Anatomy of the stomach of the collared peccary, *Dicotyles tajacu (*L., 1758) (Artiodactyla: Mammalia)[1]

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Introduction

During the late Tertiary the Tayassuidae or peccaries, a family of the even-toed Artiodactyla, inhabited North America and Eurasia (Thenius 1970). Recently a fossil species of tayassuid from the Pliocene was discovered in the Varswater formation of South Africa (Hendey 1976 a, b). Today tayassuids can only be found living in South and Central America and in southwestern United States. One species, *Dicotyles tajacu,* the collared peccary, has been found as far north as southern Arizona and New Mexico as well as southwestern Texas.

A common ancestral group of both Suidae and Tayassuidae, living during the Eocene, can be assumed (Thenius 1972). Anatomical and biochemical findings demonstrate a close systematic relation between Suidae (eight living species, Haltenorth 1963) and Tayassuidae (three living species, Woodburne 1968; Wetzel et al. 1975) as has been described by different paleontologists (Colbert 1955; Romer 1966; Thenius 1970). Subcutaneous and peritoneal fat of pigs and peccaries have similar fatty acid composition. These results of Mattson et al. (1964) show a closer similarity between Suidae and Tayassuidae than between Tayassuidae and other artiodactyls. This is further exemplified by previous investigations (Langer 1973, 1974 a) concerned with homologies of different stomach types in Artiodactyla. The gastric anatomy of the peccary is, however, more complex than that of the pig.

In this paper the macroscopic and microscopic anatomy of the stomach of *Dicotyles tajacu* is described and discussed in detail.

Review of literature

A monograph on the anatomy of the peccary was published by Tyson as early as 1683. This interesting work includes a short, but precise description of the stomach of this animal. However, still earlier reports on this subject must exist as Tyson (1683) cited publications of Falcoburgius and Grew.

Alessandrini (1857) refered to the digestive tract of the collared peccary only briefly, differentiating the three distinctive sacs, but not characterizing them in detail.

More recently Stewart (1964) described the anatomy of the alimentary tract of the collared peccary. He employed eviscerated organs for this description and named the different parts of the peccary stomach according to the gastric regions of the ruminants.

Other references to the digestive tract of the peccary can be found in papers that either deal mainly with other species (Vrolik 1843; Cordier 1893) or with the comparative anatomy or histology of the stomach in vertebrates (Cuvier 1835; Edelmann 1889; Oppel 1896; Pernkopf and Lehner 1937; Langer 1973, 1974 a, b).

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Table 1

Investigated specimens of *Dicotyles tajacu*

No.	sex	age	body weight	date of death	collected		fixative	surface of gastric compartments (cm²)			
					location	investigator		ant. bls.	upp. bls.	p. and bj.	gld. sto.
1	♀	16 months	17.9 kg	19. 2. 1976	Tucson	Langer	CF				
2	♀	3 years	25.0 kg	1. 3. 1976	Tucson	Langer	CF				
2₁	♂	fetus (62 days)	16.4 g	1. 3. 1976	Tucson	Langer	CF	1.03	1.16	7.38	10.76
3	♀	3 years	26.9 kg	9. 3. 1976	Tucson	Langer	CF	214.87	171.33	346.21	182.68
4	♀	newborn	—	29. 7. 1893	Z. Berlin	MNB	A	8.04	7.64	8.71	16.00
5	♀	adult	—	23. 2. 1926	Z. Copen.	ZMC	A	327.10	179.70	387.30	183.20
6	?	—	—	—	Z. Copen.	ZMC	i. and d.				

Abbr.: A = alcohol; ant. bls. = anterior blindsac; CF = modified Millonig's formalin (Carson et al. 1973); gld. sto. = glandular stomach; i. and d. = inflated and dried; MNB = Museum für Naturkunde, Berlin; p. and bj. = gastric poch and blindsac junction; Tucson = experimental pen of the Arizona Cooperative Wildlife Research Unit, Tucson, Ariz.; upp. bls. = upper blindsac; Z. Berlin = Zoo Berlin; Z. Copen. = Zoo Copenhagen; ZMC = Universitetets Zoologiske Museum, Copenhagen.

Material and methods

Table 1 gives a compilation of data concerning investigated specimens. The stomachs of animals Nos. 4, 5 and 6 were eviscerated organs from collections of zoological museums. The anatomy of animals Nos. 1 to 3 were investigated in situ. They were made available by the Arizona Cooperative Wildlife Research Unit, Tucson. Before being prepared for dissection the animals were housed in pens and received a pelleted domestic swine food. Animal No. 2 had access to straw.

Six to ten liters of buffered formalin (Carson et al. 1973) were perfused into the vascular system of anesthetized animals via the left or right external carotid artery. Animals were fastened to a metal frame with twine or chains to assure an upright body position.

After sufficient fixation, lasting at least one day, the animals were dissected. The different steps of dissection were documented with the help of a 6 × 6 cm camera and 25 ASA film. Whenever a subsequent section of the gastrointestinal tract was opened, its contents were collected and mixed with the same volume of formalin. Each sampling was divided into two portions, one for determining particle size and particle gravity (Langer in press); the other half was sent to Dr. R. A. Prins, Utrecht, who determined volatile fatty acid composition (VFA) in the gastric contents. This rather crude method supplied data on the rations of VFA in different parts of the stomach.

Two fetuses were obtained from female No. 2. The gestation age was determined at 62 days according to Smith and Sowls (1975). One fetus (2₁) was dissected and photographed from the left side of its body. Abdominal organs from this fetus were sampled for histological serial sections. Sections 16 µm in thickness were cut. Every tenth section was stained according to Masson and Goldner and drawings were made with a thirteenfold magnification. To facilitate identification of the different gastric parts in the embryo, a reconstruction was drawn with the help of a "Perspectomat P-40"-apparatus (F. Forster, Schaffhausen, Switzerland). The areas and contours of the different gastric compartments were measured in the magnified drawings of the sections with the MOP/AM 01-system (Kontron, München, FRG), an apparatus for quantitative picture analysis. From these measurements it was possible to calculate relative volume and relative surface area of different gastric compartments. The results were compared with measurements in newborn and adult collared peccaries previously published (Langer 1973 and in press).

Additionally, the internal surfaces of the stomachs of adult animals were projected on paper and the paper surfaces were determined with the help of paper weight.

Material for histological purposes was taken from different parts of the digestive tract and stored in Carson's buffered formalin at 4 °C. This material was sectioned at 9 µm and stained with different methods.

Specimens of gastric regions with a squamous epithelium were dehydrated according to the critical-point method, sputtered with gold, and examined with a Philips scanning electron microscope 500.

The stomach of animal No. 3 was washed in running tap water for 24 hours, then filled with plastic foam. The openings necessary for emptying the different regions were then sutured. The organ was immersed in absolute isopropanol for one week, and thereafter dried at room temperature. With an oscillating saw small openings were cut into the gastric wall and the plastic foam was removed. The specimen revealed the internal differentiation of the stomach.

Results

Macroscopic anatomy

Externally four parts can be distinguished in the stomach of the peccary (Fig. 1). The nomenclature found in the literature is compiled chronologically in Table 2. It is neither clear nor consistent. In one case (Tyson 1683) the gastric compartments have been given numbers, in other cases their position in the right or left part of the abdominal cavity has been used as characterization (Cuvier 1835; Vrolik 1843). In still other cases (Cordier 1893; Stewart 1964) names of the ruminant stomach regions have been employed.

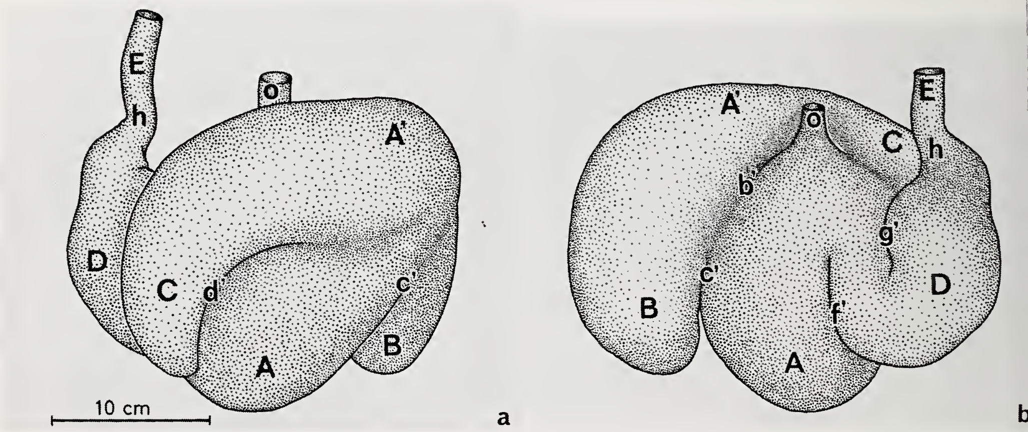

Fig. 1. Left cranio-dorsal (a) and right caudo-dorsal (b) aspect of the inflated and dried stomach of *Dicotyles tajacu* No. 6. Abbr.: A = gastric pouch; A' = blindsac junction; B = upper blindsac; C = anterior blindsac; D = glandular stomach; E = duodenum; O = esophagus; b' = fornical sulcus; c' = upper blindsac sulcus; d' = anterior blindsac sulcus; f' = ventral transverse sulcus; g' = dorsal transverse sulcus; h = pylorus

The three gastric regions that can be homologized with fornix, corpus and hindstomach are not identical with the gastric compartments that can be distinguished

Table 2

Nomenclature used by previous authors to describe different parts of the peccary stomach

FALCOBURGIUS (after TYSON 1683)	cornu in infima parte	cornu in superiore parte			
GREW (after TYSON 1683)	cone	cone	caecus ventriculus	venter magnus	
TYSON (1683)	horn	horn	second stomach	first or middle stomach	third stomach
CUVIER (1835) VROLIK (1843)	poche conique en dessous	poche conique en dessus	cul-de-sac gauche	cul-de-sac droit ou pylorique	
ALESSANDRINI (1857)	← tre sacci distinti →				
EDELMANN (1889)	blindsackartiger Anhang	blindsackartiger Anhang	linker Sack	mittlerer Sack	rechter Sack
CORDIER (1893)	extremité libre	extremité libre	cavité supérieure ou antérieure	cavité mediane=portion globulaire équivalent du rumen	cavité inférieure=troisième cavité équivalent de la caillette
PERNKOPF, LEHNER (1937)	linkes Divertikel	rechtes Divertikel	mittlerer Anhang = Fundus	oraler Sack = Vordermagen	aboraler Sack = Hintermagen
STEWART (1964)	anterior diverticulum	posterior diverticulum	rumen	reticulum	abomasum = gastric gland region
LANGER (1973, 1974 a, b) A[1]	Fornixregion=fornical region			Corpusregion= corpus region	Hintermagenregion=hindstomach region
B[2]	Parietalblindsack	Visceralblindsack	Magenbeutel Verbindungsstück d. Magenbeutels		Drüsenmagen
this paper	anterior blindsac	upper blindsac	gastric pouch blindsac junction of gastric pouch		glandular stomach

[1] A = Subdivisions according to gastric regions as they have been found during investigation of the muscular architecture of gastric wall.

[2] B = Subdivisions according to gastric compartments.

during macroscopic investigation (Langer 1973; 1974 a, b). The boundary between the fornix and the corpus is indistinct. The gastric pouch consists of parts from both regions. Also, in the glandular stomach the boundary between the corpus region and the hindstomach cannot be clearly determined without an examination of the tunica muscularis of the stomach wall.

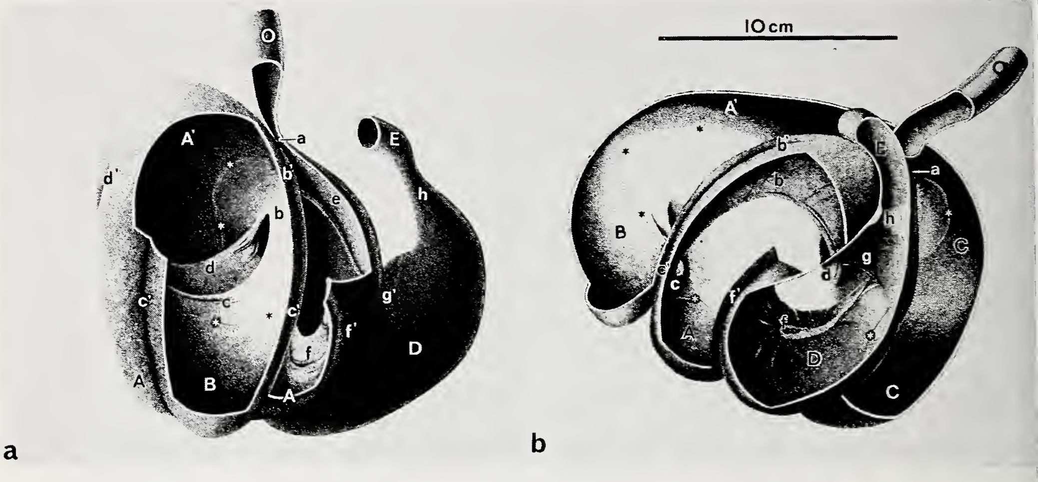

Fig. 2. Caudo-dorsal (a) and right dorsal (slightly caudal) (b) aspects of the dried and opened stomach of *Dicotyles tajacu* No. 3. Abbr.: A = gastric pouch; A' = blindsac junction; B = upper blindsac; C = anterior blindsac; D = glandular stomach; E = duodenum; O = esophagus; a = cardia; b = fornical fold; b' = fornical sulcus; c = upper blindsac fold; c' = upper blindsac sulcus; d = anterior blindsac fold; d' = anterior blindsac sulcus; e = ventricular sulcus; f = ventral transverse fold; f' = ventral transverse sulcus; g = dorsal transverse fold; g' = dorsal transverse sulcus; h = pylorus. Asterisks mark border between squamous and glandular epithelium

The gastric pouch (A in Fig. 2) represents the central compartment with other gastric parts situated around it. The esophagus (O) opens into this compartment. A ventricular sulcus (e in Figs. 2 a and 3 b) follows the lesser curvature of the gastric pouch from the cardia to the glandular stomach. An oval ostium with a diameter of 40 × 50 mm separates the gastric pouch from the glandular stomach (D). In the adult animal about 75 % of this latter compartment is lined with glandular epithelium. A ventral greater curvature as well as a dorsal lesser one can easily be distinguished. Perpendicular to the lesser curvature a transverse dorsal sulcus (g' in Fig. 2) and a corresponding fold (g) forms the dorsal contour of the ostium between gastric pouch and glandular stomach. A ventral transverse fold (f) and the corresponding sulcus (f') forms the ventral contour of the ostium. Both folds and sulci do not form a muscular ring, but rather two independent semilunar folds. The ventral transverse fold (f) is situated more to the gastric pouch, the dorsal transverse fold (g) more to the glandular stomach.

A fornical fold (b in Fig. 2), situated near the opening of the esophagus into the gastric pouch and perpendicular to the longitudinal axis of the stomach, divides the dorsal part of the pouch proper (A) from its blindsac junction (A'). A not very prominent fornical sulcus (b') can be seen externally. A wide opening between the gastric pouch proper and blindsac junction measures about 60 × 60 mm in diameter. The free edge of the cardiac fold (b) continues into folds between the blindsac junction and the upper blindsac (B) as well as the anterior blindsac (C). The upper blindsac fold (c) and the anterior blindsac fold (d) correspond to sulci c' and d' These folds and sulci run parallel to the longitudinal axis of the stomach.

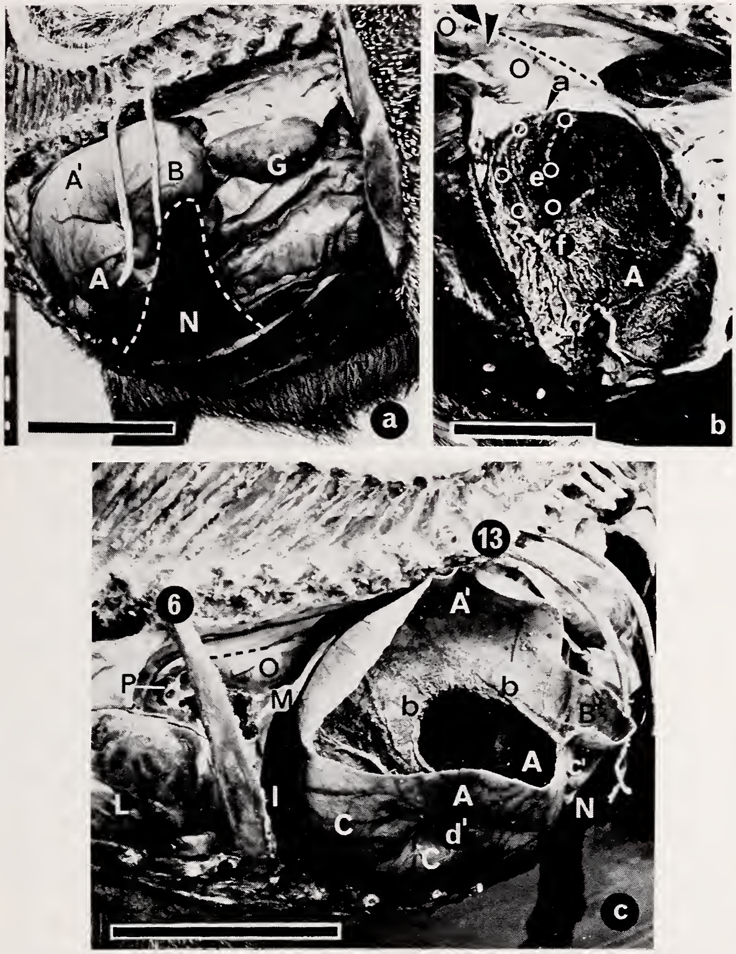

Fig. 3 a—c. a: Left caudo-dorsal aspect of abdominal situs of peccary No. 2. The last two ribs (Nos. 13 and 14) are not removed (Black scale: 10 cm). — b: Same animal as in a. Left aspect of the right wall of the opened gastric pouch (A) with ventral transverse fold (f), cardia (a) and ventricular sulcus (e), the lips of which are marked by three white circles each. The black broken line indicates the dorsal contour of the esophagus (O), the black arrow the position of the esophagus hiatus (the left part of the diaphragm has been totally removed) (Black scale: 5 cm). — c: Left cranio-dorsal aspect of the abdominal and part of the thoracal situs of Peccary No. 2 after removal of the left lung. Ribs Nos. 6 and 13 have been marked. The blindsac junction (A') of the gastric pouch (A) and the upper (B) as well as the anterior (C) blindsacs have been opened from dorsally. The black broken line separates the dorsal contour of the esophagus (O) from the descending aorta (Black scale: 10 cm). — Further abbr.: G = left kidney; I = liver; L = heart in pericardium; M = diaphragm; N = spleen; P = root of the left lung; b = fornical fold; c' = upper blindsac sulcus; d' = anterior blindsac sulcus

The stomach and its relation to other abdominal organs

As has previously been described (Langer 1973), the stomach lies transversely in the abdomen. The most cranial part of the anterior blindsac is covered by the left seventh rib and lies below the eighth thoracal vertebra (Fig. 4 a). The most caudal part of the upper blindsac lies caudal to the left fourteenth rib below the second lumbal vertebra. The glandular stomach is covered by the right eleventh and twelfth ribs and lies below the same numbered vertebra (Fig. 5 a). The ventral part of the gastric pouch (A) as well as the upper blindsac (B) touch the left abdominal wall (Figs. 3 a and 4 a). The anterior blindsac (C) lies in the left hypochondriac region. The dorsally situated blindsac junction (A') is covered by the left costal part of the cupula of the diaphragm (Fig. 4 a). Viewed from the left side of the animal the most dorsal part of the blindsac junction (A') covers the cardia. The region of the blindsac junction near the hiatus of the esophagus (black arrow in Fig. 5 b) is affixed to the diaphragm with the gastrophrenic ligament.

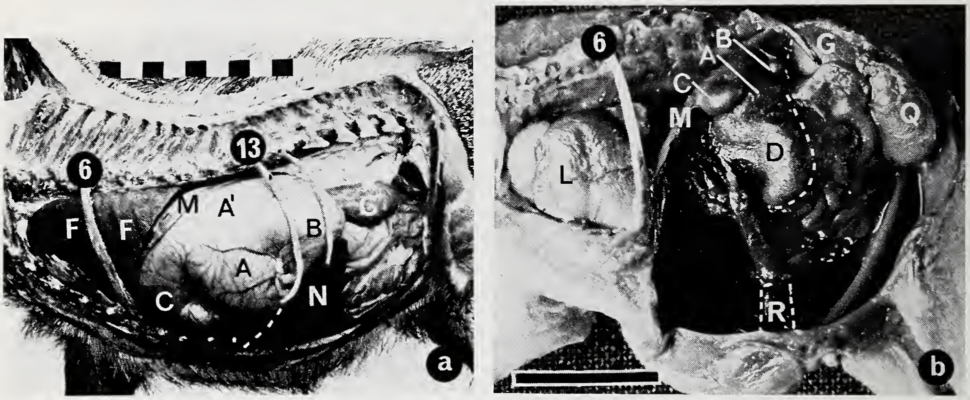

Fig. 4 a—b. a: Left aspect of the abdominal and thoracal situs of peccary No. 2. All ribs except Nos. 1, 6, 13 and 14 have been resected. (Ribs Nos. 6 and 13 have been marked.) The diaphragm (M) has been resected up to the basal border of the left lung (F). (Total scale 20 cm). — b: Left aspect of the abdominal and part of the thoracal situs of fetal peccary No. 2_1. The sixth rib is marked and the total liver has been removed. The testis (Q) is not yet descended. Note the remarkable differences in gastric proportions as compared with the adult animal in (a). The greater curvature of the glandular stomach (D) as well as the contours of the umbilical vein (R) are marked with white broken lines (Black scale represents 1 cm). Further abbr.: A = gastric pouch; A' = blindsac junction; B = upper blindsac; C = anterior blindsac; G = left kidney; L = heart in pericardium; N = spleen

The anterior wall of the anterior blindsac (C in Fig. 3 c) lies in direct contact with the left lateral lobe of the liver (I in Fig. 3 c). The right wall of this blindsac as well as the anterior wall of the glandular stomach are in contact with the right medial and lateral lobe of the liver (Fig. 5 a and b).

The glandular stomach bends ventrally at the ostium connecting it with the gastric pouch, its greater curvature being the most ventral part of the stomach (Fig. 5 b). It lies in the epigastric and right hypochondriac region. From here the pyloric part of the glandular stomach turns dorsally and opens into the duodenum (E in Fig. 5 a and b). A thickening of the muscular wall, especially near the greater curvature can be seen, although a true pyloric torus is not present (Langer 1973). The duodenum first bends dorsally, then in caudal direction at right angle. About 9 cm from the pylorus the bile and the pancreatic ducts open into the duodenum.

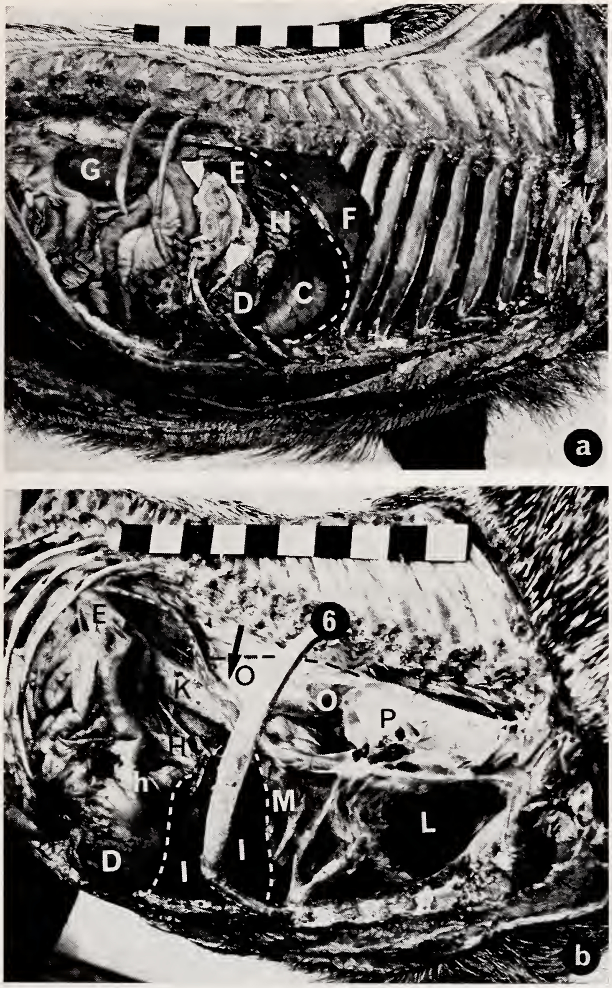

Fig. 5 a—b. a: Right aspect of the abdominal situs of peccary No. 3. Ribs Nos. 7 and 8 have been partly, ribs Nos. 9 to 12 totally removed. The diaphragm has been resected up to the basal border of the right lung (F) and is marked by a white broken line. The liver has been totally removed and the portal vessels of this organ (H) can be seen. White marks indicate the edges of the resected greater omentum. (Total lenght of scale 20 cm.) — b: Right and slightly cranial aspect of abdominal and thoracal situs of peccary No. 1 after removal of right lung and right lateral lobe of liver. The diaphragm (M) has been resected and the sixth rib has been marked. The black broken line indicates the dorsal contour of the esophagus (O). The position of the hiatus where this organ perforates the diaphragm has been marked with a black arrow. The glandular stomach (D) and the pylorus (H) lie in the right hypochondriac region. (Total length of scale 20 cm.) Further abbr.: C = anterior blindsac; D = glandular stomach; E = duodenum; G = right kidney; H = portal vessels of liver; I = liver; K = caudal vena cava; L = heart in pericardium; P = root of right lung

The dorsal end of the spleen touches the upper blindsac near its tip and caudal wall as well as the caudal wall of the gastric pouch (Fig. 3 a und 4 a). The broad ventral end of the spleen lies on the ventral abdominal wall near the ventral transverse sulcus (f' in Fig. 2) between the gastric pouch and glandular stomach.

Changes in relative surface area of different gastric compartments during ontogenetic development

It was possible to measure the inner surface of the different gastric compartments in four animals of different age. It was interesting that the results of measurements in adult animal No. 3 determined during the present investigation and animal No. 5 from an earlier publication (Langer 1973) varied only slightly; maximum differences of 7% could be found in the anterior blindsac. Data are compiled in Table 1 and Fig. 6.

The combined forestomach regions in the collared peccary show an increase in surface area from 62 days of fetal age to birth and further on to adulthood. This means that at the same time the relative surface of the glandular stomach decreases.

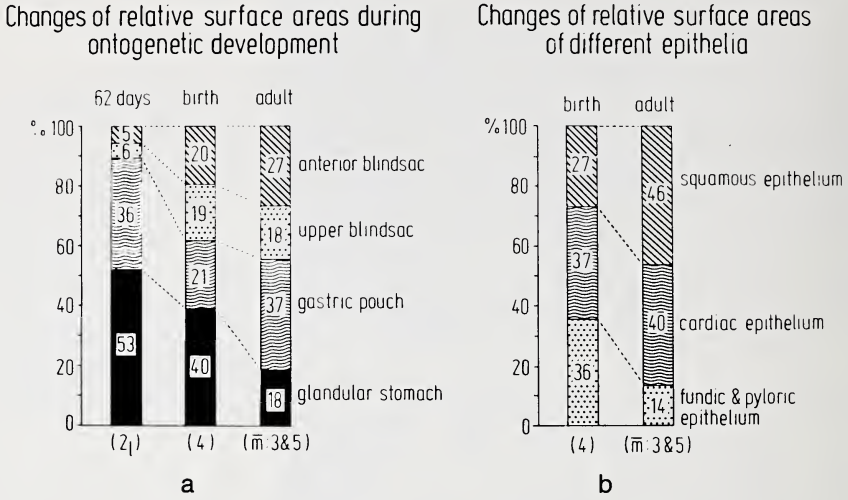

Fig. 6 a—b. a: Changes of relative surface areas of four gastric compartments of the collared peccary between 62 days of fetal age, birth and adulthood, expressed as percentage of these compartments as compared with the whole gastric surface. Values for the adult are means from animals Nos. 3 and 5. — b: Changes of surface areas of three groups of gastric epithelia between birth and adulthood are expressed as percentages of the whole gastric surface. In the fetus it was not possible to identify different types of epithelia

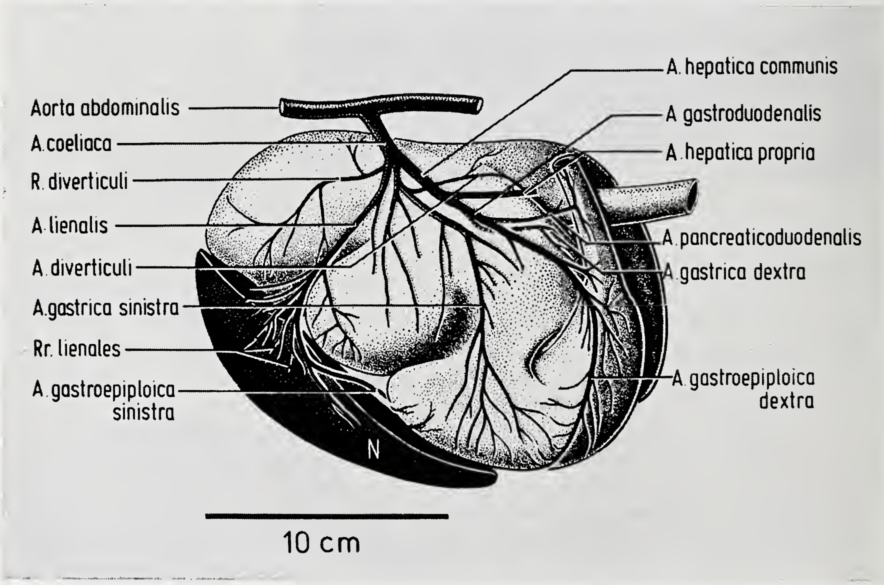

Fig. 7. Right caudo-dorsal aspect of the stomach and spleen (N) of *Dicotyles tajacu* No. 2. For orientation compare with Fig. 1b. Arteries were drawn from photographs and sketches made in situ during dissection

The gastric pouch of the adult peccary "returns" to the relative surface of a 62 day old fetus. There is a relative increase in the volume of both blindsacs between 62 days of fetal age and birth (Compare Fig. 4 a and b).

Arterial supply of the stomach

Although a short description of the arterial supply has been given (Langer 1973), new information was obtained during topographical dissection of peccary No. 2 (Fig. 7).

The coeliac artery divides into three major vessels: lienal, left gastric, and common hepatic arteries. A ramus branches off from the lienal artery and supplies the upper blindsac. Further distally rami branch off to the hilus of the spleen and a vessel with thicker caliber, the left gastroepiploic artery, runs to the ventral curvature of the glandular stomach. It forms an anastomosis with the right gastroepiploic artery.

The second branch of the coeliac artery is the left gastric artery. In the specimen described earlier (Langer 1973) the lienal as well as the left gastric artery jointly branched off from the coeliac artery. The diverticular artery, a branch of the left gastric artery, runs in the fornical sulcus (b' in Fig. 2 b) to supply the blindsac junction and anterior blindsac. The left gastric artery supplies the visceral side of the gastric pouch and glandular stomach.

The third and very prominent branch of the coeliac artery is the common hepatic artery. Its first branch is the hepatic artery proper. Further distally it divides into the right gastric artery which supplies the hepatic side of the gastric pouch and into the gastroduodenal artery with its branches to pancreas and pylorus plus proximal duodenum. As mentioned above, the right gastroepiploic artery, coming out of the gastroduodenal artery, forms an anastomosis with the left gastroepiploic artery.

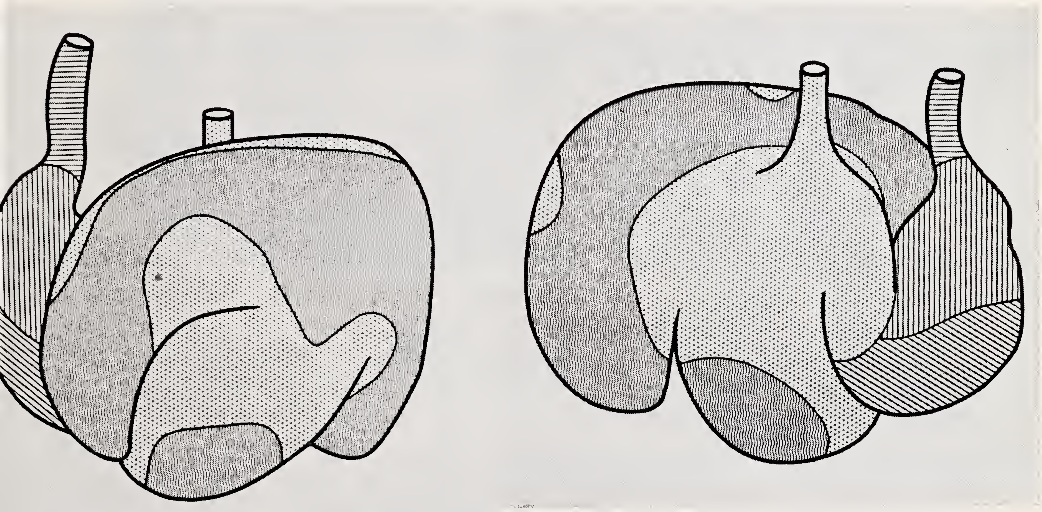

Fig. 8. Distribution of the different types of epithelial lining in the stomach of the collared peccary. The right semi-schematic figure shows the right caudo-dorsal aspect of the stomach, the left figure the left side

Microscopic anatomy

The distribution of different types of epithelia lining the stomach of the collared peccary is shown in Fig. 8. Similar figures have already been published by EDELMANN (1889), PERNKOPF (1937), STEWART (1964) and LANGER (1973).

Extensive areas of the gastric pouch as well as of the blindsac junction and the proximal part of the glandular stomach are lined with squamous epithelium. On the other hand, parts of the two blindsacs and the most ventral region of the gastric pouch are lined by glandular epithelium of cardiac type. Fundic and pyloric epithelium can only be found in the glandular stomach.

Squamous epithelium

The squamous epithelium shows considerable variations in the different gastric regions. In the ventricular sulcus this epithelium is not cornified, the nuclei are located up to the superficial layer of the epithelium. This epithelium is very similar to the uncornified structure found in the esophagus. The squamous epithelium in the blindsac junction is uncornified as well as very thin (Fig. 9 b and f).

In the dorsal part of the upper blindsac as well as in the ventral part of the gastric pouch near the border of the cardiac epithelium, a cornified squamous epithelium is found (Fig. 9 e). However, the stratum granulosum is not present and swollen cells lie below the keratinized cells of the stratum corneum. In some cases strong bacterial infiltrations on the upper cell layers of the stratum corneum can be seen as described for ruminant forestomach epithelium (STEVEN and MARSHALL 1970). The histological texture of the epithelium in different gastric regions and different individuals is variable. In many cases it is not possible to differentiate the "stratum spinosum" from the "str. granulosum" and "str. lucidum". The term "str. transitionale" as it has been used in rumen epithelia of cattle (KAUFFOLD and PIATKOWSKI 1971; KAUFFOLD 1975) seems to be appropriate.

In the proximal part of the glandular stomach cornification was variable in both investigated animals. In animal No. 1 fed only with commercial swine pellets, weak cornification was found. In animal No. 2, however, with additional straw in its food, cornification was much stronger. In both animals the free edge of the fornical fold is a region strongly exposed to mechanical stress and the epithelium shows a strong cornification (Fig. 9 a).

Measurements of epithelial thickness

Not only the degree of cornification, but also the total epithelial thickness is of importance in connection with the epithelium as a barrier between gastric lumen and blood vessels. Therefore, the shortest distances between the tips of the papillae of the lamina propria mucosae (where capillaries are located) and the epithelial surface were measured above 50 connective tissue papillae per region. The results are compiled in Fig. 10.

Glandular epithelium

In the cardiac epithelium found in the forestomach the glandular tubules vary considerable in length; being especially small in the ventral tip of the gastric pouch (Fig. 9 c). The muscularis mucosae is often perforated by the glandular tubules which can extend down into the submucosa. The tubules are loosely arranged in the lamina propria and solitary lymphatic follicles can be found in this connective tissue.

Fundic (Fig. 9 d) and pyloric epithelia show the same aspect as found in other mammals.

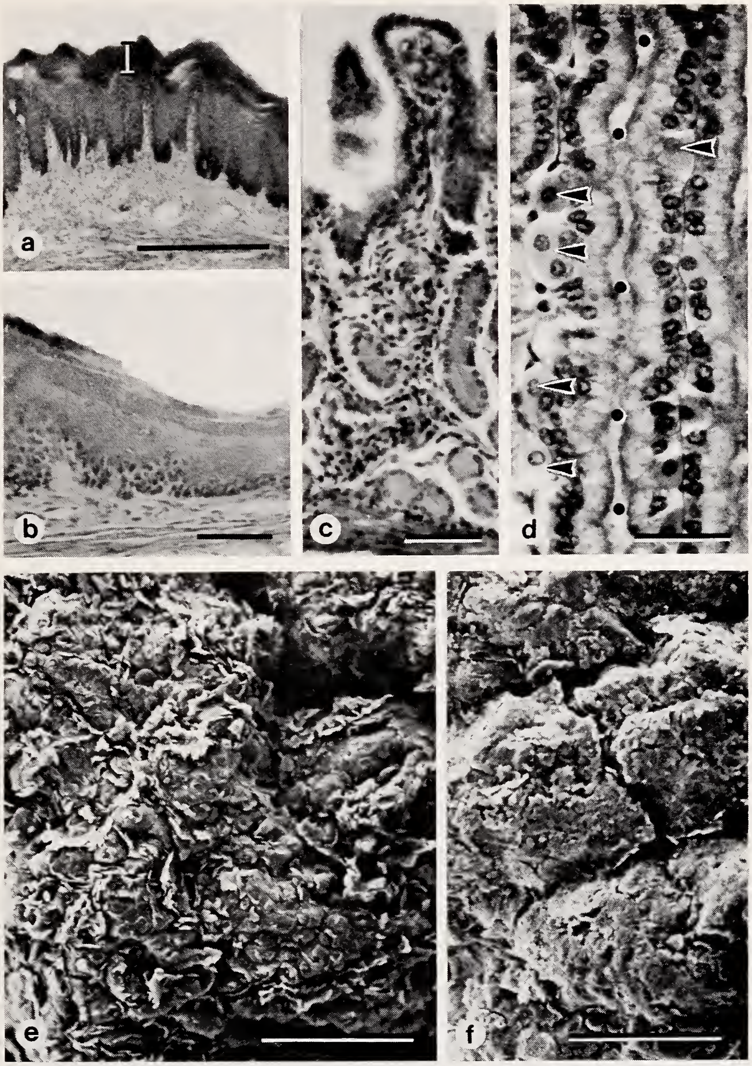

Fig. 9 a—f. a: Squamous epithelium near the edge of the cardiac fold of animal No. 2. Note the cornification (white vertical line) of the epithelium as well as its interdigitation with the lamina propria mucosae (Hematoxylin/Eosin. Scale represents 500 μm). — b: Squamous epithelium in the blindsac junction of animal No. 1. No cornfication can be seen and the epithelium shows only few interdigitations with the lamina propria mucosae. (Hematoxylin/Eosin. Scale represents 100 μm.) — c: Glandular lining of the ventral part of the gastric pouch of animal No. 1. The glandular tubules are convoluted and are not densely packed within the lamina propria mucosae. Crypts are often so wide that the surface appears papillated. (Masson/Goldner. Scale represents 100 μm.) — d: Fundic glands in glandular stomach of animal No. 1. Parietal cells are marked by arrows and the lumen of one of the densely packed glandular tubules is marked by black dots. (Masson/Goldner. Scale represents 50 μm.) — e: Scanning electron micrograph of the desquamating and cornified epithelium from the gastric pouch of animal No. 2. (Scale represents 500 μm.) — f: Scanning electron micrograph of squamous epithelium with little desquamation from the blindsac junction of animal No. 2. (Scale represents 500 μm.)

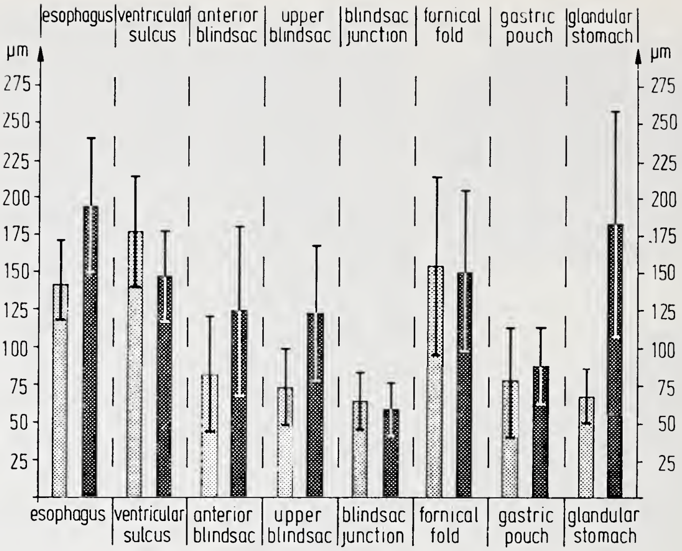

Fig. 10. Epithelial thickness and their standard deviations measured in animal No. 1 (fine stippled) and No. 2 (densely stippled). Per region 50 measurements were made between the tips of the papillae of the lamina propria mucosae and the epithelial surface

Fig. 7b shows the change of relative surface areas of different epithelia during ontogenetic development. The relative surface covered with squamous epithelium nearly doubles between birth and adulthood, the cardiac epithelium, however, remains almost constant.

Volatile fatty acids (VFA) in the gastric content

Results of the determination of VFA by Prins (pers. communication) are compiled in Table 3.

This table shows that

- in all three investigated animals VFA-concentration in the forestomach are higher than in the glandular stomach.
- molar percentages of acetic, propionic, butyric and valeric acids vary only slightly between the six regions (4 forestomach regions and 2 glandular stomach regions).
- acetic to propionic acid ratio (C_2/C_3) differs only slightly between forestomach and glandular stomach of the same animal (maximal deviation about 9 %).
- in animal No. 2, fed straw in addition to swine pellets, the C_2/C_3-ration is higher.

Discussion

In *Dicotyles tajacu* the forestomach amounts to about 85 % of the total stomach capacity (Langer, in press). This value is only slightly lower than the relative forestomach volume determined in ruminants (90 % in sheep and 88–91 % in cattle, Slijper 1946; Maynard and Loosli 1969). In the ruminant-like hippopotamus the forestomach amounts to 94 % and 95 % (Arman and Field, 1973; Langer 1975).

Tabelle 3

Volatile fatty acids in the stomach of the collared peccary

author	animal	type of food	VFA (mMol/l)		specimens	molar percentage of individual VFA					C_2/C_3	
			fore-stomach	gland. stomach		C_2	C_3	C_4	C_5	C_6	fore-stomach	gland. stomach
PRINS (pers. communication)	1	pellets	159.7	67.9	6 gastr. regions	40.9 ± 1.9	21.2 ± 0.9	26.5 ± 0.7	10.2 ± 1.9	1.3 ± 1.0	1.898	2.000
	2	pellets and straw	131.7	29.9	5 gastr. regions	39.9 ± 1.8	15.4 ± 0.9	32.3 ± 1.0	11.2 ± 1.1	1.2 ± 1.2	2.551	2.661
	3	pellets	165.5	89.5	6 gastr. regions	36.7 ± 2.9	22.4 ± 2.2	25.6 ± 1.3	11.4 ± 0.9	4.0 ± 0.9	1.693	1.551
HAYER (1961)	a	commercial supplement	92.4		whole stomach	36.5	19.6	37.5	6.4		1.862	
	b		85.9			34.2	21.5	33.5	10.9		1.591	
	c	prickly pear	176.5			45.3	36.3	16.6	1.3		1.248	
DYSON (1969)	$\bar{m}$ of 7 animals	pellets of ground milo and hay	43.7		7 different post-feeding periods	65.6 ± 6.0	24.6 ± 3.7	6.5 ± 1.6	1.7 ± 0.5		2.667	

A stomach with these quantitative characteristics is of adaptational advantage to an animal such as the collared peccary (Langer, in press). Especially the effects of behavioral thermoregulation, with rather extended periods of rest in the shade and decreased times when food is taken up, make a storage room for foodstuffs advantageous. On the other hand, in peccaries the reduction of the particle size in foodstuffs is inefficient because "the reduced pinnation and altered orientation of the elevator muscles probably restrict the amount of masticatory torque" (Herring 1975).

Microbial activity in the forestomach regions could possibly partly compensate for this inefficiency. Prins (personal communication) did not find protozoa in the gastric contents of three collared peccaries. Although direct proof for the prescence of bacteria in the forestomach of the collared peccary has not been given, the analysis of volatile fatty acids (VFA) in the gastric content gave indirect evidence (Table 3). The total VFA-concentrations in the forestomachs of three peccaries determined by Prins (personal communication) are slightly higher than those compiled by Church (1969) for domestic ruminants. In the glandular stomach VFA-values are much lower than in the forestomach. One reason for this could be the absorption of VFA through the forestomach wall. It should be kept in mind that because of technical reasons the gastric content investigated by Prins had to be treated with formalin (see Material and methods) and was not ideally suited for biochemical analysis.

It is remarkable that values for VFA-concentrations in the whole stomach of two peccaries investigated by Hayer (1961) and seven animals investigated by Dyson (1969) fed on "commercial supplement" or pellets together with milo and hay are lower than those by Prins (pers. communication). In an animal feeding on prickly pear cactus Hayer (1961) found higher VFA-concentrations in the forestomach than Prins in animal on swine pellets.

Molar percentages of individual VFA in gastric contents reflect the slightly different feeding regimes of animal No. 2, and the one hand, and animals Nos. 1 and 3, on the other. In addition to pelleted food, animal No. 2 had access to straw. It has been found by physiologists working with ruminants (reviews in Church 1969; Demeyer and Giesecke 1973) that food rich in cellulose results in an increase in acetate or a higher acetate/propionate-ratio (C_2/C_3). If less cellulose and more starch is fed or if the material is pelleted, the concentration of propionic acid increases and C_2/C_3 decreases. These conditions can be found in the results obtained by Prins (personal communication) in the collared peccary. No such differences, however, were demonstrated by Hayer (1961). Dyson (1969) administening food containing fiber, measured C_2/C_3-ratio somewhat higher than in animal 2 in the present study.

As has already been mentioned above, VFA as microbial fermentation products are likely to be absorbed through the forestomach epithelial lining. From about 60% at birth the forestomach surface as percent of total gastric surface increases to about 82% in adult animals (Fig. 7a). While cardiac epithelium remains nearly constant in relative surface, squamous epithelial surface increases considerably (Fig. 7b). The reason for this could be an increased mechanical stress from birth to weaning. Although it was not possible to obtain an idea of biochemical differentiation of the squamous epithelium, it seems at least possible that transepithelial transport takes place. Especially in the gastric pouch and in the blindsac junction where digesta are stored, epithelial thickness between 59 μm and 87 μm (Fig. 10) was almost identical with the epithelial thickness measured by Lauwers (1973) in rumen (59 μm), reticulum (62 μm) and omasum (50 μm) of cattle. Regions with high mechanical stress such as the esophagus, ventricular sulcus and fornical fold show much higher values (between 142 μm and 194 μm). These values are lower than the thickness of 302 μm in the esophagus of an adult cattle.

The question arises why the peccary stomach developed two prominent blindsacs with considerable volume. Do these areas show similar functional differentiations as the blindsacs found in the *Hippopotamus* (Langer 1975, 1976)? In this latter species it is very probable that the passage of digesta from the esophagus through the two blindsacs and the following gastric compartments successively make an intense microbial reduction of particle size probable (Langer 1976). In the *Hippopotamus* the different well developed gastric compartments are separated from each other by prominent folds. These folds probably reduce the passage rate of digesta through the stomach and make a polarized flow passing through all compartments successively very probable.

In the collared peccary folds between gastric compartments can be found as well. However, the openings between the chambers have a considerable diameter: 40 × 50 mm between gastric pouch and glandular stomach, and 60 × 60 mm between gastric pouch proper and blindsac junction. The rate of passage of digesta can be reduced by these folds. It is improbable, however, that they cause polarized flow and make the gastric content pass successively through all gastric compartments. It is probable that ingested food is transported into the gastric pouch first and from there, perhaps by contraction of the gastric wall, into the blindsacs. The more ventrally situated anterior blindsac is filled first, but it is uncertain whether the upper blindsac is filled in all cases. It is possible that a small amount of food and swallowed liquids bypass the forestomachs.

It is quite astonishing that the peccary, which can be easily held as an experimental animal, at least as long as it is young, has not been investigated more frequently, especially concerning gastric motility. Such investigations could result in a better understanding of forestomach function in general and the different strategies used by the artiodactyls to handle herbaceous food.

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Summary

A description of the macroscopic and microscopic anatomy of the stomach of the collared peccary as well as a description of its position within the abdomen and the arterial supply of the stomach is presented.

In addition to the glandular stomach with fundic and pyloric epithelium, a forestomach can be found. It is divided into a gastric pouch that is connected with a blindsac junction. This, in turn, gives access to two blindsacs. The forestomach regions are partly lined with squamous epithelium and partly with an epithelium of the cardiac type. A system of folds can be found within the stomach.

It was possible to investigate specimens of different ages from fetus to adult and to measure surfaces of different gastric compartments to determine their relative change during ontogenetic development.

The light microscopic description of the two types of forestomach epithelia suggested that a transepithelial transport takes place. Volatile fatty acids (VFA) as products of microbial metabolic activity can be found in the content of the forestomach. In this region VFA-concentrations are higher than in the glandular stomach. The reason could be the above mentioned transepithelial absorption of VFA.

The discussion of the results show that especially physiological findings are lacking to obtain a better understanding of forestomach function and the different steps of functional differentiations in the artiodactyls.

Zusammenfassung

Anatomie des Magens des Halsbandpekaris, Dicotyles tajacu (L., 1758) (Artiodactyla: Mammalia)

Es wird eine Beschreibung der makroskopischen und mikroskopischen Anatomie des Magens des Halsbandpekaris sowie eine Beschreibung seiner Lage im Abdomen und die arterielle Versorgung des Magens gegeben.

Zusätzlich zum Drüsenmagen mit seinem Haupt- und Pylorusdrüsenepithel ist auch ein Vormagen zu finden. Er besteht aus einem Magenbeutel, der in ein Verbindungsstück übergeht, welches die Verbindung mit zwei Blindsäcken herstellt. Teilweise werden die Vormagenregionen mit einem Plattenepithel ausgekleidet, zum anderen Teil mit einem Epithel vom Cardiadrüsentyp. Ein Faltensystem ist im Inneren des Magens zu finden.

Es war möglich, Tiere verschiedenen Alters zu untersuchen, vom Foetus bis zum Adultus. Die Oberflächen der verschiedenen Magenabschnitte konnten ausgemessen und ihre relative Größenveränderung während der ontogenetischen Entwicklung ermittelt werden.

Die lichtmikroskopische Beschreibung der beiden Epitheltypen im Vormagen macht es wahrscheinlich, daß transepithelialer Transport stattfindet. Flüchtige Fettsäuren (FFS) als Produkte mikrobieller Stoffwechselaktivität können im Inhalt des Vormagens ermittelt werden. In dieser Region ist ihre Konzentration höher als im Drüsenmagen. Der Grund dafür könnte die schon erwähnte transepitheliale Absorption der FFS sein.

Die Diskussion der Ergebnisse zeigt, daß vor allem physiologische Befunde fehlen, um die Vormagenfunktion und die verschiedenen Stufen funktioneller Differenzierung bei den Artiodactyla besser verstehen zu können.

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