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Morphology of Digestive Tract of the European Bison*)

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[With 24 Tables, 1 Fig. & Plates XI—XVII]

Morphological studies of the alimentary canal were carried out on 50 European bisons (34 ♂ + 16 ♀) aged from 1 day to 24 years. The values given below (apart from data for the esophagus) refer to fresh material, although fixed animals were also used. The length of the esophagus in an adult bison comes within limits of 87—104 cm, and the external diameter varies from 3 to 7.4 cm. The volume of the 4 stomach compartments forms the following sequence in adult animals: rumen — 106 l, abomasum — 11 l, omasum — 8.8 l, reticulum — 4.5 l. During postnatal development the stomach increases its volume by 33.5 times (rumen — 94, omasum — 61.8, reticulum — 39.6, abomasum — 4.4). The papillae of the rumen in European bison are longer and more densely distributed than in cattle. Primary and secondary reticular folds can be distinguished. The omasal laminae occur in numbers from 128—186 and depending on breadth and extent are divided into 5 order (there are usually 10 first-orders). Spiral folds of abomasum are more numerous (average 19) and higher (np to 12 cm) in the European bison than in domestic cattle. In newborn bisons the intestine measures on an average 15.9 m in length (84% is formed by the small intestine) and 3.9 l in volume (72% — small intestine) and during postnatal development increases its length 3.35 times (the small intestine now forms only 77%) and volume — 23.8 times (59% — small intestine). The ratio of intestinal length to body length is similar to that in domestic cattle and is 20.63:1. Either 2 *gyri centripetales* (59%) or 2½ occur in *ansa spiralis coli*.

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I. INTRODUCTION

The present study forms part of an important undertaking being carried out by the Department of Animal Anatomy, Warsaw Agricultural University, namely to obtain a knowledge of the anatomy of the European bison.

Fragmentary data on the morphology of the alimentary canal can be found in studies by Owen (1848), Müller (1852) and Wróblewski (1927). Zarzycki (1957) also described the microscopic structure of the omasum, abomasum and liver in a 10-year old male. Piękoś, Pilarski & Roskosz (1958) measured the length of the intestinum from the bodies of 16 bison. Gill (1965; 1967) defined the capacity of the alimentary canal in 6 bison [1]).

Only the mouth of the European bison has been exhaustively described (Wilkus, 1957).

II. MATERIAL AND METHODS

Examination was made of the bodies of 50 European bison, *Bison bonasus* (Linnaeus, 1758), that is, 34 males and 16 females. Their age varied from 1 day to 24 years. One fullterm foetus was also added. The animals had either died or been anaesthetized. Accurate data on the age of the animals was taken from the European Bison Pedigree Books (Żabiński, 1947—1963). These data are set out in table 1, where the results of measurements of the bodies, made in accordance with the method used by Piękoś *et al.* (1958), are given. An additional measurement (after Liskun, 1949) was introduced, termed the basic measurement, that is, the oblique length of the trunk, and indicated by the symbol »a«. The bodies were measured in the lateral position, by means of a surveying tape measure. Measurement of material before fixing was taken as a principle. In cases in which circumstances prevented this, the bodies were measured after they had been fixed, and this is indicated as appropriate in table 1. The weight of 23 bison was known, calves and some of the older bison being weighed after death, while the live bison transported to Warsaw in special packing cages were weighed before being killed.

[1]) The following publication made its appearance after this study had gone to press: Gill J., 1968: The Capacity and Weight of Walls and Digesta of the Alimentary Tract in European Bison. Acta theriol., 13, 31: 499—509.

Table 1.
Comparison of material.

No.	Name of animal	Pedigree book no.	Age yrs	Age mths	Age dys	Body measurements (cm) A	D	E	G	a	Weight (kg)
						Males					
1.	Pub				1	114	86	45	63	62	35
2.	Pon	1373			1	85	—	23	—	31	12.8
3.	Pos	1702			1	116	—	45	—	63	
4.	Pop [1, 2])	1372			3						28.5
5.	Pom [1, 2])	1364			7	107	—	44	—	67	30
6.	Plakat	1682		1	10	132	101	67	90	97	71
7.	Pomian [2])			1	19	126	98	52	86	74	57
8.	Plon *)	1292		10	—	190					
9.	Pud II *)	1086	1	—	26	200	140				318
10.	Zon	1454	1	1	23	190	137	86	—	127	240
11.	Pudzik		1	9	24	210	151	85	120	119	206
12.	Puskan		1	10	19	220	164	93	131	131	
13.	Poronin [2])	1459	2	—	8	212	156	95	130	129	
14.	Plennik *)	813	2	7	18						
15.	Pustal		2	11	2	240	170	101	135	145	
16.	Putnar	1569	3	3	24	247	171	128	137	182	408
17.	Puck [2])	1151	4	—	22	247	179	112	138	132	
18.	Pusłon	1212	4	9	3	244	168	118	135	167	500
19.	Pug II [1])	1087	6	1	25	280	184	125	151	176	806
20.	Pozew	1082	6	4	13	250	170	120	128	168	
21.	Putar [2])	1026	6	4	23	267	204	122	151	150	
22.	Plater *)	824	7	2	17	228	166	124	126	—	530
23.	Pocztowy	1281	7	3	28	290	190	135	152	170	
24.	Połamaniec *)	572	9	1	26	260	183	125	141	186	
25.	Pokorny [2])	1077	9	3	2	283	177	133	142	184	
26.	Posusz	984	10	1	12	273	202	129	131	174	
27.	Pluszcz *)	785	10	5	9	248					620
28.	Stoper	879	11	5	28	255	190	133	145	186	580
29.	Polas	985	11	7	13	282	191	118	147	165	760
30.	Plamiec	789	14	4	18	262	172	126	139	181	
31.	Pomruk	816	14	7	—						
32.	Karpacz	792	16	10	20	279	196	136	142	—	
33.	Pluvius II *)	546	17	3	5	265	173	140	137	—	920
34.	Plato *)	575	17	3	28	280	190	135	150	—	750
						Females					
1.	Foetus [2])					106	—	41	—	60	
2.	Pusza	1517			1	103	80	44	64	64	23
3.	Poja				2	106	78	44	68	67	22.5
4.	Pomiła	1564		1	12	122	95	54	81	78	54.7
5.	Purena [1, 2])	1152		2	22	103	—	48	—	67	
6.	Purata *)	943	1	5	10	192					
7.	Pukajka *)	868	1	10	2	200	140	113	111	—	
8.	Puzota *)	1148	2	8	16						217

Females

9.	Plisa *)	701	7	1	17						
10.	Powaga	977	7	7	7	251	161	115	132	135	
11.	Ponętna 1)	1073	8	5	18	252	165	133	122	183	530
12.	Pociecha 2)	909	13	10	28	238	—	127	—	187	
13.	Puszynka 2)	724	15	4	17	235	172	116	131	151	
14.	Purtanka	795	16	5	16						
15.	Pliete *)	255	18	6	21						
16.	Putka	596	20	4	13	252	197	105	141	—	
17.	Beste 2)	524	23	8	18	267	168	124	142	171	

*) — Data on intestines of these European bison were obtained from the Department of Animal Physiology and Department of Animal Anatomy of Warsaw Agricultural University; 1) — Measurements made after removing skin; 2) — Measurements made on fixed bodies; A — Body lenght (distance between the upper edge of the nasolabial plate and the tail basis); D — Distance between the utmost point of the nuchal torus and the base of the ungular capsule; E — distance between the scapulohumeral articulation and the hip tubercules; G — Distance between the ischiadic tubercule to the base of the angular capsule; a — oblique lenght of trunk (distance between the scapulohumeral articulation and the ischiadic tubercule).

The weight of »Plakat«, »Pomila« and »Plater« was determined by weighing different parts of the body.

It must be pointed out that some of the individuals examined had previously undergone anatomic pathological dissection, so that it was possible to use part of this material only.

Observations were made of both fresh and fixed material. Fixing was carried out by immersion in a 3—4% formalin water solution (calves, isolated organs) or by intraarterial injection of the bodies of the larger animals in accordance with the method given by Pilarski *et al.* (1967).

Linear measurements of the organs were made by means of a soft centimetre tape measure, a scaled ruler and slide-ruler with nonius. Capacity was determined by filling the given part with water at room temperature — the volume of water used was measured in a calibrated cylinder. The organ measured for capacity was submerged in water in order to avoid stretching the walls (cf. Kryński, 1932) and was always filled with water under a constant pressure of the water column 10 cm high.

The following procedure was used for the emptied stomach: the group consisting of the reticulum and rumen was filled through the esophagus, and the group consisting of the omasum and abomasum through the duodenum. Each of the groups was then ligated on the boundary of the chambers forming it and emptied, the amount of water flowing from it being measured. In this way despite the wide ruminoreticular and reticulo-omasal openings fully reliable results were obtained.

The length and capacity of the intestines were determined after they had been detached from the mesentery and emptied.

Measurement of the length and capacity of the intestines, and also capacity of the stomach was made, in the case of fresh material, as soon as possible *post mortem* which, however, on account of the large dimensions of the organs examined, took a few or even a large number of hours. Measurements of fixed material was made at different times, but not earlier than two weeks after the time of fixing.

The location of the organs was determined on bodies of animals which had been fixed *in toto* by intraarterial injection of the fixing medium. As it was impossible to suspend the bodies in the natural position, and also on account of the fact that no preparations were used eliminating fermentation of the ingesta of the rumen, the topographical data must be treated as approximate only.

Coefficients of growth were calculated for some of the organs examined. They were calculated, after D a v l e t o v a (1960), by means of dividing the absolute linear dimension of the given organ at an advanced age by the absolute dimension at a younger age.

Histological inspection preparations were made from the organs taken from 2 bison (»Pozew« and »Pomruk«).

The Latin anatomical terms were taken from *Nomina Anatomica Veterinaria* (1963, 1965).

III. RESULTS

1. Esophagus

The palatopharyngeal folds in the European bison take the form of low thickenings, which gradually become smaller in a posterior direction. Their junction forms the palatopharyngeal arch, which marks the entry to the esophageal vestibule. In the cross-section it is crescent-shaped, and its lumen measured along the arch is about 10 cm in an adult bison [2]). The mucous membrane of the esophageal vestibule is arranged in low, transverse and oblique folds, which become longitudinal esophageal folds without any clear dividing line. Length of the esophageal vestibule is about 5 cm.

Table 2.

Absolute length of esophagus (cm): ratio of body length (A) and oblique length of trunk (a) to length of esophagus in European bison fixed *in situ*.

Name	Cervical part	Thoracic part	Total length	A	a
Pustal	43	36	79	1:0.30	1:0.83
Polas	45	46	91	1:0.32	1:1.01
Pociecha	42	45	87	1:0.36	1:1.09
Pomruk	51	53	104	—	—
Karpacz	44	55	99	1:0.35	1:1.01

The length of the esophagus was measured from the transverse plane taken to the caudal margin of the arytenoid cartilage, and the cervical part — to the cervical margin of the first rib (Table 2).

[2]) Individuals over 5 years old were considered as adult bison. The basis for this is formed by the results of studies made by E m p e l & R o s k o s z (1963) on the skeletal structure of the legs in the European bison.

The more constant ratio of esophageal length to body length (A) than to oblique length of the trunk (a) is remarkable.

The diameter and appearance of the esophagus in an adult bison are not uniform throughout its length. The maximum diameter of the esophagus is at the final section of the thoracic part, and the minimum on the boundary between the cervical and thoracic parts (Table 3). The walls of the cervical part are sunken, and as a result the esophagus has a characteristic star-shaped lumen in the cross-section. The thoracic part has a yawning lumen. When filled with air or water the esophagus is cylindrical in shape with 5 constrictions. The first of these occupies the initial section of the esophagus lying at the level of the first few tracheal rings. It is caused chiefly by the thickening of the esophageal wall. The second constriction is situated at the terminal section of the

Table 3.
External diameter of esophagus (cm).

Name	1/5 Beginning of cervical part	1/2 Cervical part	1/5 Final cervical part	1/5 Beginning of thoracic part	1/2 Thoracic part	1/5 Final thoracic part	Immediately before diaphragm
Pustal	4.2	4.8	3.9	5.9	5.0	4.8	5.7
Puck	—	—	3.0	5.3	5.0	—	7.0
Polas	3.8	5.1	3.4	4 5	3.7	5.0	5.6
Pociecha	3.5	4.7	4.3	5.1	4.8	2.8*)	5.8
Karpacz	4.7	5.5	4.1	6.6	5.7	7.0	7.4

*) Complete compression of lumen of esophagus.

cervical part and the initial thoracic part and is caused by the »narrowness« of the thoracic inlet and also by the lowering of the esophagus to the left-lateral surface of the trachea. The third constriction chiefly affects the left surface of the esophagus and is caused by the pressure of the aortic arch. The fourth constriction, which is not always present, is formed by the pressure of the right bronchus. The fifth constriction occurs in the diaphragmatic part of the esophagus, the lumen of which is similar in shape to a vertically positioned rima. This constriction is caused by the compression of the diaphragm which is not uniform on all sides. The lateral crus of the left diaphragmatic crus presses most deeply, creating a depression up to 2 cm deep. A shallower groove can be seen on the ventral and right surface of the esophagus.

The esophageal wall in adult bison, 4/5 of which consists of muscular coat and submucosa, varies in thickness in different parts (Table 4).

The constrictions and thickenings of the lumen and walls are less distinct in the esophagus of young individuals.

The muscular membrane of the esophagus is formed throughout its length of red striated muscular fibres. They are arranged in two main layers — the external and the internal, particularly clearly visible in the cross-section of the esophagus. The thickness of the muscular membrane differs in different parts of the esophagus (Table 4). In the greater part of the esophagus the fibres of the two layers take a spiral course and thrust through each other on dorsal and ventral surface of the esophagus in such a way that the fibres of the external layer pass into the internal layer and *vice versa*. Two »sutures«, particularly clearly visible from submucosa (Photo. 1, b), are formed. Some of the fibres, however,

Table 4.

Thickness of esophageal wall (a) and its muscular coat (b) in mm.

Name		1/5 Beginning of cervical part	1/2 Cervical part	1/5 Final cervical part	1/5 Beginning of thoracic part	1/2 Thoracic part	1/5 Final thoracic part	Immediately before diaphragm
Pustal	a	2.0	1.9	2.6	2.5	2.7	2.7	3.1
	b	1.4	1.0	1.2	1.5	1.8	1.8	2.4
Polas	a	6.2	4.1	5.0	4.5	3.9	3.5	5.8
	b	4.1	3.1	4.0	3.0	2.7	2.8	3.9
Pociecha	a	7.7	5.2	4.4	4.1	3.8	8.6*)	4.5
	b	4.7	3.5	2.5	2.6	2.7	8.4*)	2.6

*) Complete compression of lumen of esophagus.

maintain an elliptic course, changing the direction of their course above the »suture«, and remaining in the previous layer. The bundles of muscular fibres of the two layers cross almost at right angles. Bundles of fibres running longitudinally (Photo. 1, a) appear on the submucosal surface of the internal layer of muscular membrane, of the preventricular part of the esophagus, and extend into the muscular membrane of the lips of the reticular groove. The majority of the fibres of the inner layer extend into the muscular membrane of the floor of the reticular groove.

Abundant submucosa includes in pharyngeal part a venous plexus composed of a dense network of blood vessels running parallel to the long axis of the esophagus connected with short, transverse »bridges«. The lumen of the veins then increases, the network becomes less close-knit and in the terminal part of the cervical part in places where the layers of the muscular membrane cross there are two veins — dorsal and ventral. Sometimes only one vessel, usually the dorsal, occurs. The mucous gland was also found to be present (Photo. 2).

The mucous membrane of the esophagus is a whitish-creamy colour. It is arranged in high longitudinal folds, and near them there are small folds which also run longitudinally. At the level of the esophageal hiatus the esophageal mucosa forms low circular folds.

The esophageal mucosa is covered with stratified squamous epithelium the thickness of which, without the *stratum corneum*, is illustrated by the above comparison of two adult males:

	Between micropapillae	Above micropapillae	Sampling site
»Pozew«	194—469 (284)	37—144 (91)	preventricular part
»Pomruk«	138—292 (215)	49—138 (94)	transition area between cervical and thoracic part

Relatively frequently, in 6 cases out of the 10 bison observed, formations occur, similar in shape to dwarf rye ears, on the mucous membrane of the esophagus, usually on the boundary line between the lips of the reticular groove. They are peduncular and formed of very numerous creamy-grey corneous »needles« similar to the conical shaped papillae on a cat's tongue. The size of these »ears« varies from 1.5 to 6.2 mm. They are not connected with the esophageal muscular membrane. They are not observed in European bison below the age of 4 and the largest number, as many as 13, were counted in a female over 20 years old.

2. Stomach

2.1. Rumen

The shape and other properties of the external structure of the rumen can best be seen in an organ only moderately filled with air (Photo. 3—6). The rumen then appears in the form of a large, laterally flattened bag, bordered by two convex curvatures, the dorsal and ventral. Both surfaces of the rumen, the parietal and visceral, are furrowed with more or less deep grooves. The size of these grooves can be judged from the figures given below for the 9-year old male (»Pokorny«); the depth of the cranial groove (Photo. 5—6e) measured in relation to the cranial end of the ventral sac of rumen is 24 cm, and in relation to the dorsal sac of rumen — 19.5 cm. The depth of the caudal groove is on an average 23 cm.

The left longitudinal groove, or strictly speaking its cranial part (Photo. 3, 5 i), forms a sort of extension of the cranial groove on the parietal surface of the rumen, and in turn this part is elongated in a straight line into the left accessory groove (Photo. 5 i′). This is a shallow and short depression not reaching to the dorsal curvature. The presence of the caudal part of the left longitudinal groove, which in cattle connects the cranial part with the caudal groove of the rumen, was not observed. There was however a more or less strongly formed depression which extended from the left accessory groove to the place in which the dorsal coronary groove disappears; this is perhaps the caudal part of the groove described situated far higher. The right longitudinal groove (Photo. 4, 6 j), and also the right accessory groove lying upwards of it (Photo. 4, 6 j′) are relatively distinct. The insula of the rumen which they demarcate is fusiform. The ventral coronary groove (Photo. 3—6 g) reaches to the ventral curvature of the rumen and is similar in shape to a closed hoop. The ventral sac of the rumen in adult bison appears to be more capacious than the dorsal sac of the rumen, the length of the two sacs being most often almost equal, although the breadth of the ventral sac of the rumen is far greater. The situation is similar in both the foetus and newborn bison, and the fact is noteworthy that the dorsal sac of the rumen covers from the front, the top and partly from the back the ventral sac (Photo. 7—10).

The dorsal coronary groove (Photo. 3—6 h) is less well defined than the ventral groove and does not reach the dorsal curvature of the rumen. The caudodorsal blind sac (Photo. 3—6 c) is conical, the axis being directed backwards and downards, and slightly to the left. In newborn animals this sac is directly downards only, and the sharp cone shape is very distinct (Photo. 9).

The caudoventral blind sac (Photo. 3—6 d) is larger than the dorsal one and is shaped like a wide cupola. *Sulcus atrioruminalis* can be observed in the European bison in the stomach viewed from the right side, in the form of an indistinct depression (Photo. 6 l). The ruminoreticular groove (Photo. 3, 5—6 m) runs beyond the dorsal curvature of the rumen and descends on its right visceral surface as a broad but shallow groove, visible only after removal of the serous coat, separating *atrium ventriculi* from the rumen (Photo. 4 and 6 n).

The capacity of the rumen in adult European bison determined on unfixed material is on an average 106 l, results being obtained in 5 out of 6 cases (Table 5) [3]) of over 100 l, but in one only 87 l. The last result refers to an individual which was fed for a week on dry fodder only for experimental purposes. Measurements made on fixed material as a rule give lower results than those presented above. In adult European bison the difference is 22% (Table 5).

Of the three layers of the ruminal wall, the serous coat covers the whole of its surface except for the following places: on the dorsal cur-

[3]) Tables with detailed measurement data are to be found in the library of the Department of Veterinary Science, Warsaw Agricultural University.

Table 5.

Volume of different compartments of stomach (in litres and in % of volume of whole stomach); relations between volume of certain compartments of stomach.

Group	N		Stomach as whole	Rumen l	Rumen %	Reticulum l	Reticulum %	Omasum l	Omasum %	Abomasum l	Abomasum %	Relations between: Ru: Ab	Ru: proventriculus
Fresh material													
Newborn	3	min	3.58	0.86	24	0.06	2	0.10	3	2.00	53	1:1.35	1:1.15
		max	4.34	1.48	40	0.16	4	0.19	4	2.96	72	1:2.99	1:2.51
		x̄	3.89	1.12	29	0.12	3	0.14	4	2.51	64	1:2.40	1:1.93
Calves 6 weeks	2	min	7.69	3.51	46	0.19	2	0.06	2	3.92	51	1:1.11	1:1.02
		max	10.80	4.93	46	0 20	2	0.21	1	5.46	51	1:1.12	1:1.03
		x̄	9.24	4.22	46	0.20	2	0.14	1	4.69	51	1:1.11	1:1.03
Young bison from 2 to 3.5 years old	2	min	53.70	36.30	68	2.75	4	5.90	7	8.75	9	4.15:1	5.14:1
		max	146.45	118.25	81	5.75	5	9.95	11	12.50	16	9.46:1	10.72:1
		x̄	100.08	77.28	74	4.25	4	7.92	9	10.62	13	6.80:1	7.93:1
Adults from 6 to 11.5 years old	6	min	114.35	87.00	76	2.50	2	4.80	4	8.00	6	5.67:1	5.46:1
		max	158.15	124.00	85	7.70	5	12.85	10	15.35	13	14.53:1	16.47:1
		x̄	130.44	106.01	81	4.50	3	8.85	7	11.03	9	10.17:1	10.11:1
Fixed material													
Adults from 6.5 to 24 years old	4	min	79.60	67.75	85	0.90	1	1.66	2	4.00	4	11.44:1	11.89:1
		max	109.34	94.50	91	4.70	4	6.60	7	8.40	8	22.50:1	23.54:1
		x̄	94.92	82.94	88	2.30	2	3.79	4	5.90	6	14.95:1	16.13:1

vature (adhesion with diaphragm, spleen and muscles of the ventral lumbar region), on the visceral surface of the ventral sac of the rumen (adhesion with the abomasum and omasum).

The muscular membrane of the rumen consists of two layers. Bundles of fibres of the external layer run longitudinally, and where they run through the region of the grooves they are arranged vertically to them and divide up into two planes, the superficial of which is weaker and does not extend to the floor of the depression. The deep, stronger plane enters into the depressions and in this way becomes an integral part of the pillars of the rumen. The internal layer of the muscular membrane is thicker than the external. The results are given below of measurements (in mm) obtained after fixing the body of a 9-year old male:

	Dorsal sac, surface		Ventral sac, surface	
	Visceral	Parietal	Visceral	Parietal
External layer	0.9	1.9	0.8	1.1
Internal layer	1.7	1.9	2.1	1.9

The fibres of this layer run parallel to the grooves and form the main supporting structure of the ruminal pillars.

The cranial pillar (Photo. 14, 17 a) is situated obliquely in relation both to the median plane (from right and top to the left and the bottom) and the transverse plane (from the bottom and front to the back and top). The free margin of this pillar forms an arch with its concave curve directed to the interior of the rumen. The length of the cranial pillar (which corresponds approximately to the depth of the cranial groove) defined in relation to the cranial end of the ventral sac is from 20—22 cm in adult European bison. Its thickness is 2.5 cm.

The caudal pillar (Photo. 14, 17, 19 c) is situated parallel to the transverse plane and obliquely to the median plane, and runs from the right side and the top to the left and the bottom. The free margin of this pillar lies at the height of the third lumbar vertebra. It is shaped like a wide lamina with thickened edges which form the start of the coronary pillars. The height of the caudal pillar in adult European bison is 93 mm and in postnatal development increases by more than five times as much (Table 6). Of the coronary pillars (Photo. 14, 17, 19 d, e) the ventral is better formed and, unlike to the dorsal pillar, forms a closed ring. The right longitudinal pillar (Photo. 17, 19 f) is similar in character to a doubling of the ruminal wall. Its height in the cross-section in an adult male (»Pokorny«) was 16 mm and thickness 11.5 mm. The right accessory pillar (Photo. 17, 19 g) is formed by the thickening (up to 10.7 mm in »Pokorny«) of the internal layer of muscular membrane. The left longitudinal pillar (Photo. 14 b) possesses only a part

Table 6.

Average dimensions and growth coefficients (g. c.) of some structures of the rumen (mm).

Group	N	Height of caudal pillar at narrowest part				Length of ruminoreticular fold				Height of ruminoreticular fold in broadest place			
		min	max	x̄	g. c.	min	max	x̄	g. c.	min	max	x̄	g. c.
2—7 days	5	14	20	17	1.26	27	45	37	2.28	8	12	10	1.29
1.5—3 months	3	19	24	22	2.90	47	103	80	1.92	11	15	13	2.38
1—5 years	7	50	85	63	1.47	140	170	153	1.40	26	35	30	1.72
6—23 years	11	85	110	93	5.39	170	240	215	5.86	40	60	52	5.32

Table 7.

Average dimensions and growth coefficients (g. c.) of reticular groove (mm).

Age group		N	Floor	Length of lips		Breadth of floor			Height of lips						Thickness of lips					
									1/3		2/3		3/3		1/3		2/3		3/3	
				l	r	1/3	2/3	3/3	l	r	l	r	l	r	l	r	l	r	l	r
1—7 days	Avg.	3	3.9	4.5	4.6	0.8	1.5	1.7	0.6	0.6	0.8	0.8	0.7	0.8	0.4	0.3	0.5	0.4	0.4	0.5
	g. c.		3.2	3.8	3.7	3.2	2.4	2.4	1.9	2.5	2.6	2.1	3.3	3.1	1.7	1.8	1.5	2.5	2.0	2.0
1—3 years	Avg.	4	12.3	17.0	17.0	2.4	3.6	4.2	1.1	1.5	2.0	1.7	2.5	2.4	0.7	0.6	0.8	0.9	0.9	1.0
	g. c.		1.4	1.3	1.3	1.1	1.0	1.1	1.5	1.0	1.0	1.5	1.4	1.2	1.8	1.9	1.8	1.5	2.0	1.7
9—17 years	Avg.	6	17.8	22.0	21.7	2.8	3.8	4.7	1.7	1.5	3.4	2.5	3.6	3 0	1.2	1.1	1.4	1.4	1.8	1.7
	g. c.		4.6	4.9	4.7	3.6	2.6	2.7	2 9	2.5	4.4	3.2	4.8	3.8	3.1	3.3	2.7	3.3	4.0	3.5

1/3, 2/3, 3/3 — indicates respectively: initial, medial and final part of reticular groove; l — left; r — rigth.

corresponding to the anterior part of the left longitudinal groove; there is no corresponding left accessory groove.

The ruminoreticular fold (Photo. 29 f) is crescent-shaped in the natural position. It lies solely on the left wall of the stomach and is smaller in extent than the ruminoreticular groove, to which it corresponds. This fold begins caudad and slightly to the left (4.5—8 cm) from the cardia, and ends on the ventral curvature and does not enter upon the visceral surface of the rumen. The dimensions of this fold increase by five times during postnatal development (Table 6).

The mucous membrane of the rumen varies in colour, depending on age, from creamy-grey in calves to brown of different shades in adult animals. The papillae of the rumen (Photo. 13—20) are distinguished by considerable variety of shape. They may take the form of narrow leaflets with slightly ragged edges, or lingulae widening towards the free ends, or low broad cones. The length of papillae in adult animals is usually more than 1 cm, but specimens were encountered 1.9 cm long, and in extreme cases — 2.4—2.6 cm (24-year old female). The longest papillae were encountered on the ventral surface of *atrium ruminis,* in both blind sacs and below the left longitudinal pillar, while the lowest cover the dorsal curvature of the rumen. In newborn calves the longest papillae of the rumen are 2.2 mm high and in 1.5 month old calves — 4 mm. The numbers of papillae per 1 cm^2 differ in different parts of the rumen and vary within wide limits — 28—65 (»Pokorny«), 54—128 (»Pudzik«). The free margins of the pillars and a large part of *insula ruminis* are free of papillae and their mucous membrane is wrinkled and similar to elephan's skin in appearance (Photo. 16).

The papillae of the rumen cover the mucous membrane of the ruminoreticular fold and also enter upon the part of the *atrium ventriculi* lying to the front of it (Photo. 29). The area they occupy is triangular in shape, the apex of the triangle directed downwards, the sides formed by the above-mentioned fold, $1/3$ of the upper part of the left lip of the reticular groove and by the line which constitutes a distinct boundary between the mucous formations typical of the rumen and reticulum.

The formations shaped like the ears of rye, which have been described in respect of the esophagus, were also found in the rumen of 6 adult European bison. They are located solely in the place situated caudally from the cardia, on the mucous membrane covered by small papillae, which in old bison is free of papillae. They do not exceed 10 in number.

The mucous membrane of the rumen is covered by flat stratified squamous epithelium, which on the micropapillae attains the thickness of 16—118 μ, average 65 μ.

The rumen occupies almost the whole left half and part of the right half of the abdominal cavity (Photo. 21). The rumen extends furthest forward to the 7—8 intercostal space. The caudal extent of the rumen is defined by a transverse plane drawn at a distance of 5—15 cm in front of the anterior margin of the pelvic symphysis (Photo. 22). This plane is reached by either the posterior ends of the two blind sacs, or the caudodorsal blind sac reaches 2—3 cm further on. The rumen extends only by the caudal part of the ventral sac to the right half of the abdominal cavity (Photo. 23, 24).

2.2. Reticulum

The reticulum is shaped like a flat sac in the anterior-posterior direction with crescent-shaped margins (Photo. 3—6, 1; 7—12 c). The length of the lesser curvature, measured on an adult male's stomach when filled with air, is 21.5 cm (near its ventral end lies the reticulo-omasal opening, oval in shape and measuring 3.0 × 3.5 cm), whereas the greater curvature is 60 cm. The breadth of the reticulum of the same male is as much as 16.5 cm, distance of the anterior wall from the posterior at the level of the reticulo-omasal opening — 15.2 cm, and height 28.2 cm.

The reticulum is the smallest of the compartments of the stomach, and in adult European bison its capacity is on an average 4.5 l (fresh material). The reticulum decreases in capacity during fixing more than the rumen, and differences in measurements are as much as 49%.

The serous coat covers almost the whole surface of the reticulum, and is absent only in places of adhesion with neighbouring organs, *i. e.* with omasum, abomasum and with the cranial end of the ventral sac of the rumen.

The muscular coat of the reticulum is thicker than that of the rumen and is formed by two layers. The external layer consists of the extension of the muscular membrane of the floor of the reticular groove and runs perpendicularly to it. It attains its maximum thickness (1.8 mm) on the diaphragmatic surface. The internal layer is a continuation of the muscular membrane of the lips of the reticular groove, and the fibres of this layer cross at different angles with the external layer. Thickness of the inner layer up to 3 mm.

The mucous membrane of the reticulum is brown in colour and similar to a honeycomb in appearance (Photo. 25—28). Two kinds of reticular folds can be distinguished among the total number, in respect of the course they take. In one case they leave the lips of the reticular groove and run divergently towards the greater curvature of the reticulum (Photo. 30). The second kind of reticular folds are arranged parallel to the reticular groove but the lines of their course are less distinct. The crossing of these two kinds of reticular fold forms four-, five- and six-sided figures, cells of the reticulum. There are secondary, lower folds on the floor of these cells, separating them from the smaller. Sometimes the latter are divided by indistinct tertiary folds into even smaller ones. The free margins of the secondary and tertiary folds, and also the floor of the cells of the reticulum, are covered with papillae of the reticulum. They are sagittate, with sharp apices, and whitish in colour. The surfaces and free margins of the main folds are slightly denticulate (Photo. 26—28). The highest reticular folds occur on the left part of the diaphragmatic surface. Their height in fully grown animals may be as much as 15 mm, and in addition they here form the smallest cells of the reticulum over the whole areas of the latter (their diagonal is only 17 mm — Photo. 26). The lowest folds (height 4.5 mm) and largest cells (diagonal over 35 mm) cover the mucous membrane of the fundus of the reticulum (Photo. 28). All three kinds of size of the reticular folds were observed even in newborn calves. The primary folds are from 2 to 2.5 mm in height and the cells which they demarcate have a diagonal of 6—7 mm.

The epithelium of the mucous membrane of the reticulum is a typical stratified squamous epithelium, the thickness of which in a 15-year old male (»Pomruk«) is on an average 56 μ (37—81).

Foreign bodies were found (nails, pieces of wire, metal rings, screws for wood) in the reticulum of 4 bison, 2 of which came from a zoo, and in one case the nail was wedged in the wall of the reticulum surrounded by connective tissue hyperplasia.

The reticulum in the European bison lies in the part of the abdominal cavity extending furthest forwards, and reaches to the 6th intercostal space or to the 7th rib (Photo. 21 b). To the rear its extent is defined by the 8th rib. The lowest part of the reticulum is situated 5—10 cm above the xiphoid process of the sternum from which it is separated by the fundus of the abomasum. In two cases it was found that the reticulum directly adjoined the xiphoid process of the sternum. The left margin of the reticulum is either completely or partially separated from the sternal part of the diaphragm by the more or less elongated spleen. On the right side the reticulum can be reached in the 6th—8th intercostal space, about 5 cm above the costochondral junction.

2.2.1. The reticular groove

The reticular groove (Photo. 29—30) runs from the cardia to the reticulo-omasal opening on the right wall of the *atrium ventriculi* and reticulum. The length of the floor of the reticular groove is 17.8 cm, and the length of the lips of the reticular groove is slightly greater. The breadth of the floor in the direction of thee reticulo-omasal opening is almost double that of the cordia. The height and thickness of the lips also increases by half as much ventrad (Table 7).

The various elements of the reticular groove do not increase uniformly in size during postnatal development. The greatest increases are observed among measurements of length — the growth coefficient calculated jointly for the floor and the two lips is 4.74. The next in order is the measurement of height of the lips — 3.59. The thickness of the lips has a coefficient of 3.40. Increase in the breadth of the floor is decidedly weakest. The length and breadth of the reticular groove, and also the height of its lips attains full development earlier than the thickness of the lips. Justification for this conclusion is formed by the high growth coefficients for calves and young bison, and low coefficients for adult animals. The development of the thickness of the lips lasts longest (Table 7).

The mucous membrane of the floor of the reticular groove is creamy or light brown in colour and is arranged in small, longitudinal folds, increasing in number ventrad, resulting in there being 3—4 distinct and 2—3 less distinct folds at the recticuloomasal opening (Photo. 30 d). As from midway along the length of the reticular groove conic bird-claw papillae appear on these folds (Photo. 30 g). The mucous membrane of the lips of the reticular groove is arranged in low folds which either change into papillae of *atrium ventriculi*, or else form the beginning of the reticular folds (Photo. 29—30).

2.3. Omasum

The outline of the omasum is shaped like a laterally flattened oval. The parietal surface is directed laterad and craniad (Photo. 4, 2; 8, 10, 12 d). It is slightly convex. The visceral surface, on the other hand, is almost flat, directed mediad. Flat grooves can be seen on both surfaces near the omasoabomasal opening. The two surface are continuous on the convex dorsal curvature, which is directed caudad and dorsad. This curvature in adult animals is 58—75 cm long. The margin of the omasum is flat and directed ventrad and slightly craniad, and is from 4—5.2 cm in length. The situation described here is only found when the omasum is in its natural position. In an isolated stomach filled with air the surfaces of the omasum are directed craniad (right) and caudad (left), the dorsal curvature laterad and dorsad, and basis omasi — mediad and ventrad. The omasoabomasal opening is oval, and measures

12.5 × 18 cm. In order to give a better idea of how large the omasum is in the European bison we have set out data for the 9-year old male (»Pokorny«) below:

Distance between surfaces	22.7 cm
Distance between cranial and caudal margins	22.5 cm
Distance between ventral and dorsal margin	27.0 cm

(all measurements were made with a slide-rule — in projection).

The average capacity of the omasum in adult European bison is 8.86 l and is 133% greater for fresh than for fixed material. The omasum shrinks as the result of fixing to a greater degree than the rumen (22%) and the reticulum (49%).

The muscular coat of the omasum is thicker than the mucous coat of the rumen and reticulum. It is thickest on the visceral surface (4.6 mm), and in the remaining regions varies from 3 to 3.6 mm. The external layer of the muscular coat is thin, since its thickness never exceeds 0.5—0.8 mm. It runs along the omasal laminae and forms a solid plane over the whole area of the omasum. The internal layer determining the thickness of the muscular coat of the omasum is arranged perpendicularly to the line of the omasal laminae. This layer forms the omasal pillar in the ventral end of the base of the omasum (Photo. 34 a). In cross-section it is oval in shape and measures 16.2 × 18.2 mm (»Pokorny«) and like a horseshoe embraces the omasoabomasical opening from the cranial, right and left side. The caudal margin remains free, since it is here that the muscle fibres disperse in fan shape into the internal muscular coat. On both surfaces of the omasum the position of the omasal pillar corresponds to the grooves described (see above).

The mucous membrane is brown in colour, lighter in calves and young animals than in adults; it forms the omasal laminae. Measurement and classification of the laminae were made on omasum transected in the medium section (Photo. 31). The total number of laminae occurring in this place varies from 128 to 186 (Table 8 a). Five orders were distinguished on the basis of the height of the laminae and their extent in relation to the reticulo-omasical opening. The highest, and simultaneously beginning closest to the opening, were classified as first-order (1), then in turn as second- (2), third- (3), fourth- (4) and fifth- (5) order. All laminae beginning near the reticulo-omasal opening, and classified as first-order, can be treated as a continuation of the longitudinal folds of the reticular groove. The shape of the laminae is similar to a wide (laminae 1—2-order) or narrow (3—4) sickle. The fifth-order laminae are similar in form to low folds (Photo. 32). The free borders of the laminae of the higher orders are more or less thickened, and may sometimes be bushy and branching. Bird-claw papillae occur, usually from 2—4 in number, on the free margins of the primary laminae lying near the reticulo-omasal opening (Photo. 33).

The surfaces of the laminae are covered with omasal papillae, which are higher in the upper portion of the omasum (about 1.5 mm) and sharp-ended, but downwards they become smaller and rounder. Laminae — secondary folds sometimes occur on the surfaces of the three highest orders, running parallel with them. In one case (10-year old male) round formations, up to 5 mm in diameter, were found in the laminae.

The stratified squamous epithelium covering the omasal laminae, varies in thickness (μ):

	Between micropapillae	Above micropapillae	*Stratum corneum*
»Pozew«	44 — 152 (79)	12 — 35 (24)	6 — 16 (11)
»Pomruk«	64 — 175 (115)	25 — 59 (40)	6 — 14 (9)

There are 8—12 first-order laminae; out of the 34 omasum observed, 10 occurred in 14 cases, 11 in 12 cases, 8 only twice, and 12 once. In females the number of first-order laminae (and therefore the remainder also) is greater than in males (Table 8 a).

The laminae of the first three orders in the group of young bisons (Table 9) are almost completely grown, but the fourth- and fifth-order laminae continue to grow in adult individuals. This conclusion is based on the low growth coefficient for the former and relatively high — for the latter laminae. The third-order laminae increase their breadth the most during postnatal development (6.52) and the fifth-order to a lesser degree (3.6).

The omasal groove is from 4.5 to 6 cm long and varies in breadth at the reticulo-omasal opening from 1.5 — 2.0 cm, and at the omasoabomasal opening from 5—10 cm. It is limited laterally by two laminae-folds, of which the right is slightly stronger and attains the height of 7—9 cm. These folds take the form of pillars, like the upper insertions of first- and second-order laminae, and they are similarly covered by horny papillae. The mucosa of the floor of the omasal groove is grey, weakly folded and covered with small papillae. The laminae-folds referred to above elongate at the level of the amaso-abomasal opening into abomasal valves. These valves attain a height of 11.5 cm (right) and 14 cm (left) (»Pokorny«). The mucous membrane of the abomasum passes beyond the free borders of the abomasal valves and occupies a belt about 4 cm wide on their omasad surface. The abomasal valves elongate into corresponding folds of the abomasum, but in the lowest part of the omasoabomasical opening are connected with each other by

Table 8.

Mean numbers of omasal laminae (a) and of spiral folds of abomasum (b).

Order of laminae	N	♂♂				N	♀♀				♂♂ + ♀♀		
		O. R.	Avg	S	C. v.		O. R.	Avg.	S	C. v.	Avg.	S	C. v.
a													
(1)	21	8—11	9.95	±0.93	9.35	13	9—12	10.46	±0.86	8.22	10.15	±0.88	8.67
(2)	21	9—12	10.95	±0.93	8.51	13	10—13	11.46	±0.86	7.90	11.15	±0.88	7 89
(3)	21	17—23	21.52	±1.73	8.04	13	18—25	21.92	±1.97	8.98	21.71	±1.77	8.15
(4)	21	37—45	40.90	±2.73	6.77	13	36—46	42.54	±3.13	7.47	41.53	±2.96	7.13
(5)	21	55—85	68.24	±5.86	5.89	13	68—90	75.46	±5.47	7.25	71.00	±8.15	11.48
Total	21	128—170	151.38	±11.19	7.39	13	141—186	162.08	±10.86	6.70	155.31	±14.10	9.08
b													
	25	16—22	19.16	±1.55	6.20	13	14—25	18.61	±2.78	21.38	18.97	±2.10	5.53

Table 9.

Average height (mm) and growth coefficients (g. c.) of omasal laminae.

Group	N	First order				Second order				Third order				Fourth order				Fifth order			
		min	max	x̄	g. c.	min	max	x̄	g. c.	min	max	x̄	g. c	min	max	x̄	g. c.	min	max	x̄	g. c.
1—7 days	6	30	50	40	5.01	24	33	28	5.58	14	23	17	5 63	4	10	7	4.14	1	3	1	2.26
1—5 years	7	120	280	202	1.09	100	210	157	1.11	55	140	97	1.16	16	52	29	1.46	1	6	3	1.59
6 to 23 years	17	155	280	222	5.49	103	240	175	6.20	62	180	113	6.52	18	80	42	6.06	1	8	4	3.60

a fold 3 cm high, the surface of which, directed towards the omasum, is almost entirely covered with the mucosa of abomasum (Photo. 35 - b). The lumen of the omasoabomasical opening is shaped like a triangle limited by the free borders of the abomasal valves and the omasal pillar.

The omasum lies in the right half of the abdominal cavity and in the lateral projection occupies the space contained between the 8th and 12th ribs (Photo. 23, 24 b). Downwards it extends below the costal arch and is separated from the floor of the abdominal cavity by the body of the abomasum. The upper reach of the omasum is defined by the middle of the 10th rib. The parietal surface contacts the right wall of the abdominal cavity in its ventral part, this taking place in the 9th—10th intercostal space, dorsally from the costochondral junction of these ribs.

2.4. Abomasum

The abomasum is piriform (Photo. 3—4, 3; 7—12 e). The ratio of length of the greater curvature to the lesser in adult animals is 3 : 2 (76 : 52), in a one-day old calf, 2 : 1 (51 : 24.5), in a fullterm foetus as 3 : 1 (42 : 15). Capacity measurements of the abomasum showed that the average value for adult European bison is 11 l. — for fresh material and about 50% less for fixed material (Table 5).

The serous coat is absent in the abomasum in the places which adhere to the reticulum, rumen and omasum.

The external layer of the muscular coat runs longitudinally, and its thickness is from 0.5—0.8 mm and only at the height of the pyloric sphincter is as much as 2.7 mm. The internal layer is from 1.0—2.4 mm thick and within the pyloric sphincter may be as much as 5.3 mm, and even 11 mm.

Torus pyloricus (Photo. 34, 35 e) lies on the lesser curvature and slightly craniad from the pyloric sphincter. It is shaped like an oval prominence measuring — length 43—54 mm and height — 35—40 mm. It is composed of a circular layer from 10—11 mm thick and abundant submucosa and mucosa. It increases by over four times as much in size during postnatal development.

The mucous membrane in the region of the body of the abomasum is shiny and velutinous, blueish-pink in colour, and in the pyloric part is lighter in shade. The spiral folds of the abomasum (Photo. 34, 35 c) are shaped like half-moons, and those lying closest to the lesser curvature form the direct extension of the corresponding abomasal valves, or begin on the fold connecting the abomasal valves which was described earlier on. These folds at first run parallel to the long axis of the abomasum, then separate and descend to its lateral surfaces, in the direction of the greater curvature. Two to three successive spiral folds begin on the surface of the valves directed towards the abomasum; after the initial parallel course they also descend on to the lateral surface, but to a lesser degree than the previous ones. The remaining folds have no connection with the valves and are formed independently near the omasoabomasal opening, behaving so that the closer they lie to the greater curvature, the more they run in a line close to the long axis of the abomasum. The above description shows that the folds do not take a spiral course.

Measurements of all the spiral folds showed that their height at the highest place varies in adult bison from 5 to 9.5 cm (males) and 6—12 cm (females); they are termed big folds. Between them there are far lower folds (in adults 1—1.5 cm high) and on this account, in order to distinguish them from the foregoing, they are known as little folds. In addition accessory folds are distinguished, which have a joint anterior part, but in the posterior part branch in the form of a letter »Y«. This phenomenon usually occurs on the folds laterally limiting the abomasal groove, and this applies to 30% of the bison examined. Another form of enlarging the active surface of the abomasum was also observed, namely in 16 bison (42%) successive folds termed secondary folds are encountered on the big folds. The total number of spiral folds (not counting the last folds) is on an average 19, males having a lower value in this respect than females (Table 8 b).

The abomasum is situated immediately on the floor of the abdomen in its cranial part (Photo. 22 — 24 c). Cranially it reaches to the 7th intercostal space, where it contacts the costal part of the diaphragm. Furthest caudad is the apex of the arch formed by the transition of the fundus of the abomasum into the pyloric part. This part lies in the elongation ventrad of the 12th intercostal space, at a distance of about 12 cm from the costal arch. In view of the fact that the pyloric part of the abomasum has no adhesions with the neighbouring organs but is merely secured by a lesser or greater omentum, it has no fixed position.

2.5. The stomach as a whole; changes due to age

The average capacity of the stomach in adult bison is 130.5, and in newborn animals — 3.9 l. (fresh material). Measurements made of fixed viscera gave results lower on an average by 27% (Table 5).

The material available made it possible to trace the formation of reciprocal capacity relations between the compartments of the stomach in bison of different ages. In the case of newborn calves the rumen forms on an average 29% and the abomasum 64% of the total stomach volume, whereas in 6-week old calves the corresponding values are 46% and 51%. In adult individuals the rumen on an average forms 81%, and the abomasum 9%, of total stomach capacity, and thus their capacity ratio is on an average 10.17 : 1, with very great individual variations (Table 5). Analysis of capacity ratios, obtained from fixed material of adult bison (Table 5), points to the relative growth of the rumen at the expense of the other parts of the stomach.

In postnatal development the stomach as a whole increases its capacity by 33.5 times, the various parts of the stomach differing in their participation in this. Thus the first place is occupied by the rumen — increase by 94.5 times, then the omasum — 61.8 times, reticulum — 39.6 times and abomasum — 4.4 times. This is conditioned by the development of the various parts of the stomach in a newborn animal, in which the abomasum forms 22.7%, reticulum — 2.6%, omasum — 1.6% and rumen — 1.1% of the volume of its corresponding parts in adult animals.

The interdependence of capacity and units of the oblique length of the trunk are defined as relative capacity (Table 10). This capacity in 6-week old calves exhibits almost double increase in comparison with newborn animals, while young bison exhibit increase of almost six times as much in comparison with calves. The relative capacity of the stomach in European bison considered as fully developed increases by 23% in comparison with the young animals.

The relative capacity of the different stomach compartments during postnatal development is as follows. The rumen in older calves in comparison with newborn animals increases on an average by 3 times. Increase in the rumen continues to exceed the linear increase in oblique length of the trunk, since in young bison capacity is almost 10 times greater than in the preceding group. On an average it is only 32% greater in adult bison in comparison with young animals.

The relative capacity of the abomasum during postnatal development is as follows: between the group of 6-week old calves and newborn calves increase is only 36%; the case is similar in respect of increase between calves and young bison. In adult individuals, however, increase drops to 7% in relation to young animals. On the basis of the foregoing it may be concluded that in calves and juveniles development in the capacity of the abomasum is characterized by greater dynamism than increase in oblique length of the trunk, whereas in bison considered as adult the trunk grows more quickly than the abomasum. The reticulum and omasum attain maximum value of relative capacity in young animals (Tab. 10).

Table 10.

Relative volume of stomach and intestine, data obtained from ratio: volume to oblique length of trunk acc. to dimension »a« (ml/cm).

Group	N		Stomach					Intestine			Alimentary canal
			Rumen	Reticulum	Omasum	Abomasum	Whole	Small	Large	Whole	
Fresh material											
Newborn	3	min	12.8	1.0	1.5	31.7	53.4	40.5	15.8	57.7	113.5
		max	23.5	2.6	3.1	47.7	70.0	48.1	19.4	67.5	127.7
		$\bar{x}$	17.6	1.8	2.3	39.2	60.9	44.3	17.5	61.8	122.7
Calves 6 weeks old	2	min	45.0	2.1	0.8	50.3	98.6	72.4	28.2	104.7	203.3
		max	50.8	2.4	2.2	56.3	111.4	98.6	32.3	126.7	238.1
		$\bar{x}$	47.9	2.2	1.5	53.3	105.0	85.5	30.2	105.7	220.7
Young bison 2—3.5 years old	2	min	305.0	23.1	49.6	68.7	451.3	221.9	118.9	331.8	783.1
		max	649.7	31.6	54.7	73.6	804.7	320.3	160.0	486.3	1291.0
		$\bar{x}$	477.3	27.3	52.1	71.1	628.0	266.6	142.5	409.1	1037.0
Adults 6.5—14.5 years	7	min	467.7	14.4	30.5	47.7	614.7	258.8	173.5	455.7	1070.7
		max	781.8	43.8	73.0	82.5	916.2	386.4	280.1	659.9	1466.6
		$\bar{x}$	629.7	26.6	51.3	65.6	772.6	326.1	220.4	546.5	1300.2
Fixed material											
Adults 6.5—24 years	3	min	448.7	6.0	9.7	36.4	527.2	208.7	113.3	330.4	857.5
		max	552.6	27.5	44.0	49.6	639.5	227.6	121.7	340.9	980.3
		$\bar{x}$	510.4	15.0	28.1	41.1	594.6	218.1	117.5	335.6	918.9

3. Intestine

3.1. Small intestine

3.1.1. Formation and location; dimensions

3.1.1.1. Duodenum. The cranial portion of the duodenum is directed from the pylorus dorsally and depending on the position of the latter (see above) slightly craniad or caudad. *Ampulla duodeni* (Photo. 23, 24 d) occupies the ventral part of this portion of the duodenum and its diameter varies from 7.5—9 cm, whereas in the dorsal part (cranial portion) it is only 6—7 cm. The cranial portion is in immediate contact with the right abdominal wall, before it disappears behind the ventral border of the right lobe of the liver. Length of the cranial portion of the duodenum in an adult bison is 25—60 cm. It is arranged in short coils, made possible by its loose junction with the lesser curvature of the abomasum and omasum by means of the lesser omentum. The sigmoid flexure is formed more or less at the level of the gall bladder. It consists of two bends lying one behind the other — a descending and ascending, which form an arch with the convexity directed ventrally. The degree of formation of the sigmoid flexure may differ and in one case (a 14-year old female) it was completely absent. The bile duct opens on the medial surface of the ascending bend of this flexure. This occurs at the level of the 13th — 14th thoracic vertebrae, a handsbreadth below the right kidney; in adult bison it is situated at an average distance of 54 cm from the pylorus (fluctuations in this distance are relatively great — from 43—70 cm). The diameter of the duodenum at the level of the opening of the bile duct is markedly constricted. At the level of the last costochondral junction (14) the duodenum again appears from behind the right lobe of the liver. In the cranial duodenal flexure which lies ventrally under the right kidney, the duodenum turns caudad at nearly a right angle and becomes the descending portion (Photo. 22—24 e). It runs horizontally, with greater or lesser deviations ventrad and forms one, and sometimes numerous, small coils. The pancreatic duct enters this part of the duodenum at a distance of 37—70 cm (average 50 cm) behind the opening of the bile duct and 85—123 cm from the pylorus. The opening of the pancreatic duct is located at the level of the 2nd — 3rd lumbar vertebra, 5—10 cm behind the last rib and about 15 cm ventrally from the transverse processes of the lumbar vertebrae; it is also indicated by a slight constriction of the diameter of the duodenum. Caudally from the opening of the pancreatic duct the descending part of the duodenum is about 15—20 cm long and reaches to approximately the level of the *tuber coxae*. Behind the caudal margin of the distal loop of the colon the duodenum turns sharply left and dorsad. This is the caudal flexure of the duodenum (Photo. 24 g); it is here that the ascending part of the duodenum begins (Photo. 38 b). It is from 40—50 cm long and ends in the duodenojejunal flexure, which is situated at the level of the first lumbar vertebra. The diameter of this part of the duodenum is 3.5—4.5 cm. The length of the whole duodenum in adult bison varies within wide limits, the average being 153 cm (Table 11).

The capacity of the duodenum in adult bison is on an average 2.74 l, which forms on an average 5% of the capacity of the whole of the small intestine and thus more than in the case of the length of the duodenum (in %). This is evidence of the greater diameter of the duodenum in comparison with the other parts of the small intestine.

The length of the duodenum in calves from 1—2 days old expressed as the percentage of the small intestine is slightly greater than in adult animals. The reverse applies to the question of capacity (Table 11). It is possible that the weakly formed *ampulla duodeni* in calves accounts for this.

3.1.1.2. Jejunum. The jejunum is arranged in short looped coils which are attached in a wide arch on the periphery of the *ansa spiralis coli*. The characteristic »garland« is formed in this way, surrounding the arrangement of the large intestine cranially, ventrally and caudally (Photo. 36—39, c). The mesentery of the jejunum is longest in the caudal part and therefore the intestinal coils suspended on this part of the mesentery have considerable freedom of movement, and may thus obtrude between the rumen and left abdominal wall.

The jejunum in respect of length and capacity forms 94% of the small intestine (Table 11). The constancy of the percentage of length, regardless of age and the slightly higher percentage of capacity in newborn animals than in the other age groups is remarkable.

3.1.1.3. Ileum. The ileum runs from the last coil of the jejunum, which lies ventrally and cranially from the apex of the cecum. Thence it runs craniad and dorsad in an almost straight line, although it may sometimes form a single coil (Photo. 37 d). The ileocecal junction lies at the level of the 3rd lumber vertebra, about 30 cm ventrally from the right transverse process. The ileum enters the large intestine on the ventro-medial surface.

The ileum is the shortest part, as it forms only 1—2% of the length of the small intestine (Table 11). The diameter of the ileum is 4—4.5 cm, and it is thus slightly narrower than the jejunum. The capacity of the ileum is also small, since in adult bison it varies from 0.410 to

Table 11.

Length in metres (m) and volume in litres (l) of different parts of the small intestine and their percentage in the small intestine as a whole.

Group	N		Duodenum				Jejunum				Ileum			
			m	l	%	%	m	l	%	%	m	l	%	%
Fresh material														
Newborn	3	min	0.59	0.08	4	3	10.93	2.42	93	95	0.17	0.02	1	1
		max	0.71	0.10	6	3	13.35	2.88	94	96	0.22	0.04	1	1
		x̄	0.67	0.09	5	3	12.51	2.72	94	96	0.19	0.03	1	1
Calves 6 weeks old	2	min	0.89	0.16	4	3	23.98	5.40	94	93	0.34	0.09	1	1
		max	1.10	0.50	4	5	24.59	8.85	95	96	0.36	0.22	1	2
		x̄	0.99	0.33	4	4	24.28	7.12	94	94	0.35	0.15	1	2
Young bison 2—3.5 years old	2	min	1.35	1.10	4	4	28.37	23.89	94	94	0.58	0.35	1	1
		max	1.82	2.96	5	5	37.38	54.70	94	94	0.64	0.64	2	1
		x̄	1.58	2.03	5	5	32.87	39.30	94	94	0.61	0.50	1	1
Adults 6—14.5 years old	7	min	1.29	1.45	3	3	34.90	42.77	93	93	0.53	0.41	1	1
		max	1.83	4.30	4	6	41.45	67.84	95	95	0.91	0.92	2	1
		x̄	1.53*	2.74	4	5	37.24	52.53	94	94	0.72	0.73	2	1
Fixed material														
Adults 6.5—24 years	9**	min	1.07	0.90	4	6	23.40	16.88	92	90	0.46	0.20	1	1
		max	1.78	3.62	6	9	37.62	35.10	94	93	1.16	0.41	4	2
		x̄	1.45	1.89	5	7	29.36	27.08	93	92	0.61	0.33	2	1

*) n = 8, **) n = 4 (volume only).

0.920 l. Further evidence of its smaller diameter in comparison with the jejunum is the lower average percentage in capacity than length of the small intestine (the reverse situation was found only in two cases).

3.1.2. Structure of the wall

The small intestine, and particularly the jejunum, is rich in lymphatic elements which lie in the mucous membrane. Peyer's patches are clearly visible with the naked eye (Photo. 40). Aggregated nodules occur regularly in the jejunum and ileum (Table 12).

Table 12.
Number and distribution of aggregated lymphatic nodules in small intestine.

Name	Total number	Length / breadth (cm)	Distribution		
			Final part of duodenum	Jejunum	Final part of ileum
Pomiła	55	—	—	+	+
Zon	37	—	—	+	+
Puslon	32	1.0 — 20.0 / 0.3 — 1.5	—	+	+
Pokorny	26	2.3 — 17.0 / 0.7 — 2.0	—	+	+
Pociecha	23	2.5 — 16.0 / 0.5 — 1.8	—	+	+
Pomruk	29	0.5 — 10.0 / 0.4 — 1.0	+	+	+
Karpacz	28	0.5 — 17.0 / 0.5 — 2.0	+	+	+

In two cases they were found in the duodenum. In »Pomruk« three small round patches 4—5 mm in diameter were observed, situated caudally from the minor duodenal papilla, whereas in »Karpacz« one patch measuring 25 × 12 mm occurred, situated 10 cm before the end of the duodenum.

In the jejunum frequency of occurrence of Peyer's patches at first increases backwards, so that in its middle part they are observed at intervals of 30—50 cm, then are more thinly scattered and in the final few metres may not occur at all. In the final part of the ileum solitary lymphatic nodules appear which gradually become denser, producing a large nodule at the opening of the intestine. The lymphatic tissue occurring near the ileocecal valve (Photo. 42 c) can be treated as a continuation of the patch from the ileum. In young bison a larger number of lymphatic patches is found than in adults (Table 12).

The major duodenal papilla (Photo. 41) forms, as it were, part of the bile duct protruding into the lumen of the duodenum. It must however be searched for not at the level of the opening of the bile duct but, as a result of its oblique course through the wall of the intestine, more caudally (—3.9 — 5.5 cm average 4.4 cm). This papilla exhibits a wide variety of forms. It most often oppears as two folds of uneven size limiting the fissure-like lumen. Measurements of the papilla: length — 7—16 mm, breadth — 7 mm; the lumen of the papilla is as much as 10 mm in length. Cranially from the papilla, on the surface of the mucosa, a distinct longitudinal prominence can be seen which is the trace of the oblique passage of the bile duct through the wall of the duodenum.

»Untypical« duodenal papillae were observed in two bison only. In one of them (a 3-year old male) the lumen of the papilla was divided into two »storeys« by a sort of fold which is nothing more than one of the numerous (largest) fold of the mucosa of the bile duct, slightly hyperdeveloped in the case in question. The major duodenal papilla in the second individual (a 24-year old female) has an unusual appearance. It consists of the base 15 mm long, which would appear to correspond to the normally formed papilla and from the two free parts running from it, similar to pendants. Their measurements are as follows: length of each 35 mm, breadth of one — 7 mm, breadth of second — 18 mm, thickness of each about 5 mm. The strongly compressed aperture of the bile duct is situated between the free parts described.

The minor duodenal papilla is a miniature of the major papilla, and protrudes into the lumen of the intestine for the height of 3 mm and length of 8 mm. The opening of the pancreatic duct is fissure-like and from 2—4 mm in length. Transition through the wall of the intestine takes place over a longer path in the case of the bile duct, since it is on the average 5.3 cm (2.7 — 8.0 cm).

In one case (15-year old male) the pancreatic duct was found to open in an unusual way. It ends in an aperture, without any special swelling, from the lateral margin of which two small thickenings run caudad. At a distance of 3 cm from this aperture the thickenings enlarge and join together, forming the beginning of an arch which limits a kind of duct-tunnel. This duct is 2.7 cm in length and ends in a minor duodenal papilla of typical appearance. Whether this is connected with the monstruous diameter of the pancreatic duct in this bison (Photo. 24 f) and where the pancreatic juice flowed is difficult to say.

3.2. Large intestine

3.2.1. Formation and location; dimensions

3.2.1.1. Cecum. The cecum in the bison is cylindrical in shape, ending gently in an apex and smooth walls (it has no taeniae or haustra

Photo. 36—39 e). The diameter of the cecum in adult bison is from 9—13 cm and may be even over the whole length, or may exhibit constriction usually halfway along the length. The length of the cecum in adult bisons is on an average 0.88 m, capacity may be as much as 7.4 l, with very great individual variations. Results 19% (length) and 35% (capacity) were obtained on fixed material — see Table 13.

Table 13.

Length (m) and volume (l) of cecum and colon together with rectum. Observed ranges and averages are given.

Group	N	Cecum		Colon with rectum	
		Length	Volume	Length	Volume
Fresh material					
Newborn	3	0.17 — 0.27 0.22	0.13 — 0.27 0.20	2.06 — 2.47 2.31	0.84 — 0.89 0.91
Calves 6 weeks old	2	0.33 — 0.35 0.35	0 44 — 0.65 0.54	3.73 — 3.88 3.80	2.08 — 2.50 2.29
Young bison 2—3.5 years old	5	0.65 — 0.77 0.71	4.28 — 5.25 4.76 *)	4.38—10.73 7.90	9.87—24.9 17.42*)
Adults 6—18.5 years old	14	0.67—1.05 0.88	3.81—11.25 7.37 **)	9.45—13.47 11.32	24.00—40.00 30.71**)
Fixed material					
Adults 6.5—24 years old	10	0.48 — 1.02 0.71	1.25 — 7.95 4.81 ***)	5.75—10.74 7 44	9.16—13.48 11.37***)

*) n = 2, **) n = 7, ***) n = 4.

The beginning of the cecum lies at the level of the 3rd lumbar vertebra. Thence it runs caudad almost horizontally in the dorsal 1/3 part of the right half of the abdominal cavity. The cranial part of the cecum (over 3/4 of the whole) connects by means of the ileocecal fold with the ileum and lower with *ansa spiralis coli*. As a result this part of the cecum has a more fixed position than the caudal part, which slips out from the omental sling and enters into the pelvic cavity, where it may reach to the transverse plane drawn through the caudal margin of the pelvic acetabulum.

Variants: in a 14-year old female, which had been fixed *in toto*, the very small measurements of the cecum are remarkable; its length is only 0.48 m and its diameter, measured on the narrowest terminal part measuring 18 cm in length, is only 2.6 mm. There is no caudal part, usually devoid of mesentery.

In the female bison »Beste« (24 years old) the apex of the cecum was bent at an acute angle ventrally and cranially. The whole suggested a tobacco pipe turned downwards.

3.2.1.2. Colon. The proximal loop of the colon (Photo. 36—38 f) consists of three elongating bends. The ventral bend begins at the ileocecal junction and has the same diameter as the beginning of the cecum. This bend, in comparison with the other bends of the colon, is a short section, only 6—10 cm. It runs craniad and lies on the level of the 2nd and 1st lumbar vertebrae. It next turns in a short sharp arch dorsad and slightly to the left, elongating in the medial bend. This bend is arranged on the previous and $^1/_3$ of the cranial part of the cecum to which it closely adheres. It runs caudad for a distance of about 40 cm and reaches to the level of *tuber coxae*. The medial bend turns sharply to the left and under the distal loop of the colon continues into the dorsal bend. The length of the dorsal bend is from 30—40 cm, while the diameter gradually decreases so that at the place of transition into the first *gyrus centripetalis* of *ansa spiralis* it measures from 5—6 cm. The length of the whole proximal loop is from 75—90 cm.

Ansa spiralis coli (Photo. 36—38 g) consists of centripetal gyri, central flexure and centrifugal gyri. The arrangement and number of coils was traced on the intestines of 29 bisons (21 males and 8 females). It was found that in 27 animals a regular pattern occurred; 16 cases were found with two centripetal gyri (12 males and 4 females) and 11 with two and a half centripetal gyri (7 males and 4 females). The number of centrifugal gyri was respectively 2 and 2.5.

What is known as the accessory loop occurs with considerable regularity on the final, most peripheral centrifugal gyrus; it was not observed in 5 animals only. It is geniculate or similar to the letter »U« in shape and usually lies on the ventrocranial or ventral part of *ansa spiralis* (Photo. 36—39). Sometimes (in 3 cases) the additionally folding last centrifugal gyrus draws the first centripetal gyrus after it. In one animal, apart from that described, two accessory loops occurred on the caudal and dorsal part of the first centrifugal gyrus. The described pattern of *ansa spiralis* was held to be regular.

In two cases (out of 29) deviation from the relations described was observed, in one animal the central flexure was arranged dorsally, instead of cranially or caudally, and two accessory coils were formed as a result (Photo. 38 g), in the second the coils were dislocated to a degree which made them unsuitable for a concise description.

The total length of the centripetal gyri was from 185—236 cm and that of the centrifugal gyri 196—230 cm. The diameter of this part of the colon was 5.5—6 cm.

The distal loop of the colon (Photo. 36, 39 h) consists of a dorsal and ventral bend, each of them measures from 35 to 40 cm in length. They also have a uniform diameter of 5—7 cm. The whole of the distal loop is similar to a letter »U« or »V« open cranially, arranged within the proximal loop.

The transverse colon is a short part only 10—15 cm long. It constitutes the extension of the ventral bend of the distal loop and craniad embraces in a backwards loop the cranial mesenteric artery and portal vein. This arch lies at the level of the 14th thoracic vertebra. The transverse colon runs from right to left and from the bottom dorsad continues into the descending colon.

The descending colon (Photo. 36—39 i) is directed caudad and after running about 50 cm, that is, at the level of the 5th, last lumbar vertebra continues into the sigmoid colon. In the bison examined the sigmoid colon was sometimes difficult to find, and as a rule did not occur in calves, and the boundary between the colon and rectum has not therefore been determined, but measurements of length and capacity of these parts made jointly (Table 13). In respect of capacity the colon and rectum form 81% of the large intestine, and in respect of length 93%. This considerable difference is due to the lesser diameter of these parts in comparison with the cecum. Beginning from the sigmoid colon the diameter of the large intestine in calves gradually increases (Photo. 36—37).

3.2.1.3. Rectum. The cranial part of the rectum, about 30 cm in length, is connected with the dorsal abdominal wall by short mesentery, while the remaining part lies in the extraperitoneal part of the pelvic cavity. The rectal ampulla may differ in shape. Either gradual increase in the diameter of the rectum was found to 9—12 cm, or its rapid dilation to 12—16 cm. In the latter case he dilated section was 17—20 cm in length (Photo. 43).

3.2.2. Structure of wall

Differences can be seen in the serous coat in different parts of the large intestine. It entirely covers the cecum only. In the colon, in places where the intestinal coils adhere closely to each other, the serous coat is unable to cover these parts of the intestine over the whole area. The peritoneum reaches further on to the rectum on its ventral than its dorsal surface. As a result the extraperitoneal part of the rectum is about 10 cm long on the ventral surface and 20—25 cm on the dorsal surface. Considerable deposits of adipose tissue collect under the serous coat of the transverse colon, descending colon and rectum, and sometimes the last centrifugal gyrus (Photo. 36—37).

The muscular coat consists of two layers. The longitudinal layer arranged on the exterior is thinner than the circular layer, which lies deeper. The thickness of the two layers increases in the cauded direction and is thickest immediately before the rectal ampulla, where it is as much as 10.8 mm — circular and 4 mm — longitudinal (»Pomruk« — fixed material). The muscular coat of the large intestine is in general evenly arranged and has no *taeniae* or *haustra*. It is only in the region of *ampulla recti* that the two layers of the muscular coat can extend into the interior of the intestine and form the supporting structure of the largest of the transverse folds (Photo. 43 b).

The mucous membrane of the large intestine is in general smooth but the mucosa of the rectum, together with its submucosa, forms high folds in the part preceding the ampular dilation. They are arranged longitudinally and are similar to the esophageal folds (Photo. 43 a). The lumen of the rectum is as a result star-shaped. The mucosa of the rectal ampulla is clearly differentiated by its browny-green colour from the creamy-grey mucosa of the remaining part of the rectum. Transverse rectal folds occur solely in the rectal ampulla. They were encountered in varying numbers and shapes in the material examined.

The smallest number, only 4, of these folds occurred in »Pomruk« (Photo. 43 b), but they were the best developed and the wall of the largest of them included, in addition to mucosa and submucosa, the two muscular layers. In the female bison »Puszynka« 6 of these folds occurred, the three largest reaching 2.5 cm in height. In the bison »Pokorny« and »Puck« there were about 10 transverse folds which were relatively low and their stroma was formed only from the circular layer of the muscular coat.

Caudad from the transverse folds described there is the columnar zone of the anus (Photo. 43 c). Its breadth is 5—9 cm. The folds, or rectal columns, occur in numbers from 6—7. They run longitudinally and are up to 2 cm high. The free borders of these folds are usually thickened and incline towards the anus. The surface of the columns and depressions lying between them are covered with small secondary folds mainly running transversely. The denticulate anorectal line separates the rectum from the anus, the structure of which is not included in the scope of the present study.

The concentration of lymphatic tissue in the cecum take the form of lymphatic nodules, varying greatly in number and size.

Situations were encountered in which the whole mucous membrane was densely covered with them (»Zon«), or they occurred solitarily (»Karpacz«, »Pokorny«) or when they were concentrated in three places: near the ileocecal orifice, in the central part and near the apex of the cecum (»Pomruk«). No lymphatic nodules at all were observed in the cecum of the female bison »Pociecha«.

In the area of the mucous membrane of the colon, in the immediate vicinity of the ileocecal valve, the is an area of lymphoid tissue with a craterlike surface (Photo. 42 c). It never encroaches upon the mucosa of the cecum and does not cover the valve from all sides. In the remaining part of the colon solitary and thinly scattered lymphatic nodules are encountered, the numbers of which decrease in a caudal direction, again to occur in great abundance in the rectal ampulla.

3.2. The intestine as a whole; changes due to age

In calves 1.5 months old the small intestine almost doubles its length in comparison with 1—2 day old calves (Table 14). This is evidence of the intensive growth of the small intestine during this period. The mean length of the small intestine in bison considered adult is about $^1/_3$ greater than the average for young individuals. The small intestine increases 3.07 times in length during the whole of postnatal development.

In newborn calves the capacity of the small intestine is on an average 2.836 l (Table 15), which forms only 5% in relation to adult bison (in the case of length — 39%). In older calves (1.5 months old) there is an almost treble increase in capacity in relation to newborn animals. This confirms the rapidity of growth of the small intestine. In the young bison examined there a further almost 6 times greater increase in this intestine in relation to the previous group. The small intestine in adult animals has a capacity nearly $^1/_4$ greater than its capacity in young bison. During postnatal development the small intestine increases almost 19.7 times in capacity.

The large intestine (Table 14 and 15) in calves 1—2 days old in comparison with the state in animals considered as adult, forms 21% in respect of length and 3% in respect of capacity. Six-week old calves have a large intestine more than 1.5 times longer and with almost twice greater capacity than newborn animals. The increase in length of the large intestine in young bison is more than twice and capacity almost 9 times greater, in relation to the preceding group. During postnatal development the large intestine increase its length 4.83 times and capacity 34.13 times. The following conclusions can be drawn on the basis of the foregoing:

1. Stronger development of the large intestine than the small intestine is observed during postnatal development.

2. In the case of both the small and large intestine increase in capacity greatly predominates over increase in length.

The total length of the intestine in newborn animals form 30% of this measurement in adult bison; in calves at the age of 1.5 months the

Table 14.

Observed ranges and averages of length of different parts of intestine (m).

Group	N	Small intestine m	Small intestine %	Large intestine m	Large intestine %	Intestine as whole	Ratio of small intestine to large intestine
Fresh material							
Newborn	3	11.80—14.03 13.37	81—86 84	2.23— 2.74 2.53	14—19 16	14.54—16.90 15.90	4.31:1—6.29:1 5.35:1
Calves 6 weeks old	2	25.23—26.03 25.63	86—86 86	4.08— 4.23 4.16	14—14 14	29.46—30.11 29.79	5.96:1—6.38:1 6.17:1
Young bison 2—3.5 years old	7	27.40—39.87 31.83	77—85 80	5.15—11.38 8.30	15—23 20	34.30—51.22 40.13	3.41:1—5.86:1 4.11:1
Adults 6—18.5 years old	14	35.27—48.12 41.06	75—80 77	10.20—14.46 12.21	20—25 23	45.72—61.79 53.27	2.95:1—4.08:1 3.38:1
Fixed material							
Adults 6.5—24 years old	10	25.54—39.90 30.86	76—83 80	6.26—11.76 8.14	17—24 20	32.14—51.66 39.00	3.25:1—4.39:1 3.82:1

Table 15.

Changes of the volume of intestine (l) depending on the age of animals. Observed ranges and averages are given.

Group	N	Small intestine		Large intestine		Intestine as whole	Ratio of small intestine to large intestine
		l	%	l	%		
Fresh material							
Newborn	3	2.51— 2.97 2.84	70—74 72	1.06— 1.22 1.12	26—30 28	3.58— 4.25 3.95	2.36:1—2.80:1 2.55:1
Calves 6 weeks old	2	5.64— 9.56 7.60	69—78 73	2.52— 2.73 2.62	22—31 27	8.16—12.30 10.23	2.24:1—3.50:1 2.87:1
Young bison 2—3.5 years old	2	25.34—58.30 41.82	64—66 65	14.15—30.21 22.18	34—36 35	39.49—88.51 64.00	1.79:1—1.93:1 1.86:1
Adults 6—14.5 years old	7	44.84—69.94 56.00	55—65 60	27.82—51.25 38.08	35—46 40	72.65—82.41 94.07	1.24:1—1.86:1 1.50:1
Fixed material							
Adults 15.5—24 years old	3	18.47—38.92 29.64	56—67 62	14.31—19.38 17.35	33—44 38	32.78—58.30 46.99	1.29:1—2.01.1 1.67:1

length is almost doubled. Young bison have an intestine nearly as long as that proper to individuals considered as adult. The total length of the intestine increases by 3.35 times during postnatal development.

The capacity of the whole intestine immediately after birth forms only 4% of the capacity of the intestine in adult bison. In older calves we observed more than 2.5 times increase in this measurement. Considerable increase in the capacity of the intestine in comparison with the previous group continues to be observed. This is not, however, a completed process, as the capacity of the intestine in adult bison is almost half as great again (Table 15). During postnatal development total capacity increases by 23.81 times.

Analysis of tables 14 and 15 shows that in respect of length the small intestine in newborn and 6-week old calves forms a greater percentage of the whole of the intestine than it does in respect of capacity. Beginning with these animals a gradual decrease is observed with increasing age in the participation of the small intestine, and increase in the large intestine in length (lesser) and capacity (greater) in the whole of the intestine (Fig. 1).

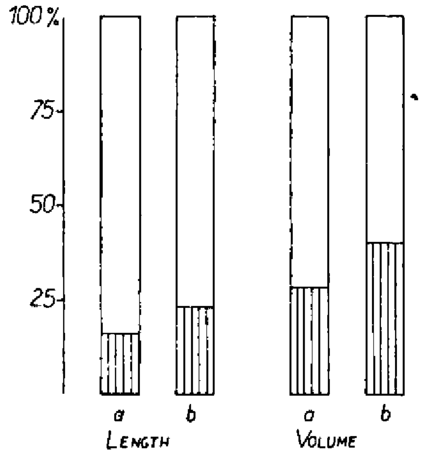

Fig. 1. Percentage formed by small intestine (unshaded field) and large intestine (shaded field) of whole intestine.
a — newborn animals, b — adult animals.

The mean value of the ratio: measurement »A«:length of the small intestine is highest in 6-week old calves, and lowest in newborn animals (Table 16). So considerable a difference in this ratio proves that the small intestine in calves at the age of 6 weeks increases more quickly than body length. Differences in the values of this ratio between young and adult bison are small and show that the linear development of small intestines reaches a state close to the final one at an early age.

Other conclusions arise from comparison of body length with length of the large intestine. This relation expressed by average values through the older calves and young bison to fully-grown bison. This gives grounds for concluding that the linear increase in the large intestine is more even and lasts longer than that of the small intestines.

The ratio of body length to length of intestine as a whole also changes with age, being greatest in 6 week old calves. In young and adult bison, however, it is lower than in older calves but higher than in the youngest calves.

Table 16.

Ratio of body length acc. to measuremens »A« and oblique length of trunk acc. to measurement »a« to the length of intestine.

Group	N		A			a		
			Small intestine	Large intestine	Whole of intestine	Small intestine	Large intestine	Whole of intestine
Fresh material								

Newborn	3	min.	1:10.17	1:2.10	1:12.53	1:18.73	1:3.33	1:23.08
		max.	1:13.24	1:2.36	1:15.34	1:23.03	1:4.35	1:27.25
		x̄	1:11 98	1:2.25	1:14.23	1:20 90	1:3.93	1:24.87
Calves 6 weeks old	2	min.	1:19.72	1:3.09	1:22.81	1:26.83	1:4.21	1:31.04
		max.	1:20.68	1:3.47	1:24.15	1:32.35	1:5.42	1:37.77
		x̄	1:20.20	1.3.28	1:23.48	1:29.59	1:4.82	1:34.41
Young bison 1—3.5 years old	6	min.	1:13.70	1:2.58	1:17.15	1:21.89	1:6.25	1:28.14
		max.	1:16.35	1:4.61	1:20.74	1:25.53	1:7.49	1:33.02
		x̄	1:14.91	1:3.60	1:18.71	1:24.29*)	1:6.87*)	1:31.16
Adults 6—17 years old	11	min.	1:14.32	1:4.29	1:18.79	1:20.10	1:6.59	1:26.69
		max.	1:20.84	1:5.74	1:26.08	1:27.26	1:8.10	1:35.36
		x̄	1:15.83	1:4:80	1:20.63	1:22.95**)	1:7.21**)	1:30.16
Fixed material								
Adults 6.5—24 years old	9	min.	1:10.44	1:2.52	1:12.96	1:14.70	1:3.97	1:19.22
		max.	1:14.95	1:4.40	1:19.35	1:23.33	1:6.88	1:30.27
		x̄	1:12.06	1:3.15	1:15.21	1:18.89	1:4.93	1:23.82

*) n = 3, **) n = 8.

Calculation of the ratio occurring between the oblique length of the trunk (measurement »a«) and length of the small intestine, large intestine, was made on less numerous material (Table 16) and this may affect the average values for the age groups (greater for young animals than for adults).

The relative volume of the small intestine (Table 10) increases in 6-week old calves almost twice as much in relation to newborn animals, but in young animals over 3 times as much in relation to calves. We observe an increase of 22% for adult bison in comparison with young animals. In relation to this the relative capacity of the large intestine increases as follows: in older calves it is over twice greater than in new-born calves, and in young bison over 4 times as great as in the latter. An increase of 55% is observed between young and adult bison.

Sexual differences in capacity and length of intestines expressed in absolute figures are minimum (Table 17). The relative size of the intestines is, however, always greater in females. This undoubtedly results from the fact that with almost equal intestines the females are smaller than males (Table 1). The limited number of observations, particularly in relation to females, does not justify drawing a conclusion as to the existence of sexual dimorphism in respect of length and capacity of intestines in European bison.

Table 17.
Comparison of length and volume of intestines in adult females and males — fresh material.

	Small intenstine		Large intenstine		Intestine as whole	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Length (m)	41.00	41.16	12.36	11.93	53.36	53.09
Length (as % of whole)	77	78	23	22	—	—
Volume (l)	56.68	54.30	37.49	39.53	94.17	93.82
Volume (as % of whole)	60	59	40	41	—	—
Ratio of length of intestine to measurement »A«	15.77:1	16.06:1	4.74:1	5.05:1	20.51:1	21.11:1
Ratio of length of intestine to measurement »a«	22.01:1	25.66:1	6.95:1	8.00:1	28.99:1	33.66:1
Relative volume (ml)/cm of measurement »a«	320.5	340.2	211.3	243.0	531.8	583.3
Ratio of length of small intestine to large intestine	—	—	—	—	3.33:1	3.48:1
Ratio of volume of small intestine to large intestine	—	—	—	—	1.53:1	1.42:1

The length of the small intestine in fixed adult bison is 25%, and of the large intestine 43% smaller than is fresh animals (Table 14). Losses in capacity due to fixing are: 47% — small intestine and 54% — large intestine (Table 15). The relative capacity (Table 10) in fixed bison decreases by 33% (small intestine) and by 47% (large intestine) in relation to fresh material. The values of the ratio of body length and length of trunk to the length of the small intestine are smaller respectively by 24% and 18% and the large intestine by 35% and 32% (Table 16). The percentage of the large intestine in length (Table 14) and capacity (Table 15) of the whole intestine decreases in fixed bison.

IV. DISCUSSION AND CONCLUSIONS

Only Piękoś (unpubl.) states that the esophagus in a 3-year old female measures 125 cm in length, and in a 18-year old female — 95 cm. Both measurements apply to unfixed material and were made under field conditions. The length of the esophagus, according to the author's own measurements made on fixed bodies, is slightly lower (Table 18).

Table 18.
Comparison of length of esophagus in European bison and domestic cattle (cm).

	Total length	Cervical part	Thoracic part	Abdominal part (diaphragmatic)
Domestic cattle				
Rubeli (1890)	76			
Martin & Schauder (1938)	110—125	50	67	3
Sisson & Grossman (1960)	90—105			
Wilkens & Rosenberger (1957)	90—95	42—45	48—50	
Rogovskyy (1959)	78 94(104)	42—52(55)	33—50	0.4—2.5
European bison				
Author's own observations	87—104	42—51	45—55	

The ratio of the oblique length of the trunk to the length of the esophagus in Sindhi Red cows is 1 : 0.6 (Villegas, 1960) and in the bisons — 1 : 1.01 to 1 : 1.09. So great a difference between the representatives of *Bovinae* given here is most certainly due to the small absolute length of the esophagus on the cow (70.0—77.5), with relatively great trunk length (117—135). The constrictions of the esophagus described in the present study occur, with the exception of the fourth, in cattle also (Rogovskyy, 1959). The observation made in relation to cattle of the lumen of the esophagus being greatest in the preventricular part (Rubeli, 1890, Rogovskyy, *l. c.*) has also been confirmed in the case of the bisons. The structure of the esophageal wall in the European bison corresponds in broad outlines to the description given for cattle, but *m. esophageus longitudinalis lateralis* distinguished by Martin & Schauder (1938) does not occur in the bisons. In addition the third layer, lying deepest, of the muscular coat takes a longitudinal course in the European bison (Photo. 1), thus differing from its transverse position in cattle (Rogovskyy, *l. c.*).

The occurrence in the European bison of formations similar to the ears of rye on the mucous membrane, of the esophagus, initial parts of the lips of the reticular groove and *atrium ventriculi* were described in respect of domestic ruminants by Rubeli (*l. c.*). Comparison of the author's own description with the photograph on p. 334 of the textbook by Nieberle & Cohrs (1962) shows that these are »pinselförmiges papilloma filiforme und disseminierte knotige Aktinomykose« in the submucosa of the esophagus. That these formations are of this character is shown by their connection with age — they occur only in European bison over 4 years old.

Esophageal glands in cattle occur only up to the level of the cricoid cartilage (Rubeli, *l. c.*). A mucous gland was also found in the bisons, in the preventricular part of the esophagus.

The description of the external structure of the rumen in the European bison applies, in broad outlines, to cattle. Exceptions occur in respect of the absence in the European bison of the caudal part of the left longitudinal groove and the pillar corresponding to it. Also the cranio-ventral blind sac was not distinguished in the rumen of bison, and in fact its existence is questioned in relation to cattle, indirect proof of which is the lack of a term for it in the proposed NAV nomenclature (1963).

Müller (1852) states in respect of the muscular coat of the rumen that it is thicker than in cattle. This is a general opinion, not supported by measurements. The relevant comparison given in the present study shows that the thickness of the muscular coat of the rumen in the European bison differs in different parts, and is as much as 3.8 mm in the thickest place. This is, as can be seen, an imposing thickness, although if we accept (after Martin & Schauder, 1938) that the thickness of the external layer of the muscular coat of the rumen in cattle is 1.5 mm, there is no fundamental difference in favour of the European bison. The pillar of the rumen would however appear to be more strongly developed in the bison than in cattle.

Owen (1848) states in relation to the papillae of the rumen that their appearance is midway between that of the ox and the American bison, and writes: »In the Aurochs the villi are shorter than in the Bison, and broader, being compressed and clavate, terminating in an even rounded margin: they are smaller and more numerous than in the Common Ox«. Müller (1852) writes of the mucosa of the rumen that it is smooth on the pillars, but that the »spade-shaped«, unusually densely distributed papillae lying by them attain the length of 8—9 lines. Wróblewski (1927) on the other hand, comparing the papillae of the rumen in the bison with those in red deer, demonstrates that »with equal length they are however 3 times broader than the stomach papillae in the red deer«. The author's own observations show that the papillae of the rumen in the European bison, depending on the place in which they occur, differ in shape, size and density of distribution. Therefore in order to make it possible to compare the European bison, American bison, domestic cattle or red deer, it is essential to maintain unity of place. It would seem that the shape of the ruminal papillae in cattle and European bison does not differ greatly. In respect of the number of papillae occurring on an area 1 cm^2 of the mucosa of the rumen Müller's (*l. c.*) opinion on their density of distribution can be confirmed. In other ruminants we find (Lihačev, 1964): cattle — 30—40, buffalo — up to 60, elk and reindeer — 50—60. Akajevskij (1939) found from 52—108 ruminal papillae, depending on the place examined, in the reindeer.

The papillae are already well developed in newborn bison, in which they are up to 2.5 mm long, and this length is doubled within 6 weeks. In newborn domestic calves, however, they are less than 1 mm at birth, but within 7—8 weeks attain their normal size and shape (Tamate *et al.* 1962). On the strength of the foregoing it may be concluded that these papillae are higher in newborn bison than in cattle and that they grow longer and attain greater dimensions in European bison.

The external structure of the reticulum in the European bison, possibly on account of its similarity to the reticulum in domestic cattle, has not attracted much attention from the authors already referred to (Owen, 1848; Müller, 1852; Wróblewski, 1927), but all of them recorded details of the appearance of its mucosa. Müller, after Owen, states that the cells of the reticulum are hexagonal only in shape and that there are no secondary folds, whereas on the basis of the author's own observation it may be said that the shape and size of the folds and also the cells of the reticulum in the bison depend on their localisation and Schels's studies (1956) showed that they also depend on the phase of action of the muscular membrane (contraction and expansion). The cells of the reticulum thus differ in shape, and are not only hexagonal; in addition to the first-order folds, second-order and third-order folds also occur. This agrees with the observations made by Wróblewski (1927).

The description of the reticular groove agrees with the descriptions known to the author relating to domestic cattle (Schmaltz, 1894 a, Ellenberger, 1895; Ellenberger, 1898; Kolda, 1930—1931). The dimensions of its component elements are similar to those in cattle (Massig, 1907, cited after Kolda, Martin & Schauder, 1938). The regularities of postnatal development of the reticular groove observed in the present study have been confirmed in studies on domestic cattle (Ščetinov, 1963).

The bird-claw papillae described here have also been recorded in European bison by Wróblewski (1927): »The corneous bird-claw papillae constantly encountered in horned cattle and the European bison in the passage from the second to third stomach, and serving to break up the large particles of food, do not occur at all in the red deer«. Knobloch (1935) described these papillae in 3 moose.

Müller (1852) states in respect of the omasum in bison that it is »rounded, compressed flat, soft to the touch«. On the basis of the author's own observations it is confirmed that this conveys the most significant features of the omasum, but the consistency of the omasum depends on the quality of food and the degree to which the organs is filled with it (Schön, 1953). According to Müller (*l.c.*) omasal laminae of 4 categories occur in the omasum, whereas Owen (1848) distinguishes only 2 kinds of them — »large and small, the larger kind presenting two size«. Wróblewski (*l.c.*) writes: »The omasum in European bison has five orders of laminae (quinqueplicata)«. The lack of agreement in this respect should not be surprising since even in relation to cattle opinions can be encountered in literature that there are five orders of laminae (Ellengerger & Baum, 1881; Pernkopf, 1931; Martin & Schauder, 1938; Friedrich, 1942; Schön, 1953; Silinja, 1962; Backer *et al.*, 1963) or four orders (Klimov, 1960; Nickel *et al.*, 1960; Sisson & Grossman, 1960; Žedenov, 1965). The total number of omasal laminae in bison is from 128 to 186, and they are divided into 5 orders, there being most often 10 of the longest laminae, with variations within limits of 8—12, whereas in the case of cattle the majority of the authors cited state that there are 12—14 first-order laminae and from 90—130 in all. The apparent inconsistency arises from the fact that the number of laminae depends on the part of the omasum (Backer *et al.*, 1963) and thus if results are to be comparable they must refer to the same region.

As distinct from cattle (Martin & Schauder, 1938) the mucosa of the abomasal valve in the European bison (also termed the omasal valve — Klimov, 1960, or *vela omasoabomasica* — Nickel *et al.*, 1960) encroaches from the side of the abomasum on to the omasad surface, covering it in a belt about 4 cm wide. What is even more interesting is that a similar situation is found in sheep and goats (Kolda, 1930—1931).

The shape and structure of the abomasum in bison is similar to that in cattle. Müller (1852) drew attention to this. The ratio of length of the greater curvature to the lesser corresponds to this ratio in cattle (Schwalbe, 1930), but the number of spiral folds of the abomasum would appear to be different in the species compared. In European bison they number on an average 19 (14—25), whereas in cattle: 12—16 (Martin & Schauder, 1938; Friedrich, 1942) 13—14 (Schwalbe, 1910; Klimov, *l. c.*), 12—25 (28) — Silinja, 1962. The height of these folds is greater in European bison than in cattle. Owen (1848) however assesses these »folds as only $1^1/_2$ inches in breadth«. The results of our observations also fail to confirm Owen's (*l. c.*) observations that the spiral folds »subside towards the pyloric half, where the chief object is the valvular protuberance which overhangs the aperture leading into the duodenum«. The fold, occurring in bison, connecting the two abomasal valves (Photo. 35 b) has not been described in the literature known to me.

The stomach capacity of an adult European bison is on an average 130 litres, making 21.9 l per 100 kg of body weight. A similar result was obtained by Wróblewski (1927). According to Gill (1965, 1967) the capacity of the ruminoreticulum in bison varies between 58.6—120 l, and the omasum with abomasum — 10.0—39.0 l.

Comparison of results of observations on stomach capacity obtained by different authors is risky on account of the lack of uniformity in the methods used. On this account the table 19 gives only measurements obtained under similar conditions (Paloheimo, 1944, cited after Warner, 1965).

Table 19.

Comparison of stomach volume in European bison and domestic cattle.

Species	N	Rumen + reticulum		Omasum		Abomasum	
		l	%	l	%	l	%
Domestic cattle	26	105—225	88	6—20	6	7—15	6
European bison	6	118—166	84	48—129	7	8—15.3	9

This comparison would appear to show that the bison has a smaller rumen and greater abomasum than cattle. The opposite conclusion is reached when we analyse the ratio of rumen:abomasum. In an adult bison it is 10,17:1 and in cattle 10:1 (Schmaltz, 1894 b) and 9.1:1 (Auernheimer 1910).

The method of measuring volume, today almost classic, has been accepted as a criterion of the development of the stomach in the present study. It has also been applied in recent years as well by such authors as: Krasota (1954), Tamate (1957), Višnevskaja (1969), Church *et al.*, (1962), Tamate *et al.* (1962), Silinja (1962), Gill (1965).

It is clear from Table 20 that the European bison is born with a better developed abomasum than domestic cattle. A certain weakness of this comparison is due to the fact that data on cattle and elk refer to weight, and on European bison to capacity, but weight and volume data are supposed to be analogical (V i š n e v s k a j a, 1960).

The author's own observations as to the percentage of the rumen (29%) and abomasum (64%) in the volume of the whole stomach in a newborn European bison are close to data for cattle — 28% and 68% (V i š n e v s k a j a, 1960) and 28% and 64% (B r ü m m e r, 1876). The results of our investigations on balancing of proportions between rumen and abomasum agree with A u e r n h e i m e r's data (1910) on cattle: in both species this takes place at the age of 6 weeks. This is certainly evidence that the change over of these animals from milk only to a mixed diet takes place at the same time.

Table 20.

Size of stomach in a newborn animal as a percentage of stomach in adult animals.

	Visnevskaja (1964)		Author's investigations
	Domestic cattle (weight)	Elk (weight)	European bison (capacity)
Whole stomach	1.38	1.92	2.75
Rumen	0.87	1 14	1.06
Reticulum	1.53	3	2.53
Omasum	0.87	1.91	1.62
Abomasum	5	8	22.72

The length of the duodenum in the European bison greatly exceeds data obtained by P i ę k o ś *et al.* (1958) for this species (78—112 cm). This may perhaps be due to this author's measurements not being sufficiently accurate, due to difficulties with field investigations. Thus the relatively long duodenum in the European bison (4% of the length of the whole small intestine) exceeds that of the duodenum in cattle also, for which the figures of 90—120 cm are most often given (M a r t i n & S c h a u d e r, 1938; E l l e n b e r g e r & B a u m, 1943; N i c k e l *et al.*, 1960) and 2.5 of the length of the small intestine (Ž e d e n o v, 1965).

The distribution of the openings of bile and pancreatic ducts in European bison comes in principle within the range of variations given for cattle (M a r t i n & S c h a u d e r, *l. c.*).

Although the appearance of the duodenal papillae is similar in European bison to that in cattle, the way in which the corresponding ducts pass through the intestinal wall would appear to be more like that in small domestic ruminants (E l l e n b e r g e r & B a u m, *l. c.*).

The number of aggregated lymphatic nodules in the small intestine in European bison may be as many as 55, with less in adult animals (23—28). For cattle the figures of 18—40 are given, and 20—58 for young animals (Ellenberger & Baum, *l. c.*) or: 18 in cattle, 25 in sheep and goats (Titkemeyer & Colhoun, 1955). The lymphatic nodules of intestines in European bison are smaller than in cattle.

Measurements of length of the cecum confirmed Müller's observations (1852) that it is longer in European bison than in cattle.

The 2 centripetal gyri (59% cases) and $2^1/_2$ (41% of cases) found in *ansa spiralis coli* differ from the number of coils in cattle. The following figures are given in textbooks: $1^1/_2$ (Klimov, 1960; Poplewski, 1948), $1^1/_2$—2 (Martin & Schauder, *l. c.*; Ellenberger & Baum, *l. c.*; Nickel *et al.*, 1960). These figures were confirmed by studies made on a larger number (735) of animals; Smith & Meadows, 1956, according to whom 2 centripetal gyri are found in 71% and $2^1/_2$ in 24% of cases. Bearing in mind the increasing number of coils in *ansa spiralis*, we can draw up the following sequence:

$1^1/_2$ — 2	— domestic cattle
2 — $2^1/_2$	— European bison
$2^1/_2$ — 3 — $3^1/_2$	— goat (Smith, 1959, Paiva & Borelli, 1965)
3 — $3^1/_2$	— sheep (Smith, 1955)
4	— camel (Myczkowski, 1965)
$5^1/_2$ — 6	— reindeer (Akajevskij, 1926)

As we observed a colon pattern in only 8 females and 21 males in our material we did not even attempt to establish sexual dimorphism characters, but statistical calculations made on a very great amount of material revealed the absence of sexual influence in sheep (Smith, 1957).

The occurrence of an accessory loop on the final, most peripherally situated centrifugal gyrus would appear to be a feature characteristic of the European bison. This may be a manifestation of the formation of a new gyrus or a tendency to separate this gyrus from the remainder, as is the case in sheep and goats (Kolda, 1931).

During postnatal development the length of intestines in domestic cattle, elk (Višnevskaja, 1964) and European bison increase by the following number of times:

	Whole intestine	Small intestine	Large intestine
Cattle	4.2	3.81	7.24
Elk	4.6	3.82	6.93
European bison	3.35	3.07	4.83

The relatively lower growth coefficients in European bison may show that bison calves are born with intestines already well developed (Table

21). The results I obtained are higher than the results of Piękoś *et al.* (*l. c.*) and do not confirm the conclusion put forward by the above author that intestines in females are longer (in absolute figures) than those of males. The results of our calculations, however, bear out the observations made by Piękoś *et al.* (*l. c.*) that in females the ratio of body length acc. to measurement »A« to length of intestines is greater than in males (Table 22).

Table 21.

Author	N		Whole intestine		Small intestine		Large intestine	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Piękoś *et al.* (1958)	4	7	44.57	48.29	35.04	37.15	9.54	11.14
Author's observations	9	5	53.36	53.09	41.00	41.16	12.36	11.94

Table 22.
Ratio of body length to intestinal length.

Author	N		Whole intestine		Small intestine		Large intestine	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Piękoś *et al.* (1958)	6	10	1:17.25	1:19.60	1:13.74	1:15.36	1:3.26	1:3.86
Author's observations	9	2	1:20.51	1:21.11	1:15.77	1:16.06	1:4.74	1:5.05

Certain differences between the ratios are due, *inter alia*, to the fact that my own data refer solely to adult European bison, whereas Piękoś *et al.* (*l. c.*) give mean values for animals, among which in addition to adults there were also young animals. This is a certain shortcoming since a chance in this ratio is observed during postnatal development — *e. g.* in the European bison — from 1 : 14.23 — in newborn animals to 1 : 20.63 in adults (in Persian sheep correspondingly — 1 : 34.27 and 1 : 45.00 — Bogoljubskij, 1954).

My own observation did not confirm the conclusion of Piękoś *et al.* (*l. c.*) that the ratio of body length of intestinal length in European bison is lower than in cattle, since according to my own calculations this was 1 : 20.63, whereas for cattle they give 1 : 20 (Ellenberger & Baum, 1943; Sisson & Grossman, 1960). It must, however, be emphasised that Piękoś *et al.* made their observations under field conditions, during frost in the winter, and referred to animals which had died of foot-and-mouth disease. It must be mentioned here that in an old Americon bison the intestine measured 157 feet (47.85 m) in length (Crisp, 1864).

The length of the large intestine is greater in the European bison than in cattle (Table 23). Piękoś *et al.* (*l. c.*) drew an identical conclusion from their investigations. I cannot, however, support the formulation of the above authors that the intestines as a whole and the small intestine are shorter in European bison than in cattle. Wróblewski (1927) also stated on the subject of the size of intestines in

Table 23.

Comparison of intestinal length in European bison and domestic cattle (m).

Author	Whole intestine	Small intestine	Large intestine
Domestic cattle			
Schmaltz, 1884 b	47—53 (50)	40—45 (41)	6.4—10.5 (8.5)
Auernheimer, 1910	49.3	36.5—45	—
Ellenberger & Baum, 1943	39—63	40—49	6.4—11
Arutjunjan, 1953	49.95	40.09	9.86
European bison			
Author's observations	53.27	41.06	12.21

Table 24.

Volume of intestines in European bison and domestic cattle.

Author	Whole intestine	Small intestine	Large intestine
Domestic cattle			
Schmaltz, 1884 b	84—118 (101)	—	12—24 (18)
Auernheimer, 1919	—	65—67	—
Arutjunjan, 1953	89.9	62.32	27.58
European bison			
Author's observations	94.1	56.0	38.1

European bison that »the small intestine measures up to 50 m in length and has a volume of 100 litres in a bison weighing 16 hundredweight«. This was an individual of a weight not encountered today (Table 1) hence the high values, since the volume of the small intestine in my own observations was only 44.8 to 69.9 l. It will be seen from Table 24 that the volume of the large intestine is greater but that of the small intestine lesser, in bison than domestic cattle.

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MORFOLOGIA PRZEWODU POKARMOWEGO ŻUBRA

Streszczenie

Opracowanie morfologii przewodu pokarmowego żubra oparto na materiale pochodzącym od osobników obojga płci (34 ♂♂ i 16 ♀♀) w wieku od 1 dnia do 24 lat (Tabela 1). Obserwacje prowadzono głównie na materiale świeżym, wykorzystano też materiał utrwalony. Cytowane niżej wartości (poza danymi dla przełyku) dotyczą materiału świeżego. Pojemność narządów oznaczano przez napełnienie ich wodą pod stałym ciśnieniem słupa wody o wysokości 10 cm.

Długość przełyku dorosłego żubra mieści się w granicach 87—104 cm, a średnica zewnętrzna waha się od 3—7,4 cm (Tabela 2—4). Żołądek żubra ma ogólny plan budowy podobny do żołądka bydła domowego (Fot. 3—12) — składa się więc z czterech komór, które u dorosłych osobników tworzą następujący szereg: żwacz — pojemność średnia 106 l, trawieniec — 11 l, księgi — 8,8 l, czepiec — 4,5 l (Tabela 5). W rozwoju pozapłodowym żołądek, jako całość powiększa swą pojemność 33,5 razy (żwacz — 94, księgi — 61,8, czepiec — 39,6, trawieniec — 4,4).

Brodawki żwacza żubra dłuższe i rosną gęściej niż u bydła (Fot. 13—20). Listewki czepca żubra (Fot. 25—27), podobnie jak u bydła dzielą się na główne i wtórne; tworzą również 4-ro, 5-cio, i 6-cio boczne figury. Blaszki ksiąg występują w liczbie 128—186 i w zależności od szerokości i zasięgu dzielą się na 5 kategorii (Fot. 31—32); pierwszorzędowych jest przeważnie 10 (Tabela 8a). Fałdy spiralne trawieńca żubra są liczniejsze (średnio 19 szt.) i wyższe (do 12 cm) niż u bydła domowego (Fot. 34—35, Tabela 8b).

U noworodka żubra jelito wynosi średnio 15,9 m długości (84% przypada na jelito cienkie), 3,9 l pojemności (72% — jelito cienkie, Tabela 14—15) i w rozwoju postnatalnym powiększa swą długość 3,35 razy (na jelito cienkie przypada teraz tylko 77%) a pojemność — 23,8 razy (59% — jelito cienkie, Ryc. 1). Stosunek długości jelita do długości ciała u żubrów jest podobny jak u bydła i wynosi 20,63:1 (Tabela 16). W błędniku spiralnym okrężnicy występują bądź 2 zawoje dośrodkowe (59% przypadków), bądź też 2,5 (41% przypadków, Fot. 36—39).

EXPLANATION OF PLATES

Plate XI

Photo 1. Muscular coat of esophagus of European bison (♂ Pomruk, 15 years old): seen from side of submucosa.
a — fasciculi of fibres running longitudinally, b — so-called »sutures«.

Photo 2. Cross-section through gland of mucous membrane of esophagus in European bison (♂ Pozew, 6 years old, approx. about 70×).

Photo 3. Stomach of European bison (♂, Pomruk, 15 years old): seen from left side.

Photo 4. Stomach of European bison (♂, Pomruk, 15 years old): seen from right side.

Photo 5. Rumen and reticulum in European bison (♂, Pokorny, 9 years old): seen from left side.

Photo 6. Rumen and reticulum in European bison (♂, Pokorny, 9 years old): seen from right side.
a — dorsal sac of rumen, b — ventral sac of rumen, c — caudodorsal blind sac, d — caudoventral blind sac, e — cranial groove, f — caudal groove, g — ventral coronary groove, h — dorsal coronary groove, i — left longitudinal groove, i′ — left accessory groove, j — right longitudinal groove, j′ — right accessory groove, k — insula of rumen, l — *sulcus atrioruminalis*, m — ruminoreticular groove, n — *atrium ventriculi*, 1 — reticulum, 2 — omasum, 3 — abomasum.

Plate XII

Stomach of European bison

Photo 7. Full-term foetus (♀): seen from left side.

Photo 8. Full-term foetus (♀): seen from right side.

Photo 9. Newborn bison (♂, Pos): seen from left side.

Photo 10. Newborn bison (♂, Pos): seen from right side.

Photo 11. Calf (♂, Plakat, 6 weeks): seen from left side.

Photo 12. Calf (♂, Plakat, 6 weeks): seen from right side.
a — esophagus, b — rumen, c — reticulum, d — omasum, e — abomasum. f — duodenum.

Plate XIII

Mucous membrane of rumen in European bison.

Photo 13. Section from left surface, immediately by dorsal curvature (♂, Pomruk, 15 years old).

Photo 14. View from left side (♂, Puck, 4 years old).

Photo 15. Section from *atrium ruminis* (♂, Pomruk, 15 years old).

Photo 16. Section from right longitudinal pillar (♂, Pomruk, 15 years old).

Photo 17. View from right side (♂, Puck, 4 years old).

Photo 18. Section from ventral sac (♂, Pomruk, 15 years old).

Photo 19. Caudal end (♂, Pomruk, 15 years old).

Photo 20. Section from ventral coronary pillar (♂, Pomruk, 15 years old).
a — cranial pillar, b — left longitudinal pillar, c — caudal pillar, d — ventral coronary pillar, e — dorsal coronary pillar, f — right longitudinal pillar, g — right accessory pillar.

Plate XIV

Abdominal topography in European bison.

Photo 21. View from left side (♂, Puck, 4 years old).
a — spleen, b — reticulum, c — rumen, 1 — IX rib, 2 — last (XIV) rib.

Photo 22. View from right side (♂, Polas, 12 years old): after transecting abdominal wall.

Photo 23. View from right side (♂, Pomruk, 15 years old): after transecting superficial wall of greater omentum.

Photo 24. View from right side (♂, Pomruk, 15 years old): after transecting deep wall of greater omentum.
a — liver, b — omasum, c — abomasum, d — duodenal ampulla, e — descending duodenum, f — pancreatic duct, g — caudal flexure of the duodenum, h — ventral sac of the rumen, i — cecum, j — proximal loop of the colon, k — coils of jejunum, 1 — xiphoid process, 2 — last (XIV) rib, 3 — *tuber coxae*.

Plate XV

Photo 25. Mucous membrane of reticulum in European bison (♂, Puck, 4 year old): seen from left side.

Photo 26. Section from diaphragmatic surface of reticulum in European bison (♂, Pokorny, 9 years old).

Photo 27. Section from lateral surface of reticulum in European bison (♂, Pomruk, 15 years old).

Photo 28. Section of fundus of the reticulum (♂, Pomruk, 15 years old).

Photo 29. Mucous membrane of *vestibulum ventriculi* (♂, Pokorny, 9 years old).

Photo 30. Reticular groove of European bison (♂, Pomruk, 15 years old): lips opened to show floor.
a — left lip, b — right lip, c — cardia, d — floor of reticular groove, e — reticulomasal opening, f — ruminoreticular fold, g — bird-claw papillae.

Plate XVI

Photo 31. Omasum of European bison (♂, Pomruk, 15 years old): cross-section.

Photo 32. Omasum of European bison (♂, Pokorny, 9 years old): cross-section along greater curvature.

Photo 33. Bird-claw papillae (adult European bison of both sexes).

Photo 34. Abomasum of European bison (♂, Pokorny, 9 years old): cross-section along greater curvature. Fixed material.

Photo 35. Abomasum of European bison (♂, Pudzik, 2 years old): cross-section along greater curvature. Fresh material.
a — omasal pillar (transected), b — fold connecting abomasal valves, c — spiral folds of abomasum, d — fold of pyloric part of abomasum, e — *torus pyloricus*, f — omasal laminae.

Plate XVII

Photo 36. Intestine of European bison (♂, Pub, 1 day old): seen from left side. Regular pattern of *ansa spiralis*.

Photo 37. Intestine of European bison (♂, Pub, 1 day old): seen from right side.

Photo 38. Intestine of European bison (♀, Pos, 1 day old): seen from left side. Irregular pattern of *ansa spiralis*.

Photo 39. Intestine of European bison (♂, Pudzik, 2 years old).
a — descending duodenum, b — ascending duodenum, c — jejunum, d — ileum, e — cecum, f — proximal loop of the colon, g — *ansa spiralis*, h — distal loop of the colon, i — descending colon.

Photo 40. Aggregated lymphatic nodules of small intestine of European bison (♂, Pokorny, 9 years old).

Photo 41. Major duodenal papilla in European bison (♂, Pomruk, 15 years old).

Photo 42. Ileocecal valve in European bison (♂, Pokorny, 9 years old).
a — colon, b — cecum, c — lymphoid tissue.

Photo 43. Cross-section through rectum in European bison (♂, Pomruk, 15 years old).
a — longitudinal folds, b — transverse rectal folds, c — rectal columns, d — mucous membrane of anus.

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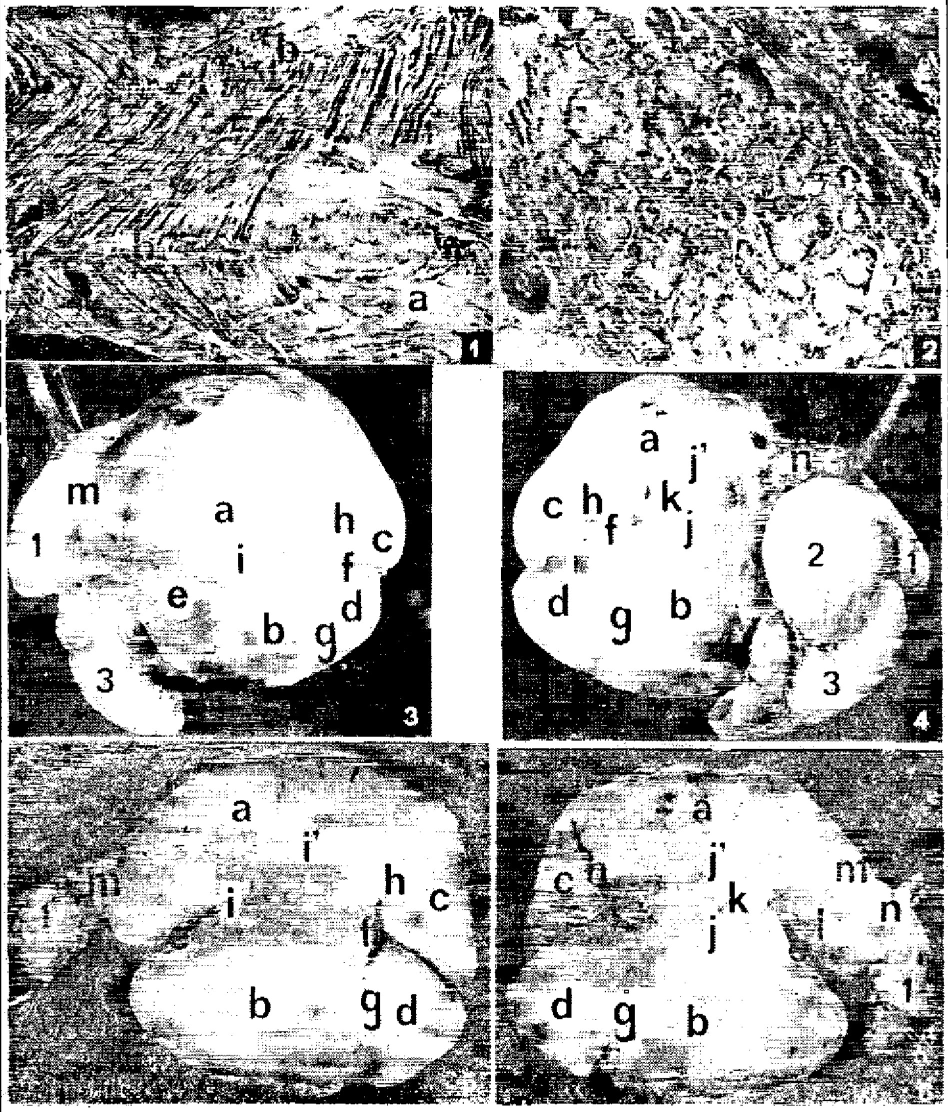

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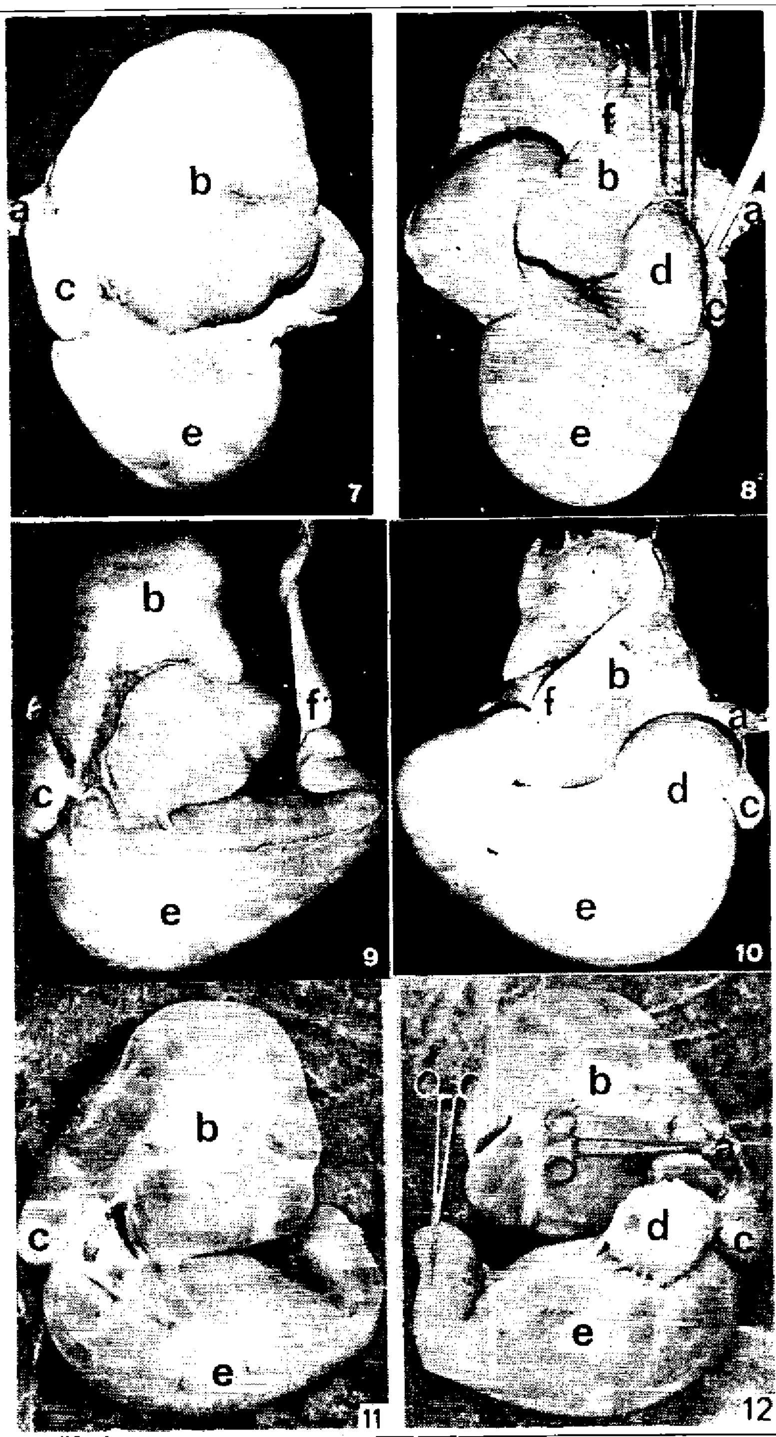

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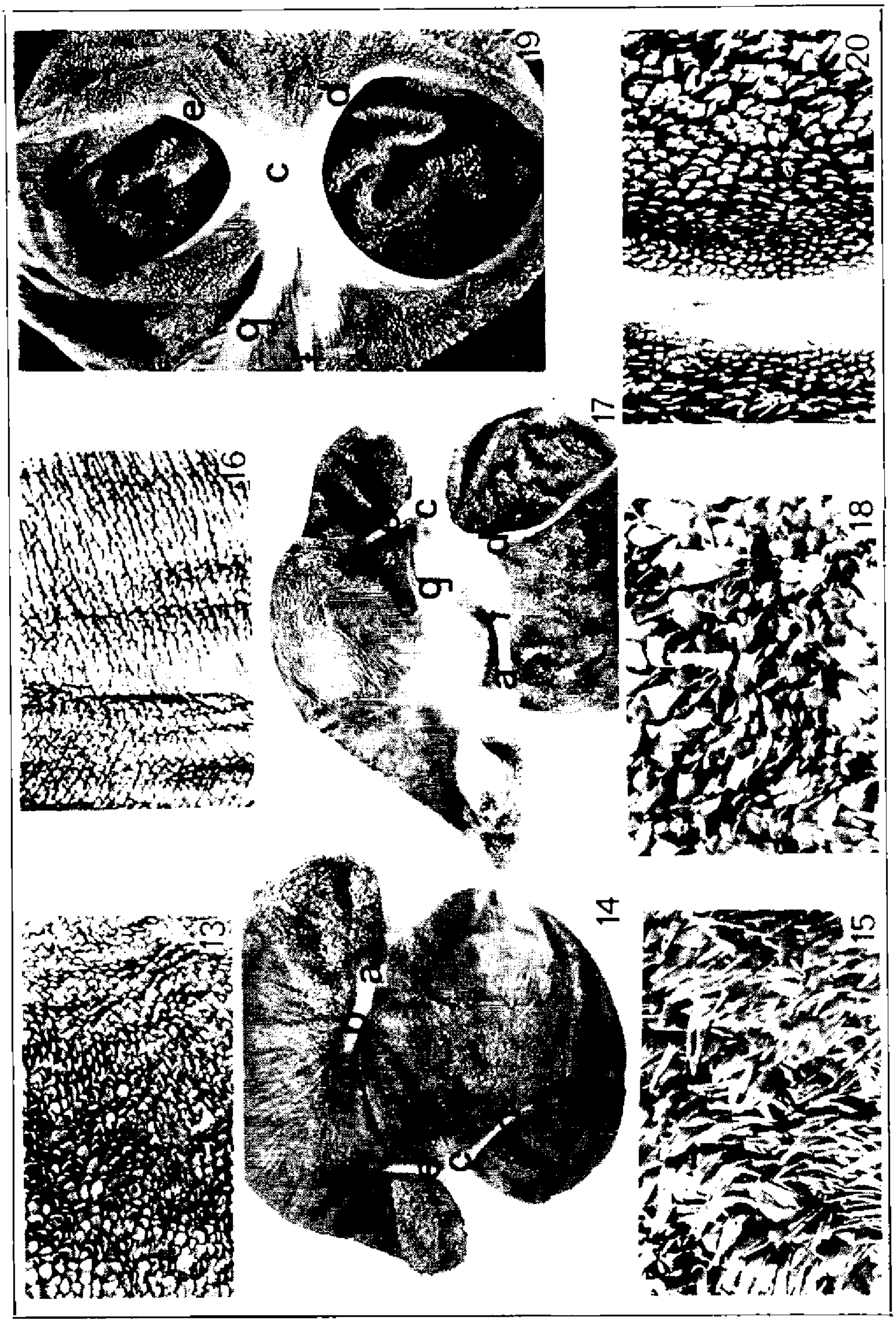

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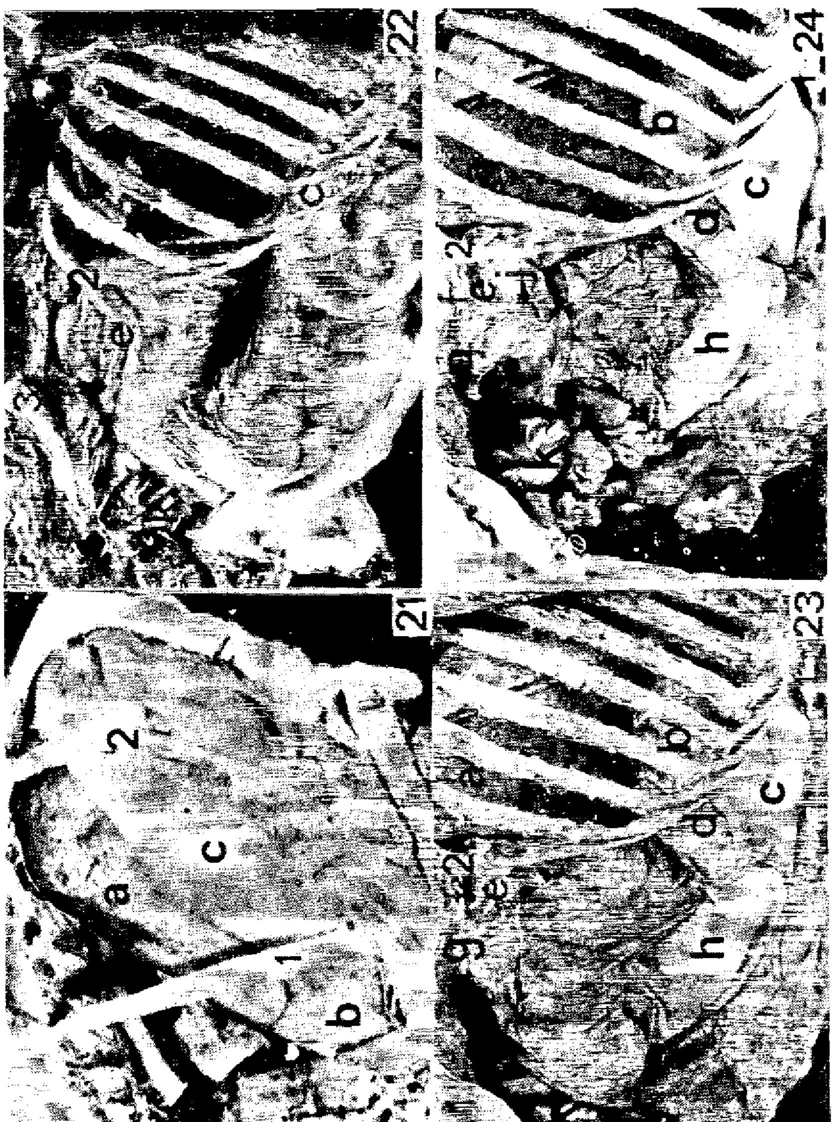

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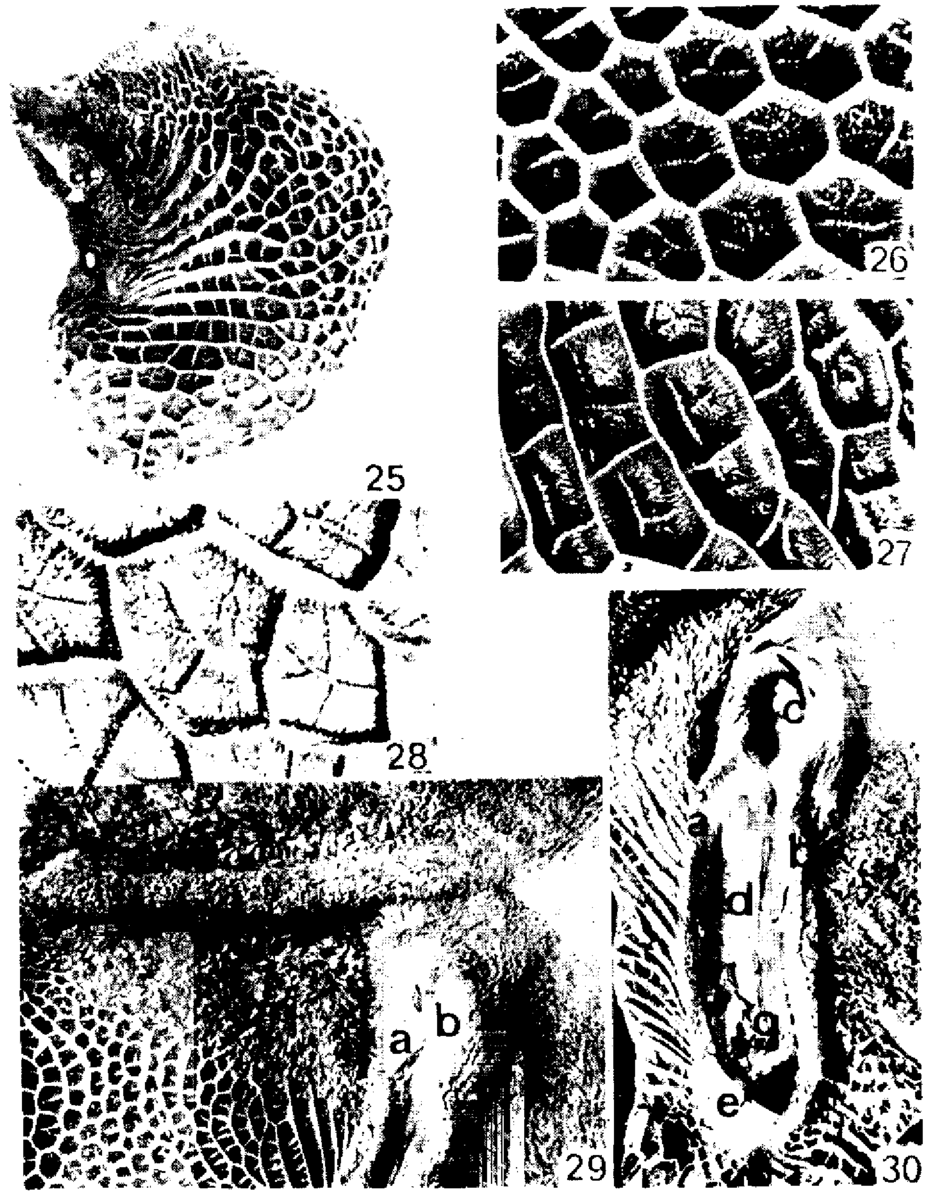

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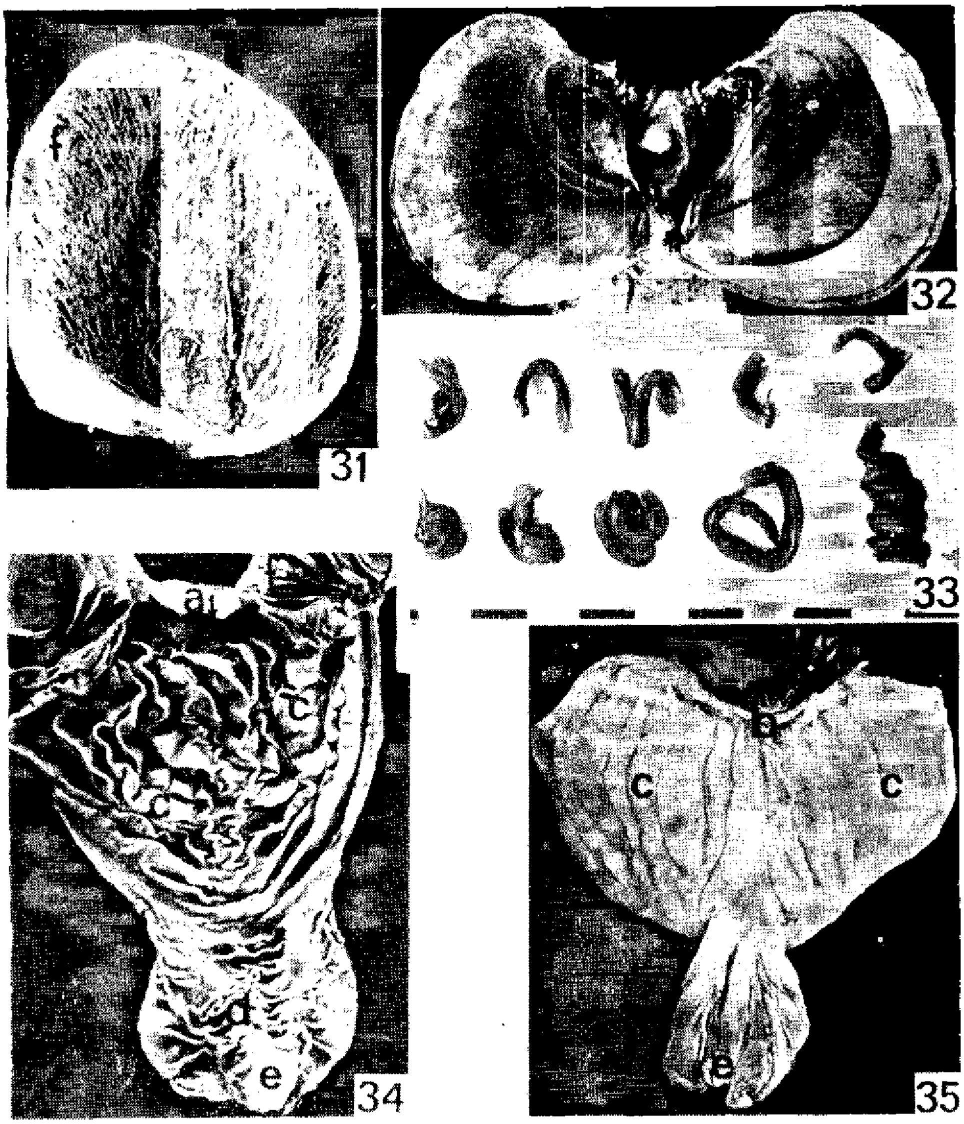

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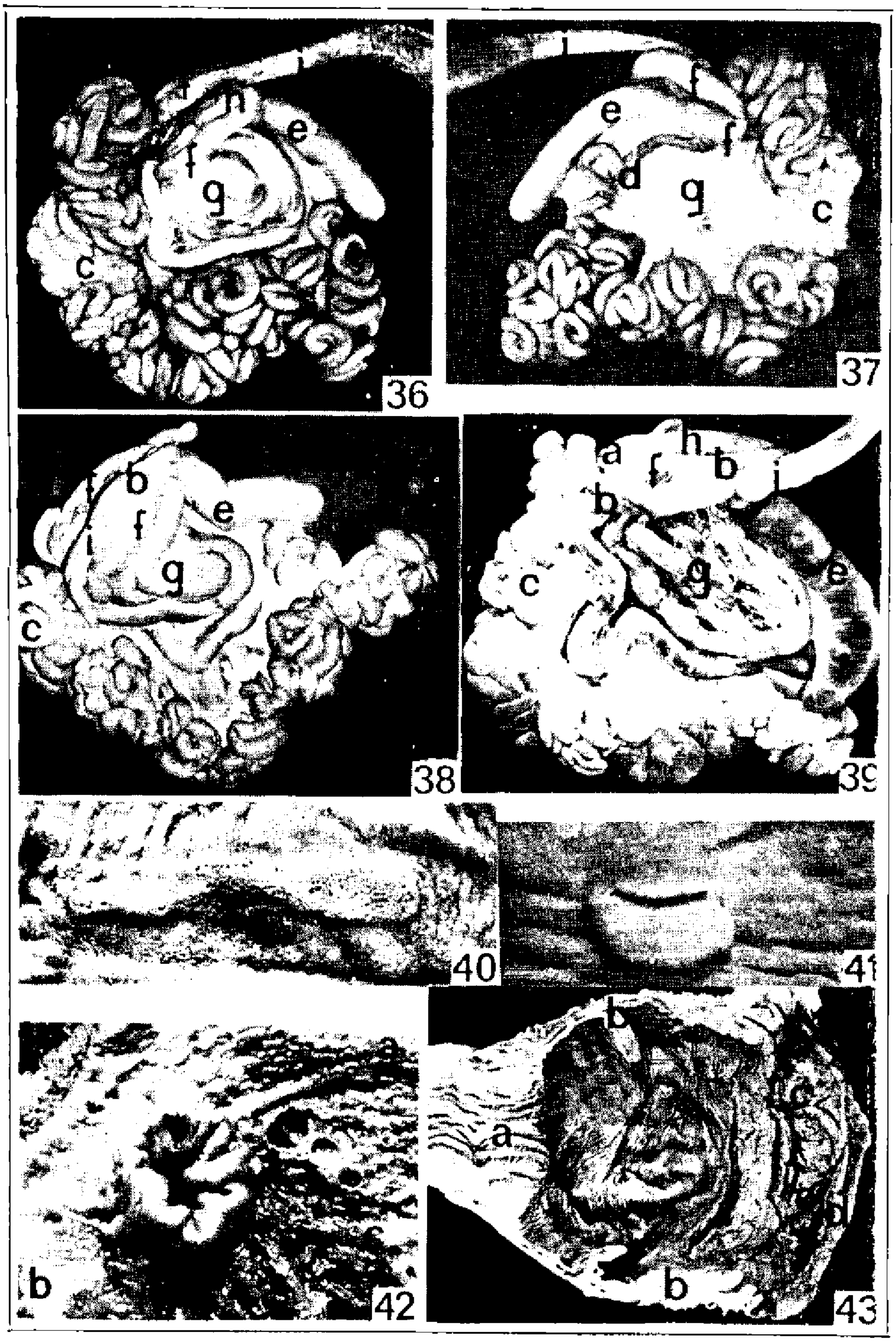

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