Original Research

Skulls of Neolithic Eurasian Beavers (*Castor fiber* L.) in Comparison with Skulls of Contemporary Beavers from Natural Biotopes of Wielkopolska Region (Poland)

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Abstract

The present work describes the morphological distance of a cranium between specimens of *Castor fiber* from Neolithic period and contemporary specimens which live in the same region of Poland. Two well-preserved skulls of Neolithic beavers and 32 skulls of contemporary beavers were available. In order to compare the skulls, first the age of the animals was estimated followed by 22 measurements of each skull. On the basis of Principal Components Analysis it was found that the skull in the beaver changes its dimensions with age. Moreover, a strong positive allometry was found of the external sagittal crest in relation to age. The other craniometric features showed negative allometry. The PCA method also made it possible to determine that the skull of a 3-year old Neolithic beaver is as big as skulls of 4- to 5-year old contemporary ones. The skull of the second Neolithic beaver, a 5-year old, is the largest among skulls of contemporary beavers in its age group.

Keywords: *Castor fiber*, skull, cranial features, reintroduction

Introduction

The beaver as an amphibious animal plays a tremendous role in regenerating the natural environment. The reintroduction and conservation of mammals, including the beaver, are often difficult. One of the reasons is the fact that contemporary species reintroduced into the biotope frequently differ in size and genetic makeup from the former ones living in the earlier historic and prehistoric epochs [1, 2]. Since reintroduced animals come from other sites, they have no genetic contact with populations living previously in a given area. Being slightly different genetically from those animals which had died out, they had to again adapt to the new habitats. Moreover, contemporary biotopes, in which wild animals live at present, differ considerably from those of earlier periods [3]. The size of animals is routinely monitored within the framework of species protection programs. Successive generations are compared to verify whether a given population turns out to be prone to diseases and degeneration [4]. Apart from the comparison of successive generations it is also worthwhile to refer the dimensions of contemporary species to animals living in the same territory before their extinction. Among the recent studies on this subject a study by Kitchner and Lynch [5] is especially valuable. Those authors verified which of the extant populations of beavers in Europe are most similar to the fossil remains of British beavers. Those investigations were to aid the reintroduction of the beaver in Scotland. The similarity was established on the basis of skulls. As the authors stated, it would not be acceptable to use these specimens for molecular analysis, since this would require their complete or partial destruction and the successful extraction of useable DNA cannot be guaranteed.

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Apart from the above-mentioned study, osteological comparative studies of old and present-day forms of beavers have been conducted by several authors [6-9]. Among elements of the skeleton, the skull especially provides a large amount of information. It is the site of many taxonomical traits and thus using it is possible to assess the size of a given animal. Recent valuable data on the welfare of beavers in Russia, both reintroduced and aboriginal, were supplied by Saveljev and Milishnikov [10]. However, those authors regret there have been few studies on cranium sizes, as cranium parameters facilitate a more comprehensive assessment of morphology of beavers. In studies of this kind the biggest problem is the limited number of fossil skulls and their sometimes unsatisfactory condition. Moreover, as reported by Piechocki [11], some dimensions of skulls change during the lifetime of a given animal, also after reaching maturity. This may occasionally be misleading, especially if researchers do not have a large sample at their disposal.

This study had two primary objectives. The preliminary aim was to verify whether the age of a beaver affects changes in skull dimensions. The primary aim was to determine whether the two Neolithic skulls of beavers found in the Wielkopolska region (Poland) differ in size from skulls of contemporary beavers from their age group.

Although it is difficult on the basis of a scarce sample to draw far-reaching conclusions, the unique experimental material justifies such a comparison.

Material and Methods

The main objects of study were two skulls of beavers from Neolith found in the Wielkopolska region, one in the area of Murowana Goślina and the other near the town of Żnin. Their metric parameters are presented in comparison to 32 skulls of contemporary beavers also living in the Wielkopolska region. Contemporary skulls come from the collection of the Department of Animal Anatomy and the Department of Zoology of the Agricultural University of Poznań.

The first stage of the study was to determine the age of all animals. Age was determined using the standard and widely used method developed by Larson and Van Nostrand [12] supplemented with later observations by Stiefel and Piechocki [13]. This method consists of the observation of the degree of tooth root closure and the deposition of cementum on buccal teeth. On the basis of this method the age of Neolithic beavers was assessed as 3 and 5 years. The age of contemporary beavers ranged from 0.5 to 8 years.

A total of 22 measurements were taken on skulls (Fig. 1). They were:

- AP – total length of the skull – the distance between points: Akrokranion and Prosthion
- CbasLen – condylobasal length: border of the occipital condyles – Prosthion
- BasLen – total length of the cranial base: Basion – Prosthion
- BSt – basal-palatal length: Basion – Staphylion
- StP – median palatal length: Staphylion – Prosthion
- ANas – median frontal length: Akrokranion – Nasion
- NasP – upper length of the viscerocranium: Nasion – Prosthion
- NasRh – length of the nasals: Nasion – Rhinion
- ZygZyg – zygomatic breadth: Zygion – Zygion
- SupProc – breadth across the supraorbital processes
- PorbBrea – postorbital breadth: Frontostenion – Frontostenion
- EntEnt – least breadth between the orbits: Entorbitale – Entorbitale
- MxtLen – length of the tooth row in the maxilla
- PremP – length between the first premolar tooth and Prosthion
- SagCrest – length of the external sagittal crest
- NuchCrest – length of the nuchal crest
- EuEu – neurocranium breadth: Euryon – Euryon
- OccCond – breadth of the occipital condyles
- ParaOcc – breadth at the bases of the paraoccipital processes
- IncisBrea – breadth of the incisive bone
- MxBrea – breadth of the maxilla beside infraorbital foramens
- PalaBrea – greatest palatal breadth

The statistical method applied in this study was the Principal Component Analysis [14]. On its basis it was possible to show the metric variation of skull in terms of age, as well as visualize skulls of Neolithic beavers in comparison to skulls of contemporary beavers. The next stage of the study was to show proportions in which cranial parameters change in relation to age. For this purpose the allometric function was used in the form:

$$y = ax^b$$

In the last stage of the study craniometric parameters were referred to specimens from the Neolithic Age to the dimensions of contemporary specimens of respective age classes.

Analyses were performed using Statistica v. 6.0 software, as well as Statgraphics v. 5.0.

Results

Principal Components Analysis

On the basis of PCA two components were revealed. They exhibit a high degree of representation because they explain jointly 85.5% of the variance which is determined by all 22 metric features. After the varimax rotation was performed, each variable was given a load, being the correlation coefficient reflecting the linkage of a variable with a given component. The highest loads (>0.7) in Table 1 are marked in bold.

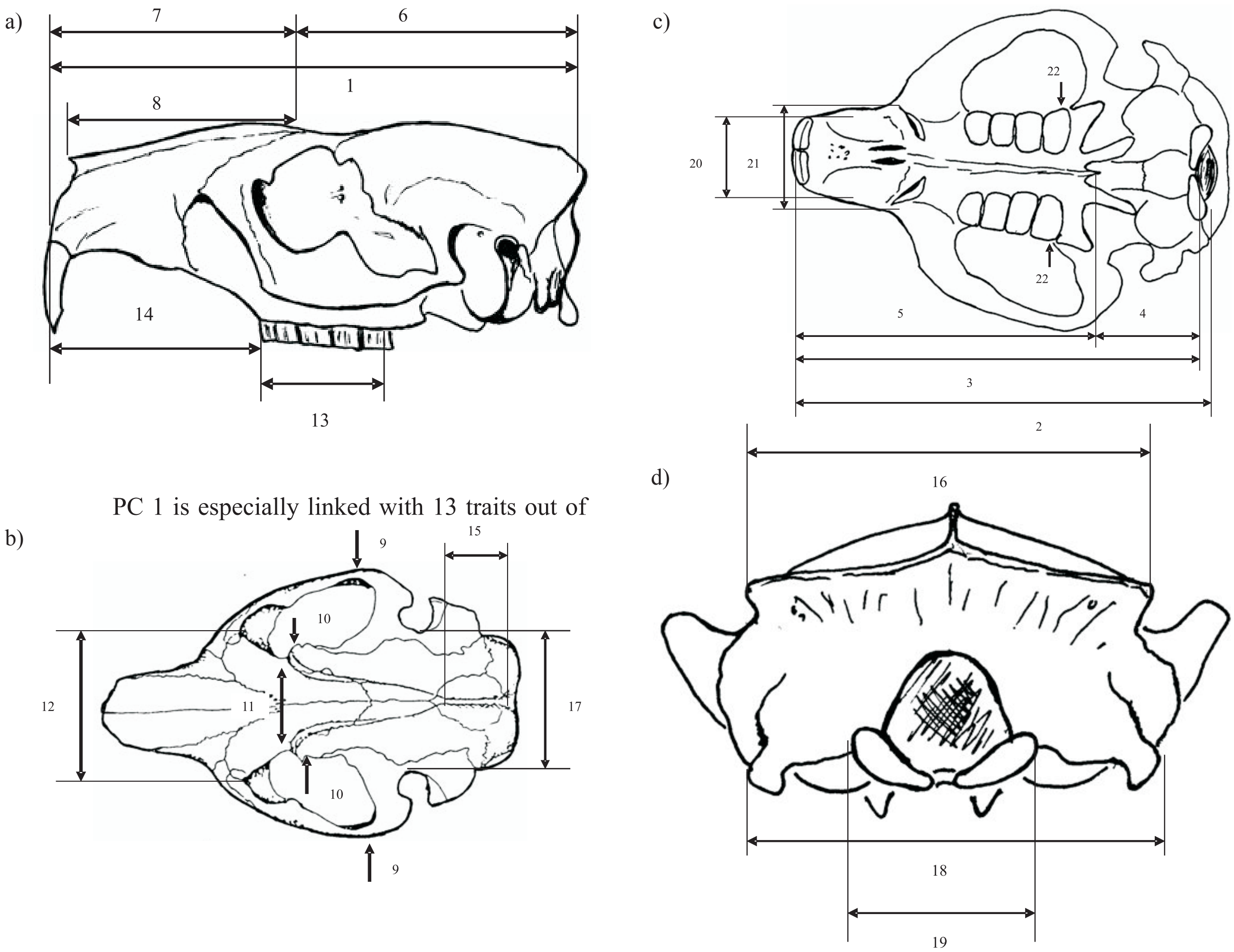

Fig. 1. Cranial measurements used in this study. a) left side view. b) dorsal view. c) basal view. d) nuchal view. Number references in the text.

PC 1 is especially linked with 13 traits out of 22. PC 2 defines mostly four variables. The plot of PC1 against PC2 shows the dispersion of factor scores for the skulls of each beaver. This distribution is connected with aging of the individuals (Fig. 2).

It needs to be emphasized that the skull of a 3-year-old Neolithic beaver is placed among skulls of contemporary beavers aged 4–5 years. Thus it is larger than skulls of contemporary beavers of the same age. In turn, the skull of a Neolithic beaver whose age was assessed at 5 years is the largest of skulls in its age group.

Allometry

In order to determine how metric parameters of the skull increase with age, allometric regression equations were applied for each pair of variables. In the formula $y = ax^{b,}$ age was used as an independent variable, while successive features of the skull were the dependent variable. In accordance with the assumption of this method [15, 16], when exponent (b) was bigger than 1, a given characteristic increased faster than age-positive allometry, b equal to 1 indicated an isometric increase of variables, while b lower than 1 meant negative allometry. Values of the exponent and values of the intercept are presented in Table 2.

Only the length of the external sagittal crest (SagCrest) exhibited very strong positive allometry. The allometric equation showing the growth rate of this character in relation to age is presented in Fig. 3. However, for the purpose of age prediction, the linear model: $y = a + bx$ shows a better fit (Fig. 4.).

Among other traits, the CbasLen (Fig. 5) and ZygZyg parameters are of special importance, since on the basis of these traits age classes of the beaver may be established using the method proposed by Piechocki [11] (Fig. 6).

Age has a negligible effect on three variables, in which the allometric slope was close to 0. They are PorbBrea, OccCond and EuEu.

A Comparison of Cranial Parameters of Neolithic Beavers with Contemporary Ones

Parameters of skulls of 3-year old Neolithic beavers are listed below next to mean values of skulls of contemporary beavers of its age group (Table 3). This animal considerably exceeded mean values of contemporary beavers of his group in terms of as many as 18 parameters.

The Neolithic 5-year old beaver, also in terms of most dimensions, exceeded mean cranial dimensions of contemporary animals (Table 4).

Discussion

The Effect of Age on the Variation in Contemporary Beaver Subspecies

Not all authors comparing skulls of the Eurasian beaver in different populations emphasize sufficiently the process of skull modelling progressing with age. When researchers have sufficiently numerous material at their disposal it may be assumed that in the analyzed groups age variances are going to be homogenous. In such a situation age should not affect the interpretation of results. However, there is some risk when we compare relatively scarce material. Similar conclusions were reached by Frahnert [17], who did not recommend comparisons of juvenile animals with adult or old animals when identifying subspecies. That author showed that in the process of ontogenesis the skull grows rather in length than breadth, i.e. she observed a slight negative allometry of the greatest breadth of the skull (ZygZyg in this study) to its basal length (BasLen). It was also shown in this study that in the ontogenetic development these parts of the skull are relatively constant, which protect the brain and sense organs. However, the trait exhibiting strong positive allometry is the length of the external saggital crest. Those conclusions were also confirmed in our study.

The problem of changes in the condylobasal length (CbaLen) and zygomatic breadth (ZygZyg) with age has been investigated in several studies [17-19]. These observations along with his own findings were summed up by Piechocki [11]. That author prepared seven age classes of the beaver, where he added values of parameters CbasLen and ZygZyg. Excluding the juvenile age, individual variation in a given animal after reaching sexual maturity may be considerable. After summing up the length and breadth of the skull into one parameter, the difference between a two-year old beaver and a 15-year old one should be 8 cm.

In accordance with the allometric regression line plotted in our study it may be assumed that the skull grows especially strongly in length and breadth in the beaver up to the age of 4.5 years. Above this age the increase in these features is slower. However, this observation needs to be confirmed on a more numerous material. When comparing beavers of different ages it is advisable to focus on these cranial parameters, which grow least with age. These characters include especially parameters located on bones protecting the brain (except for the sagittal crest) and those around sense organs.

If we consider craniometric variation connected with sexual dimorphism, many authors do not include it in their studies, saying that it has a slight effect on morphological characteristics [5, 20, 21].

Table 1. Component loading matrix after varimax rotation.

Variable	PC 1	PC 2
AP	**0.839**	0.530
CbasLen	**0.842**	0.521
BasLen	**0.843**	0.526
BSt	**0.835**	0.382
StP	**0.793**	0.584
ANas	**0.837**	0.303
NasP	**0.772**	0.597
NasRh	0.641	0.659
ZygZyg	**0.776**	0.607
SupProc	0.258	**0.882**
PorbBrea	0.442	**0.748**
EntEnt	0.669	0.661
MxtLen	0.447	**0.707**
PremP	**0.771**	0.546
SagCrest	**0.816**	0.437
NuchCrest	**0.858**	0.386
EuEu	0.526	0.660
OccCond	0.591	0.560
ParaOcc	**0.729**	0.591
IncisBrea	0.481	**0.731**
MxBrea	0.696	0.539
PalaBrea	**0.718**	0.595

Contemporary and Fossil Eurasian Beavers

The problem of comparing contemporary beavers with fossil and subfossil osseous materials has been analyzed several times, especially when searching for an appropriate population for reintroduction to a given area. Kitchner and Lynch [5] found that there is a high craniometric variation in Castor fiber in Europe. Among the beaver populations in this continent, the biggest variation is found in Germany, followed by England, France and Scandinavia. Skulls of three animals from early Holocene from Scotland, available to the researchers, were metrically most similar to those of the extant beavers from Scandinavia.

Data on Neolithic beavers coming from the Caucasus were supplied by Burczak-Abramowicz [6]; however, it was based on only 1 incomplete skull. That author did not determine the age of that animal. The skull was markedly wider than Neolithic skulls investigated in our study, as the ZygZyg parameter was 120 mm. However, the PorbBrea measurement was comparable – 27 mm. This may indicate that the animal from the Caucasus was much older, since as it was shown in our study, parameter ZygZyg increases in value with age to a bigger extent than parameter PorbBrea. Unfortunately, length parameters could not be compared.

Valuable comparative data for our study were supplied by Chmielewski [7]. That author also investigated Neolithic beavers and beavers from the early Middle Ages from the Wielkopolska region, Poland. On the basis of craniometric data he stated that extinct beavers of that time were bigger than contemporary animals. Similarly, Kurten [22] indicated that the reduction in body size is commonly seen in Holocene mammals. Moreover, at least in the last several centuries all European beaver populations have undergone severe population bottlenecks [23].

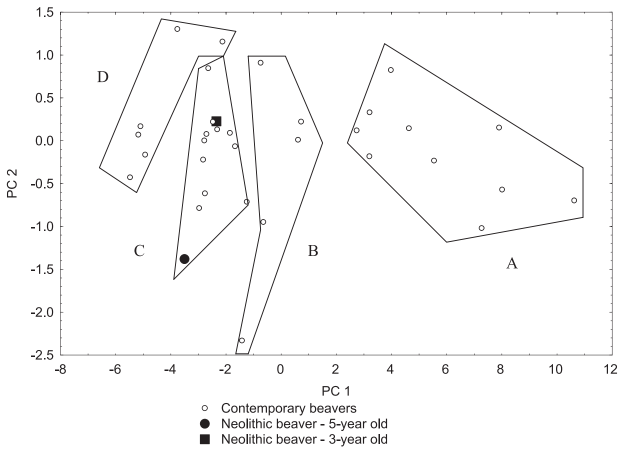

Fig. 2. Principal Component (PC) plot. Polygons enclose contemporary beavers of different age groups.
A) 0.5 – 2-year old; B) 3-year old; C) 4 – 5-year old; D) 6 – 8-year old

History of Contemporary Beavers in the Wielkopolska Region (Poland)

Contemporary beavers of the Wielkopolska region are not descendants of Neolithic beavers of this region. After World War II in Poland only one family stand of beavers was found, on the Marycha River, a tributary of the Czarna Hańcza [24]. However, the number of beavers in eastern Poland increased as a result of natural migrations from the Niemen River and its tributaries [25, 26]. However, in the Wielkopolska region beavers had not been reported for the previous six centuries. Their return to this area was not a natural process. The first beavers were introduced to the Warta River in the area of Biedrusko in 1974, which initiated a successful process of restoration of this species in the Wielkopolska region [27]. Most reintroduced animals (71%) came from the Popielno fur farm of the Polish Academy of Sciences and the Wiartel Fur Animal Farm. The rest consisted of animals from a natural site in the Suwalsko-Augustowska Primeval Forest. The latter may thus be considered to be typical representatives of subspecies *Castor fiber vistulanus*. In the case of fur farm beavers, a considerable share in their gene pool originated from animals coming from a reserve near Voronezh, representing the subspecies *Castor fiber pohlei* [28, 29].

Here a question may be raised on the similarity – both craniometric and genetic – of Eurasian beaver subspecies. Babik et al. [30] showed genetic identity of beaver sub-

Table 2. Values of the allometric model in which age was the independent variable.

Dependent variable	Intercept (a)	Slope (b)
SagCrest	0.95	2.38
NasP	52.55	0.20
BSt	28.47	0.19
NasRh	43.47	0.19
ZygZyg	77.35	0.17
PremP	42.87	0.17
EntEnt	34.16	0.17
BasLen	101.29	0.17
CbasLen	105.94	0.17
AP	110.48	0.16
StP	72.87	0.16

Dependent variable	Intercept (a)	Slope (b)
NuchCrest	37.46	0.16
PalaBrea	30.47	0.15
MxtLen	27.12	0.15
ANas	65.74	0.13
ParaOcc	45.12	0.13
MxBrea	28.23	0.13
IncisBrea	23.14	0.11
SupProc	30.41	0.10
PorbBrea	23.59	0.09
OccCond	27.71	0.08
EuEu	42.93	0.06

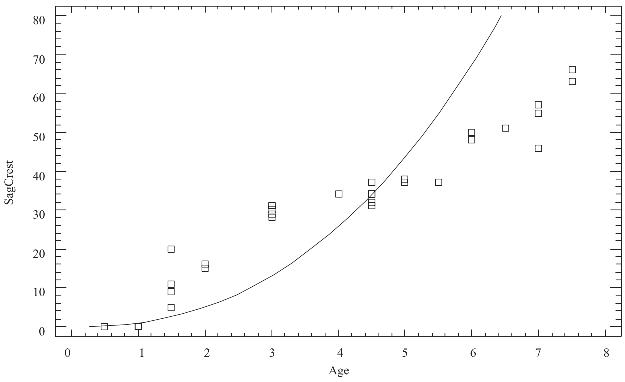

Fig. 3. The allometric equation: SagCrest = 0.95 $Age^{2.38}$

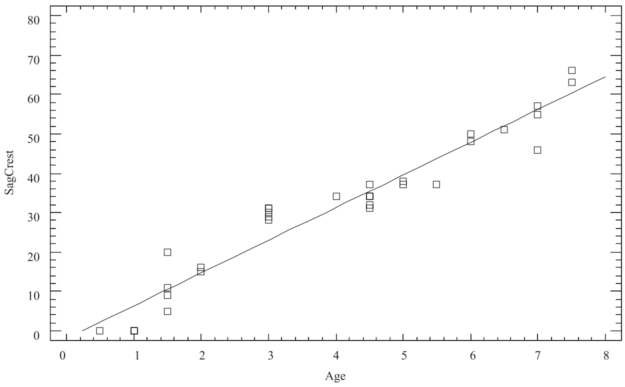

Fig. 4. Linear model: SagCrest = -1.94 + 8.30 Age

species on the basis of alleles of the MHC DRB gene connected with immune response. Those authors stated that there was no close similarity in allele sequences between geographically proximate populations. In other, more recent studies on beaver subspecies, Gabryś and Ważna [31] emphasized how important it is to introduce native subspecies to their historically documented localities. Firstly, it may significantly increase the probability of successful reintroduction. Secondly, it may also prevent undesired intersubspecific crosses and reduce the risk of foreign taxon expansion. Also Saveljev and Milishnikov [10] stressed that aboriginal subspecies as a product of natural selection are important components of recent biodiversity. In view of the above conclusions the comparison of skeletons of beavers reintroduced in the Wielkopolska region with those of native Neolithic beavers is justified.

As shown in the Principal Component Analysis, the two analyzed Neolithic skulls are larger than skulls of contemporary beavers of the same age. Reliable conclusions may hardly be drawn based on two animals. However, it seems likely that Neolithic beavers living in that area exceeded in size representatives of the contemporary population. These observations confirm studies by Chmielewski [7] and Niezabitowski [32]. Those authors stated that not only Neolithic beavers, but also those from the early Middle Ages were larger than the contemporary representatives of this species. The question arises on the cause of this difference. As reported by Żurowski [4], during reintroduction only a small percentage of animals coming from fur farms participated effectively in reproduction. This resulted in an increased inbreeding effect in beavers in the Wielkopolska region. In many mammalian species one of the effects of inbreeding is a decrease in the dimensions of the skeleton, including the skull [33].

On the other hand, it is not known whether changes in the natural environment have ever had an effect on the reduction in bodily dimensions of beavers. Although the population of beavers in the Wielkopolska region is presently prospering, the tolerance limit of this species is not known [4]. Fustec et al. [34] showed that as a result of anthropopressure, beavers move to less advantageous habitats, which also might affect the reduction of their size through the insufficient nutrition base. Kamiński [35] studied native habitats of the beaver in Poland in terms of ecology – tributaries of Lake Wigry, including the Czarna Hańcza River. He stated that the biogenetic role of these biggest European rodents as well as beaver's ecology in overpopulated conditions is not sufficiently investigated. Also Niewolak [36], when studying the pollution rate of this lake, noted the presence of a beaver reserve. In the areas where beavers have repeatedly passed through a genetic bottleneck there are many negative morphological changes observed in those animals [10]. These changes pertain also to the maxillary bone, especially teeth.

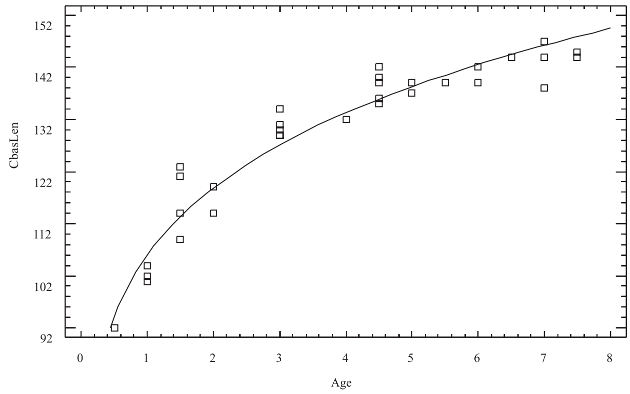

Fig. 5. The allometric equation: CbasLen = 105.94 $Age^{0.17}$

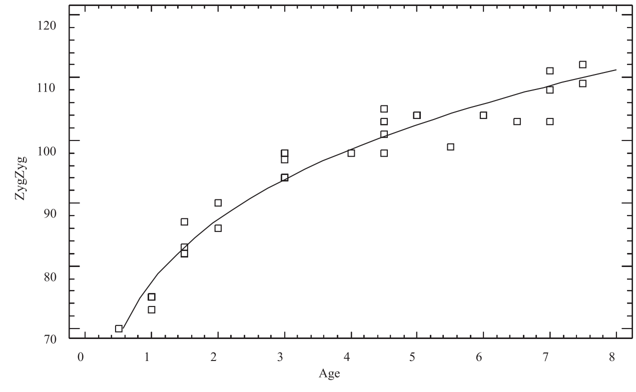

Fig. 6. The allometric equation: ZygZyg = 77.35 $Age^{0.17}$

Table 3. The comparison of the skull of 3-year-old Neolithic beaver with contemporary ones.

Variable	Mean value 3-year old contemporary beavers (5 specim.)	Value 3-year old Neolithic beaver
AP	136.6	144.0
CbasLen	130.6	143.0
BasLen	125.6	137.0
BSt	36.2	42.0
StP	89.4	96.0
ANas	78.8	86.0
NasP	67.4	68.0
NasRh	53.4	57.0
ZygZyg	96.2	100.0
SupProc	35.0	37.0
PorbBrea	26.8	28.0
EntEnt	42.6	48.0
MxtLen	35.8	35.0
PremP	53.6	57.0
SagCrest	29.8	28.0
NuchCrest	44.6	50.0
EuEu	45.8	46.0
OccCond	30.2	30.0
ParaOcc	52.4	54.0
IncisBrea	27.0	27.0
MxBrea	33.2	33.0
PalaBrea	36.6	37.0

Table 4. The comparison of the skull of 5-year-old Neolithic beaver with contemporary ones.

Variable	Mean value 4-5-year old contemporary beavers (11 specim.)	Value 5-year old Neolithic beaver
AP	142.4	145.0
CbasLen	136.5	141.0
BasLen	131.2	134.0
BSt	37.9	37.0
StP	93.3	97.0
ANas	81.6	80.0
NasP	70.9	74.0
NasRh	56.9	61.0
ZygZyg	100.1	103.0
SupProc	34.7	38.0
PorbBrea	26.8	30.0
EntEnt	43.6	51.0
MxtLen	33.5	37.0
PremP	55.2	60.0
SagCrest	35.0	31.0
NuchCrest	48.5	49.0
EuEu	47.5	48.0
OccCond	31.2	32.0
ParaOcc	55.2	59.0
IncisBrea	27.5	29.0
MxBrea	34.6	33.0
PalaBrea	37.7	37.0

Conclusions

– Beaver age has an effect on metric parameters of its skull. Traits which markedly increase in their dimensions with ageing of an animal include the external sagittal crest, upper length of the viscerocranium, basal-palatal length and length of the nasals.
– Both skulls of Neolithic beavers from the Wielkopolska region are larger than skulls of contemporary beavers in this region in their age class.

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