

Variability of the Skull Shape in Hybrids between European bison and Domestic Cattle

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Kraśńska M., 1988: Variability of the skull shape in hybrids between European bison and domestic cattle. Acta theriol., 33, 12:147—186 [With 8 Tables, 2 Figs, & Plates VII—XIV].

The study was carried out on 59 (28,31) skulls of hybrids between European bison and domestic cattle of the Polish red breed and black and white lowland breed. The percentage of cattle's blood increased from 50% in F₁ generation to 93.75% in three backcross generations. In order to compare the data for hybrids, 40 (6,34) skulls of domestic cattle were measured and the data for European bison were taken from literature. Adult F₁ hybrids exceeded both European bison and the cattle as well as backcross hybrids in basal length of a skull, length of *dorsum nasi* and *mandibula*, and in capacity of *cavum cranii*. Most remaining cranial dimensions in F₁ hybrids and the shape of F₁ male skulls were intermediate between the parental forms. The features of European bison which distinctly predominated in hybrid skulls were: the breadth of occiput, the size and shape of *processus cornuales* in F₁ hybrids of both sexes as well as telescopic *annuli orbitales* and the height of a skull in F₁ males. The cattle features predominated in: the skull shape of F₁ females and backcross hybrids, *calvaria* formed entirely of *ossa frontalia*, composition of *planum nuchale*, hind situation of *processus cornuales*, and the height of *fossa temporalis*. The growth rate of F₁ hybrids skulls during the second year of their life was faster than that in European bison. However, in European bison which were older than 4 yrs breadth dimensions of a skull grew more intensively than in cattle. Sexual dimorphic features in hybrid crania occurred in the *calvaria* and *planum nuchale* and in the size of *processus cornuales*. In adult hybrids the variability of linear cranial dimensions was rather low whereas structural differentiation was higher. In backcross hybrids the skulls became more similar to those of the cattle as the percentage of cattle's blood increased.

[Mammals Res. Inst., Polish Acad. Sci., 17-230 Białowieża, Poland].

1. INTRODUCTION

Seventy-one hybrids between European bison and domestic cattle of both breeds: the Polish red (pr) and the black and white lowland (bwl) were obtained at Białowieża during the period 1958—1976. The percentage of bison blood in these hybrids decreased from 50% to 6.25% (Dehnel, 1960; Demiaszkiewicz, 1961; Kraśńska, 1963, 1967, 1971a, 1976, 1979a). The postnatal development of these hybrids was studied (Kraśńska, 1969, 1971b, 1979b) as well as their fertility (Fedyk & Kraśńska,

Table 1

List of examined hybrids between European bison and domestic cattle. Abb.: white lowland breed of cattle; rp×simt. — the red Polish×Simental breed of M — male; F — female; rp — the red Polish breed of cattle; bwl — black and white cattle; E.b. — European bison.

No.	Name	Sex	Parents		Age (mth)	Place of birth
			Mather	Father		
F ₁ Hybrids						
1	Lowicz	M	cattle	E.b.	16	Lękno
2	Luk	M	cattle	E.b.	17	"
3	Lan	M	cattle	E.b.	17	"
4	Lotysz	M	cattle	E.b.	20	"
5	Lowca	M	rp.	E.b.	24	"
6	Lobez	M	rp.×simt.	E.b.	24	"
7	Fakir	M	bwl	E.b.	63	Białowieża
8	Farad	M	bwl	E.b.	77	"
9	Filip	M	E.b.	rp.	96	"
10	Facet	M	bwl	E.b.	136	"
11	Filon	M	E.b.	rp.	156	"
12	Lysica	F	cattle	E.b.	18	Lękno
13	Lajza	F	cattle	E.b.	20	"
14	Ląka	F	bwl	E.b.	24	"
15	Latka	F	bwl	E.b.	24	"
16	Lawica	F	bwl	E.b.	29	"
17	Filutka	F	E.b.	rp.	84	Białowieża
18	Fama	F	rp.	E.b.	96	"
B ₁ bos Hybrids						
19	Feid	F	Fama F ₁	bwl	19	Białowieża
20	Fellach	M	Famela F ₁	bwl	24	"
21	Festyn	M	Figa F ₁	bwl	29	"
22	Feg	M	Filutka F ₁	bwl	41	"
23	Fen	M	Fama F ₁	bwl	43	Białowieża
24	Feb	M	Filutka F ₁	bwl	43	"
25	Fey	M	Famela F ₁	jersey	49	"
26	Fez	M	Filutka F ₁	bwl	52	"
27	Fetysz	M	Fama F ₁	bwl	53	"
28	Fenix	M	Fama F ₁	bwl	66	"
29	Fell	M	Fanny F ₁	bwl	84	"
30	Felly	F	Famela F ₁	bwl	15	"
31	Ferma	F	Fama F ₁	bwl	17	"
32	Fema	F	Fama F ₁	bwl	28	"
33	Feta	F	Filutka F ₁	bwl	39	"
34	Felpa	F	Fatima F ₁	bwl	53	"
35	Feska	F	Figa F ₁	bwl	54	"
36	Fewa	F	Filutka F ₁	bwl	66	"
37	Fera	F	Figa F ₁	bwl	78	"
38	Femina	F	Fanny F ₁	bwl	90	"
39	Fenny	F	Fanny F ₁	bwl	96	"

continued on p. 149

Table 1. concluded.

B ₂ bos Hybrids						
40	Fenek	M	Fenny B ₁	bwl	16	Białowieża
41	Fenyl	M	Fenny B ₁	bwl	27	"
42	Fenomen	M	Femina B ₁	bwl	51	"
43	Fen II	M	Fera B ₁	bwl	52	"
44	Fenol	M	Feska B ₁	bwl	53	"
45	Fela	F	Femina B ₁	bwl	30	"
46	Fetwa	F	Fewa B ₁	bwl	34	"
47	Felga	F	Fenny B ₁	bwl	38	"
48	Fenicja	F	Femina B ₁	bwl	41	"
49	Fedala	F	Feska B ₁	bwl	41	"
50	Ferajna	F	Fera B ₁	bwl	50	Białowieża
51	Fela II	F	Felpa B ₁	bwl	52	"
52	Fega	F	Fema B ₁	bwl	53	"
53	Ferrara	F	Fera B ₁	bwl	56	"
54	Festa	F	Feska B ₁	bwl	65	"
B ₃ bos Hybrids						
55	Feliks	M	Fela II B ₂	bwl	25	Białowieża
56	Felba	F	Fela II B ₂	bwl	12	"
57	Fedra	F	Fedala B ₂	bwl	12	"
58	Ferta	F	Festa B ₂	bwl	16	"
59	Feda	F	Fedala B ₂	bwl	26	"

1971, 1980). Also the heredity of morphological and physiological features have been followed (Buchalczyk *et al.*, 1971; Krasińska & Pilarski, 1977; Krasińska & Sumiński, 1981), and the utility value of these hybrids has been estimated (Pietrzykowski & Krasińska, 1971; Szulc *et al.*, 1971).

The proportions and a form of a skull of European bison differs from those of domestic cattle, especially in *regio parietalis* and *regio frontalis* (Sokolov, 1953; Heptner *et al.*, 1961), so it is interesting to learn the trends of the changes in the skull form in hybrids with different percentage of bison blood. The morphology of skulls of hybrids between European bison and domestic cattle was analyzed earlier, in the pre-war years, on the small group of animals, which came from the Askania Nova (USSR) (Andreeva, 1935; Bogoljubskij, 1935).

2. MATERIAL AND METHOD

The study was carried out on the skulls of 59 (28,31) hybrids between European bison and domestic cattle; F₁ generation and three backcross generations (B₁bos: 25% European bison, 75% cattle; B₂bos: 12.5% European bison, 87.5% cattle, and B₃bos: 6.25% European bison, 93.75% cattle) (Table 1). The skulls originated from 1—13 years old animals of two breeding stations: at Białowieża (50) and Lękno State Farms (9). All the skulls are included to the collection of Mammals Research Institute of Polish Academy of Sciences. By comparison with that, 40 (6,34) skulls

of domestic cattle adult specimens of red Polish breed (pr) and the black and white lowland breed (bwl) were measured. All they, except of the bull Richtje, are from the collection of the Department of Animal Anatomy, Warsaw Agriculture University. The dimensions of European bison skulls were taken from the paper by Empel (1962) and the needed averages were counted. The only measurement Sm—Sm, not measured by Empel (1962) but important for the comparison, was taken particularly for this study in the Department of Animal Anatomy, Warsaw Agriculture University by Dr. F. Kobryńczuk. The measurements comprised both the Empel's materials and the specimens collected later ($n=35$). The age of hybrids was known from the breeding documents, the age of the cattle was estimated on the basis of an obliteration of the skull sutures.

Thirty-four measurements, listed below, were taken according to Duerst's (1928) and Krysiak's (1983). Two measurements (12 and 19) were taken according to Empel's (1962) instructions. The capacity of *cavum cranii* was measured with use of grain after tightening of the larger holes of a skull. The measurements were taken either directly or in projection. The main measuring points of a skull are shown in Fig. 1.

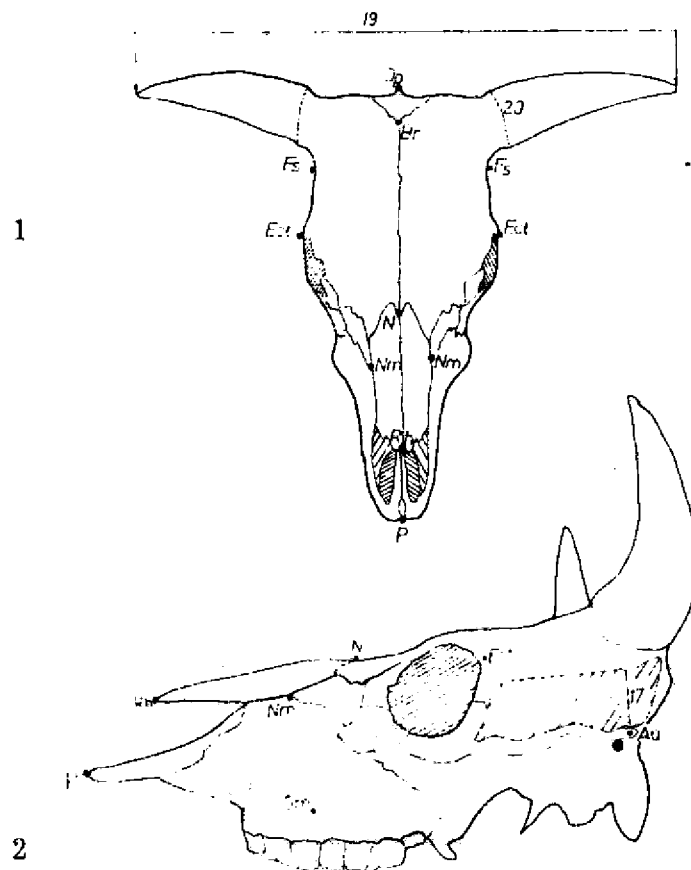


Fig. 1. See explanation on p. 151

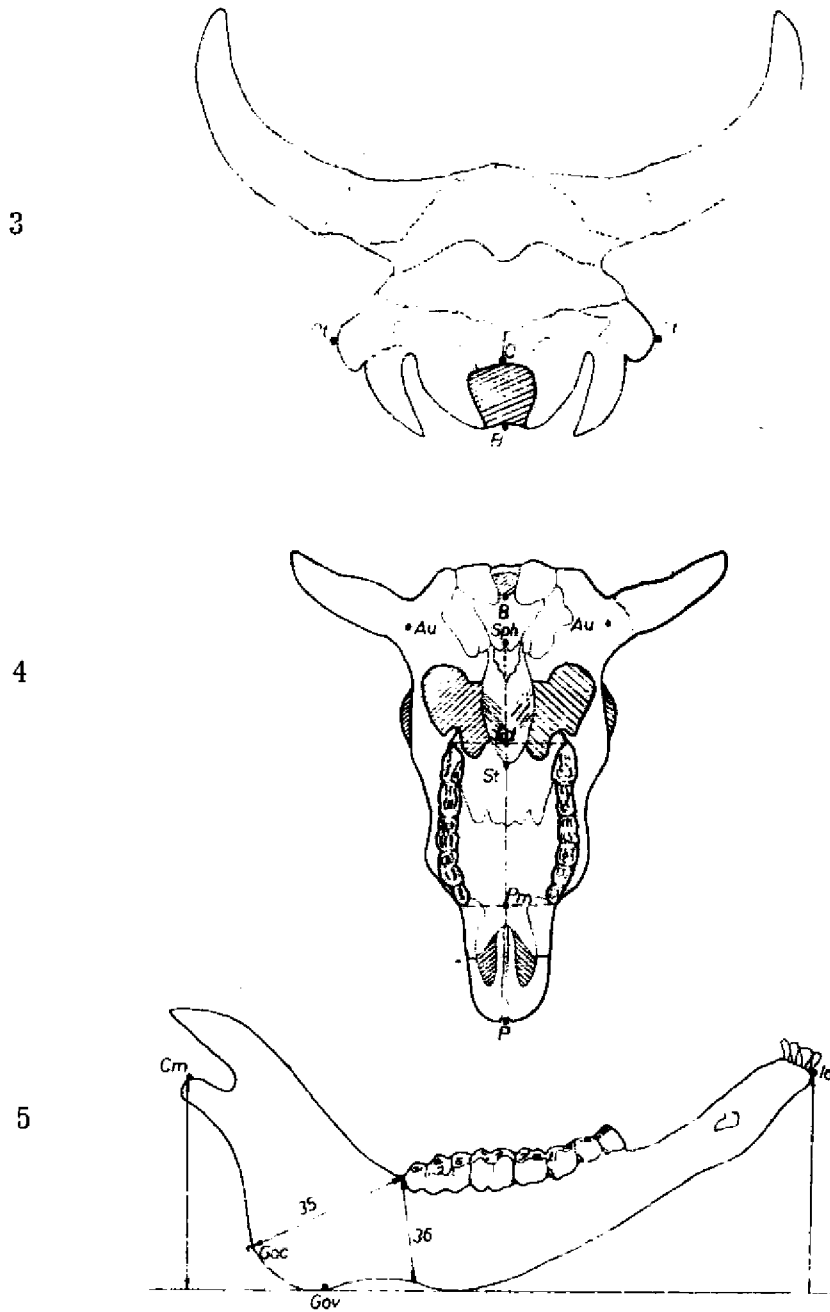


Fig. 1. Measuring points of a skull. See text (p. 152) for the definitions of measurements. 1 — *Norma verticalis*, 2 — *Norma lateralis*, 3 — *Norma nuchalis*, 4 — *Norma basilaris*, 5 — *Mandibula*.

Measurements of Length

1. *Cb* — the length of skull from the hind surface of *condyli occipitales* to the point *Prosthion (P)*
 2. *B-P* — *Basion-Prosthion*
 3. *Op-P* — *Opisthocranium-Prosthion*
 4. *Op-Br* — *Opisthocranium-Bregma*
 5. *N-Op* — *Nasion-Opisthocranium*
 6. *N-Rh* — *Nasion-Rhinion*
 7. *N-P* — *Nasion-Prosthion*
 8. *St-B* — *Staphylion-Basion*
 9. *St-P* — *Staphylion-Prosthion*
 10. *Pm-P* — *Praemolare-Prosthion*
 11. *Pm-Pd* — *Praemolare-Postdentale*
- Measurements of Height**

12. the height of skull (Empel, 1962) — the distance from the highest point of the *calvaria* to the line drawn across *Staphylion-Basion*
13. *Basion-linea nuchae*
14. *St-N* — *Staphylion-Nasion*
15. *Sph-Br* — *Sphenobasion-Bregma*
16. *B-O* — *Basion-Opisthion*
17. the height of *Fossa temporalis* (Fig. 1, 2)

Measurements of Processus Cornualis

18. the length of horn core measured along external curve
19. the greatest spread of horn cores
20. horn core base circumference

Measurements of Breadth and Capacity

21. *Ect-Ect* — *Ectoorbitale-Ectoorbitale*
22. *Fs-Fs* — *Frontostenion-Frontostenion*
23. *Nm-Nm* — *Nasomaxillare-Nasomaxillare*
24. *Ot-Ot* — *Otion-Otion*
25. *Sm-Sm* — *Supramolare-Supramolare*
26. *Au-Au* — *Auriculare-Auriculare*
27. the breadth of *processus zygomaticus ossis frontalis* measured along the suture which connects it with *processus frontalis ossis zygomatici*
28. Capacity of *cavum cranii*

Measurements of Mandible

29. *Id-Cm* — *Infradentale-Condylon mediale*
30. *Id-Goc* — *Infradentale-Gonion caudale*
31. *Cm-Gov* — *Condylon mediale-Gonion ventrale* in projection
32. *Id-Gov* — *Infradentale-Gonion ventrale* in projection
33. the breadth of *ramus mandibulae (BRM)*
34. the height of *corpus mandibulae* behind M_3 (*HCM*)

The following cranial indices have been calculated in order to find out the proportions of a skull:

1. $Ect-Ect \times 100 / BP$
2. $Sm-Sm \times 100 / ST-P$
3. $B-St \times 100 / St-P$
4. $Sm-Sm \times 100 / Ect-Ect$
5. $St-N \times 100 / Sph-Br$
6. $St-N \times 100 / St-P$
7. $Sph-Br \times 100 / B-St$
8. $Op-N \times 100 / B-P$
9. $Op-N \times 100 / N-P$
10. height of *corpus mandibulae* behind $M_3 \times 100 / BRM$
11. the height of corpus mandibulae behind $M_3 \times 100 / Id-Goc$
12. $B-linea nuchae \times 100 / Ot-Ot$

In hybrids both mandibles of every individual have been measured and the arithmetic mean was assumed to be the result. Individual dimensions of the skulls of all hybrids are compiled in the tables annexed to the typescript of this paper, which is kept in the Library of the Mammals Research Institute PAS in Białowieża.

The postnatal development of the hybrids' skulls could not be followed due to lack of material. The detailed analysis of the shape of hybrids' skulls as well as of the heredity of cattle's and European bison's features was made on the material of adult individuals.

Taking into account three measurements: *Ect-Ect*, *Ot-Ot* and the height of a skull, which show the greatest significant differences between the European bison and the cattle, I compiled a table of average differences in these measurements of adult hybrids of F_1 , B_1bos and B_2bos generations, as well as the young ones of B_3bos (there was no adult individual) and a random sample picked out from the material in question. The sample contained: 6 (3,3) skulls of European bison, 3 skulls of domestic black and white lowland cows and the bull Richtje, which was the father of most of the backcross hybrids. The number of picked out skulls of European bison and domestic cows was limited in order to simplify the calculations since the material was rather homogenous (low values of CV). At the same time, six skulls of domestic bulls were quite heterogeneous (high CV of most of the measurements) and that is why I picked out the skull of the one, which was closely related to the hybrids. Obtained data were classified by the method of spanning tree ordering, so-called the method of Wrocław taxonomy (Perkal, 1958).

The whole studied material was considered in two age groups: young individuals from 1 to 4 years old and the adult ones, more than 4 years old. In this paper, the term skull (*cranium*) means the whole skeleton of head i.e. facial part (*splanchnocranium*) and neural part (*neurocranium*) after Krysiak (1983). The significance of the differences in the average values of measurements and indices was compared with the Student *t*-test for independent groups.

Table 2

Measurements of the skull length in hybrids between European bison and the cattle and in the parental forms. Generation of hybrids: F₁ — 50% European bison, 50% cattle; B₁bos — 25% European bison, 75% cattle; B₂bos — 12.5% European bison, 87.5% cattle; B₃bos — 6.25% European bison, 93.75% cattle.

Generation sex	n(name)	Age, (mth)		C-B	B-P	Op-P	Br-Op	N-Op	N-Rh	N-P	St-B	St-P	P-Pm	Pm-Pd
F ₁ Males	5	60—156	\bar{x}	557.2	525.8	580.0	46.0	260.4	226.2	332.4	213.0	313.4	156.0	151.0
			SD	30.6	21.9	24.6	48.9	9.5	14.3	18.0	12.7	15.2	2.1	12.4
			CV	5.5	4.2	4.2	106.2	3.6	6.3	5.4	6.0	4.8	1.4	8.2
	6	12—24	\bar{x}	471.0	436.2	480.0	30.2	216.8	188.2	266.0	171.2	259.3	135.0	148.7
			SD	10.5	9.0	15.5	4.9	6.0	10.6	11.7	9.1	9.5	6.6	10.1
			CV	2.2	2.1	3.2	16.3	2.8	5.6	4.4	5.3	3.6	4.9	6.8
F ₁ Females	Filutka Fama 5	84 96 12—24	\bar{x}	522.0	485.0	531.0	22.0	231.0	207.0	312.0	177.0	305.0	149.0	156.0
			SD	509.0	475.0	515.0	38.0	231.0	196.0	293.0	182.0	294.0	145.0	151.0
			CV	471.2	438.4	474.2	32.2	207.2	196.8	273.2	172.4	268.4	137.8	140.2
	5	12—24	\bar{x}	471.2	438.4	474.2	32.2	207.2	196.8	273.2	172.4	268.4	137.8	140.2
			SD	9.4	7.0	1.1	9.9	3.6	7.5	4.8	7.0	4.1	4.2	7.5
			CV	2.0	1.6	0.2	30.6	1.8	3.8	1.8	4.0	1.5	3.0	5.4
B ₁ bos Males	5	48—84	\bar{x}	520.0	487.2	524.8	15.0	237.8	190.8	292.0	193.0	297.6	150.0	150.4
			SD	15.2	12.2	24.4	5.5	11.9	18.3	17.6	8.6	7.1	6.7	10.6
			CV	2.9	2.5	4.6	36.8	5.0	9.6	6.0	4.4	2.4	4.4	7.1
	6	12—48	\bar{x}	490.2	453.7	488.3	18.5	228.2	182.2	268.2	180.3	277.3	134.0	152.7
			SD	21.0	22.5	19.3	16.7	12.4	15.5	14.2	10.0	16.2	9.0	9.7
			CV	4.3	5.0	3.9	90.4	5.4	8.5	5.3	5.6	5.8	6.7	6.4
B ₁ bos Females	6	48—96	\bar{x}	499.5	467.8	496.8	10.7	214.2	191.5	287.2	176.7	291.8	141.3	146.2
			SD	10.2	7.5	16.1	6.8	14.7	9.6	4.3	6.7	5.5	1.9	5.3
			CV	2.0	1.6	3.2	63.8	6.9	5.0	1.5	3.8	1.9	1.3	3.6
	4	12—48	\bar{x}	434.3	401.3	443.5	10.0	205.8	170.0	252.8	157.0	243.5	120.0	133.0
			SD	32.5	34.2	27.6	6.1	11.2	10.0	12.3	11.5	22.9	14.7	9.9
			CV	7.5	8.5	6.2	60.5	5.5	5.9	4.9	7.3	9.4	12.3	7.4
B ₂ bos Males	3	48—60	\bar{x}	511.7	486.7	509.7	10.3	223.3	193.5	288.7	190.0	297.0	146.0	150.3
			SD	19.4	16.1	18.6	4.0	17.2	—	6.5	10.8	9.5	8.2	4.0
			CV	3.8	3.3	3.6	39.1	7.7	—	2.3	5.7	3.2	5.6	2.7
	5	48—72	\bar{x}	440.0	403.0	457.0	37.0	213.0	—	243.0	170.0	240.0	126.0	146.0
			SD	500.0	457.0	500.0	10.0	237.0	183.0	268.0	196.0	267.0	134.0	139.0
			CV	500.6	464.0	511.2	11.8	233.0	185.2	280.0	182.8	283.8	141.6	146.2
B ₂ Females	5	48—72	\bar{x}	500.6	464.0	511.2	11.8	233.0	185.2	280.0	182.8	283.8	141.6	146.2
			SD	19.1	25.3	30.6	8.9	18.1	13.3	14.5	7.7	17.3	10.9	5.0
			CV	3.8	5.4	6.0	75.3	7.8	7.2	5.2	4.2	6.1	7.7	3.4
5	12—48	\bar{x}	462.8	427.6	469.8	18.2	214.8	176.8	261.6	174.0	267.2	130.8	142.6	

			SD	32.9	31.2	31.8
			CV	7.1	7.3	6.8
B ₂ bos Male	Feliks	23		485.0	445.0	476.0
B ₂ bos Females	4	12—36	\bar{x}	417.0	384.5	421.0
			SD	34.1	34.1	29.5
			CV	8.2	8.9	7.0
Cattle Males	6	ad	\bar{x}	504.6	478.4	521.4
			SD	46.9	50.2	53.2
			CV	9.3	10.5	10.2
Cattle Females	34	ad	\bar{x}	463.9	433.4	482.4
			SD	16.9	17.1	18.0
			CV	3.6	3.9	3.7
Bison Males *	16	48—264	\bar{x}	—	478.8	532.1
			SD	—	14.6	15.2
			CV	—	3.0	2.9
	Pułan	13		—	—	387.0
	3	12—28	\bar{x}	—	386.7	—
			SD	—	27.5	—
			CV	—	7.1	—
				—	—	—
				—	—	444.0
Bison Females *	17	48—324	\bar{x}	—	443.6	486.9
			SD	—	11.9	10.6
			CV	—	2.7	2.2
			\bar{x}	—	375.2	409.4
	5	12—36	SD	—	41.5	48.9
			CV	—	11.1	11.9

* after Empel, 1962

6.6	14.5	19.0	16.0	6.0	9.3	4.3	3.8
36.5	6.8	10.8	6.1	3.4	3.5	3.3	2.7
26.0	228.0	178.0	256.0	180.0	276.0	132.0	147.0
25.3	195.5	147.7	232.5	149.3	234.0	119.3	122.0
7.9	16.4	7.4	26.8	14.0	25.7	7.2	14.6
31.2	8.4	5.0	11.5	9.4	11.0	6.1	12.0
—	234.0	193.4	281.4	187.0	287.4	148.8	141.0
—	26.3	22.2	28.3	27.7	27.9	20.2	12.3
—	11.2	11.5	10.0	14.8	9.7	13.6	8.7
—	221.0	173.5	264.4	165.4	269.9	133.2	129.1
—	11.9	11.1	13.3	7.8	12.3	6.5	9.1
—	5.4	6.4	5.0	4.7	4.5	4.9	7.1
—	256.1	184.7	298.9	188.7	292.8	145.5	140.9
—	11.8	9.0	11.3	10.9	8.1	4.9	5.1
—	4.6	4.9	3.8	5.8	2.8	3.4	3.6
—	205.0	—	—	—	—	—	—
—	—	138.7	—	154.0	235.0	—	—
—	—	21.8	—	9.2	18.2	—	—
—	—	15.7	—	5.9	7.7	—	—
—	—	—	236.0	—	—	—	—
—	218.0	—	244.0	—	—	117.0	—
—	231.4	172.1	276.0	167.8	275.6	133.3	135.5
—	9.1	8.7	8.3	8.4	6.8	5.1	5.8
—	3.9	5.1	3.0	5.0	2.5	3.8	4.3
—	204.6	142.0	225.0	144.6	230.8	115.4	141.0
—	27.9	16.9	28.6	14.6	27.0	10.1	—
—	13.6	11.9	12.7	10.1	11.7	8.8	—

Tabela 3

Measurements of the skull breadth in hybrids between European bison and the cattle and in the parental forms. See Table 2 for abbreviations of hybrid generations and European bison

Generation, sex n(name)	Age, (mth)		<i>Ect</i>	<i>EctFs</i>	<i>FsNm</i>	<i>NmOt</i>	<i>OtSm</i>	<i>SmSm</i>	<i>Au-Au</i>	<i>Proc</i> <i>zyg.</i>
F ₁ Males 5	60—156	\bar{x}	295.6	231.2	87.4	258.4	193.6	272.6	39.8	
		SD	15.6	8.9	3.0	18.8	17.5	22.2	9.5	
		CV	5.3	3.9	3.5	7.3	9.0	8.2	23.9	
6	12—24	\bar{x}	241.8	213.0	80.3	209.3	156.8	217.0	22.2	
		SD	8.0	6.8	6.1	8.3	5.2	8.7	3.3	
		CV	3.3	3.2	7.6	4.0	3.3	4.0	14.9	
F ₁ Females Filutka	84		241.0	189.0	61.0	217.0	165.0	218.0	31.0	
	Fama	96	241.0	187.0	74.0	207.0	180.0	215.0	26.0	
5	12—36	\bar{x}	228.0	183.4	73.6	193.4	153.2	200.0	24.0	
		SD	7.4	7.7	4.0	1.5	3.3	3.5	1.7	
		CV	3.3	4.2	5.5	0.8	2.2	1.8	7.2	
B ₁ bos Males 5	48—84	\bar{x}	257.8	196.2	77.0	230.4	179.6	237.8	36.6	
		SD	20.2	14.8	11.2	19.3	9.9	21.6	9.1	
		CV	7.8	7.6	14.6	8.4	5.5	9.1	24.8	
6	12—48	\bar{x}	237.2	194.0	67.0	203.2	161.7	211.7	27.3	
		SD	9.9	6.9	3.9	13.1	11.6	11.4	6.3	
		CV	4.2	3.6	5.9	6.4	7.2	5.4	23.0	
B ₁ bos Females 6	48—96	\bar{x}	224.8	174.0	53.0	198.7	166.0	202.3	27.0	
		CV	4.3	6.3	18.3	4.9	3.9	4.4	16.0	
		\bar{x}	197.3	156.5	58.8	174.0	141.5	179.5	21.3	
4	12—48	SD	7.7	6.6	10.4	12.1	11.2	10.4	5.3	
		CV	3.9	4.2	17.8	7.0	7.9	5.8	25.0	
		\bar{x}	263.7	203.7	85.0	236.7	183.7	242.3	34.7	
B ₂ bos Males 3	48—60	SD	9.5	10.8	—	8.5	5.8	1.5	1.2	
		CV	3.6	5.3	—	3.6	3.1	0.6	3.3	
		Fenek	16	224.0	192.0	61.0	172.0	152.0	184.0	24.0
Fenvl	27	271.0	227.0	79.0	216.0	180.0	230.0	33.0		
B ₁ bos Females 5	48—72	\bar{x}	226.8	169.2	64.8	206.4	164.4	209.8	24.6	
		SD	12.2	11.3	11.1	8.0	5.7	10.1	5.1	
		CV	5.4	6.6	17.2	3.9	3.5	4.8	20.8	
5	12—48	\bar{x}	222.6	171.8	58.0	192.6	158.4	195.4	23.4	
		SD	14.4	14.2	6.6	7.3	8.0	6.5	3.9	
		CV	6.5	8.3	11.4	3.8	5.0	3.3	16.7	
B ₁ bos Male Feliks	23		247.0	195.0	74.0	209.0	177.0	224.0	41.0	
B ₁ bos Females 4	12—36	\bar{x}	196.5	147.0	48.0	168.8	143.8	177.0	20.8	
		SD	15.3	12.6	3.5	14.2	13.1	9.8	4.9	
		CV	7.8	8.6	7.2	8.4	9.1	5.6	23.7	
Cattle Males 6	ad	\bar{x}	239.0	186.7	68.5	218.8	170.5	224.2	27.7	
		SD	29.6	21.4	11.0	35.5	24.0	38.2	9.4	
		CV	12.4	11.4	16.1	16.2	14.1	17.1	34.0	

continued on p. 157

Table 3. concluded.

Cattle Females									
34	ad	\bar{x}	206.7	156.9	54.1	191.1	155.0	193.6	24.6
		SD	9.8	7.6	4.7	8.9	9.3	10.1	4.3
		CV	4.7	4.8	8.6	4.7	6.0	5.2	17.3
Bison Males *									
16	48—264	\bar{x}	315.8	251.1	100.6	252.9	183.2	248.5	35.5
		SD	17.1	10.9	7.0	10.7	9.3	10.4	6.3
		CV	5.4	4.3	6.9	4.2	5.1	4.2	17.7
3	12—28	\bar{x}	225.0	213.0	70.3	178.7	152.7	201.5	17.7
		SD	17.7	—	12.7	14.7	16.6	31.4	2.5
		CV	7.9	—	18.1	8.2	10.9	15.6	14.2
Bison Females *									
17	48—324	\bar{x}	263.8	212.1	81.8	208.1	168.3	208.0	24.6
		SD	8.4	8.1	4.7	4.5	7.0	6.7	3.5
		CV	3.2	3.8	5.7	2.2	4.1	3.2	14.1
5	12—36	\bar{x}	204.0	182.0	65.0	164.6	141.5	177.5	15.4
		SD	29.1	16.9	9.0	23.8	16.9	22.0	3.4
		CV	14.3	9.3	13.8	14.5	11.9	12.4	21.8

3. RESULTS

3.1. General Proportions of Skull and its Size

General size of a skull was characterized by two measurements: basal length (*BP*) and the breadth (*Ect-Ect*). The longest *BP* was found in mature F_1 hybrids (Table 2, 3). It was significantly longer than in European bison ($p < 0.001$). In adult hybrids of backcross generations *BP* was similar in length to that observed in European bison. Basal length of a skull in F_1 males was significantly greater than *BP* in the skulls of backcross hybrids ($0.02 < p < 0.05$). In comparison with the skulls of the cattle *BP* was distinctly longer in F_1 hybrids, but in males the difference was not significant, while in backcross hybrids it was longer only in females ($B_1\text{bos}$: $p < 0.001$, and $B_2\text{bos}$: $0.001 < p < 0.002$) and in males it was similar to that of the cattle.

In the material of mature individuals the skulls of European bison were the broadest ones. The dimension *Ect-Ect* in the crania of European bison was significantly greater than that in adult hybrids of all generations (F_1 : $0.02 < p < 0.05$; $B_1\text{bos}$ and $B_2\text{bos}$: $p < 0.001$) (Table 3). In comparison with the cattle the skulls of F_1 hybrids of both sexes and $B_1\text{bos}$ and $B_2\text{bos}$ females were broader (F_1 : $0.005 < p < 0.01$; $B_1\text{bos}$ and $B_2\text{bos}$: $p < 0.001$). Crania of F_1 males were significantly broader than those of backcross hybrids ($0.02 < p < 0.05$). Of young hybrids F_1 cows had the longest, and broadest skulls while $B_1\text{bos}$ males had the longest and $B_2\text{bos}$ the broadest crania of all male hybrids (Table 2, 3).

Basal length of a skull in mature hybrids and European bison showed slight individual variability (CV lower than 6%), while in domestic bulls

which were examined it was rather variable (CV=10.5%) (Table 2). In young individuals of European bison and backcross hybrids this dimension showed distinctly higher variability than in mature specimens (Table 2). Measurement *Ect-Ect* of adult European bison, F_1 and B_2 bos hybrids also showed slight variability. Higher variability of this measurement was observed in B_1 bos males and the highest in mature domestic bulls. In the group of young animals the measurement *Ect-Ect* showed slight variability in F_1 and B_1 bos hybrids and the highest in European bison (Table 3).

The breadth-length index (1) properly characterized the general proportions of a skull (Table 4). The highest index was found in European bison and the lowest one in the cattle. The differences in the value of this index between European bison and the cattle were highly significant ($p < 0.001$). Of adult hybrids the highest values of this index were observed in F_1 , next in B_2 bos and at last in B_1 bos hybrids, but the differences between them were not significant. Among young hybrids the animals of B_2 bos generation showed inconsiderable higher values of this index in comparison with F_1 and remaining backcross hybrids (Table 4).

None of adult hybrids reached the value of breadth-length index which was embraced in its range of European bison (the highest index of F_1 male "Facet" — 59.4, the lowest one of European bison — 60.9). Young F_1 hybrids and European bison showed similar values of the index, and the differences appeared only in adult animals. So in European bison older than 4 years the skulls grew in breadth more intensively than in hybrids.

The breadth-length index in all adult hybrids was significantly lower than in European bison ($p < 0.001$). Only in F_1 males it was higher in comparison with the cattle ($0.02 < p < 0.05$). So, the general proportions of hybrids' skulls were similar to those of the cattle rather, than of European bison, except for F_1 males, in which they were intermediate. No distinct differences in general proportions of the skulls, which could be connected with the effect of father or mother, were found in F_1 hybrids, but this might be due to the scarcity in F_1 material.

There was a great variety in the general appearance of the skulls of all hybrids. The skulls of F_1 hybrids were distinctly larger (longer and broader) than those of backcross hybrids. Of F_1 males the skull of "Facet" (Plate VII, Photo 1) was most similar to the European bison one. This bull was the progeny of the cross ♂ European bison × ♀ *bwl* cattle. Hybrid "Fakir", which came from the same combination, had the longest skull. Crania of F_1 cows were long and narrow. They differed distinctly from the skulls of European bison (Plate VII, Photo 2). The more similar to that of the cattle (Plate VIII, Photo 3). Most skulls were

long and slender (Plate VIII, Photo 4). Only four B₁bos and B₂bos males had comparatively broader crania (Plate IX, Photo 5).

The skulls of European bison were significantly higher than cattle skulls. In females this difference was highly significant ($p < 0.001$) (Table 5). Empel (1962) connected the great height of skull of adult European bison with the presence of *tuberositas frontalis*. In spite of a lack of this tuberosity in hybrids the skulls of F₁ males were, on average, somewhat higher than those of European bison (F₁: 194.0 ± 6.8 , European bison: 191.4 ± 8.9). In F₁ cows and B₁bos backcross hybrids of both sexes height of the skull was smaller than that in European bison (B₁bos and ♂♂ B₂bos: $0.002 < p < 0.005$ and ♀♀ B₂bos: $0.02 < p < 0.05$). Hybrid females had higher skulls than domestic cows (B₁bos and B₂bos: $p < 0.001$). Skulls of F₁ males were distinctly higher than the cattle skulls but the difference were not significant. In backcross hybrids the height was similar to that of cattle. This measurement showed rather low individual variability in adult hybrids, European bison, and domestic cows. Only the skulls of domestic bulls showed high variability of this measurement. The coefficient of variation of this dimension in young animals is higher than in adult ones (Table 5).

The comparison showed that the skulls of F₁ males were as high as those of European bison, while the crania of backcross males were similar in height to the cattle's ones. In cow hybrids of all generations the height of skull was intermediate between European bison and the cattle.

Taking into account the measurements which significantly differ between European bison and the cattle (*Ect-Ect*, *Ot-Ot* and the height of a skull, I counted the average differences (see Material and Method) and then arranged them by the Wrocław taxonomy. An analysis of the dendrite (Fig. 2) showed that the skulls of F₁ males were most similar, in respect of breadth and height, to the European bison's ones. Most backcross males were similar in this respect to the domestic bull. However, F₁ cows and most backcross females had these features intermediate between females European bison and domestic cows. In young B₃bos heifers the features in question showed the greatest similarity to those in domestic cows (Fig. 2).

The greatest capacity of *cavum cranii* was observed in F₁ hybrids. It excelled the data for both European bison ($0.002 < p < 0.005$) and cattle (Table 5). This capacity in European bison was significantly greater than in cattle ($p < 0.001$) (Table 6). In B₁bos hybrids of both sexes and B₂bos females the capacity was similar to that in European bison. But in B₂bos males it was significantly smaller ($p < 0.001$). The capacity of *cavum cranii* of backcross hybrids: B₁bos males ($0.01 < 0.02$) as well as B₁bos

Table 4

Indices of the structure of the skull in hybrids between European bison and the cattle and in the parental forms. See Table 2 for abbreviations of hybrids generations and European bison. Indices: 1. *Ect-Ect*×100/*B-P*; 2. *Sm-Sm*×100/*St-P*; 3. *B-St*×100/*St-P*; 4. *Sm-Sm*×100/*Ect-Ect*; 5. *St-N*×100/*Sph-Br*; 6. *St-N*×100/*St-P*; 7. *Sph-Br*×100/*B-St*; 8. *Op-N*×100/*B-P*; 9. *Op-N*×100/*N-P*; 10. *HCM*×100/*BRM*; 11. *BRM*×100/*Id-goc*; 12. *B. — Linea nuchae*×100/*Ot-Ot*. See text for the definitions of measurements.

Generation, n(name)		Age	Indices:												
			1	2	3	4	5	6	7	8	9	10	11	12	
Males															
F ₁	5	ad	\bar{x}	56.24	61.76	68.02	64.80	96.24	58.48	90.12	49.56	78.50	61.66	18.50	60.3
			SD	2.72	4.84	4.03	3.11	11.95	3.07	7.64	1.76	4.67	7.28	1.27	2.5
			CV	4.83	7.83	5.92	4.80	12.41	5.24	8.47	3.55	5.94	11.80	6.86	4.2
	6	juv	\bar{x}	55.62	60.51	65.34	67.20	88.90	56.78	100.60	49.94	81.58	—	—	64.8
			SD	1.53	2.15	2.52	1.53	—	2.43	—	1.52	2.81	—	—	—
			CV	2.75	3.55	3.85	2.36	—	4.27	—	3.04	3.44	—	—	—
B ₁ bos	5	ad	\bar{x}	52.92	60.40	64.84	68.80	87.82	53.42	93.92	48.82	81.60	69.04	19.80	56.7
			SD	3.95	3.98	2.43	2.58	3.76	1.57	4.16	1.71	5.02	3.26	0.94	5.0
			CV	7.46	6.58	3.74	3.75	4.28	2.93	4.42	3.50	6.15	4.72	4.74	8.8
	6	juv	\bar{x}	52.30	58.43	65.13	68.20	84.61	52.56	95.80	50.33	85.26	75.58	20.88	65.0
			SD	2.07	5.00	3.97	4.71	5.64	1.49	5.04	2.59	5.76	2.82	0.61	6.0
			CV	3.95	8.55	6.09	6.91	6.66	2.83	5.26	5.14	6.75	3.73	2.92	9.3
B ₂ bos	3	ad	\bar{x}	54.20	61.93	64.03	69.30	84.30	50.33	93.50	45.83	77.33	71.30	20.06	54.1
			SD	2.84	3.84	3.87	3.21	5.84	1.93	0.91	2.33	5.03	5.81	1.47	0.9
			CV	5.23	6.20	6.04	4.60	6.92	3.83	0.97	5.08	6.50	8.14	7.32	1.6
B ₃ bos Bison bonasus *	Fenek	juv	\bar{x}	55.60	63.30	70.80	67.80	82.40	58.30	100.00	52.90	87.70	82.70	22.70	72.1
			SD	59.30	67.40	73.40	66.40	78.90	56.20	96.90	51.90	88.40	70.60	22.00	63.4
			CV	53.90	62.30	65.20	71.60	80.60	52.50	100.00	51.20	89.10	74.30	21.50	58.8
	Feliks	ad	\bar{x}	65.68	—	64.83	58.50	110.40	56.93	—	53.46	85.78	53.44	15.49	54.0
			SD	2.38	—	3.68	2.29	3.65	1.45	—	2.30	4.85	6.17	1.54	2.6
			CV	3.62	—	5.67	3.90	3.30	2.54	—	4.30	5.65	11.54	9.94	4.8
Pułan	3	juv	\bar{x}	—	—	—	—	—	—	—	57.70	—	—	65.4	
			SD	58.20	—	65.60	—	—	—	—	—	—	—	—	—
			CV	2.00	—	1.99	—	—	—	—	—	—	—	—	—
Cattle	Pułkownik Plecotus	6	ad	\bar{x}	—	—	—	—	54.70	—	—	—	—	—	
				SD	—	—	—	54.00	—	56.10	—	54.50	89.30	—	60.5
				CV	3.43	—	3.03	—	—	—	—	—	—	—	—
	6	ad	\bar{x}	52.18	61.94	67.62	72.50	78.01	53.56	99.15	50.10	85.10	77.90	22.30	80.0
			SD	2.48	1.29	2.62	2.60	5.97	1.24	4.21	1.35	1.52	5.17	0.20	8.0
			CV	4.75	2.08	3.87	3.60	7.65	2.31	4.24	2.69	1.78	6.63	0.89	10.1

		Females			
F ₁	Fama	ad		50.70	61.20
	Filutka	ad		49.70	54.10
	5	juv	\bar{x}	52.04	57.10
			SD	2.32	2.02
			CV	4.45	3.53
B ₁ bos	4	ad	\bar{x}	48.06	56.86
			SD	1.59	2.20
		CV	3.30	3.86	
	4	juv	\bar{x}	49.32	58.22
		SD	2.31	3.09	
			CV	4.68	5.30
B ₂ bos	5	ad	\bar{x}	48.90	58.06
			SD	1.24	3.33
		CV	2.53	5.73	
	5	juv	\bar{x}	52.18	59.68
		SD	3.55	2.90	
			CV	6.80	4.85
B bos	6	juv	\bar{x}	51.12	61.57
			SD	1.05	3.01
		CV	2.05	4.88	
<i>Bison bonasus</i> *	17	ad	\bar{x}	59.47	—
			SD	1.49	—
		CV	2.50	—	
	6	juv	\bar{x}	54.22	—
		SD	1.91	—	
			CV	3.52	—
Cattle	34	ad	\bar{x}	47.79	57.41
			SD	1.66	2.49
		CV	3.47	4.33	

61.90	74.70	98.70	52.40	85.70	48.60	78.80	66.20	18.90	58.4
58.00	68.50	103.10	54.10	90.40	47.60	74.00	69.80	18.20	57.6
64.24	67.00	91.80	53.64	87.30	47.30	75.86	—	—	63.0
2.76	2.97	—	0.86	—	0.97	1.51	—	—	2.9
4.29	4.43	—	1.60	—	2.05	1.99	—	—	4.6
60.56	72.10	88.16	49.65	93.33	45.73	74.56	70.80	19.40	64.7
2.42	1.50	5.78	1.41	4.72	2.54	4.72	7.00	1.10	5.6
3.99	2.00	6.55	2.83	5.05	5.55	6.33	9.88	5.67	8.7
64.57	69.00	83.92	52.30	96.60	51.42	81.40	78.72	21.70	62.9
1.95	4.89	2.90	1.55	2.64	2.48	1.36	7.35	1.43	4.1
3.01	7.01	3.45	2.96	2.73	4.82	1.67	9.33	6.58	6.5
64.52	71.20	82.38	50.94	96.04	50.18	83.26	69.16	19.68	57.4
3.11	4.90	5.70	2.75	3.63	1.78	5.47	1.56	0.66	2.4
4.82	6.80	6.91	5.39	3.77	3.54	6.56	2.25	3.35	4.0
65.20	69.00	83.76	51.94	95.40	50.32	82.20	72.14	20.54	61.0
3.79	4.06	5.42	2.27	5.82	2.97	5.20	8.17	2.12	2.0
5.81	5.88	6.47	4.37	6.10	5.90	6.32	11.32	10.32	3.3
63.92	72.00	81.72	51.85	99.85	50.97	84.77	68.02	21.52	60.2
3.89	1.65	6.07	1.10	7.79	4.17	11.07	3.86	0.09	6.6
6.08	2.26	7.42	2.12	7.80	8.18	13.05	5.67	0.41	11.0
60.91	62.70	99.90	54.26	—	52.18	83.95	54.90	15.40	59.3
2.86	1.70	8.90	1.65	—	1.92	4.79	4.44	0.77	2.0
4.69	2.70	8.90	3.04	—	3.67	5.70	8.08	5.00	3.4
62.76	64.20	—	54.10	—	54.46	92.50	64.30	17.70	64.4
2.42	2.38	—	2.37	—	2.25	4.94	—	0.98	1.1
3.85	3.71	—	4.38	—	4.13	5.34	—	5.53	1.6
61.35	75.50	84.12	48.45	94.47	51.01	83.76	69.22	20.69	61.8
3.08	3.00	6.81	2.00	6.87	2.47	6.02	6.59	1.70	3.0
5.02	4.00	8.09	4.12	7.27	4.84	7.18	9.52	8.21	4.9

Table 5

Measurements of the skull height in hybrids between European bison and the cattle and in parental forms. Abbreviations of hybrid generations and European bison as in Table 2.

Generation, sex, n(name)	Age, (mth)		Height of skull	<i>B-linea nuchae</i>	<i>St-N</i>	<i>Sph-Br</i>	<i>B-O</i>	Height of fossa temp.
F₁ Males								
5	60—156	\bar{x}	194.0	155.6	183.0	191.8	47.6	57.0
		SD	6.8	6.0	7.2	17.6	2.4	6.5
		CV	3.5	3.8	3.9	9.2	5.0	11.4
6	12—24	\bar{x}	173.0	139.0	147.2	180.0	46.0	47.5
		SD	—	—	7.1	—	—	6.8
		CV	—	—	4.8	—	—	14.3
F₁ Females								
Filutka	84		162.0	125.0	165.0	160.0	45.0	51.0
Fama	96		166.0	121.0	154.0	156.0	41.0	58.0
5	12—36	\bar{x}	167.6	121.8	144.0	158.0	40.4	54.2
		SD	1.5	4.6	2.2	—	0.9	2.0
		CV	0.9	3.8	1.5	—	2.2	3.8
B₁ bos Males								
5	48—84	\bar{x}	175.8	130.2	159.0	181.2	42.2	60.8
		SD	5.5	9.1	5.9	8.1	2.8	10.3
		CV	3.2	7.0	3.7	4.5	6.6	16.9
6	12—48	\bar{x}	166.3	131.7	145.7	172.5	42.7	55.7
		SD	9.1	11.2	6.6	7.7	2.7	5.2
		CV	5.5	8.5	4.5	—	6.4	9.3
B₁ bos Females								
6	48—96	\bar{x}	163.8	121.7	145.0	164.8	46.3	59.2
		SD	7.6	3.7	6.6	9.4	8.6	3.2
		CV	4.6	3.0	4.6	5.7	18.6	5.4
4	12—48	\bar{x}	148.8	109.3	127.3	151.5	41.3	52.0
		SD	9.0	5.6	10.6	8.5	2.6	2.8
		CV	6.0	5.1	8.3	5.6	6.4	5.4
B₂ bos Males								
3	48—60	\bar{x}	171.0	128.0	149.3	177.7	39.3	52.3
		SD	11.8	2.6	1.2	11.7	3.8	5.5
		CV	6.9	2.1	0.8	6.6	9.6	10.5
Fenek	16		161.0	124.0	140.0	170.0	33.0	52.0
Fenyl	27		179.0	137.0	150.0	190.0	34.0	46.0
B₂ bos Females								
5	48—72	\bar{x}	167.6	118.4	144.4	175.6	44.0	62.0
		SD	9.6	4.7	9.4	10.7	1.0	4.3
		CV	5.7	3.9	6.5	6.1	2.3	6.9
5	12—48	\bar{x}	160.0	117.2	138.6	166.2	39.0	58.4
		SD	10.7	6.6	4.2	14.7	3.2	4.7
		CV	6.7	5.7	3.0	8.8	8.3	8.0
B₃ bos Males								
Feliks	23		178.0	124.0	145.0	180.0	42.0	56.0
B₃ bos Females								
4	12—36	\bar{x}	140.0	102.0	121.3	148.8	36.3	56.0
		SD	14.4	13.9	12.2	15.5	3.1	4.9
		CV	10.3	13.6	10.1	10.4	8.4	8.7
Cattle Males								
6	ad	\bar{x}	174.5	126.2	145.0	185.0	39.0	63.3
		SD	27.9	12.0	26.5	25.4	1.8	5.8
		CV	16.0	9.5	18.2	13.8	4.7	9.1

continued on p. 163

Table 5. concluded

Cattle Females								
34	ad	\bar{x}	150.6	117.8	130.7	156.1	39.1	64.1
		SD	8.7	4.5	7.0	11.3	3.4	4.9
		CV	5.8	3.8	5.3	7.2	8.8	7.7
<i>Bison bonasus</i> *								
Males								
16	48—264	\bar{x}	191.4	136.1	166.1	155.5	39.9	17.3
		SD	8.9	8.5	6.8	6.0	1.7	3.9
		CV	4.6	6.2	4.1	3.8	4.3	22.8
3	12—28	\bar{x}	150.5	110.5	136.0	140.6	37.5	20.5
		SD	—	—	—	16.8	—	—
		CV	—	—	—	11.9	—	—
<i>Bison bonasus</i> *								
Females								
17	48—324	\bar{x}	176.0	123.4	149.5	142.5	39.7	20.1
		SD	5.5	4.4	4.5	4.6	2.3	3.6
		CV	3.1	3.5	3.0	2.1	5.7	18.1
5	12—36	\bar{x}	150.2	106.2	128.0	123.6	38.6	20.2
		SD	17.9	14.1	20.5	14.7	2.6	3.8
		CV	11.9	13.3	16.0	11.9	6.7	19.0

and B₂bos females ($p < 0.001$) was significantly greater as compared to that of the cattle. Of young animals B₃bos cows had the smallest, and B₂bos males had the greatest capacity of *cavum cranii* (Table 6). This measurement showed high variability in mature male hybrids and in domestic bulls as well as in B₂bos cows (CV=10.7—16.5), while in European bison it was moderate (CV=6.5—6.8). This variability was distinctly lower in young animals. The differentiated CV indicates that the capacity of *cavum cranii* of different hybrids, which are 4+ yrs, old, changes irregularly.

The proportion of *neurocranium* in relation to *splanchnocranium* were rendered by the indices 4, 5, 9 (Table 4). The length of *neurocranium* to *splanchnocranium* ratio in adult European bison was similar to that of the cattle (Table 4). In F₁ hybrids *splanchnocranium* was longer than *neurocranium*, which resulted in the value of the index 9, which was lower than that observed in the parental forms. Similar proportions were observed in young F₁ hybrids (Table 4).

Breadth ratio of both parts of *cranium* (index 4) in adult animals showed another pattern (Table 4). Average value of this index in European bison differed significantly from that in the cattle ($p < 0.001$), because the breadth of *neurocranium* in relation to the breadth of *splanchnocranium* in European bison was greater than that in the cattle. The value of this index in all hybrids was always different from European bison's one. Of all hybrids, the F₁ ones had the lowest value of this index. It was lower than that observed in the cattle ($0.01 < p < 0.02$), but it is still significantly higher than the value of this index typical

of European bison ($p < 0.001$). The proportion of *splanchnocranium* to *neurocranium* was similar in hybrids of different generations. The comparisons showed that the proportion of the breadth of *splanchnocranium* to *neurocranium* in all hybrids assumed intermediate value between those observed in the skulls of European bison and the cattle, although this ratio approximated rather the value characteristic of the cattle than of European bison. This feature was not very much variable in material studied. In young animals the ratio of *splanchnocranium* to *neurocranium* breadth was rather similar in males, only in B_3 bos male *splanchnocranium* was relatively broader. However, *splanchnocranium* of F_1 females was relatively narrower than those of remaining cow hybrids (Table 4).

The height proportion between *splanchnocranium* and *neurocranium* (index 5) of European bison differed significantly from the cattle's ($p < 0.001$) (Table 4). It resulted from the fact that the height of *splanchnocranium* in European bison excelled that of *neurocranium*, contrary to the cattle. In F_1 females this index was alike that of European bison females, in F_1 males it was intermediate between European bison (index 5 was significantly lower, $p < 0.001$) and the cattle ($0.02 < p < 0.05$). In adult males it was very much variable ($CV = 12.4\%$). In backcross hybrids the values of index 5 were lower than those in F_1 ones but not significant, which evidenced that their skulls become similar in the proportions to the cattle's. The above mentioned proportions of both parts of skull were similar in young hybrids and adult ones (Table 4).

Presented above comparisons of the shape and the proportions between both parts of skull evidenced that the size ratio between *splanchnocranium* and *neurocranium* in F_1 hybrids assumed intermediate between European bison and the cattle. *Splanchnocranium* of F_1 hybrids was longer, broader, but lower in relation to *neurocranium* than that of European bison. It was also narrower and higher in comparison with those of the cattle. In backcross hybrids the size proportion of both parts of a skull was similar to that of F_1 hybrids, but there was a tendency to the changes toward the features which are typical of the cattle's skull.

3.2. Dorsal Wall of a Skull

Dorsal walls of the skulls of all hybrid generations were bordered from the back with *sutura frontoparietalis*, just as in the cattle, and with *processus nasales ossium nasalium* from the front, as opposed to European bison in the skull of which hind border of *calvaria* is formed by *linea nuchae* (Empel, 1962). At the hind one third length of *calvaria* stick out on both sides *nuli orbitales*. *Processus cornuales* grow to the sides from close to the hind margin of *calvaria*.

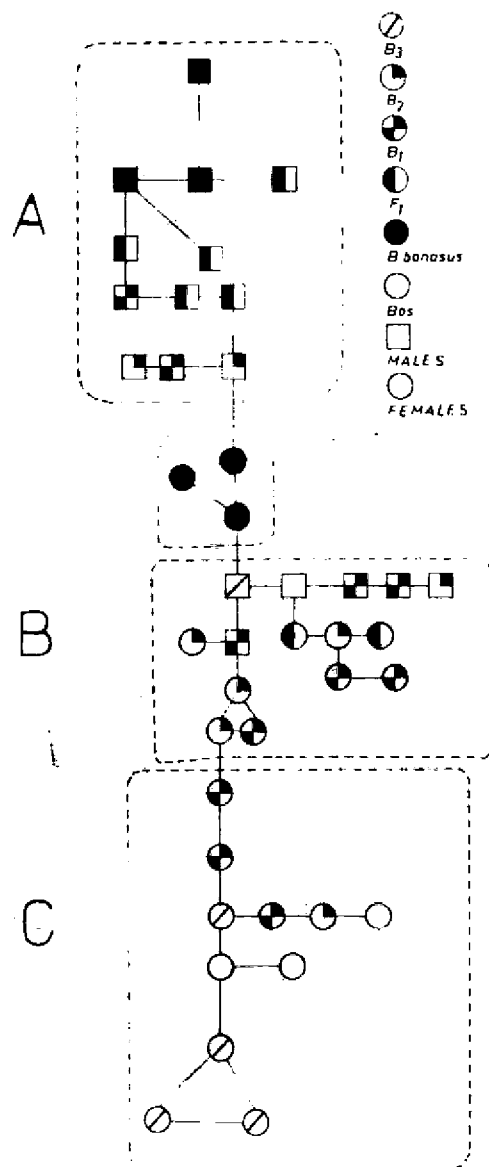


Fig. 2. Classificatory dendrite of the skulls. The selection of material and measurements are given in the text (p. 149—153).

3.2.1. *Calvaria*

In the skulls of all hybrid generations *calvaria* was formed entirely of *ossa frontalia*, such as in the cattle crania, but unlike in European bison, in which *calvaria* was composed of *ossa frontalia* and of *os interparietale* united with *ossa parietalia* (Sokolov, 1953, 1963; Heptner *et al.*, 1961; Empel, 1962; Krysiak, 1983). In the central part of *ossa frontalia* most lowland European bison had a node, which Empel (1962) called *tuberositas frontalis*. This node was absent in the cattle. It was not observed in any of the hybrid skulls, either.

Anuli orbitales of adult European bison distinctly stuck out to the sides, which differentiated skulls of European bison from the cattle (Sokolov, 1953; Heptner *et al.*, 1961). Only in the skulls of F_1 males *anuli orbitales* distinctly stuck out to the sides, although lesser than those of European bison. In backcross hybrids they were formed just as in the cattle.

Frons of F_1 hybrids showed intermediate size between those of European bison and the cattle. Both breadth dimensions of *frons* (*Ect-Ect*, *Fs-Fs*) in F_1 hybrids were smaller than in European bison ($0.02 < p < 0.05$ and $0.001 < p < 0.002$), but they were greater than in the cattle ($0.002 < p < 0.005$), while its length (*N-Op*) was similar in these three forms. In backcross hybrids *frons* was shorter and narrower than in European bison. In male hybrids its size was similar to that of the cattle, in cow hybrids it was broader. The greatest difference between both breadth dimensions of *frons* resulted from the occurrence of distinct narrowness behind orbits. This feature, which was typical of European bison, was observed, although less so, in F_1 hybrids, but it did not occur in backcross hybrids. Of young hybrids B_1 bos and B_2 bos males had the longest *frons* and F_1 hybrids and B_2 bos males had the broadest ones (Table 2, 3).

The ratio: sagittal length of *frons* to basal length of a skull (index 8) only inconsiderably differed between European bison, the cattle and both adult and young hybrids (Table 4).

3.2.2. *Processus Cornuales*

The situation of *processus cornuales* on the skull of European bison distinctly differed from that of the cattle. In the cattle *processus cornuales* grew on the top border of *planum frontalis*. They were directed to the side, usually horizontally (Krysiak, 1983). *Processus cornuales* of European bison grew more rostral than those of the cattle, before hind margin of *calvaria* and in the middle of the distance: *orbita* — *linea nuchae*. Empel (1962) distinguished two types of *processus cornuales* in

European bison — the curved and the straight ones. *Processus cornuales* of F₁ hybrids grew nearer the hind margin of *calvaria* than in the European bison, except for one F₁ bull. This feature showed a great individual variability. *Processus cornuales* of F₁ hybrids were situated more rostral than those of the cattle. In backcross hybrids they usually grew close to the hind margin of *calvaria*, just as in the cattle (Plate IX, Photo 5).

Protuberantia intercornualis was typical of the cattle (Poplewski, 1947; Krysiak, 1983). In F₁ hybrids it was poorly developed, while in B₁bos hybrids it showed high individual variability. In the extreme cases it could be underdeveloped or pushed above *planum nuchale* as *torus*. In B₂bos generation the skulls in this respect similar to the cattle's (presence of *torus*) grew in number. In the skulls of young B₃bos hybrids *protuberantia intercornualis* was poorly developed.

In hybrids the shape of *processus cornuales* showed high individual variability. In this respect F₁ hybrids were very much alike European bison. Their *processus cornuales* ran to the sides and they were curved upwards in relation to the frontal plane (Plate VII, Photos 1, 2). *Processus cornuales* of F₁ bull "Filip" (Plate IX, Photo 6) were most similar in shape to those of European bison, although they grew at the back, just as in the cattle. In B₁bos hybrids *processus cornuales* ran to the sides and upwards just as in European bison (Plate VIII, Photo 4) or to the sides and forward just as in the cattle (Plate IX, Photo 5). *Processus cornuales* of most B₂bos and B₃bos hybrids ran to the sides and forward alike the cattle. The shape and the settling of *processus cornuales* on *calvaria* were very much differentiated. One could observe the cases with *processus cornuales* similar in shape to European bison ones, but settled in the manner typical of the cattle.

Processus cornuales of mature F₁ hybrids and European bison were similar in size. In F₁ males only the circumference of horn core base was similar to that of the cattle, remaining dimensions were significantly greater ($0.02 < p < 0.05$). All dimensions of *processus cornuales* were greater in F₁ females than in domestic cows. *Processus cornuales* of backcross hybrids were smaller than those of F₁ hybrids. In B₁bos and B₂bos hybrids only the greatest spread of horn cores was significantly lower than that in European bison ($0.02 < p < 0.05$ and $0.002 < p < 0.005$, respectively).

In backcross cows all dimensions of *processus cornuales* were significantly greater than those in the cattle while in male hybrids they were alike the cattle's (Table 6). In young F₁ hybrids the dimensions of *processus cornuales* were greater than those of backcross generations (Table 6).

Table 6

Measurements of *processus cornuales* and capacity of *cavum cranii* in hybrids between European bison and the cattle and in parental forms. See Table 2 for abbreviations of hybrids generations. Expl.: 1 — Horn core length measured along external curve; 2 — The greatest spread of horn cores; 3 — Circumference of horn core base; 4 — Capacity of *cavum cranii*.

Generation & sex	n, name	Age, (mth)		Measurement				
				1	2	3	4	
F ₁ Males	5	60—156	\bar{x}	289.4	646.0	251.0	826.0	
			SD	25.7	45.2	36.7	88.8	
			CV	8.9	7.0	14.6	10.7	
	6	12—24	\bar{x}	222.5	522.3	204.7	850.0	
			SD	41.2	52.8	11.3	—	
			CV	18.5	10.1	5.5	—	
F ₁ Females	Filutka	84		184.0	425.0	175.0	—	
			Fama	226.0	450.0	179.0	720.0	
	5	12—36	\bar{x}	218.4	414.5	159.4	—	
			SD	15.2	34.1	5.8	—	
			CV	6.9	8.2	3.6	—	
			\bar{x}	231.0	568.5	204.4	692.0	
B ₁ bos Males	5	48—84	SD	36.7	64.6	17.6	114.1	
			CV	15.9	11.4	8.6	16.5	
			\bar{x}	221.2	509.7	212.5	590.0	
	6	12—48	SD	25.2	55.6	16.6	20.0	
			CV	11.4	10.9	7.8	3.4	
			\bar{x}	222.0	427.5	161.3	635.0	
B ₁ bos Females	6	48—96	SD	58.7	51.3	20.8	28.8	
			CV	26.5	12.0	12.9	4.5	
			\bar{x}	132.8	325.5	131.3	535.0	
	4	12—48	SD	25.1	18.6	13.3	23.8	
			CV	18.9	5.7	10.1	4.4	
			\bar{x}	263.3	528.5	214.3	560.0	
B ₂ bos Males	3	48—60	SD	24.1	16.1	3.8	60.8	
			CV	9.1	3.0	1.8	10.5	
			\bar{x}	145.0	425.0	174.0	540.0	
	Fenek	16		251.0	590.0	215.0	750.0	
			Fenyl	181.8	402.0	160.4	648.0	
			\bar{x}	29.0	55.6	23.8	74.6	
B ₂ bos Females	5	48—72	SD	15.9	13.8	14.9	11.5	
			CV	206.5	365.3	147.8	532.0	
			\bar{x}	49.0	130.2	26.2	27.7	
	5	12—48	SD	23.7	35.6	17.7	5.2	
			CV	182.0	480.0	187.0	500.0	
			\bar{x}	87.3	270.8	103.8	490.0	
B ₃ bos Male	Feliks	23	SD	15.9	44.7	15.5	26.5	
			CV	18.2	16.5	14.9	5.4	
			\bar{x}	184.2	478.7	205.8	535.0	
B ₃ bos Females	4	12—36	SD	74.1	121.9	53.9	62.8	
			CV	40.2	25.5	26.2	11.7	
			\bar{x}	145.8	349.9	123.0	526.5	
	Cattle Males	6	ad	SD	32.1	47.8	18.7	47.7
				CV	22.0	13.7	15.2	9.1
				\bar{x}	251.3	656.5	276.8	721.5
Cattle Females	34	ad	SD	36.8	51.9	18.7	48.8	
			CV	14.6	7.9	8.3	6.8	
			\bar{x}	162.8	455.5	155.5	600.0	
	Bison Males*	3	12—28	\bar{x}	159.9	473.9	172.6	655.0
				SD	31.5	35.1	12.4	42.3
				CV	19.7	7.4	7.2	6.5
Bison Females*	17	48—324	\bar{x}	157.5	390.4	126.4	526.0	
			SD	36.4	49.4	12.5	39.1	
			CV	23.1	12.7	9.9	7.4	

Nearly in the whole analyzed material the measurements of *processus cornuales* showed the high variability, greater than other cranial dimensions. Horn core length measured along external curve in F_1 hybrids showed moderate variability while it was very much variable in backcross hybrids, European bison, and domestic cattle (Table 6). The coefficient of variation of the greatest spread of horn cores indicated moderate variability in young and mature F_1 hybrids and adult European bison as well as high variability in backcross hybrids and the cattle. The circumference of horn core base showed high variability in F_1 hybrids, the cattle, and backcross cows and moderate variability in European bison and backcross males.

3.2.3. Dorsum Nasi

There were no significant differences in the length of *ossa nasalia* ($N-Rh$) between European bison and cattle. *Ossa nasalia* of F_1 hybrids and backcross cows were significantly longer (F_1 and European bison: $p < 0.001$; F_1 and the cattle: $0.02 < p < 0.05$; B_1 bos: $p < 0.001$, and B_2 bos: $0.02 < p < 0.05$). In male backcross hybrids $N-Rh$ was similar in length to those of European bison and the cattle. In adult hybrids this measurement showed moderate variability but it was very much variable in domestic bulls. In young B_2 bos hybrids and European bison CV was higher than in mature animals.

Contrary to the length, the breadth of *ossa nasalia* ($Nm-Nm$) was significantly greater in European bison than in the cattle ($p < 0.001$). In F_1 hybrids this dimension was smaller than in European bison ($p < 0.001$) but greater than in the cattle ($0.005 < p < 0.01$) (Table 3). In backcross hybrids *ossa nasalia* were narrower than in F_1 hybrids and their breadth only inconsiderably excelled the values typical of the cattle. In young hybrids F_1 *dorsum nasi* was longer and broader than in backcross hybrids and European bison (Table 2, 3). In mature F_1 hybrids $Nm-Nm$ showed slight variability, in European bison it was moderate and in backcross hybrids of both sexes it became high. The variability of this dimension was higher in most young animals than in mature ones (Table 3).

The comparison showed that *dorsum nasi* was distinctly longer in F_1 hybrids than in their parents, and its breadth was intermediate. In backcross hybrids the proportions of this portion of the skull were similar to those of F_1 hybrids, but they trended towards the proportions typical of the cattle.

3.3. Planum Nuchale

There was substantial difference in the form of *planum nuchale* between European bison and the cattle. In the cattle its central part was composed of *squama occipitalis*, from above it was bordered by

interconnected *ossa parietalia* and *os interparietale*, the lower part was composed of *partes laterales ossium parietalium* with *processus mastoidei ossium temporalium* on their sides. On the border line between *planum frontale* and *planum nuchale* lay *protuberantia intercornualis* (Poplewski, 1947; Krysiak, 1983). However, in European bison *planum nuchale* was composed of *squama occipitalis* and *partes laterales ossis occipitalis* as well as *processus mastoidei ossium temporalium*. The top border was delimited by *linea nuchale* (Empel, 1962).

Planum nuchale in all hybrids was composed of identical bones as in the cattle (Plate X, Photo 7), and nuchal part of *ossium parietalium* showed various degree of reduction (Plates X, XI, Photos 8, 9, 10). So that, in hybrids one could observe the verticality of postcornual part of the skull, *i.e.* the feature of a skull characteristics of the cattle. Nuchal parts of *ossium parietalium* were developed best in F_1 hybrids and occupied 1/3 to 1/4 area of *planum nuchale*. In backcross hybrids the reduction of these parts intensified, though individual variability of this feature was very high.

The upper margin of *planum nuchale* in hybrids, just as in the cattle, was formed by *protuberantia intercornualis*. It was poorly developed in F_1 hybrids (Plate X, Photos 7, 8) and well developed in B_2 hybrids (Plate XI, Photos 9, 10).

The breadth of *planum nuchale* measured as the breadth of occiput ($Ot-Ot$, Table 3) in mature European bison was high significantly greater than in the cattle (males: $0.001 < p < 0.002$; females: $p < 0.001$). In F_1 hybrids this dimension was somewhat greater than in European bison (Table 2). In backcross hybrids, except B_2 bos females, $Ot-Ot$ was significantly smaller than in European bison ($p < 0.05$) but it was inconsiderably greater than in the cattle. Among young animals the breadth of occiput in F_1 hybrids, B_2 bos cows, and B_3 bos bull was greater than in European bison. The variability of this measurement was moderate or low, except for young animals, in which it was higher than in mature specimens and in the cattle.

The height of occiput ($B - \textit{linea nuchae}$) was highest in mature F_1 males. It considerably exceeded those of European bison, the cattle, and backcross hybrids. In these last the height of occiput only inconsiderably exceeded that of the cattle. In young animals this dimension was highest in F_1 hybrids of both sexes. In all young hybrids, except B_3 bos cows, it excelled the data of European bison. So, it can be concluded that occiput grew to height and to breadth at different rates in European bison and in hybrids. In this material the height of occiput showed low or moderate variability, except young B_3 bos cows and young European bison, in which it was rather high.

There were distinct differences in the shape of occiput between mature male European bison and the cattle (index 12, Table 4). In the skulls of domestic bulls the occiput was higher in relation to its breadth, contrary to European bison (index 12 was significantly higher in domestic bulls, $p < 0.001$). The shape of occiput in F_1 males was intermediate between parental forms (index 12 was significantly lower than in domestic bulls and higher than in European bison, $0.001 < p < 0.002$) (Table 4). In adult male backcross hybrids the shape of occiput was similar more to European bison's than to the cattle's. There were no distinct differences in the proportions of occiput in adult female European bison, domestic cows, and female hybrids. In the crania of most young hybrids and European bison index 12 was higher than in adult animals. It evidenced that in mature animals the breadth of occiput ($Ot-Ot$) grew more intensively than its height. High individual variability of the index under discussion could be observed in domestic bulls and B_3 bos cows ($CV > 10\%$).

3.4. *Paries Lateralis*

On this cranial surface the form of two elements distinctly differed between European bison and the cattle. They were orbit and *fossa temporalis*. In European bison *fossa temporalis* was long and narrow (slot-shaped) and in older individuals it was markedly narrowed as an effect of increasing *processus cornuales* (Empel, 1962). Since in European bison *processus cornuales* stuck out before the hind margin of the *calvaria*, a fragment of *fossa temporalis* on the lateral wall was visible behind *processus cornualis*. In the cattle *fossa temporalis* was short and broad, bordered from the top entirely by *os frontal* (Plate XII, Photo 11). In F_1 hybrids one could observe great individual differences in the shape of *fossa temporalis*. In three individuals ("Filon", "Filip", "Filutka") which mother was European bison it was similar to *fossa temporalis* of European bison (Plate XII, Photo 12), while in the progeny of domestic cow and European bison ("Facet", "Fakir", "Farad", "Fama") it was similar to that of the cattle (Plate XIII, Photo 13). In most backcross hybrids the shape of *fossa temporalis* was similar to that, observed in the cattle skull, although there were some individual differences in the breadth, length and the situation of the narrowing (Plate XIII, Photo 14).

The height of *fossa temporalis* in all mature hybrids was similar to that of the cattle (Table 5), and it was almost three times as high as in European bison. The height of *fossa temporalis* showed high variability in male hybrids, nevertheless it was lower than the variability of this dimension observed in European bison. In young animals high variability of this measurement occurred in F_1 males and in European bison.

3.4.1. Orbita

Contrary to the cattle (Plate XII, Photo 11) *anuli orbitales* of European bison stuck out far away to the sides. Among hybrids only mature F_1 males had telescopic orbits similar to those of European bison (Plates XII, XIII, Photos 12, 13), though they were poorer developed. In backcross hybrids, except for one B_{1bos} bull (Plate XIII, Photo 14), this feature got atrophied.

3.5. Basis

A detailed description of the form of basal length of a skull (BP) is given in section 3.1. It was greatest in F_1 hybrids. The length proportion of *neurocranium* basis to *splanchnocranium* basis (index 3, Table 4) was similar in all hybrids and parental forms.

Length of maxillary toothrow P^1 to M^3 was greatest in the skulls of F_1 hybrids. In backcross cows it was also greater than in European bison and the cattle (Table 2). The dimension of cranial basis showed low or moderate variability ($CV=2.7-8.7$), except young B_3 cows (Table 2).

3.6. Mandible

There were distinct differences in the form of mandible between European bison and the cattle, although its length did not differ significantly. *Corpus mandibulae* and *ramus mandibulae* of European bison were lower than those of the cattle ($p<0.001$). Both indices which characterized the proportions of mandible (10, 11 — Table 4) were significantly greater in the cattle than in European bison ($p<0.001$).

In this material adult F_1 hybrids of both sexes had the longest mandibles ($Id-cm$). They exceeded the dimensions of mandibles of the cattle, European bison ($p<0.001$), and backcross hybrids (significant differences observed only in males: $0.02<p<0.05$). Also mandible of female backcross hybrids was significantly longer than that of European bison (B_{1bos} : $0.01<p<0.02$; B_{2bos} : $0.02<p<0.05$) and the cattle (B_{1bos} : $p<0.001$, and B_{2bos} : $0.001<p<0.002$). In young animals (there was no F_1 material) the longest mandibles were observed in male European bison and B_{1bos} females (Table 7). The length of mandible showed low variability, it was higher only in young European bison (Table 7).

In all backcross hybrids the height of *ramus mandibulae* ($Cm-gov$) was significantly greater than in European bison ($p<0.001$). There were no distinct differences in this dimension between F_1 and B_{1bos} hybrids and the cattle. In B_{2bos} hybrids the height of *ramus mandibulae* ex-

ceeded that of the cattle ($0.01 < p < 0.02$). The variability of this dimension was moderate in adult hybrids and European bison while it was rather high in cow hybrids and the cattle.

Height of *symphysis mandibulae* (*Id-gov*) in F_1 hybrids, B_1 bos and B_2 bos males was similar to that of European bison and smaller than in the cattle while in B_1 bos and B_2 bos females it exceeded that of the cattle ($0.002 < p < 0.005$). It was the most variable dimension of mandible, and in adult hybrids and parental forms it was particularly high. Only in young female hybrids it was moderate (Table 7).

Table 7

Measurements of mandible in hybrids between European bison and the cattle and in parental forms. See Table 2 for abbreviations of hybrids generations and European bison. Definitions of measurements are given in the text.

Generation, sex, n(name)	Age, (mth)		<i>Id-cm</i>	<i>Id-goc</i>	<i>Cm-gov</i>	<i>Id-gov</i>	<i>BRM</i>	<i>HCM</i>
F_1 Males								
5	60—156	\bar{x}	473.4	441.9	167.4	148.5	133.7	81.7
		SD	16.9	19.3	13.1	20.8	13.7	4.4
		CV	3.6	4.4	7.8	14.0	10.2	5.3
F_1 Females								
Filutka	84		438.5	406.5	164.5	155.5	106.0	74.0
Fama	96		432.5	409.5	170.5	122.0	117.0	77.5
B_1 bos Males								
5	48—84	\bar{x}	443.7	419.2	167.9	152.2	120.4	83.0
		SD	11.8	10.8	13.9	23.3	7.9	4.8
		CV	2.7	2.6	8.3	15.3	6.6	5.8
6	12—48	\bar{x}	412.3	385.6	167.2	139.1	106.6	80.4
		SD	18.7	17.9	13.4	17.2	6.2	2.1
		CV	4.5	4.7	8.0	12.3	5.8	2.6
B_1 bos Females								
6	48—96	\bar{x}	422.9	401.6	170.6	152.1	110.4	77.8
		SD	9.5	7.3	13.7	22.3	6.7	4.1
		CV	2.2	1.8	8.0	14.7	6.1	5.2
4	12—48	\bar{x}	355.5	331.8	137.0	115.3	91.5	72.1
		SD	19.8	22.1	14.7	8.7	3.7	8.3
		CV	5.6	6.7	10.7	7.5	4.0	11.5
B_2 bos Males								
3	48—60	\bar{x}	427.5	406.8	182.3	151.7	114.5	81.5
		SD	4.3	10.1	10.4	13.9	5.3	5.0
		CV	1.0	2.5	5.7	9.2	4.6	6.1
Fenek	16		367.0	345.5	139.0	140.5	95.0	78.6
Fenyl	27		404.5	382.5	170.0	148.5	119.0	84.0
B_2 bos Females								
5	48—72	\bar{x}	426.2	402.5	175.1	157.4	114.7	79.2
		SD	22.6	20.0	11.1	22.3	9.2	4.7
		CV	5.3	5.0	6.3	14.2	8.1	6.0
5	12—48	\bar{x}	410.3	388.2	164.8	145.0	110.7	79.4
		SD	25.1	21.5	8.7	13.3	9.0	5.2
		CV	6.1	5.5	5.3	9.1	8.1	6.5

continued on p. 175

Table 7. concluded.

B ₃ bos Male Feliks	23		418.5	391.0	151.5	182.5	113.0	84.0
B ₃ bos Females 4	12—36	\bar{x}	350.9	338.6	124.0	122.6	106.6	72.5
		SD	27.7	24.7	23.2	9.1	5.2	5.4
		CV	7.9	7.3	18.7	7.4	4.9	7.5
Cattle Males 3	ad	\bar{x}	439.3	412.3	168.7	172.0	118.7	92.0
		SD	26.8	26.3	29.3	30.1	14.0	6.1
		CV	6.1	6.4	17.3	17.5	11.8	6.6
Cattle Females 40	ad	\bar{x}	386.4	368.7	155.5	129.5	110.5	76.3
		SD	23.8	21.4	15.3	15.3	8.8	7.4
		CV	6.1	5.8	9.8	11.8	8.0	9.7
Bison Males * 16	48—264	\bar{x}	435.6	410.9	125.7	153.2	119.6	63.6
		SD	11.6	12.1	8.0	16.3	9.6	6.1
		CV	2.7	3.0	6.4	10.6	8.0	9.5
Pulan Pułkownik	13 22		319.0 355.0	350.0 361.0	96.0 105.0	142.0 141.0	— —	— —
Bison Females * 17	48—324	\bar{x}	410.3	387.8	120.9	135.6	108.9	59.8
		SD	9.1	8.3	8.5	16.8	5.8	3.0
		CV	2.2	2.1	7.1	12.4	5.3	5.0
5	12—36	\bar{x}	341.4	326.8	101.0	141.5	98.0	64.5
		SD	43.0	39.6	8.5	20.1	—	—
		CV	12.6	12.1	8.4	14.2	—	—

Height of *corpus mandibulae* behind B₃ (HCM) in hybrids was distinctly greater than in European bison (F₁, B₁bos and B₂bos females: $p < 0.001$, B₂bos males: $0.002 < p < 0.005$). In comparison with the cattle the height of *corpus mandibulae* of only male hybrids was inconsiderably smaller (significant difference in F₁ males: $0.02 < p < 0.05$). This dimension showed moderate variability in adult animals, it was higher only in young B₁bos hybrids.

There were no significant differences in the breadth of *ramus mandibulae* (BRM) between adult European bison, the cattle, and backcross hybrids. This dimension was greater only in F₁ males in comparison with that of European bison ($0.02 < p < 0.05$) and it showed high variability in F₁ males and domestic bulls, while in remaining animals the variability was moderate or low. I had both mandibles of hybrids at my disposal and I found that they were asymmetrical. Only in 12 cases (of 59 ones examined) the dimensions of both mandibles were almost identical. In remaining hybrids the left and the right mandibles differed in both their height and length.

It was interesting that both dimensions, which distinctly differed between European bison and the cattle (HCM and Cm-gov), in hybrids were similar either to those of European bison (F₁ hybrid "Filon")

or to the cattle's ("Facet" — Plate XIV, Photo 15) or one dimension was similar to that of European bison and another to the cattle (other F₁ hybrid — Plate XIV, Photo 16). In backcross hybrids the shape of mandible grew more and more similar to that of the cattle as the percentage of cattle blood increased (Plate XIV, Photo 16). Of B₁bos hybrids four animals and three individuals of B₂bos generation had lower *corpus mandibulae* (Plate XIV, Photo 17) but it was still higher than in European bison. In young B₃bos hybrids the proportions of mandible were similar to those of the cattle.

The comparison, presented above, showed that European bison's mandible was characterized by lower *corpus mandibulae* and, in males, by smaller height of *symphysis mandibulae* than those of the cattle. The differences in the length were rather small. Hybrids' mandibles, especially those of F₁ hybrids, were longer than those of European bison and the cattle while their height of symphysis approximated the cattle's. However, in backcross males and F₁ hybrids the height of *symphysis mandibulae* was rather alike in European bison.

3.7. Sexual Dimorphism

Taking into account absolute values of cranial dimensions published by Empel (1962) I ascertained significance of differences in average measurements of male and female skulls. Significant differences were found in the following measurements: *Ot-Ot*, *Ect-Ect*, *Fs-Fs*, *Nm-Nm* and the greatest spread of horn cores ($p < 0.001$), which confirmed the earlier conclusions of Empel (1962). Most of remaining mean measurements of male European bison's skull were also greater than those in females. However, in young male European bison only two measurements — the capacity of *cavum cranii* and the horn core base circumference were significantly greater than those in females ($0.02 < p < 0.05$), which indicated that the dimorphic differences in skull of European bison developed with age.

Most cranial dimensions of domestic bulls were greater than those of cows, alike European bison. The greatest significant differences were observed in the following measurements: horn core base circumference, *Fs-Fs*, *Ect-Ect*, *Nm-Nm*, *Sph-Br*, the greatest spread of horn cores, *Ot-Ot*, and the height ($p < 0.001$, Tables 2, 3, 4, 5, 6).

In the skulls of F₁ hybrids the differences related to the sex were visible earlier than in European bison. In two-year-old male F₁ hybrids the measurements *Ect-Ect* and *Fs-Fs* were significantly greater than those in females, which was not so visible in the skulls of European bison. In adult F₁ hybrids the greatest differences related to the sex

were found in the following dimensions: *Ect-Ect*, *Fs-Fs*, *Ot-Ot*, *Nm-Nm*, the height of a skull and the greatest spread of horn cores so that alike parental forms.

In young B_1 bos males the dimensions of a skull were, in general, greater than those of females. In young animals the greatest differences were observed in the measurements: the greatest spread of horn cores and the circumference of horn core base ($0.005 < p < 0.01$), smaller ones in the breadth and the length of a skull ($0.01 < p < 0.02$) as well as in its height ($0.02 < p < 0.05$).

In the group of young B_2 bos hybrids some dimensions were greater in males. They were: the breadth *Ect-Ect* and *Fs-Fs*, the capacity of a skull, the circumference of horn core base, and the greatest spread of horn cores. In adult B_2 bos males the measurements: *Sm-Sm*, *Ot-Ot*, *Ect-Ect* ($0.005 < p < 0.01$) and three measurements of *processus cornuales* ($0.01 < p < 0.02$) were significantly greater than those in females. Most dimensions of young B_3 bos male were greater than the analogous dimensions of females.

The formation of sexual dimorphism in the skulls of adult animals could be investigated by analysis of dendrite (Fig. 2), on the basis of the similarity in the measurements of breadth (*Ect-Ect*, *Ot-Ot*) and the height of a skull. Distinct division of sexes on the basis of three measurements was observed in adult European bison, F_1 hybrids, and in the cattle as well as in young B_3 bos hybrids. In B_1 bos and B_2 bos hybrids the division of sexes on the basis of these measurements was possible only in some animals. This resulted from the fact that backcross cows had relatively large skulls, which dimensions exceeded those of domestic cows.

To sum up, it can be said that the most distinct differences in the size of a skull which were connected with sex and which occurred in hybrids and parental forms referred to the breadth of a skull and *planum nuchale* as well as to the size of *processus cornuales*. The differences in skull's breadth which were connected with sex developed earlier in life in hybrids than in European bison. This indicated different rates of development of the skulls in these animals.

4. DISCUSSION

In the evolutionary process of *Bovinae* frons has grown longer and broader and postcornual part of the skull has been transformed. These transformations proceeded different ways in different phylogenetic branches of the groups: *Bison*, *Bibos*, and *Bos*, which resulted in creation of different forms. In *Bison* line the divergance of a skull found expres-

Table 8

Collation of the age (in months) of the earliest full obliteration of *suturae capitis* in hybrids between European bison and the cattle and in parental forms. Abbreviation of hybrid generations as in Table 2; B₃ hybrids — only animals 1—2 years available; Data for cattle, after Krysiak (1975). Abb.: E.b. — European bison, after Empel (1962); l — lateral; m — medium; a — anterior; p — posterior.

Suturæ	Hybrid generation or species					
	F ₁	B ₁ bos	B ₂ bos	B ₃ bos	E.b.	Cattle
<i>Dorsum nasi</i>						
<i>S. internasalis</i>		8	7	—	—	22
<i>S. nasofrontalis</i>	l	6.5	—	—	—	14
	m	11.0	—	—	—	—
<i>Calvaria</i>						
<i>S. parietofrontalis</i>	l	6.5	2.5	4.2	2	5
	m	5.5	2.5	2.2	2.2	5
<i>S. frontalis</i>	a	8	—	—	—	7—12
	m	6.5	4.5	—	—	6
	p	5.5	2.5	4.2	—	6
<i>Planum nuchale</i>						
<i>S. squamosooccipitalis</i>		5.5	3	2.5	2.2	3
<i>S. occipitomastoidea</i>		5.5	4	4.2	—	5
<i>Fossa temporalis</i>						
<i>S. parietofrontalis</i>		5.5	—	—	—	12
<i>S. parietotemporalis</i>		5.5	7.5	—	—	9
<i>S. zygomaticofrontalis</i>		5.5	4.5	—	—	6
<i>Orbita</i>						
<i>S. frontolacrimalis</i>		5.5	5.5	—	2.2	14
<i>S. sphenofrontalis</i>		5.5	5.5	—	—	14
<i>Facies facialis</i>						
<i>S. lacrimomaxillaris</i>		—	—	—	—	10—15
<i>S. zygomaticolacrimalis</i>		5.5	—	4.2	—	6
<i>S. zygomaticomaxillaris</i>		8	—	—	—	14
<i>S. frontolacrimalis</i>		5.5	—	—	—	7—8

sion in slight shortening of postcornual part of the skull, in broadening of frons and in horizontal situation of *regio parietalis*, which is of interparietal type. The postcornual part of the skull has changed most of all in the *Bos* line. Their *calvaria* is composed entirely of elongated *ossa frontalia*, while postcornual part of the skull, which is very much shortened, gets vertical and it lies in the same plane as occiput. In *Bos* the top border of *calvaria* is formed by *protuberantia intercornualis* which interconnects the base of horn cores while in *Bison linea nuchae* formed this border (Sokolov, 1953).

I attempted to investigate the trend of heredity of cranial characters. In the skulls of hybrids of all generations the features which were typical of *Bos* distinctly prevailed. They were verticality of postcornual

part of the skull and the reduction of nuchal parts of *ossium parietalium*, although in hybrids it was less reduced than in cattle. In backcross hybrids the size of this region grew smaller as the percentage of cattle's blood increased. In hybrids also *calvaria* was composed entirely of *ossa frontalia*, alike the cattle. In skulls of juvenile, hybrids originating from the Askania Nova *regio parietalis* was similar to that of the cattle (Bogoljubskij, 1935). The form of *regio parieto-occipitalis* approximated that observed in European bison skull as the age of these hybrids increased (Andreeva, 1935). B₁ hybrids of the Askania Nova, in this respect, were alike cattle.

Most of features of skulls of F₁ hybrids from Białowieża were intermediate between those of European bison and the cattle, but some of them were alike European bison and other were similar to those of the cattle. In F₁ males the general proportions of a skull as well as the value of *splanchnocranium* to *neurocranium* ratio were intermediate between parental forms. In F₁ hybrids of both sexes the size of frons and the breadth of *ossa nasalia* were also intermediate as well as the height of a skull in females of all hybrid generations. In F₁ hybrids of both sexes the similarity with European bison appeared in the breadth of occiput, the size of *regio parietalis*, and in the shape of *processus cornuales*. In F₁ males it appeared in an arching of *anuli orbitales*, as well. Also the height of *symphysis mandibulae* in F₁ hybrids and backcross males was more characteristic of European bison than of the cattle.

However, the similarity with the cattle apart from mentioned above verticality of postcornual part of the skull and form of the *calvaria*, appears in general proportion of a skull in F₁ females and backcross hybrids as well as in the height of *fossa temporalis* in all hybrids. Most of remaining cranial dimensions in backcross hybrids approximated those of the cattle and this similarity increased as the percentage of cattle blood grew higher.

Similar regularities could be observed when comparing the structure of hybrid's skull with the form of its whole body. The form of F₁ hybrid's body was of intermediate character and some of features were inherited from European bison while other from the cattle, just as in its skull. The bodies of F₁ males had more features alike European bison, just as it was observed in their skulls. The heads of F₁ males showed intermediate form while the heads of females were alike the cattle's, which was in accordance with the observations of general proportions in hybrid skulls. Exterior similarity with the cattle increased in backcross hybrids as the percentage of cattle blood grew higher (Krasíńska, 1969, 1971b, 1979b).

Juvenile skulls of hybrids of the Askania Nova were similar to the

cattle skulls although the differences in the skull form between hybrids, European bison, and the cattle were considerably smaller in new-born calves than those in older animals (Bogoljubskij, 1935). In two older F_1 hybrids of the Askania Nova the height of *fossa temporalis*, the breadth of nasal bones and the shape of horns showed distinct domination of cattle features. In hybrids from Białowieża this last feature approximated that of European bison. Alike backcross hybrids of Białowieża, in two B_1 hybrids of the Askania Nova the skull form was similar to the cattle's, but some dimensions were greater than those of the cattle.

Cranial dimensions of one mature F_1 cow of the Askania Nova ("Galka", ♂ European bison × ♀ grey Ukrainian breed of cattle) were similar to those observed in hybrids of Białowieża, only her *frons* was broader. The dimensions of the skulls of B_1 hybrids of the Askania Nova were similar to those of analogous hybrids of Białowieża, only the breadth of *frons* (*Ect-Ect*) and the height of occiput (*B-linea nuchae*) were greater.

The skulls of adult hybrids of Białowieża were relatively homogeneous, not very differentiated material. The coefficients of variation (CV) of most measurements were lower than 6%. The domestic bulls examined were different in this respect. Most of their measurements had high CV, which indicated, among others, that the material was very much differentiated. In hybrid *crania* only dimensions of *processus cornuales*, the height of *fossa temporalis*, the capacity of *cavum cranii* of male skulls and some dimensions of *mandibula* showed high variability. The cranial dimensions of young animals were more variable in most cases than those of adult ones. This phenomenon was observed as well in European bison (Empel 1962; Kobryńczuk & Roskosz 1980) as in other mammals (Buchalczyk & Ruprecht, 1977; Ruprecht, 1974).

In hybrid *crania*, which were rather homogeneous material in respect of linear dimensions, occurred many differences which could not be expressed in numbers. They may refer, *i.e.*, to only one bone with some features inherited from European bison and others from the cattle, just as in the case of mandible or *processus cornuales ossium frontaliium*. High variability was observed in the shape of *fossa temporalis* and in the development of *protuberantia intercornualis*. Also verticality of post-cornual part of the skull inherited from cattle goes together with different degree of development or reduction of nuchal parts of *ossium parietaliium*. European bison features of a skull (*Ect-Ect*, *HCM*, the shape of *processus cornuales*) which were observed in some backcross hybrids, apart from F_1 hybrids, could be inherited only by single individuals of a given backcross generation. So that, the comparison of average values

of the dimensions did not form a proper pattern of the differentiation of cranial features inherited from European bison or from the cattle in hybrids of all generations. It also indicates that the heredity of these features is very much complicated. It was found that the skulls of F_1 hybrids grew faster in early youth of these animals of European bison. It refers to most dimensions of length, breadth, and the height of a skull. Also dimensions of *processus cornuales* and most of measurements of *mandibula* (except for *Id-Gov*) were greater in 12–24 month old F_1 hybrids than in European bison of the same age. The comparison of linear dimensions in the skulls of adult animals indicates the differences in the rates of growth between hybrids and European bison. The breadth of a skull (*Ect-Ect*, *Fs-Fs*, *Nm-Nm*) and the size of occiput were significantly greater in adult European bison than those in hybrids, contrary to the young animals. It evidences that the skull grew in breadth more intensively in European bison which were older than 4 yrs than in hybrids. It remains in accordance with Empel's (1962) observation which suggests that some dimensions of European bison skull increase even in animals more than 5 years old. During the earliest 24 months of life the rate of growth was faster in hybrids than in the parental forms, or it is at least as intensive as that of the cattle. Adult F_1 hybrids exceeded both parental forms in body size. Their constitution approximated the proportions of the cattle rather than of European bison, although there were many intermediate features (Krasieńska, 1969). So, it can be concluded that the faster rate of growth of F_1 hybrids during the early stages of postnatal development can be the feature inherited from the cattle or it is an effect of heterosis.

Some similarities as well as differences between hybrids, European bison and the cattle were visible in the rate of obliteration of skull's sutures. In hybrids of all generations, just as in European bison (Empel, 1962) and the cattle, the sutures of *planum nuchale* ossified earliest of all (Table 7). Such an early obliteration could be observed in backcross hybrids in respect to some sutures on the *calvaria*. The sutures: *inter-nasalis*, *nasofrontalis (pars media)* and *lacromaxillaris* ossified in hybrids alike in parental forms *i.e.* sporadically or late in age. In backcross hybrids the obliteration of the sutures on the surfaces of *fossa temporalis*, *orbita*, *facies facialis* occurred earlier in life than the obliteration of these sutures in parental forms.

Heterosis is one of the most interesting phenomena which accompanies hybridization. It can appear in the changes of metabolism, faster rate of growth, in large body size or greater productivity *etc.* In general, heterosis was observed in hybrids of first generation. In all F_1 hybrids between European bison and the cattle, obtained so far, it was distinctly

visible. Hybrids bodies in both the birth-weight and the weight of adult animal exceeded those of the parental forms (Karcov, 1903; Iwanow & Philiptschenko, 1916; Krasińska, 1969; Małecka *et al.*, 1976; Małecka & Sumiński, 1976). The great weight of body was related to the increase in the weight of internal organs (Krasińska & Pilarski, 1977; Pytel *et al.*, 1977), muscles (Szulc *et al.*, 1971) and skin (Pietrzykowski & Krasińska, 1971). The heterosis of body size and its weight was not observed in most backcross hybrids. Merely three calves of B₁bos generation had greater birth-weight (Krasińska, 1971b). Heterosis was also recorded in the form of crania of F₁ hybrids just as in the constitution of their bodies. Most cranial dimensions of young F₁ hybrids were greater than those of European bison and backcross hybrids. In adult F₁ hybrids the base of a skull, mandible (*Id-CM*) and *ossa nasalia* were longer and the capacity of *cavum cranii* was greater than those of European bison and the cattle. In F₁ males also the height of *occiput* was distinctly greater than that in European bison and the cattle. It is interesting that the crania of two F₁ hybrids of the Askania Nova were not larger than the skulls of parental forms (Andreeva, 1935). However, in Askanian backcross hybrids many of cranial dimensions were greater than in the cattle (Andreeva, 1935). In the material from Białowieża this phenomenon was observed in B₁bos and B₂bos cows.

The material for craniometric analysis of hybrids came from hybridization between European bison and different breeds of cattle, so it was not homogeneous in respect of origin. Also many age classes were not represented in it because of the need for other studies on these animals. Hybrids of the Askania Nova were the progeny of European bison and grey Ukrainian and Metis-Simental cows, while the remaining hybrids came from black and white lowland and the Polish red breeds of cattle. All backcross hybrids of Białowieża were the progeny of black and white lowland bulls. Some of backcross hybrids had the blood of only black and white lowland cattle, others had the blood of both black and white lowland and the Polish red breeds. Craniometric analysis has not revealed any features of the skull related to the breed of cattle crossed with European bison. The differences in the skulls between hybrids of the Askania Nova and those of Białowieża resulted rather from individual variability than from the differences in the breeds of domestic cattle which were hybridized with European bison.

Acknowledgments. I thank the director and research workers of Department of Animal Anatomy, Warsaw Agricultural University for giving me the run of their collection of skulls and for the consultations, and Dr. F. Kobryńczuk for the measurements of *Sm-Sm* in European bison. I would like to thank Mr. Jerzy Dackiewicz and Mr. Maksymilian Szuma of Mammals Research Institute, PAS for technical help.

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Received 20 September 1985. Accepted 12 February 1988.

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KRANIOMETRYCZNA ZMIENNOŚĆ KSZTAŁTU CZASZKI HYBRYDÓW ŻUBRA Z BYDŁEM DOMOWYM W PORÓWNANIU DO FORM WYJŚCIOWYCH

Streszczenie

Badania wykonano na 59 (28, 31) czaszkach hybrydów żubra z bydłem domowym rasy czp i ncb o rosnącym udziale krwi bydła od 50% do 93,75%. Zwierzęta te reprezentowały 4 pokolenia hybrydów: F_1 (50% bydło, 50% żubr), B_1 bos (75% bydło, 25% żubr), B_2 bos (87,5% bydło, 12,5% żubr), B_3 bos (93,75% bydło, 6,25% żubr). Szczegółową analizę porównawczą przeprowadzono na czaszkach osobników dorosłych (Tabela 1). Do porównań wykonano wymiary 40 (6, 34) czaszek bydła domowego, a z literatury zaczerpnięto dane dla żubra (Empel, 1962). Na każdej czaszce wykonano 34 pomiary (Ryc. 1), które użyto do wyliczenia 12 wskaźników (Tabela 4). Czaszki dorosłych hybrydów wykazują małą zmienność wymiarów linio-

wych ($CV < 6\%$). Spotyka się jednak zróżnicowania w strukturze czaszki hybrydów, których nie można wyrazić pomiarami.

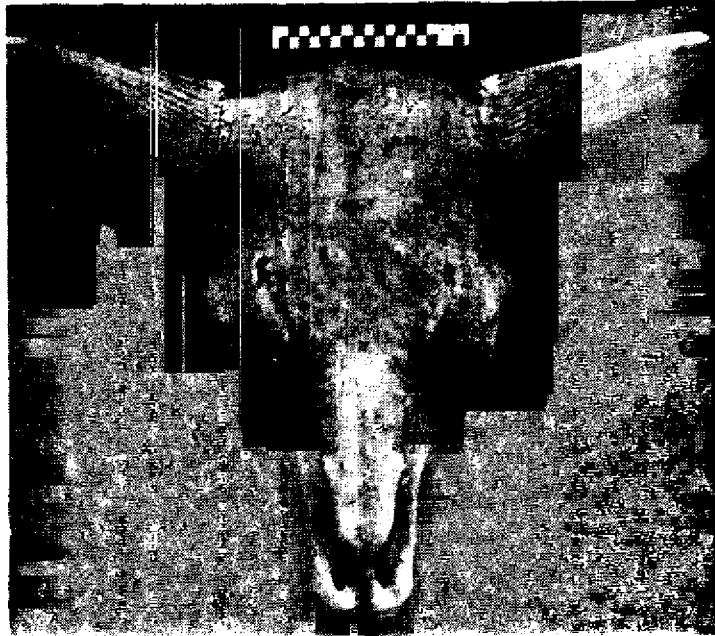
U hybrydów F_1 w budowie czaszki zaznacza się efekt heterozji, przejawiający się w większej niż u żubra i bydła długości podstawy czaszki, długości żuchwy ($Id-Cm$), długości kości nosowych oraz pojemności jamy czaszki (Tabele 2—7). Większość pozostałych wymiarów czaszki dorosłych hybrydów F_1 ma wartości pośrednie w stosunku do form wyjściowych, przy czym są cechy podobne do żubra, inne do bydła. U samców F_1 kształt czaszki jest pośredni, jak również stosunek wielkości trzewio- i mózgowiczaszki czy kształt potylicy. Wielkość czoła u hybrydów F_1 oraz szerokość sklepienia nosowego mają wartości pośrednie, podobne jak wysokość czaszki u samic hybrydów wszystkich pokoleń (Tabele 2—7). Podobieństwo do żubra zaznacza się w szerokości potylicy, wielkości i kształcie mózżeni u hybrydów F_1 obu płci. Również u samców F_1 wysokość czaszki oraz wysklepienie pierścieni oczodołowych są podobne do żubra. Wysokość spojenia żuchwy ($Cm-Gov$) jest u hybrydów F_1 i samców pokoleń wstecznych bliższa danym dla żubra (Tabela 7).

Podobieństwo do bydła zaznacza się w pionizacji zarogowej części czaszki, która leży u wszystkich hybrydów razem z potylicą na tarczy karkowej oraz w budowie sklepienia czaszki, utworzonego wyłącznie przez kości czołowe. Kształt czaszki samic F_1 oraz hybrydów wstecznych jak również wysokość dołu skroniowego u hybrydów wszystkich pokoleń są podobne do bydła. Większość pozostałych wymiarów czaszki hybrydów wstecznych jest zbliżona do czaszki bydła, przy czym podobieństwo to rośnie w miarę wzrostu udziału krwi bydła. Jednak nawet u sztuk o niskim procencie krwi żubra mogą pojawiać się indywidualne cechy zbliżone do żubra (kształt mózżeni, szerokość czoła, wysokość trzonu żuchwy za M_3). W żuchwie obie cechy różniące się wyraźnie u żubra i bydła (wysokość trzonu żuchwy za M_3 i tylna wysokość gałęzi żuchwy w projekcji) dziedziczą się u hybrydów F_1 albo obie po żubrze albo obie po bydle, albo jedna po żubrze a druga po bydle (Tablica XIV, Fot. 15—17).

Większość wymiarów długości, szerokości i wysokości czaszki młodych (12—24 miesiące) hybrydów F_1 jest większa niż u żubrów. Natomiast u zwierząt dorosłych wymiary szerokości czaszki ($Ect-Ect$, $Fs-Fs$, $Nm-Nm$, $Ot-Ot$) są wyraźnie większe u żubrów niż u hybrydów. Wskazuje to, że w pierwszych latach życia czaszka hybrydów rośnie intensywniej niż u żubrów, co może wynikać z efektu heterozji oraz wpływu tempa wzrostu czaszki odziedziczonego po bydle. Natomiast u żubrów w wieku powyżej 4 lat czaszka powiększa się na szerokość intensywniej niż u hybrydów.

Duże podobieństwa ale i pewne różnice, obserwuje się również w tempie obliteracji szwów kostnych czaszki między hybrydami i formami wyjściowymi (Tabela 8). U hybrydów wszystkich pokoleń podobnie jak u żubra i bydła najwcześniej kostnieją szwy *planum nuchale*. U hybrydów pokoleń wstecznych również wczesną obliterację obserwuje się w części szwów leżących na sklepieniu czaszki. U hybrydów wstecznych proces kostnienia szwów na powierzchni dołu skroniowego, oczodołu i powierzchni twarzowej trzewioczaszki zachodzi wcześniej niż u form wyjściowych.

Dymorfizm płciowy jest wyraźnie zaznaczony u hybrydów F_1 i B_3 bos podobnie jak u żubrów i bydła. U hybrydów B_1 bos i B_2 bos wyraźnie tylko u samic, których czaszka jest podobnej wielkości jak u krów domowych (Ryc. 2). Największe różnice związane z dymorfizmem płciowym dotyczą u hybrydów pomiarów $Ect-Ect$ i $Fs-Fs$ na sklepieniu czaszki oraz $Ot-Ot$ na tarczy karkowej jak również największej szerokości czaszki na mózżeniach, podobnie zresztą jak u żubra i bydła.



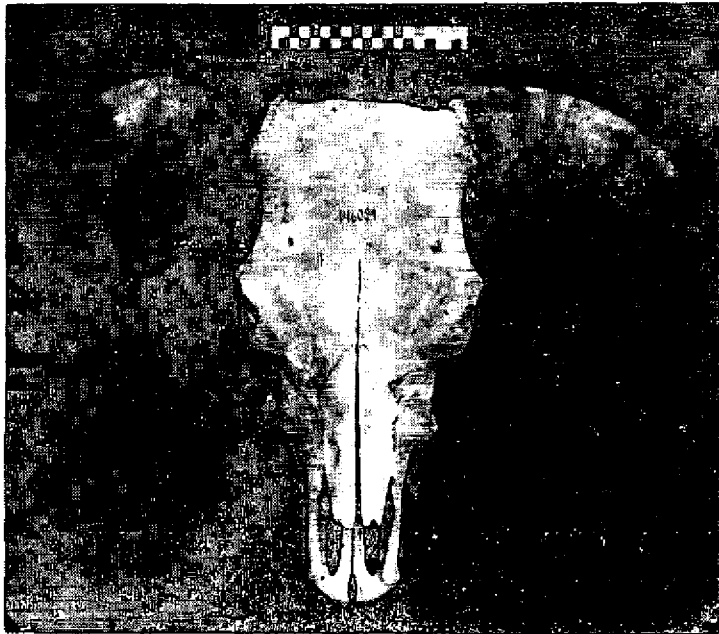
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S. Buszko *phot.*



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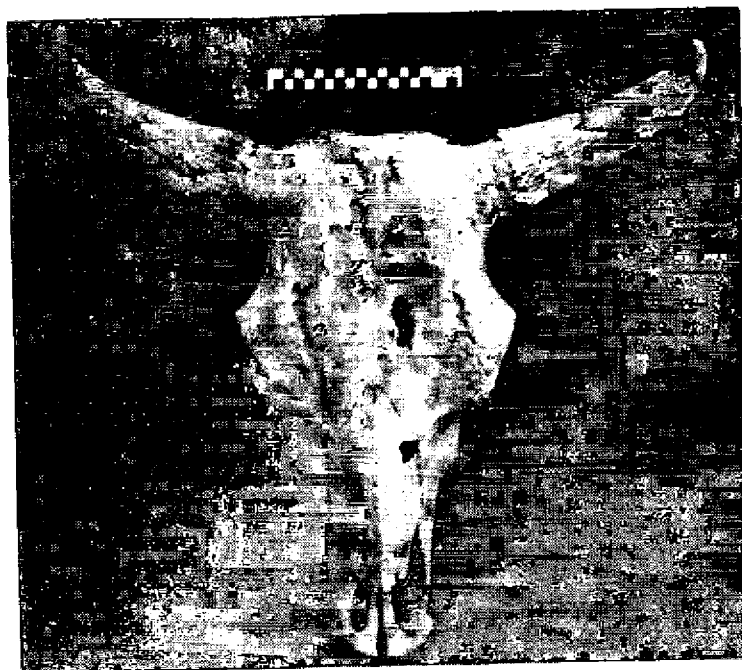
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M. Krasieńska

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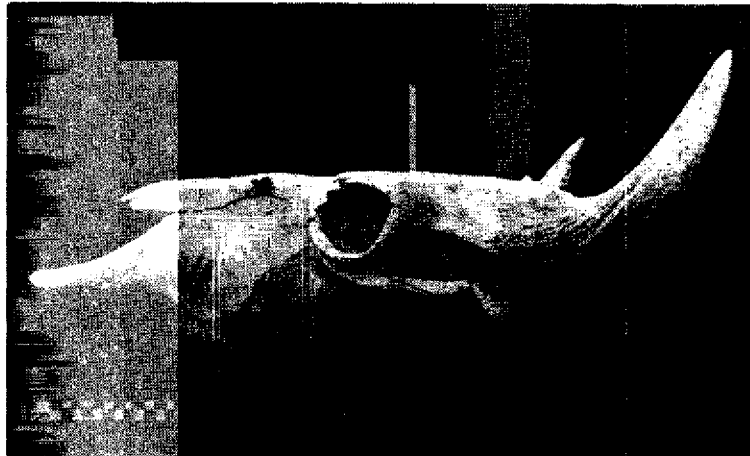
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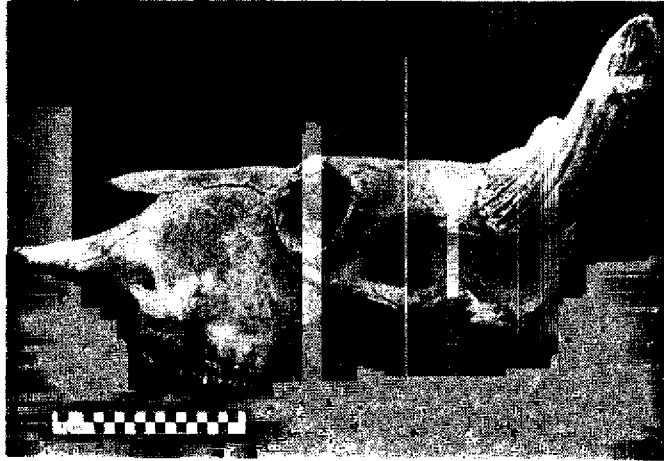
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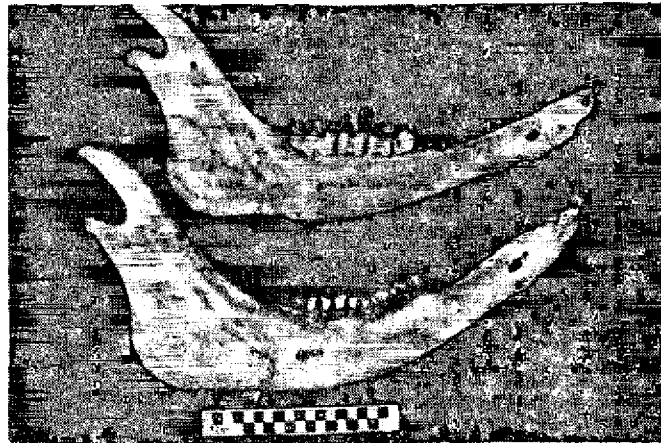
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S. Buszko *phot.*



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16



17

M. Krasíňska

Uzyskane wyniki porównano z danymi analizy morfologicznej czaszek hybrydów żubra z bydłem uzyskanymi z Askanii Nowej (Andreeva, 1935; Bogoljubskij, 1935). Stwierdzono dużo podobieństwa ale i pewne różnice, między innymi brak wpływu heterozji na wielkość czaszki krowy F_1 . Zbyt mały materiał porównawczy skłania do przypuszczenia, że różnice te są raczej wynikiem zmienności indywidualnej niż wpływu różnych ras użytych do krzyżowania z bydłem.

EXPLANATION OF PLATES

The following abbreviations were used:

F_1 — F_1 hybrids (50% European bison, 50% cattle),

B_1 bos — 25% European bison, 75% cattle,

B_2 bos — 12.5% European bison, 87.7% cattle,

E.bis — European bison,

bwl — black and white lowland cattle,

rp — red Polish cattle,

M — male,

F — female.

Plate VII

Cranium, Norma verticalis

Photo 1. "Facet", M, F_1 (E.bis×bwl) 11.5 yrs.

Photo 2. "Filutka", F, F_1 (rp×E.bis) 7 yrs.

Plate VIII

Cranium, Norma verticalis

Photo 3. Domestic bull bwl, 5 yrs.

Photo 4. "Fenny", F, B_1 bos, 8 yrs.

Plate IX

Cranium, Norma verticalis

Photo 5. "Fen" II, M, B_2 bos, 4 yrs.

Photo 6. "Filip", M, F_1 (rp×E.bis), 8 yrs.

Plate X

Cranium, Planum nuchale

Photo 7. "Łąka", F, F_1 (E. bis×bwl) 2 yrs.

Photo 8. "Filip", M, F_1 (rp×E. bis) 8 yrs.

Plate XI

*Cranium, Planum nuchale*Photo 9. "Fela", F, B₂bos, 2.5 yrs.Photo 10. "Festa", F, B₂bos, 5 yrs.

Plate XII

Cranium, Norma lateralis

Photo 11. Domestic bull, bwl, 5 yrs.

Photo 12. "Filip", M, F₁ (rp×E. bis) 8 yrs.

Plate XIII

*Cranium, Norma lateralis*Photo 13. "Facet", M, F₁ (E. bis×bwl) 11.5 yrs.Photo 14. "Fell", M, B₁bos, 7 yrs.

Plate XIV

*Mandibula*Photo 15. "Filon", M, F₁ (rp×E. bis) 13 yrs."Facet", M, F₁ (E. bis×bwl) 11.5 yrs.Photo 16. "Fakir", M, F₁ (E. bis×bwl) 5 yrs."Feta", F, B₁bos, 3.2 yrs.

Photo 17. Domestic bull, bwl, 5 yrs.

"Fenny", F, B₁bos, 8 yrs.