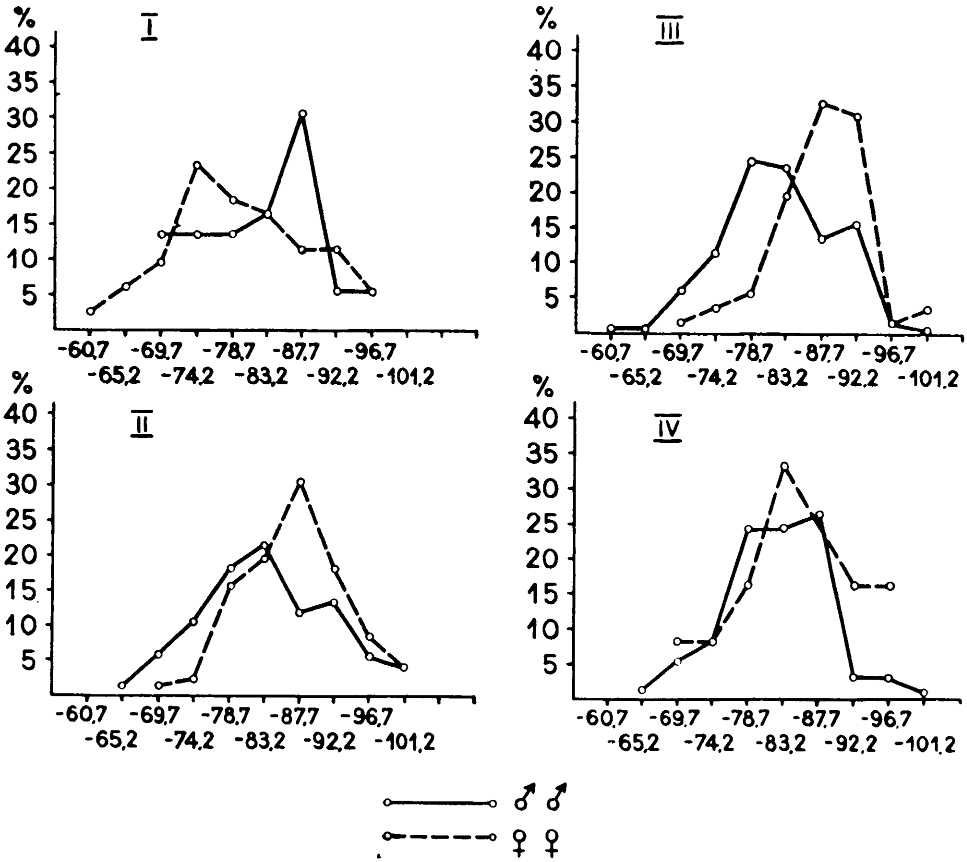


Fig. 12. Changes in index $\frac{Nsi—N \times 100}{M—M}$ with age in males and females (Roman numerals indicate age groups).

measurement between males and females is the greatest and attains 8.5 mm. In age class II this difference is smaller, 6.2 mm, but increases in the next group to 8.0 mm.

Index *Op—O*$\times$100/*con—con* (Fig. 13) increases in females from 69.1 to 72.3 (means for groups I and III), then decreases in group IV, which is connected with the reduction in height of the *planum nuchale*.

In males this index is observed to remain at the same level in groups I and II — 75, and in the third its value decreases to 73.9 — which agrees with the actual reduction of *planum nuchale* as from this age class. In group IV we observe a slight increase in the value of the index to 74.1 which is connected with the simultaneous decrease in condylo--occipital breadth. In group I the apices of the curves in the diagram

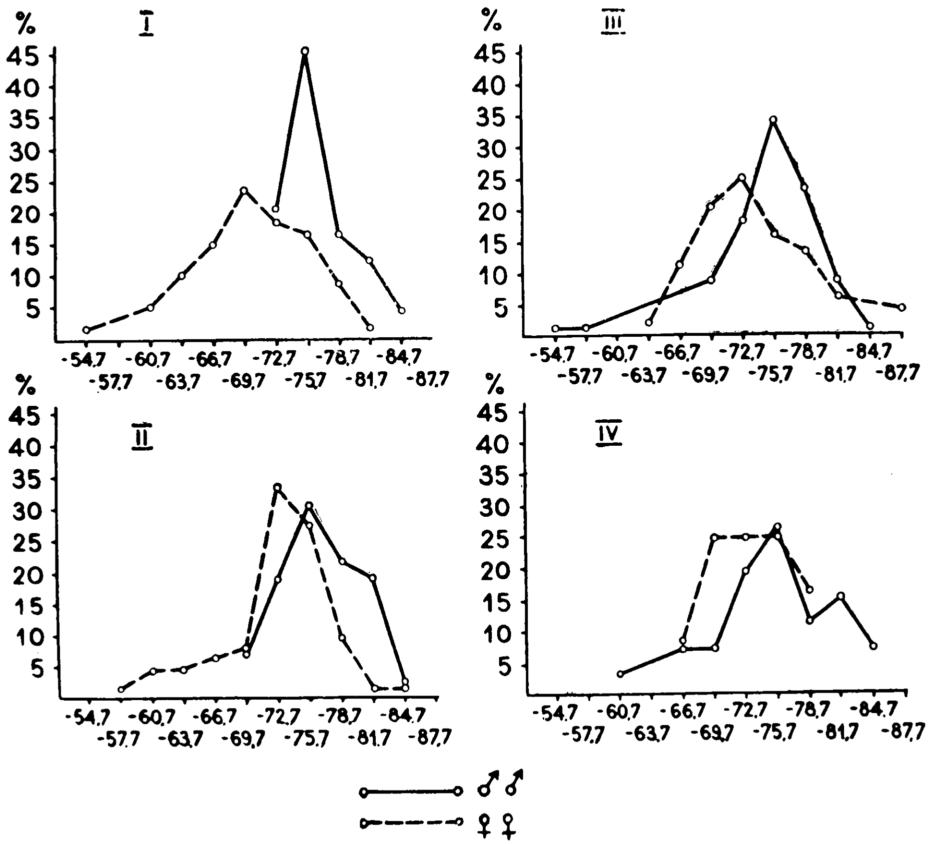


Fig. 13. Changes in index $\frac{Op—O\times100}{con—con}$ with age in males and females
(Roman numerals indicate age groups).

exhibit the maximum shift in relation to each other, this shift being visible in group II and even in group III, but in group IV the two curves coincide.

Maximal breadth of the braincase, *eu—eu* increases up to age group IV, reaching in this group an average of 105.9 mm for males and 91.9 mm for females. The maximum difference connected with sex dimorphism can be seen in this group (difference between averages is as much as 14.0 mm).

Index *eu—eu*×100/*St—B* (Fig. 14) illustrates changes in the shape of the neurocranium in males and females depending on age. Proport-

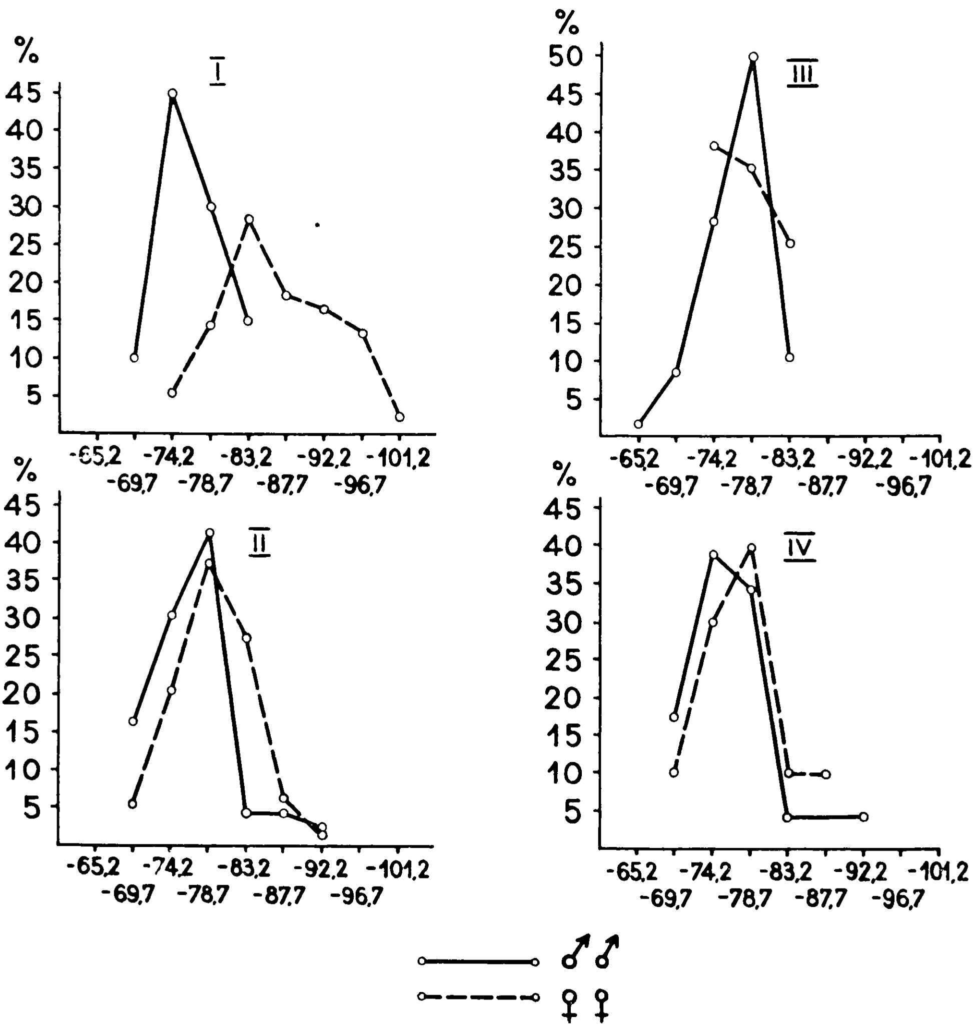


Fig. 14. Changes in index $\frac{eu—eu \times 100}{St—B}$ with age in males and females (Roman numerals indicate age groups).

ions between maximum breadth of the neurocranium and length of its base in males hardly alters at all with age. Mean value of the index for males is 74 in all age groups. In the case of females this index decreases from 84.6 to 75.6 (averages for groups I and IV) which is connected with the rapid increase in basal length of the skull on the one hand and fairly slow increase in its breadth on the other. Maximum differences in the value of this index between skulls of both sexes occur in the youngest individuals (age group I). In later groups the two curves coincide and differences are difficult to perceive (Fig. 14).

Increase in mandibular length (*if—goc*) continues throughout the animal's life. The greatest difference in the size of this measurement between males and females takes place in age group I, when it is 54.9 mm. In older individuals it is reduced to 21.9 mm, to increase in group IV to 24.3 mm. The difference between averages of measurement of mandibular height (*gov—cr*) in males and females attains 22.5 mm in group I.

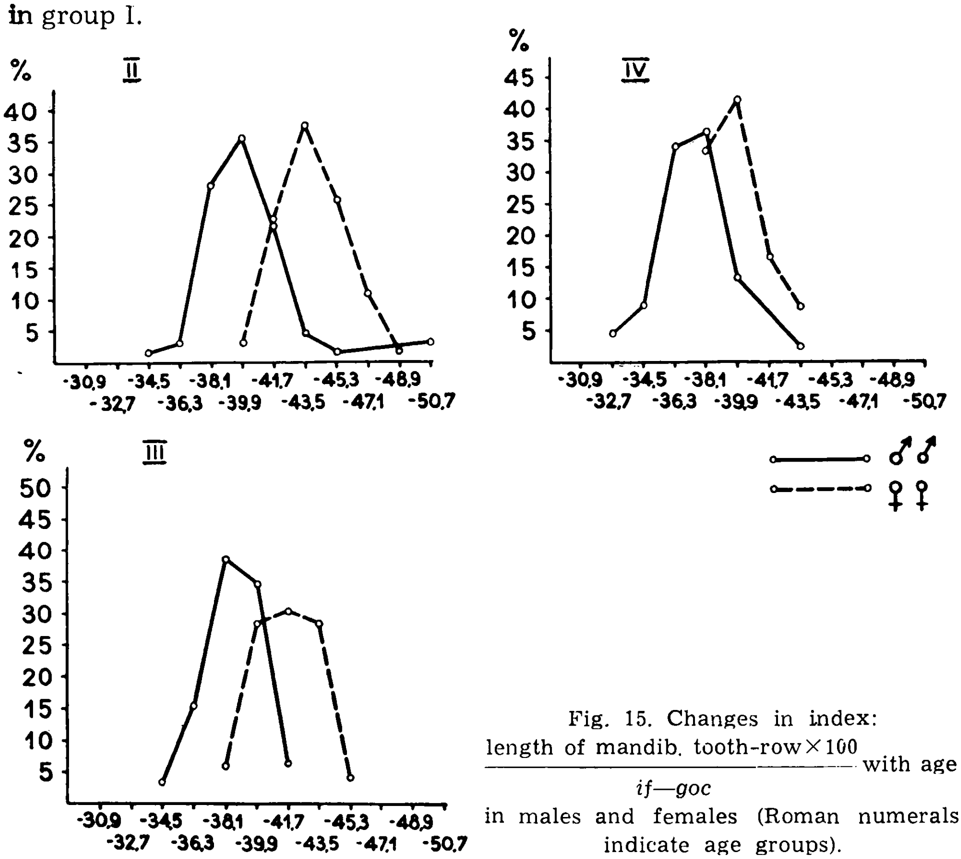


Fig. 15. Changes in index: $\frac{\text{length of mandib. tooth-row} \times 100}{if\text{—}goc}$ with age in males and females (Roman numerals indicate age groups).

Length of the mandibulary tooth-row decreases with age in a similar way to that of the maxillary tooth-row. The size of this measurement decreases in males from 120.7 mm to 117.1 mm and in females from 121.9 mm to 116.3 mm (averages of this measurement in groups II and IV). This is the only measurement, the average of which in age group

II is smaller in males than in females. This difference is evened up in age group III. It may be said that the length of the mandibulary tooth-row is almost the same in individuals of both sexes in age groups III and IV (the difference is 0.9 mm in group III and 0.8 mm in group IV).

Index: mandibulary tooth-row length × 100/*if*—*goc* (Fig. 15) decreases

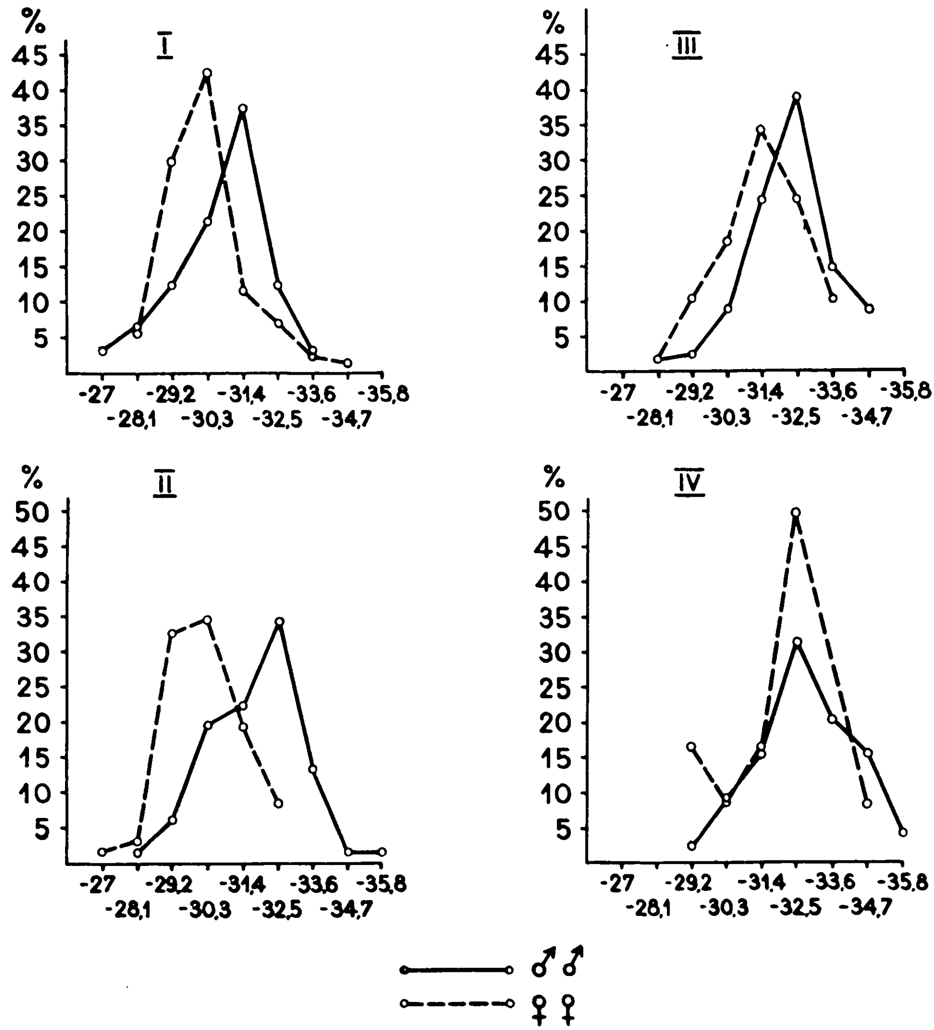


Fig. 16. Changes in index $\frac{\text{length of } \textit{margo adent. mandib.} \times 100}{\textit{if—goc}}$ with age in males and females (Roman numerals indicate age groups).

with age, in males from 39.3 to 36.5 and in females from 43.1 to 39.2 (averages for groups II and IV). Hence the apices of curves can be observed to shift to the left on the diagram. This decrease in the value of the index is connected with the shortening of the tooth-row with age on the one hand, and increase in total length of the mandible on the other. Length of tooth-row is similar in both sexes but as mandibular length is greater in males the value of the index in the latter is lower. This is why fairly considerable shift of the apices of the two curves in relation to each other can be observed on the diagram, which illustrates sex dimorphism.

The length of *margo adentalis mandibulae* increases with age up to group IV. Dimorphic differences are greatest in group I, in which they attain a value of 18.7 mm, while in later years they decrease, reaching 10.9 mm in group IV. The index: length *of margo adentalis mandib.* × 100/ /*if—goc* increases in both groups of skulls up to age group IV. The greatest differences between males and females in this index can be seen in age groups I and II (Fig. 16). These differences can still be perceived in group III, but in group IV the apices of the two curves on the diagram coincide.

VI. RATE OF GROWTH

1. Growth of Different Skull Measurements

The first age group was divided into three smaller ones in order to grasp age changes more accurately and fully. Group Ia includes the skulls of animals shot at ages varying from 6 to 12 months, i. e. up to one year old; Ib, from 12 to 24 months; Ic, from 24 to 36 months. Group Ia was taken as the initial 100%, and figures illustrating increase in all the other groups were related to it.

Numbers of individuals in groups a, b, c of age class I are as follows:

Group	Ia	Ib	Ic
♂♂	3	12	21
♀♀	40	26	20

Values of percentage increase in measurements with age in relation to group Ia are set out in table 8. Changes in skull measurements with increasing age of the animals must be considered separately for males and females, since fairly considerable differences occur here connected with sex dimorphism.

1. 1. Females. The diagram (Fig. 17) shows the increase in all skull measurements of females from group Ia to IV. Attention should first of all be directed here to the division of the lines (illustrating increase in different measurements) into two groups: the group of measurements of neurocranium increasing only slightly throughout the animals' life, and the second larger group of measurements, increase in which is considerable, that is, all measurements of the viscerocranium, *St—B* and *Zl—Op*.

Table 8.
Value of increase in percentage of measurements with age in relation to age group Ia in males and females.

Age class	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
	3. P-Op		4. Zl-P		5. Zl-Op		6. Op-Br		7. Br-N		8. P-Br	
Ia	100	100	100	100	100	100	100	100	100	100	100	100
Ib	7.1	21	3	27.0	5.1	12.6	5.1	5.8	0.2	16.1	7.4	23.4
Ic	13.1	24	9.5	32.3	11.1	13.9	8.9	5.8	1.5	16.4	13.2	27.8
II	15.8	30.4	12.6	40.7	13.2	17.6	10.2	8.4	5.0	23.0	17.7	35.0
III	19.1	33.7	17.0	46.3	16.5	18.7	10.9	8.7	7.6	24.2	20.9	39.1
IV	19.3	34.7	16.0	47.2	17.7	19.7	12.6	8.9	8.4	27.8	22.3	40.1
	9. Nsl-N		10. St-B		11. St-P		13. Pm-P		14. Pm-MoMo		15. Pm-Pa	
Ia	100	100	100	100	100	100	100	100	100	100		
Ib	17.4	30.3	11.2	16.3	8.7	23.8	5.9	24.3	12.4	23.0		
Ic	29.0	40.5	12.3	18.7	16.0	30.0	13.0	25.5	19.3	23.5	100	100
II	34.8	47.3	12.3	24.2	18.9	37.1	17.3	33.0	23.1	32.7	-3.7	-3.3
III	38.9	54.4	19.0	26.5	22.6	41.1	20.6	39.1	27.5	40.7	-5.4	-5.2
IV	39.8	49.6	23.8	30.4	22.0	40.4	22.0	43.1	29.3	44.0	-9.2	-10.3
	16. Mo-Mo		17. Nl-Nl		18. Nm-Nm		19. M-M		20. zy-zy		21. Ect-Ect	
Ia	100	100	100	100	100	100	100	100	100	100	100	100
Ib	6.4	16.1	7.7	18.6	12.6	12.9	8.3	15.2	6.3	11.8	6.8	11.0
Ic	14.2	19.3	17.3	26.5	19.8	18.0	13.6	20.6	10.8	14.3	11.9	13.9
II	19.7	28.3	24.6	32.8	24.8	21.1	19.5	26.2	15.8	19.9	16.6	18.3
III	26.1	33.5	35.4	37.7	28.8	25.8	23.4	31.4	20.1	21.9	26.0	21.0
IV	28.4	39.3	37.7	37.2	42.4	22.7	25.3	34.3	21.3	24.1	22.0	22.5
	22. Da-Da		23. fs-fs		24. eu-eu		25. Ot-Ot		26. con-con		27. Nsl-margo adentalis	
Ia	100	100	100	-	100	100	100	100	100	100	100	100
Ib	6.0	12.7	0.6	-	2.2	4.6	7.7	10.2	7.7	4.0	4.3	14.7
Ic	13.5	17.6	3.2	-	6.6	5.4	12.6	11.8	12.6	3.7	10.6	16.6
II	18.7	22.6	4.6	-	9.7	6.5	18.6	16.8	10.0	5.8	13.6	23.5
III	23.8	26.6	8.1	-	13.9	7.3	24.4	18.7	13.7	6.8	18.5	25.8
IV	24.5	29.5	10.8	-	15.1	8.6	25.5	18.3	11.1	5.7	19.4	24.6
	28. St-N		29. Sph-Br		30. Op-O		31. if-goo		32. Length-m. ad. mand.		33. Mand.-tooth-row	
Ia	100	100	100	100	100	100	100	100	100	100		
Ib	9.1	13.5	100	5.5	12.3	12.7	7.4	22.8	7.7	21.1		
Ic	14.1	14.0	4.7	8.3	16.4	12.7	14.9	26.6	21.6	23.1	100	100
II	18.5	19.1	8.2	9.7	19.4	14.2	16.9	34.2	23.8	32.2	-3.6	-0.9
IIII	22.1	21.2	12.9	9.7	17.0	16.4	17.9	37.6	29.0	40.8	-4.4	-3.4
IV	22.1	20.9	16.5	12.5	14.5	14.4	20.8	40.1	32.7	44.7	-6.5	-5.4
			34. gov-cr		Capacity of cranial cavity							
Ia			100	100	-	100						
Ib			6.8	17.4	-	10.2	100	100				
Ic			10.9	20.5	-	15.2						
II			11.8	25.0	-	16.2	12.9	8.6				
III			14.9	27.2	-	17.3	18.6	9.6				
IV			16.5	27.9	-	25.8	5.0	17.5				

The most rapid increase in mesurements of the neurocranium takes place between the first and second year of life, being most intensive in the case of height of *squama ossis occipitale*, *Op—O* — 12.7%. In the third year of life there is a slight increase in breadth of braincase, *eu—eu*, slightly more rapid increase in its height, *Sph—Br*, while the height of *planum nuchale*, *Op—O* and length, *Op—Br*, do not change at all (Table 8).

In group II all measurements increase, whereas between age groups II and III intensive increase is exhibited only by height of *planum* *nuchale, Op—O* — 16.4%. The three other measurements described either do not increase at all, such as the height of the cranium, or else this increase is very slow (Table 8). Height of the skull increases intensively between age groups III and IV, while the height of *planum nuchale* descreases markedly.

All the measurements of the viscerocranium increase most rapidly (like the neurocranium) between the first and second year of life. Breadth of the skull on the posterior walls of the orbits (*Ect—Ect* — 11.0%) increases least at this age, and length of nasal bones the most (*Nsi—N* — 30.3%).

In the third year of life some measurements continue to increase, but not as intensively as in the second year, and in the case of some increase is almost completely inhibited. These are: length of *ossa frontalia, Br—N,* length of *margo adentalis maxillae, Pm—Mo—Mo* and height of viscerocranium, *St—N* (Table 8). Continued increase between the third year of life and age group II takes place more rapidly, and its even rate, illustrated by the parallel lines on the diagram (Fig. 17), is remarkable.

As from age group II increase is more rapid only in length of *margo adentalis maxillae, Pm—Mo-Mo* (of 8.0%) and in length of *margo adentalis mandibulae* (of 8.6%).

In group IV certain measurements have a tendency to reduce their values, as follows: length of nasal bones, *Nsi—N,* and their maximum and minimum breadth, *Nm—Nm, Ni—Ni* (Tab. 8).

The majority of the measurements increase up to age group IV, although this increase is very slight between groups III and IV. There are, however, exceptions to this, and breadth on intermaxillary bones increases intensively even in group IV. Increase is even greater here than between age groups II and III. Increase in basal length of the neurocranium, *St—B* and length of *os frontale, Br—N* also follows the same pattern (Table 8, Fig. 17). It must be emphasised that the maximum increase throughout the individual's life is shown by length of nasal bones *(Nsi—N)* and lateral length of the viscerocranium *(Zl—P)* (Table 8). Breadth of the braincase, *eu—eu,* changes and increases least during the animal's life time (age group IV, 8.6%).

1. 2. M a l e s. Contrary to females, the skull of males in general grows far less intensively. The only measurement which increases considerably with age is breadth of the nasal bones (*Nm—Nm,* 42.4%) (Table 8).

The neurocranium and viscerocranium increase similarly and thus in the case of males we cannot observe two groups of curves on the diagram (Fig. 18) as we can for females. The majority of increases in different measurements come within limits of 12 to 25%.

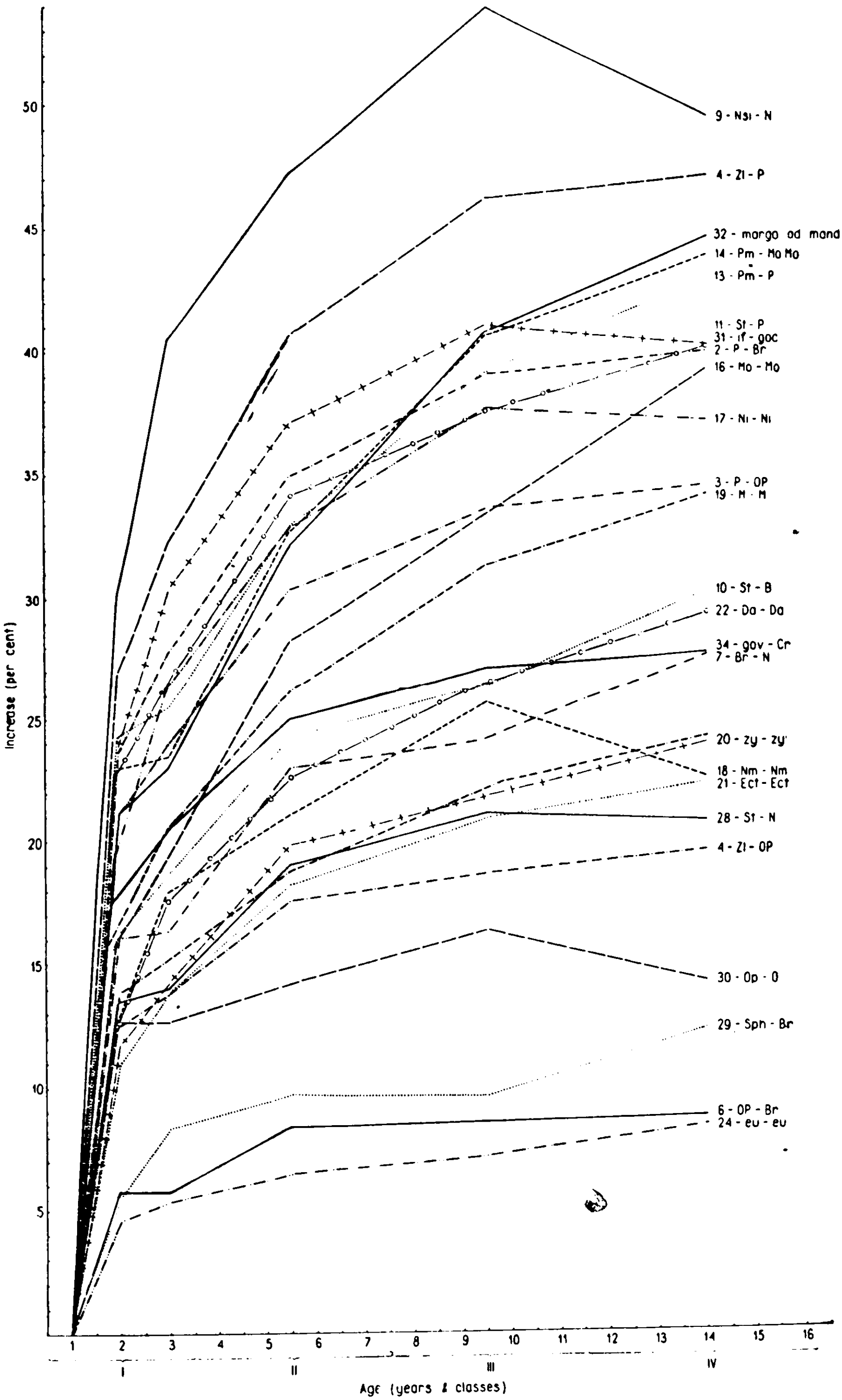


Fig. 17. Percentage of increase with age of all skull measurements in females.

Between the first and second year of life the increase in measurements is not as rapid as that observed in females. It is true that certain skull bones grow most rapidly during this period, and that this jump in growth is not repeated later on e.g. height of *planum nuchale* (*Op—O* — 12.3%) but increase in the majority is distributed almost evenly between the

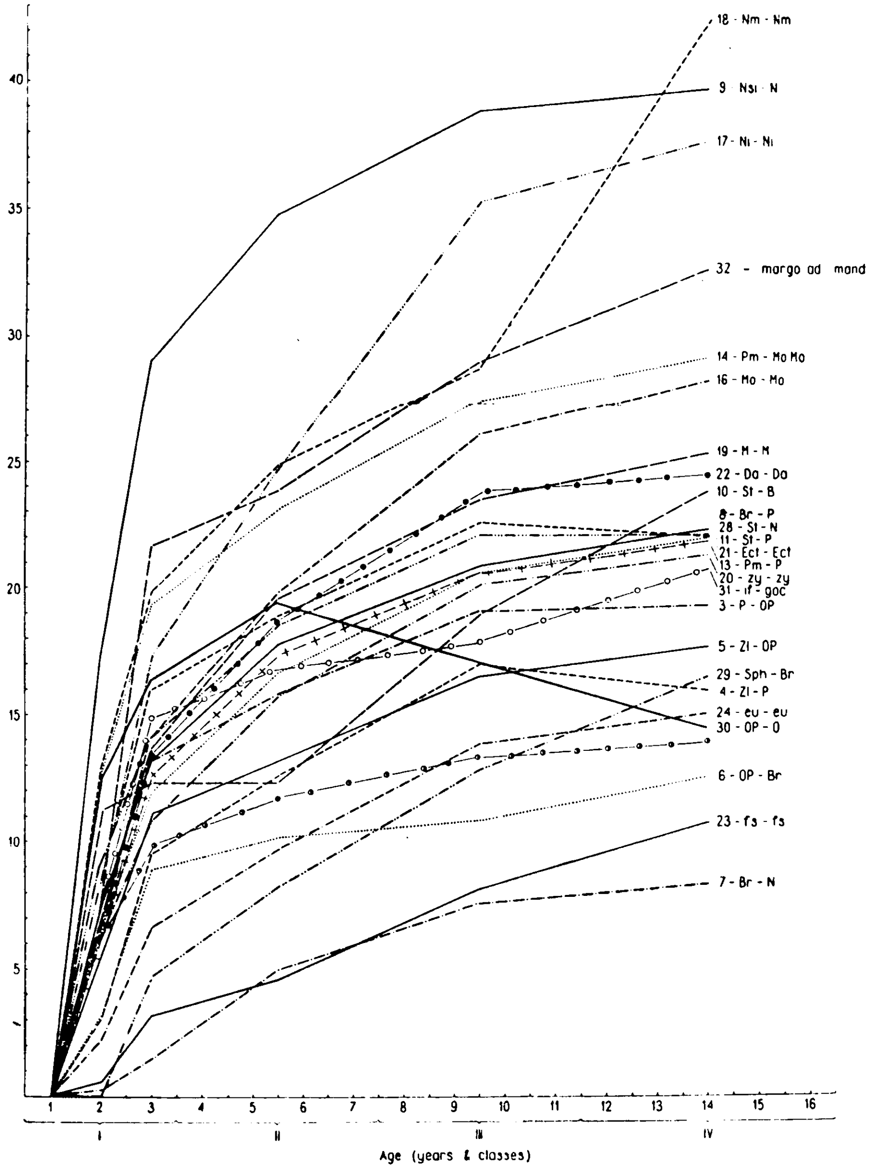


Fig. 18. Percentage of increase with age of all skull measurements in males

second and third year of life. An example of this is the increase in the minimum breadth of *ossa frontalia* on the orbits, *Da—Da,* which increases by 6.0% in the second year, and by 13.5% in the third, or breadth of *ossa intermaxillaria, Mo—Mo,* which increases in the second year by 6.4%, and in the third by 14.2%. There are more of such measurements, as can be seen from the diagram (Fig. 18, Tab. 8).

The majority of the measurements continue to increase up to age class II almost evenly, with the exception of basal length of the neurocranium — *St—B,* the growth of which is inhibited in group II (Fig. 18). In later years growth is similar except that basal length of the skull, *St—B,* increases more rapidly in groups III and IV than other measurements (19.0% increase in group III and 23.8% in group IV).

Measurement of height of *planum nuchale, Op—O,* takes a different course, its value decreasing as from group III (age group II, increase 19.4%, III — 17.0%, and IV — 14.5%).

There is very little increase, if any, in measurements between group III and IV. An exception here is the maximum nasal breadth, *Nm—Nm,* which increases to 42.4% (increase between groups III and IV is 13.6%).

Maximum nasal length, *Nsi—N,* also exhibits very great increase, of 39.8%, but it must be pointed out that increase in this length takes place almost evenly in all age groups (Table 8).

Increase in three measurements differs slightly from this general pattern: height of braincase, *Sp—Br,* minimum breadth between bases of antlers, *fs—fs,* and length of *ossa frontalia, Br—N.*

Attention must be drawn primarily to measurement of height of the braincase, which does not increase in the second year of life. Increase in this measurement does not begin until the third year and lasts until the fourth (group IV) age group, with almost unvarying intensity (Table 8, Fig. 18).

Measurements *fs—fs* and *Br—N* are distinguished by very small increase in the second year of life of the animals (first of these measurements 0.6%, second 0.2%). Both these values increase rapidly in the third year, then continue increasing fairly evenly up to the group IV.

2. Sex Dimorphism

As can be seen from the preceding part of this section, the majority of females grow most intensively in the second, and of males in the second and third year of life, and apart from this, grow fairly regularly in later years. The most distinct differences connected with sex dimorphism should therefore be expected in the second year of life. This is illustrated by diagrams made similarly to those in Figs. 17 and 18, but in this case the values of increase in only one measurement made on the skulls of males and females have been set out (females — indicated by broken line, males by continuous line).

It is possible to distinguish several groups of measurements, increase in which differs for each sex:

2. 1. The majority of skull measurements of females increase with age more than in males, but this is not an unalterable rule. This is clearly evident in the case of lateral length of the viscerocranium, *Zl—P* (Fig. 19A). The maximum increase in this measurement in males is 16.0% (3% in the second year of life) and in females 47.2% (27.0% in the second year). The rate of growth is slightly similar in both sexes only in the third year of life (Table 8, Fig. 19A). Increase in palatine length *St—P*, takes a similar course as do length of *ossa frontalia, Br—N, Br—P*, maximum length of skull, *P—Op*, mandibular length, *if—goc* (Table 8). Breadth of *pars facialis, M—M*, is similar, increasing in males to 25.3% and in females to 34.3% in group IV (Fig. 19B). Attention must be drawn to the fact that these measurements describe in the main increase in length and breadth of the viscerocranium in red deer.

2.2. A fairly similar growth rate can be observed in both sexes in the case of certain measurements, primarily measurement of breadth on the posterior walls of the orbits, *Ect—Ect* (Fig. 19C). It is true that in the second year of life the skulls of females exhibit slightly greater increase than that of males (11.0% and 6.8% resp.), but the more rapid growth rate in this measurement in males in the third year of life (11.9%) balances this difference to some extent. In both sexes this breadth increases up to group IV, attaining an increase of 22.0% in males and 22.5% in females.

Very similar growth with age is shown by: zygomatic breadth, *zy—zy*, breadth of *ossa frontalia* on the orbits, *Da—Da*, and lateral length of the neurocranium, *Zl—Op* (Table 8). The growth rate of height of the viscerocranium, *St—N*, also is very similar in both sexes (Table 8, Fig. 19D). Of course in the second year of life this height in females increases more rapidly, attaining 13.5% (9.1% in males) but similarly to the case described previously, in the third year of life increase in the measurement in females is far slower (by 0.5%) whereas in males intensive increase takes place which balances the previous difference (5.0%). In group II the difference is slight, 0.6%, in favour of females, but as from group III increase in this measurement in males attains 22.1%, remaining unchanged in group IV. Females attain maximum increase in group III — 21.2%.

2.3. Group III is formed by measurements which increase more in males than in females. The most striking example of this is breadth of

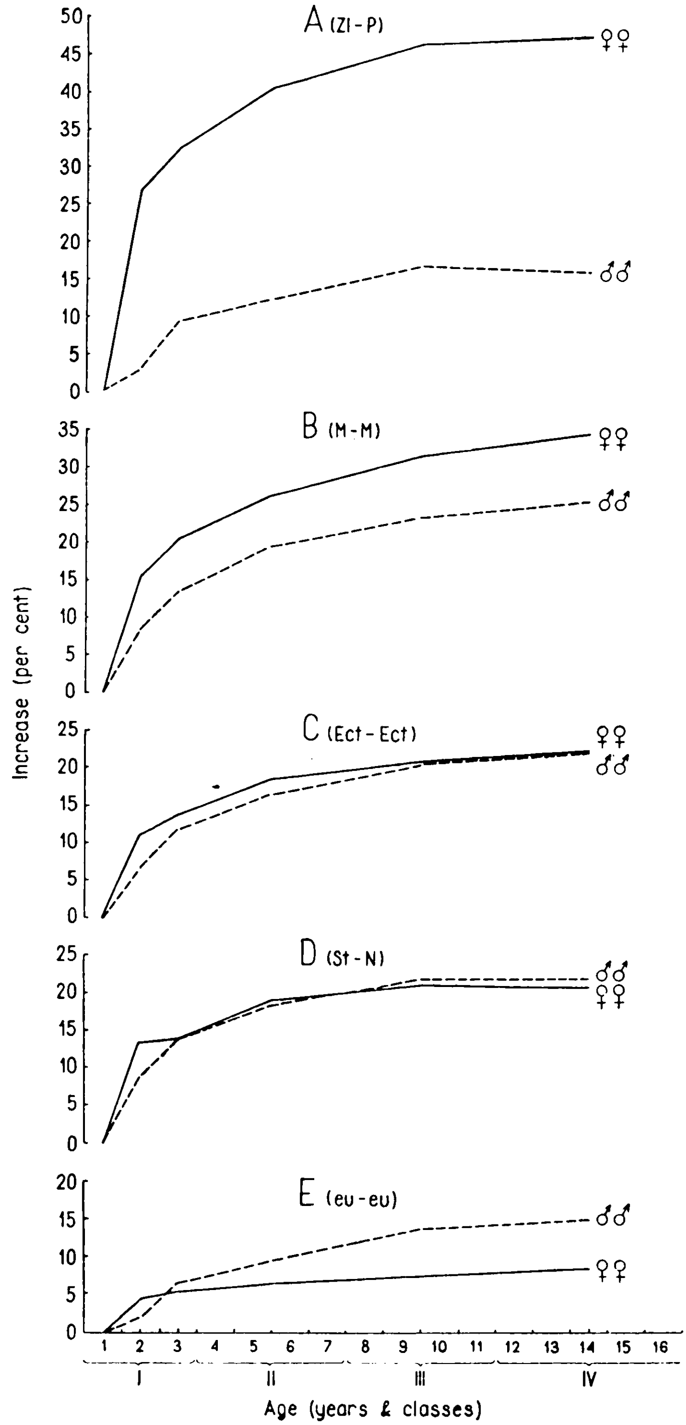
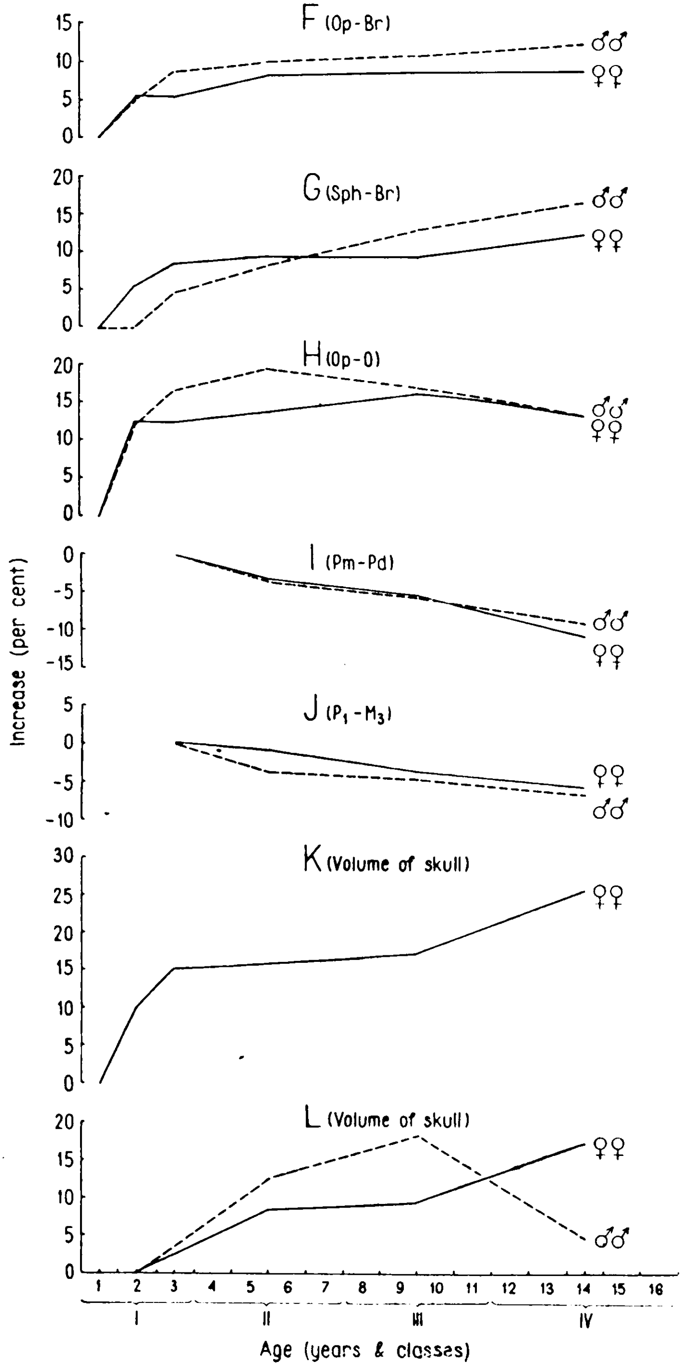


Fig. 19. Percentage of increase with age of various skull dimensions in red deer. A — lateral length of viscerocranium, *Zl—P*; B — Breadth of viscerocranium, *M—M*; C — Breadth of cranium, *Ect—Ect*; D — Height of viscerocranium, *St—N*;



E — Breadth of braincase, *eu—eu*; F — Length, *Op—Br*; G — Height of neurocranium, *Sph—Br*; H — Height of *planum nuchale, Op—O*; I — Length of tooth-row, *Pm—Pd*; J — Length of mandib. tooth-row, *P1—M3*; K — Capacity of *cavum cranii* in females (age group Ia taken as 100%), L — Capacity of *cavum cranii* in males and females (age group I taken as 100%.

the braincase, *eu—eu*. Increase in this breadth is more rapid in females in the second year of life than in males (females 4.6%, males 2.2%) (Table 8, Fig. 19E). In the third year fairly intensive increase begins in this measurement in males, attaining increases of 6.6% in the third year, 9.7% in age group II, 13.9% in age group III and 15.1% in age group IV. In females this increase also lasts up to group IV, in which it is only 8.6%. Breadth, *Ot—Ot* (Table 8) and length, *Op—Br* (Table 8, Fig. 19F) increase almost identically with age. Increase in the latter measurement in the second year of life is almost the same in males as in females (the difference is 0.7% still in favour of females). In later years increase is greater in males.

Measurement of *Sp—Ba* exhibits similar changes, although in this case males attain greater increase than females in age group III (Fig. 19G). It must be emphasised that this height in females hardly increases at all between the third year of life and age group III (8.3% and 9.7%). Increase is not observed until age group IV — 12.5%.

2.4 Only two measurements: condylo-occipital breadth, *con—con*, and height of *planum nuchale*, *Op—O*, cannot be allocated to any of the three groups described. Increase in *con—con* is greater in males than in females in all the age groups (Table 8). In the second year of life this measurement increases in males by 7.7%, and in females by 4.0%. Increase is most intensive during this period in both sexes. Maximum increase is attained in age group III (males, 13.7%; females, 6.8%).

Increase in height of *planum nuchale*, *Op—O*, takes place in a similar way (Fig. 19H). The almost identical growth rate in both sexes in the second year of life is remarkable (males 12.3%, females 12.7%). This height increases in males up to age group II, when it there attains its maximum — 19.4%, then decreases to 17.0% in age group III and 14.5% in age group IV. Increase is inhibited in females between the second and third year. Maximum increase is attained in age group III — 16.4%, and decreases in group IV to 14.4%. As in the second year of life the percentage of increase is almost identical in this group in both sexes (Table 8).

2.5. The only measurements which do not increase, but decrease, during the individual's life are: length of maxillary tooth-row, *Pm-Pd*, and of mandibulary tooth-row, P_1—M_3 (Fig. 19 I—J)[5]).

Progessive reduction in the length *Pm—Pd* is parallel in both sexes up to age group III, being slightly greater in males. In group IV decrease is more intensive in females than in males (males — 9.2%, females —

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[5]) In this case class Ic, in which individuals have already complete sets of permanent teeth, was taken as the initial group — 100%, to which the values of other groups were related.

10.3%). Decrease in the length of the mandibulary tooth-row takes a similar course, except that decrease in length is more intensive in males than in females throughout the animals' entire life.

VII. CAPACITY OF THE CRANIAL CAVITY (*CAVUM CRANII*)

Faulty preparations of skulls intended as hunting trophies made it impossible to measure capacity in a large number of males, it proving possible to make this measurement on 29 individuals only. The number of skulls of females measured was 146.

Table 9 shows that the highest mean capacity of the brain case of females in age group IV (356 cm^3) corresponds to the mean value for males in group II (358 cm^3). Males attain maximum average value of this measurement in age group III, of 376 cm^3.

Table 9.
Capacity of *cavum cranii* (in cm^3).

Age class	♂♂				♀♀			
	n	Min.	Avg.	Max.	n	Min.	Avg.	Max.
I	3	275	317	365	61	215	303	370
II	8	325	358	390	45	270	329	430
III	13	325	376	440	32	275	332	390
IV	5	295	333	360	8	285	356	410

In hinds there is constant increase in skull capacity up to age group IV, and it is most intensive between the first and second year of life — 10.2% (Fig. 19 K, Table 8), then no significant but constant slow increase up to group III is observed in these values. Between age group III and IV increase again becomes rapid (25.8%). In the case of males it is difficult to conclude in which age group increase is most intensive on account of the small amount of material available (group I — only 3 individuals [6]). If therefore we take the mean value for group I as a whole as 100% then most rapid increase in this measurement will be between age groups I and II — 12.9%. The value of this measurement increases up to age group III (18.6%), and in group IV decreases to 5% (Table 8, Fig. 19 L).

[6]) Hence the double diagram for this measurement: Fig. 20 K, on which increase in capacity of the skull cavity has been given for females only, and where age class Ia has been taken as the initial group, and Fig. 20 L, in which age group I has been taken as the initial group for females and males.

VIII. BODY WEIGHT

The carcass weight [7]) of Polish lowland red deer comes within limits of 67 to 194 kg for males and from 25 to 103 kg for females (Table 10). The average weight of adult stags in age group III is 138.0 kg, and of hinds 73.7 kg. Sex dimorphism is therefore very distinctly manifested here.

Increase in the animals' body weight with age is illustrated by Table 11, Fig. 20. Increase in body weight continues up to age group IV. It is a characteristic fact that in both sexes the increase of this value in the third year of life slows down (females) or is completely inhibited (males).

Table 10.
Variations in body weights of males and females in different age groups (in kg).

Age class	♂♂				♀♀			
	n	Min.	Avg.	Max.	n	Min.	Avg.	Max.
I	59	67	95.8	151	61	25	55.7	86
II	103	68	118.2	187	43	56	74.9	103
III	112	78	138.0	194	33	56	73.7	102
IV	53	101	141.7	192	9	65	79.6	92

Table 11.
Increase in body weight in different age groups (group Ia taken as 100%).

Age class	Ia	Ib	Ic	II	III	IV
♀♀	100	37.0	41.0	62.8	60.2	73.0
♂♂	100	11.7	10.6	25.5	46.8	50.0

In later years while males increase in weight fairly considerably, and continue to increase up to age class IV, the body weight of females increases up to age group II, then there is a period of stagnation between group II and III, or even a decrease in weight. It begins increasing again as from group III. Age groups II and III form a period of intensified reproduction in females, which undoubtedly affects the animals' condition.

The most intensive increase in body weight in males is observed

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[7]) All the values for body weight given in this study refer to females from 8 months upwards and males from one year upwards. Data relating to females refer to body weight together with the head, while the males were weighed after the head, together with the antlers, had been cut off. It may be taken that the head without antlers weighs from 5 to 9 kg.

between age group II and III (21.3%) and in females in the second year of life (37.0%).

IX. DISCUSSION AND SUMMARY OF RESULTS

1. Characteristic Features of the Skull of the Red Deer

In the morphological description of the skull I have tried to draw attention particularly to the characters distinguishing the skull of red deer from the skulls of other ruminants previously described and to characters which describe sex dimorphism.

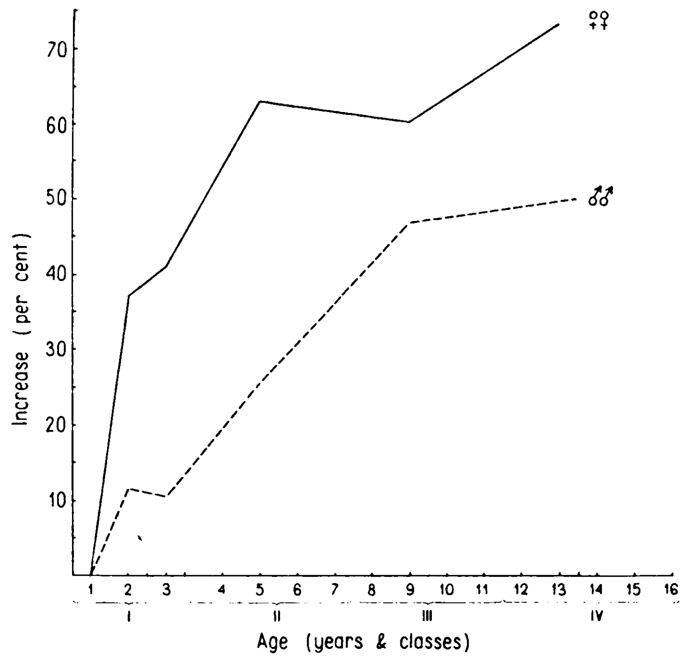

Fig. 20. Percentage of increase with age in body weight of males and females.

In males abortion of *linea nuchalis superior* in the structure of the skull fornix is observed, contrary to females, in which this line is better formed. This is connected, with the formation of a deeper and more extensive *fossa temporalis,* which is the place of insertion of the temporal muscle, better formed in stags.

Structure of *ossa frontalia* in red deer differs from the general pattern of skull structure in domestic ruminants. In males the posterior part of the squama of the paired bones forms massive bases with antlers.

The laminae of the paired *ossa frontalia* are characteristically bent upwards and backwards in males. In connection with the formation of antlers a transverse and lengthways kink or indentation can be observed in their medial part which is more distinctly visible, the older the individual and the more massive the antlers which it grows. *Crista frontalis ext.* does not occur in males, which is connected with the formation of antlers. Female skull is lighter, not so massive, and the laminae of *oss. frontalia* are more flat and do not bend to the same degree as in males.

The orbits of males and females are strongly protruded to the lateral side so that the *margo supraorbitale* is situated diagonally in a direction from front to back and sideways.

The anterior part of the fornix is formed by *ossa nasalia,* individual variations playing an important role in their formation. The lateral processes of these bones thrust between the *os frontale* and *os maxillare,* reaching to *hiatus lacrimalis.* The size of these processes varies greatly. In the material examined there were also cases in which they were completely absent, and then the *ossa frontalia* contacted *ossa maxillaria.* The end of the free parts of the nasal bones from the front also varies greatly and is not dependent on sex or age.

The very strong formation of *linea nuchalis superior* is noticeable in the structure of *planum nuchale.* This line is far more distinct in males and forms a kind of bony ridge. This strong development of the crest is connected with development of the nuchal muscles moving the head which is burdened with antlers.

Two openings characteristic of the red deer occur on the sides of the *squama occipitalis* — these are *forr. supramastoidea* connecting with the posterior part of *cavum cranii.*

For. postglenoidaeum is exceptionally large in the red deer and may be compared in respect of size to the size of the *porus acusticus ext.*

The structure of *os zygomaticum* is remarkable on account of the formation of a bony crest surrounding *annulus orbitalis* from the bottom and forming with it a kind of thin lamina bent downwards. This crest extends forwards to the suture between *os zygomaticum* and *os maxillare.* Below it there is a long depression, more distinct in males and older individuals.

A characteristic feature of the mandible in red deer is the occurrence in the majority of individuals of an opening situated on the external anterior side of the corpus, caudad from the *for. mentale.* In the posterior and lower angle of the mandible there is a bony crest characteristic of the red deer which runs to an arch from bottom upwards, ending halfway along *ramus mandibulae* in a protuberation which is more distinct in older individuals and in males.

2. Comparison of Skull Size in Red Deer from Poland and from Other Areas

Data are given in table 12 on measurements of the skull of red deer from areas in Northern Europe (Norway, Denmark, Sweden), Eastern Europe (Soviet Union) and Southern Europe (Czechoslovakia, Hungary, Rumania). Skull measurements are also given for other European subspecies (Crimea, Causasus) similar in dimensions to the Polish population.

The maximum length of skull in Polish lowland red deer is decidedly exceeded by that in Scandinavian red deer, which even exceeded the sizes of this measurement given by Gromov *et al.* (1963) for the subspecies of *Cervus elaphus* from the Soviet Union.

The Polish population of lowland red deer is similar in respect of maximum skull length to the High Tatra population of Czechoslovakia, but inferior to red deer from East Slovakia and Hungaria. In the latter case this applies both to males and females. Possibly the Hungarian, East Slovakian and Rumanian red deer have already become a different subspecies. The above-mentioned authors (data, table 12) in describing these populations do not give a final opinion as to the subspecies appurtenance of the individuals examined, although they consider that the Carpathian red deer should be segregated into a separate subspecies, *Cervus elaphus montanus* Botezat, 1903.

The Crimean red deer (*Cervus elaphus brauneri* Charlemagne, 1920), of the European subspecies, are most similar to the Polish red deer in respect of maximum skull length.

The mean maximum skull lengths for Caucasian red deer (*Cervus elaphus maral* Ogilby, 1840) markedly exceed the average for Polish red deer.

The skulls of lowland red deer are broader than the skulls of Rumanian and Crimean red deer. The mean value of the measurement of zygomatic breadth is only similar in Polish and Caucasian individuals.

The following measurements have a similar range in the Polish and Crimean red deer: lateral length of the viscerocranium, *Zl—P*, palatine length, *Pm—P*, and breadth of *ossa frontalia* at points *Da—Da*. A distinct difference in favour of Polish individuals occurs only in the measurement of condylo-occipital breadth.

Dimensions of the skull in Polish red deer are similar to the dimensions in Crimean red deer and sometimes even exceed them, as in the case of measurement of zygomatic and condylo-occipital breadth. Skull length in Crimean red deer is, however, greater than in Polish individuals, the skulls of these latter being slightly shorter and broader. Unfortunately data on values of measurements of the braincase of these later were not

Table 12.

Comparison of skull measurements of red deer from Northern, Central and Southern Europe with corresponding Polish lowland red deer (after data given by different authors) (in mm)

Measurement	Country	Locality, population	Males			Females			Auther
			Min.	Max.	Avg.	Min.	Max.	Avg.	
P - Op	Poland	lowland	381.0	464.0	418.5	324.4	406.3	372.6	Mystkowska*
	Poland	Carpathian	443.0	495.0	473.8	-	-	-	Szaniawski /1966/
	USSR		403	440	-	-	-	-	Gromov et al. /1963/
	Czechoslovakia	High Tatras	359	468	414.4	-	-	-	Bališ /1959/
	Czechoslovakia	East Slovakia	398	497	435.3	-	-	-	Bališ /1959/
	Hungary		-	-	446.5	-	-	396.4	Szunyoghy /1963/
	Rumania		470	540	-	-	-	-	Philipowicz /1961/
	USSR	Crimea	405	454	-	311	378	-	Geptner & Nasimovič /1961/
	USSR	Caucasus	447	482	472	-	-	-	Flerov /1952/, Beme /1957/
CB	Poland	lowland	361.0	418.0	405.1	306.4	394.1	360.7	Mystkowska*
	Denmark	lowland	-	-	364.0	-	-	340.9	Ahlen /1965/
	Sweden		-	-	381.3	-	-	344.0	" "
	Norway		-	-	366.1	-	-	327.9	" "
zy - zy	Poland	lowland	160.0	199.0	175.3	135.4	161.0	147.8	Mystkowska*
	USSR	Crimea	127	167	148.8	128	146		Beme /1957/
	USSR	Caucasus	178	184	171.6	-	-	-	Flerov /1952/, Beme /1957/
	Rumania		140	180	-	-	-	-	Philipowicz /1961/
Zl - P	Poland	lowland	206.0	270.0	241.8	189.4	236.8	219.5	Mystkowska*
	USSR	Crimea	190	273	235.5	176	234	-	Beme /1957/
	USSR	Caucasus	262	289	283.0	-	-	-	Flerov /1952/, Beme /1957/
Pm - P	Poland	lowland	112.0	153.0	128.7	106.2	129.0	118.1	Mystkowska*
	USSR	Crimea	109	154	-	100	134	-	Beme /1957/
Pm - Pd	Poland	lowland	91.0	118.0	105.6	91.9	124.4	104.7	Mystkowska*
	USSR	Crimea	92	124	-	96	116	-	Beme /1957/
Da - Da	Poland	lowland	107.0	133.0	120.5	90.4	113.6	102.3	Mystkowska*
	USSR	Crimea	92	130.5	113.2	90	106	98.8	Beme /1957/
	USSR	Caucasus	125	136	80.9	-	-	71.6	Flerov /1952/
con - con	Poland	lowland	68.0	80.0	73.9	58.4	74.8	65.9	Mystkowska*
	USSR	Crimea	60.5	78.0	69.7	54.0	69.0	-	Beme /1957/
	USSR	Caucasus	73	79	77.8	-	-	-	Flerov /1952/, Beme /1957/
$\frac{\text{Mo-Mo} \times 100}{\text{Pm - P}}$	Poland	lowland	47.6	60.2	53.5	44.8	57.8	49.3	Mystkowska*
	USSR	Beloveżska Pušča	46.0	48	47	-	-	-	Geptner & Calkin /1947/
	USSR	Caucasus	46.0	53	50.5	-	-	-	Geptner & Calkin /1947/

*) data for age group III (7—12 years).

available for comparison. Probably greater differences, in favour of the Crimean red deer, would occur in its length.

Polish red deer exceed in respect of the index value *Mo—Mo*×100/ /*Pm—P* not only individuals from the Soviet part of the Białowieża Primaeval Forest, but also Caucasian red deer, which points to the lesser breadth of *pars facialis* in these latter.

To sum up it must be said that Polish red deer, as Central European representatives, are inferior in skull dimensions to the red deer of Southern Europe, but exceed in this respect individuals from Western Europe. The High Tatra population of red deer, and also individuals from the Soviet part of the Białowieża Primaeval Forest, are very similar to Polish representatives.

It is difficult to give an opinion on the subspecies appurtenance of the lowland red deer (which in any case was not the purpose of this study). The majority of authors (Geptner & Calkin, 1947; Flerov, 1952; Gromov, *et al.*, 1963) find that the subspecies *Cervus elaphus elaphus* occurs in Central Europe. Since the differences between red deer from Western, Central, Eastern and Southern Europe (Table 12) are slight, it is difficult to speak of subspecies appurtenance, particularly as the most similar European subspecies, the dimensions of which almost entirely coincide with the measurements made in this study, is the Crimean red deer, *C.e. brauneri.*

3. Sex Dimorphism

Sex dimorphism in red deer is best characterised by measurements of breadth: zygomatic breadth, breadth on facial tuber, condylo-occipital breadth; of length: maximum skull length, mandibular length and of height: height of braincase and height of *pars rostralis.* Of the indices, that which best illustrates sex dimorphism is the index: *Nsi—margo adentalis*×100/*Pm—Pd.*

The males of the Polish red deer differ from the females by the greater dimensions of their skulls. It is only in the measurement of length of maxillary tooth-row that differences are almost imperceptible but length of the mandibulary tooth-row is even very slightly greater in females than in males in age group II.

Breadth of the viscerocranium is, proportionately to length, greater in males than in females.

4. Rate of Growth

4.1. Growth Rate of the Skull in Females and Males

Growth rate of the skull differs in the two sexes. The skull of females grows most intensively in the second year ,and this jump in value is generally never repeated throughout the whole life of the individual. Inhibition of growth rate in the third year of life, or even its complete interruption, is remarkable. This applies both to measurements of the viscerocranium and neurocranium, and is also connected with smaller increase in body weight. This may be due to some physiological causes. An exception to this is the breadth of the viscerocranium which increases in this period also.

The majority of the bones of the viscerocranium grow up to age group IV except for the nasal bones, maximum growth of which is attained in age group III.

The very rapid increase in length of *pars rostralis* is remarkable. As from the third year of life this is expressed in the rapid increase in the measurement, *Pm—Mo-Mo* and in length *Pm—P* preceeding parallel to it, and on length of *margo adentalis mandibulae* (Fig. 17). The exponential of this considerable elongation of *pars rostralis* and simultaneously of increase in breadth of the viscerocranium is the enormous increase of *Zl—P*.

The neurocranium grows far less than the viscerocranium during postnatal life. Basal length, *St—B*, increases most intensively, also lateral length, *Zl—Op*, it being possible to connect increase in the measurement *Zl—Op* with the intensive increase in zygomatic breadth, which may render the picture less clear.

Breadth of the braincase is the most stable measurement, which changes very little over the animal's life, increasing slowly up to age group IV. The capacity of *cavum cranii* increases similarly up to group IV, but increase in this measurement is incomparably quicker in relation to the majority of measurements of the neurocranium, particular to *eu—eu*.

It is worth while drawing attention to the fairly intensive increase of *Sph—Br* in group IV coinciding with reduction in the height of *planum nuchale, Op—O*. This is probably connected with the fornication in females (to a certain degree similarly to that in males) of the frontal bones above the orbits.

Growth of different bones of the viscerocranium in males, in the third year of life is equally intensive as in the second year and takes place up to group III at a very slightly slower rate. It is not until class IV that development of the skull is inhibited, or takes place very slowly (Fig. 18).

Increase in the majority of measurements of the neurocranium is not very intensive in the second year of life, and growth rate is not more rapid until the third. Thus *Sph—Br* does not increase at all in the second year of life. There is little increase in the third, and most intensive increase as from group II which lasts until group IV. There is increase in the length of the frontal bones. This is undoubtedly connected with the growth of increasingly massive antlers by the males and in consequence considerable fornication of the frontal bones between the antlers. There is parallel increase in the measurement *fs—fs*. This change in the frontal bones, or rather their fornication is possible on the one hand owing to the rapid increase in the length of the frontal bones, *Br—N*, and on the other is connected with the slower but constant increase in the length *Op—Br*. These changes in the formation of the skull are accompanied by decrease in the height *Op—O*.

One of the few measurements which passes through a sort of stagnation period during the development of the skull in males is *St—B*. Its growth is inhibited between group Ic and II. In later age groups this length increases very intensively.

The value of the measurement *zy—zy* increases up to age group IV, both in males and females. It would therefore be difficult to agree with the conclusion reached by Szunyoghy (1963), who found on the basis of Hungarian material that increase in this breadth ends in females at the age of 22—26 months. As in the case of certain other measurements there is far more rapid growth in the second year of life, but the process itself continues up to age group IV.

The length of the maxillary tooth-row, *Pm—Pd*, and mandibulary tooth-row, P_1—M_3, decreases with age in both males and females. Similar observations were made by Ingebrigtsen (1927) on Norwegian material, on Caucasian red deer by Biome (1957) and on Hungarian red deer by Szunyoghy (1963). Biome connects this phenomenon with the process of tooth wear. I find it difficult to agree with this view since I made measurements of the length of the tooth row in the middle of the hard palate (see description of measurements and Fig. 1) and therefore tooth wear could not have affected the result of the measurement. Possibly this is connected with the increase of the viscerocranium in breadth with age.

4.2. Dimorphic Differences in the Increases in Some Measurements

When comparing skull growth in males and females it is remarkable how the measurements can be divided into there groups: (1) measurements, the value of which increases with age more in females than in males. Profile lenght of the skull, *P—Op*, and the majority of measurements of the viscerocranium belong to this group. (2) The second group is formed by measurements which increase similarly in males and females. i.e. measurements of the medial part of the skull, and thus its breadth, *(Ect—Ect, zy—zy* and *Da—Da)* and length *(Zl—Op).* This is probably due to the zygomatic breadth exerting a considerable influence on the size of this latter measurement. Height of viscerocranium, which exhibits a similar growth rate in both sexes, belongs more or less to this group of measurements. (3) The third group is formed by measurements of the neurocranium which increase more slowly in males than in females during the first years of life. The more rapid growth rate in old males not only balances up the difference but leads to greater increase in these measurements. Breadth of the braincase *(eu—eu),* the increase in which is 6.5% higher in males than in females, breadth, *Ot—Ot,* 7.2% higher, and height *Sp—Br,* 4.0% higher, belong to this group.

Sex dimorphism does not therefore affect the growth of the medial part of the skull, which increases similarly in both sexes. This central intermediate zone forms, as it were, a band surrounding the skull in the region of *ossa frontalia* between the orbits, on *arci zygomatici* and *ossa palatina.* Distinct differences can, however, be observed in the growth of the viscerocranium and neurocranium between the two sexes.

5. Capacity of the Cranial Cavity

The capacity of *cavum cranii* in males greatly exceeds that in females. Increase in this measurement ends in males in age group III, while in group IV fairly considerable decrease occurs in this value. As breadth of the braincase increases up to group IV it might be assumed that bony tissue is deposited inside the cranial cavity which decreases its capacity. Empel (1962) observed a similar phenomenon in his examinations of the skull of the European bison.

The process of increase in the capacity of the braincase in females is most intensive in the second year of life, which confirms Szunyoghy's investigations (1963). In age groups II and III growth is slight, not becoming more rapid until age group IV. This inhibition in the growth rate of cranial capacity occurring in age groups II and III takes place during the period of most intensive reproduction, which ends in group IV. A certain degree of confirmation of the above hypothesis is provided by the similar inhibition in increase of body weight in females between age groups II and III.

When comparing Polish individuals with Hungarian material

(Szunyoghy, 1963) it is found that the capacity of the skulls of Hungarian hinds of an age corresponding to group I in our material the capacity value was, e.g. 373.5 cm^3 and thus greatly exceeds the same values for Polish stags of the same age, and even the skull capacity of Polish hinds in age group III — 332 cm^3.

The skull capacity of Hungarian hinds 9 or 10 years old is, according to this same author, 401 cm^3. This value is even higher than the majority of the mean values for Polish stags in all age classes.

6. Body Weight

I found very few craniometrical data on red deer in the literature at my disposal, but there were many studies both on body weight and on structure and weight of antlers. These two characters are undoubtedly connected with each other and there is a certain relation between them as shown by Beninde's studies (1940). Despite the fact that the body weight is usually proportional to the weight of the antlers, a few cases do occur which appear to contradict this rule. Red deer distinguished by small body weight and fairly considerable antler mass, and *vice versa,* have been encountered in the same game areas in addition to red deer average for those areas.

During the last 300 years a sharp decrease in body weight of red deer in Poland has been noted. A similar phenomenon was described by Ingebrigtsen (1927) and Beninde (1940) on Norwegian and German material. Müller-Using (1953) reached similar conclusions when examining red deer antlers from excavations on Wolin Island.

Data relating to the Mazurian region (Mager, 1941) show that the mean body weight of 41 red deer killed in 1617 was 314 kg (i.e. weight of individuals before gralloching). 69 males hunted during the period from 1890 to 1898 had an everage body weight of 155 kg. From 1899—1906 the mean body weight of 135 red deer was 147.3 kg. Stags, 117 in number, hunted during the period from 1907 to 1912, had an average body weight of 143 kg. In the following period from 1918 to 1938 the best males killed in the area now forming the Olsztyn province weighed on an average 211 kg (mean of 6 inidividuals). Red deer shot in the Olsztyn province from 1960 to 1962 had body weights within limits of 67 to 192 kg, the average weight for adult stags (age group III) being 154.9 kg. It would appear from the above that body weight fall sharply up to 1912, and has risen again during recent years, i.e. since that time.

For purposes of comparison I have given in table 13 the values of body weights of adult Polish stags and the same data for red deer from Eastern, Western and Southern Europe, after different authors.

Polish red deer exceed in body weight red deer from the west of Europe: Norway, Scotland, England and Germany, but are inferior in this respect to stags from the south and east Europe: Soviet Union — Białowieża Primaeval Forest, Hungary, Rumania and Yugoslavia. The above comparison confirms the generally held opinion (Ingebrigtsen, 1927; Beninde, 1940) that differences exist in body dimensions and

Table 13.
Comparison of body weight of red deer from Western, Eastern and Southern Europe — after data given by different authors (in kg).

Country	Place	Min.	Max.	$\bar{x}$	Author
Norway	Hitra Island	90	100*	—	Ingebrigtsen 1927)
Norway	continent	130	160*	—	Ingebrigtsen 1927)
Scotland	—	—	—	95	Taylor Page (1964)
England	—	—	189	—	Taylor Page (1964)
Germany	Schwarzwald	—	—	96.6	Ingebrigtsen 1927)
Germany	Potsdam	—	—	100.0	Beninde (1940)
Germany	Taunus	—	—	105.0	Beninde (1940)
Germany	Schorfheide	120	130	—	Beninde (1940)
Poland	lowland populat.	78	194	138.0**	Mystkowska
USSR	Beloveżkaja Pušča	143.5	208.0	180.1*	Sablina (1955)
Hungary		178	285***	—	Botezat (1922)
Hungary					Szunyoghy (1963)
Rumania		—	241	—	Szunyoghy (1959)
Yugoslavia		—	350	—	Valentinčič (1958)

* These data apply to the period before rutting, whereas the body weight values given by me mainly refer to the rutting period and winter, when the red deer decrease sharply in weight (30—40 kg — Heptner & Calkin, 1947).

**) The body weight given here applies to adult males in age group III.

***) The weight of individuals before gralloching. For comparison with other data it is necessary to deduct about 25% of weight for entralis and about 5—9 kg for head without antlers,

antler strength depending on the geographical habitat. Red deer inhabiting the west Europe are distinguished by smaller body weight and poorer antlers in comparison with the red deer from the east of Europe. This is probably due not to the western forms being primitive, but that they have gone back slightly as the result of habitat conditions. Beninde (1940) states that red deer find their optimum conditions in a continental climate.

The Polish lowland red deer, as a component of the fauna of Central Europe, are intermediate forms and are distinguished by greater body weight and antler strength than those from Western Europe, but lesser than red deer from Eastern and Southern Europe.

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MORFOLOGICZNA ZMIENNOŚĆ CZASZKI I CIĘŻARU CIAŁA JELENIA NIZINNEGO

Streszczenie

Celem pracy było przedstawienie zmienności morfologicznej czaszki jelenia nizinnego, *Cervus elaphus* Linnaeus, 1758, w zależności od wieku i płci osobników, jak również zmienności w zakresie ciężaru ciała. Zagadnienia te nie były dotychczas wyczerpująco opracowane w literaturze polskiej. W dostępnym mi piśmiennictwie obcym nie spotkałam się także z opisem morfologicznym czaszki jelenia ani innych przedstawicieli *Cervidae*. Większość prac odnosi się do budowy poroża i ciężaru ciała.

Materiał do badań liczył 483 czaszki (w tym 260 samców i 233 samice) i pochodził z okresu trzech sezonów łowieckich, z lata 1960—1962 (Tabela 1). Wiek osobników oznaczony został na podstawie starcia zębów. Na czaszkach tych wykonano 34 pomiary, wzorując się na pracy Duersta (1926).

W opisie morfologicznym czaszki starano się uwypuklić cechy charakteryzujące dymorfizm płciowy jelenia, wpływ wieku oraz cechy różniące jelenia od innych przeżuwaczy. Proces obliteracji szwów przebiega nierównolegle u samców i samic. U samców większość szwów zaciera się szybciej co prawdopodobnie pozostaje w związku z obciążeniem czaszki przez poroże (Tabele 2 i 3).

Drugą część pracy stanowi kraniometria i wskaźniki zestawione w tabele liczbowe (Tabele 4, 5, 6). Cały materiał podzielono na cztery grupy wiekowe: I grupa — osobniki 1 do 3 lat, II — od 4—7 (młode); III grupa — od 8 do 12 (dojrzałe) i IV grupa — powyżej 12 (osobniki stare).

Starano się zwrócić szczególną uwagę na te pomiary i wskaźniki, które charakteryzują najlepiej dymorfizm płciowy jelenia nizinnego i te które można porównać z pomiarami i wskaźnikami czaszek jeleni z innych terenów jak Związek Radziecki, Węgry, Norwegia.

Pomiarami, które najlepiej obrazują różnice pomiędzy czaszkami obu płci są przede wszystkim pomiary szerokościowe, tj. szerokość jarzmowa, szerokość na guzach policzkowych, szerokość kłykci potylicznych a poza tym dwa pomiary długościowe i dwa wysokościowe: długość największa czaszki, długość żuchwy, wyskości częściej rostralnej i wysokość mózgoczaszki. Istotność stwierdzonych różnic sprawdzono metodami statystycznymi (Tabela 7).

Wskaźnikiem najlepiej ilustrującym dymorfizm płciowy jest: wysokość części rostralnej×100/długość szeregu zębów szczęki. (Tabela 6, Ryc. 9).

Pojemność jamy czaszkowej jest większa u samców niż u samic. Najwyższa średnia wielkość tej jamy u samic w IV grupie wieku, odpowiada średniej samców grupy II (Tabela 9).

Porównywując opisany materiał badawczy z danymi odnoszącymi się do czaszek jeleni z terenu Związku Radzieckiego, Węgier i Norwegii można stwierdzić, że polskie jelenie nizinne przewyższają znacznie długością czaszki jelenie norweskie, ustępują natomiast jeleniom węgierskim. Dotyczy to zarówno samców jak i samic. Spośród podgatunków europejskich, najbardziej zbliżone do polskich jeleni nizinnych są jelenie krymskie *Cervus elaphus brauneri* Charlemagne, aczkolwiek te ostatnie przewyższają wielkością pomiarów czaszki polskich osobników (Tabela 12).

Przy opracowaniu tempa wzrostu czaszki I grupę wieku podzielono na trzy mniejsze. Za grupę wyjściową — 100%, do której odnoszono cyfry obrazujące wzrost wszystkich pozostałych grup, przyjęto klasę I a, obejmującą czaszki osobników w wieku od 6 do 12 miesięcy.

Najbardziej intensywny wzrost czaszki samic odbywa się pomiędzy pierwszym a drugim rokiem życia. W trzecim roku zwraca uwagę zahamowanie tempa wzrostu. W dalszych latach wzrost odbywa się, ale tempo jest znacznie wolniejsze. Większość wymiarów wzrasta aż do IV grupy wieku. Trzewioczaszka samic rośnie bardziej intensywnie niż mózgoczaszka, która w ciągu życia przyrasta niewiele (Ryc. 17). Czaszka samców rośnie naogół mniej intensywnie, a przyrost mózgoczaszki i trzewioczaszki jest podobny. Najszybszy przyrost wymiarów czaszki samców odbywa się w drugim i trzecim roku. W dalszych latach wzrost jest wolniejszy i trwa do III lub IV grupy wieku (Ryc. 18).

Wszystkie pomiary można podzielić na trzy grupy: (1) takie, których wielkość przyrasta z wiekiem bardziej u samic niż u samców (Ryc. 19 A i B): (2) przyrost pomiarów u obu płci jest podobny (Ryc. 19 C i D); (3) przyrost u samców jest większy niż u samic (Ryc. 19 e, 20 A i B).

Jedynymi pomiarami, które z wiekiem maleją są: długość szeregu zębów szczęki i żuchwy (Ryc. 20 D i E).

Ciężar ciała jeleni nizinnych wynosi u samców od 67 do 194 kg, a u samic od 25 do 103 kg (dane dla I i IV grupy wieku) (Tabela 10).

W ciągu ostatnich 300 lat notowany jest gwałtowny spadek ciężaru tuszy jeleni na terenie Polski. Podobne zjawisko opisywano było przez autorów węgierskich, niemieckich i norweskich.

Polskie jelenie nizinne, wchodzące w skład fauny Europy środkowej, odznaczają się większym ciężarem ciała i rozmiarami czaszki w porównaniu do zachodnio-europejskich, ale mniejszym do wschodnio-europejskich.