

COMPARATIVE GASTRIC HISTOLOGY OF
SELECTED AMERICAN BATS

By

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PREFACE

There are many gaps in zoologists' knowledge concerning comparative anatomy in general and comparative histology in particular. Hopefully these gaps will eventually be filled. This histological study of bat stomachs is undertaken to fill some of these gaps.

I am deeply indebted to Dr. Bryan P. Glass, my major adviser, who suggested a study of this type and offered helpful advice and criticism during the preparation of this manuscript. Drs. L. Herbert Bruneau, John H. Venable, and Margaret H. Brooks served on my committee and also assisted in the preparation of this manuscript. I sincerely wish to thank Dr. Robert Baker for taking time out during his own research in Mexico to collect specimens for this project. Dr. Harley W. Reno provided invaluable assistance by lending me his personal microscope and camera as well as suggesting techniques applicable to a study of this type. Dr. Milton R. Curd provided valuable advice concerning techniques for the preparation of histological materials and techniques of photomicrography. Mr. George C. Rogers assisted in the collection of many of the bats used in this study. I am especially indebted to my wife, Sharon, for her assistance in typing this manuscript and her patience during its preparation.

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CHAPTER I

INTRODUCTION

This study of the gastric histology of Tadarida brasiliensis (Molossidae), Myotis velifer (Vespertilionidae, Vespertilioninae), Antrozous pallidus (Vespertilionidae, Nyctophilinae), Leptonycteris sanborni (Phyllostomatidae, Glossophaginae), and Desmodus rotundus (Desmondontidae) is undertaken to add to the present knowledge of the anatomy of bats. Although comments on the stomachs of bats appear occasionally in the literature, most are concerned only with gross morphology.

Huxley (1865) and Robin (1881) cited Cuvier (1805), possibly the earliest author on the topic, as classifying the stomachs of Chiroptera into three specific types: the frugivorous, being transversely elongated and tubular; the insectivorous, being globular with closely approximated cardiac and pyloric orifices; and the sanguivorous, being longitudinally elongated and conical with a pyloric caecum. Huxley went on to describe the unusual stomach of Desmodus as belonging to a fourth category, an elongated-intestiniiform type with closely approximated esophageal and pyloric orifices.

Home (1807) noted longitudinal folds of the mucosa in "long-eared" bats and presented a schematic drawing of the everted stomach of this and the "vampire" bat. Owen (1868) briefly commented on the stomach of bats and added his own interpretation of how bat stomachs might be

classified into three types related to diet. Robin's paper (1881) presented the first careful comparative morphological study of the digestive tract in bats. He discarded for the most part the classification of Cuvier (1805) and Owen (1868) as being inconsistent with his findings, observing that the forms of the stomach were not strictly related to diet. Robin noted the following three general characteristics of the stomachs of bats: there was never a cardiac valve; there were three shapes as represented in the Pteropidae, Microchiroptera, and Desmodontidae; and there were three patterns of mucosal foldings, the longitudinal and parallel folds in the insectivorous bats, the similar folding but with numerous anastomoses in the Desmodontidae, and the sponge-like foldings in the frugivorous Microchiroptera. Robin's histological observations indicated that the mucosa of the Murin (Myotis myotis), Rhinolophus euryale, and Pteropus medius contained tubular glands similar to those typical of most mammals. He further noted that the parietal cells were less numerous in Pteropus medius than in the two Microchiroptera.

Grasse (1955) summarized the work of Robin adding that the stomach of Diphylla had a much shorter caecum than that of Desmodus. He also stated that the different categories of gastric glands were well-developed in all the Chiroptera except the Desmodontidae in which glands of the fundic type, containing chief and parietal cells, emptied between high villi.

Weidersheim (1907) noted that the stomach undergoes more numerous modifications in mammals than in any other vertebrate class. He also described the stomach of Desmodus as having a pyloric caecum.

Park and Hall (1951) reported on the gross morphology of the

stomachs of Glossophaga soricina, Choeronycteris mexicana, Leptonycteris nivalis, Carollia perspicillata, Artibeus jamaicensis, Macrotus californicus, and Eptesicus fuscus, and redescribed that of Desmodus rotundus (which is a synonym of D. rufus of Huxley, 1865). They noted that the cardiac and pyloric orifices in nectivores are usually close together, although Leptonycteris nivalis proved an exception to this generalization.

Heidenhain (1870) (as cited by Bensley, 1896, 1898, 1902, 1963, and Frey, 1880), though not known to have investigated the stomachs of bats, must be credited with much of our knowledge and nomenclature concerning the histology of stomachs. He discovered and subsequently named the two functionally-important cell types in the gastric glands, the chief cells and parietal cells (which he called "Hauptzellen" and "Belegzellen", respectively).

A similar but independent investigation by Rollett (1871) (as cited by Bensley, 1963; Frey, 1880; and Langley, 1880-82) resulted in similar findings, but he coined the terms "adelomorphous" for the chief cells and "delomorphous" for the parietal cells. According to Langley (1880-82), Rollett did study the stomach of a bat, noting few parietal (delomorphous) cells in the mucosa of a hibernating bat, but many in that of an active bat. Langley considered this observation of Rollett's questionable.

Langley's own work (1881-82) included histological observations on the stomach of a bat. He reported that the wall of the fundic portion of the stomach of the bat was thinner than the wall of the rest of the stomach. He also noted that the glands of the fundus were short, containing only one or two parietal cells each, and that the glands of the

greater curvature were nearly twice as long as those of the fundus and had the median portion of the gland composed entirely of parietal cells and the basal portion of chief cells. Unfortunately, he did not name the species of bat used. His observations correspond very closely to the morphology of Myotis velifer. Langley's most important contribution to gastric histology was his description of the histological changes that occur before and during secretion in the stomach.

Bensley (1896, 1898, 1902) first distinguished the pyloric and cardiac glands from the proper gastric glands in the mammalian stomach, although Bischoff (1838) (as cited by Grossman, 1959) and Edelmann (1889) (as cited by Bensley, 1898) recognized that the glands of the pyloric region of the stomach were different from those glands later characterized as containing both chief and parietal cells. Heidenhain (1870) and Langley (1880-82) seemingly did not recognize a functional difference between the pyloric and fundic areas, and indicated no awareness of the cardiac glands at all.

The earliest published record found devoted to the histology of the digestive tract in bats was that of McMillan and Churchill (1947). The stomach of Myotis lucifugus was described as being the size and shape of a lima bean, and containing rugae covered by mucosa surfaced with columnar cells. They observed that: the mucosa contained parietal cells, chief cells and numerous blood vessels; the tunica muscularis was much thicker on the greater curvature of the stomach with some of the muscles arranged obliquely; and in the pyloric part of the stomach there were several long, slender projections resembling the villi of the upper intestine.

In Andrew's textbook of comparative histology there is only one

mention of the stomach of bats, namely that the chief cells are more abundant in the caecal pouch of the bat stomach than elsewhere, and that the blood-sucking and fruit-eating bats show a greater elongation of the caecal pouch.

Recently a fine structural study of gastric mucosa of Myotis lucifugus by Ito and Winchester (1963) has been published. Their study established that the cell types in the stomach of this species were essentially the same as those in other mammals studied to date, the only differences being in the relative numbers and distribution of cell types.

The food habits of the bats considered in the present study might be considered important factors relating to the gross and histological nature of their stomachs. While the food habits of the species used in this study have not been studied extensively, work of others and personal observations allow placement of these species in rather broad categories.

Ross (1961) studied the stomach contents of seven stomachs of T. brasiliensis in Arizona and found that moth remains were by far the most abundant, although some homopteran and dipteran remains were found also. Another researcher (Storer, 1926) found similarly that the identifiable remains in guano produced by T. brasiliensis in Texas were predominantly (over 90%) those of moths.

Myotis velifer is considered insectivorous (Ward, 1956) and occupies a similar habitat to that of T. brasiliensis, but there do not seem to be any published data concerning its diet.

The reports of Orr (1954), Grinnell (1915), Hatt (1923), Borell (1942), and Ross (1961) on the insects eaten by Antrozous pallidus

indicate that it subsists primarily on larger insects caught both in flight and on the ground. No study has been made of the food habits of this bat in Oklahoma.

Leptonycteris usually has been referred to as a nectivore. However, Hoffmeister and Goodpaster (1954) observed that the stomach contents of six L. nivalis in southern Arizona contained on the average 92% pollen grains and 8% remains of insects. They suggested that the pollen probably was that of Jimson weeds. It was not shown whether pollen was the primary food or was secondarily acquired while obtaining nectar.

Desmodus rotundus is well known as a sanguivore. A few insect remains were observed in the stomach of one specimen, which supports the observation of Arata (et al. 1967) who found several Desmodus rotundus stomachs containing insect remains as well as blood. Wimsatt and Guerriere (1962) suggested that the vampire bat must have some rather specialized physiological adaptations in order to subsist and thrive on blood, one of these being the absorption of large quantities of water into the blood stream from the stomach. Their suggestions were based on two observations: that most mammals that they had studied were incapable of living on a diet of blood; and that vampires began urinating immediately after ingesting a meal of blood.

CHAPTER II

METHODS AND MATERIALS

Bats used in this study were killed by ether asphyxiation or cervical dislocation. The stomach was then removed along with a short (a few mm.) length of esophagus and small intestine. The organ was immediately immersed in about 20 ml. of fixative. Whenever practical, the animals were fasted for 24 hours before killing.

The descriptions included in this study were based on materials from 22 Myotis velifer, 18 Tadarida brasiliensis, 6 Antrozous pallidus, 3 Desmodus rotundus, and 3 Leptonycteris sanborni. M. velifer, T. brasiliensis, and A. pallidus were collected in western Oklahoma caves. The specimens of D. rotundus and L. sanborni were collected in Mexico.

Ten of the 22 M. velifer used in this study were hibernating when collected. A. pallidus, the only other hibernator among the species studied, was collected only while active during the summer.

Fixatives used were Bouin's, 10% formalin, 10% neutral buffered formalin, Zenker's fluid, Gilson's fluid, and AFA (Alcohol-Formalin-Acetic Acid). The most satisfactory of these proved to be AFA, 10% neutral buffered formalin, and 10% formalin, in that order. Bouin's and Zenker's-fixed material proved very difficult to section due to the tissue becoming excessively hard and brittle.

After 24 hours to two weeks the fixative was washed out of the tissue, which was then transferred to 50% isopropanol for storage.

Stomachs fixed in aqueous fixatives were washed in water; those fixed in Bouin's and alcoholic fixatives were washed in 50% isopropanol. A few drops of alcoholic iodine were added to the stored material that had been fixed in mercuric chloride to insure complete removal of mercuric chloride.

After dehydration in absolute isopropanol and clearing in benzene, the tissues were infiltrated in either Tissuemat or paraplast at 58° C. for three hours, with one change after the first two hours and another prior to embedding. Tissue-Tek embedding molds proved most satisfactory for embedding.

After trimming the blocks and exposing the tissue on the cutting surface, the blocks were soaked in ice water for two hours. Sectioning was accomplished with an American-Optical rotary microtome and 125 millimeter Lipshaw microtome knife. Section thickness was usually 6 microns, but was thicker when difficulties were encountered in sectioning. It was possible to cut smooth, intact sections at a maximum of 9 microns in all but one case. The engorged stomach of Desmodus rotundus, distended with what appeared to be fibrin, proved to be almost impossible to section. The stomach content became so hard after embedding that the knife would scarcely cut it. A few 12 micron sections were obtained after soaking the blocks overnight in tap-water. Desmodus rotundus was the only species in which it proved impossible to embed the stomach wholly within one block. The organ had to be cut into one-centimeter lengths, which were embedded separately.

After sectioning, appropriate lengths of ribbons were placed on slides overlaid with an aqueous gelatin solution containing a few drops of formalin. The slides with ribbons floated on the affixative solution

were placed on a warming tray at 45^o C. until the sections became flattened. The affixative was then drained from the slides and the slides blotted with a paper towel to remove all excess liquid. The slides with affixed sections were then dried for several minutes on the warming tray before being stored for future staining.

Sections were stained with hematoxylin and eosin, Masson's triple stain (Humason, 1962), or Gomori's (1950) aldehyde fuchsin followed by alcian blue as described by Spicer and Meyer (1960). Aldehyde fuchsin selectively stains elastic fibers, some mucins, chief cells, and argentaffine cells (Scott et al. 1953). Alcian blue selectively stains sialic acid-containing and other non-sulfated acid mucopolysaccharides (Spicer and Meyer, 1960).

Semidiagrammatic drawings were made by tracing a projected representative section of stomach on a sheet of drawing paper. Photomicrographs were taken with a 35 mm. camera on a triocular American Optical microscope or Polaroid camera mounted on a Bausch and Lomb microscope.

CHAPTER III

OBSERVATIONS

Insectivores: Myotis velifer, Tadarida brasiliensis,
and Antrozous pallidus

The stomachs of these three species are strikingly similar in gross and histological features. Grossly, the stomach of these species conforms to the simple type common to many mammals. A fundic or cardiac caecum is present in all three species, being somewhat longer in Antrozous and Myotis than in Tadarida. In A. pallidus the caecum is sharply bent cranial. The esophageal and pyloric orifices tend to be somewhat closer together in the two vespertilionids than in Tadarida. Figs. 1, 2, and 3 show these stomachs in sagittal section.

The walls of the stomach of these species are composed of the typical four layers, tunica mucosa, tunica submucosa, tunica muscularis, and tunica serosa, found in the digestive tract of mammals generally. The mucosa and submucosa are involved in the formation of several longitudinal rugae (Figs. 4 and 5) which traverse the entire length of the stomach, ending at the gastroesophageal and gastroduodenal junctions. The rugae tend to be effaced in the elastic portion of the stomach when it is fully distended. The elastic portion of the stomach in these three species is easily discernable when the stomach is fully distended, being a bulbous distention including all of the fundic caecum and extending aborally to about the mid-portion of the greater curvature. In

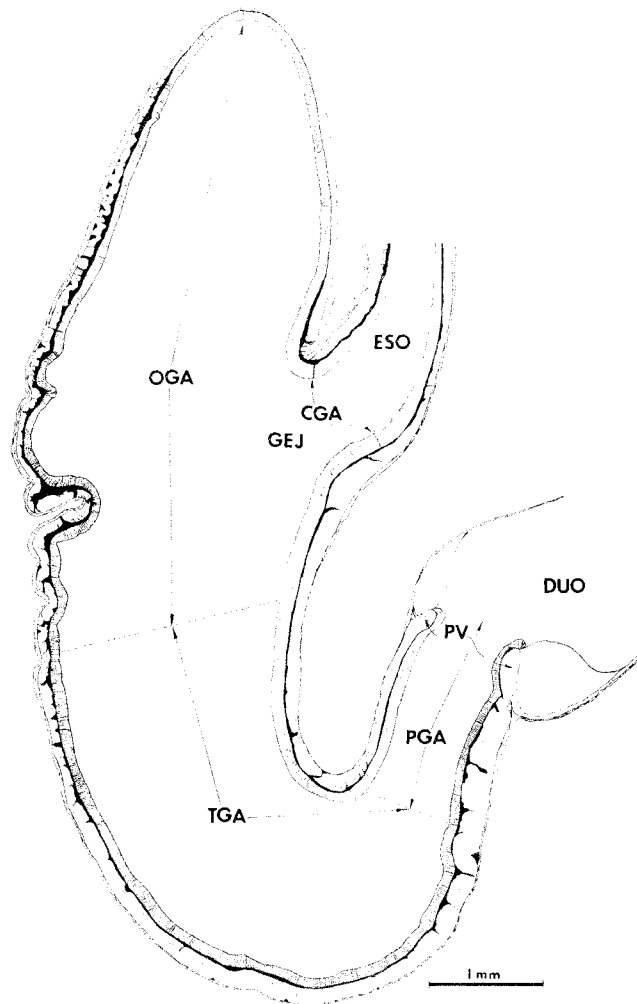


Figure 1. Sagittal section of stomach of Tadarida brasiliensis, dorsal view. Top of page represents the anterior. Note the bundles of muscle along greater curvature and thin outer muscle layer of lesser curvature. ESO, esophagus; CGA, cardiac gland area; GEJ, gastroesophageal junction; OGA, oxyntic gland area; TGA, transitional gland area; PGA, pyloric gland area; PV, pyloric valve. Longitudinal hatching, longitudinal layer of tunica muscularis; Stippling, circular layer of tunica muscularis; Solid black, tunica submucosa; Vertical hatching, tunica mucosa. Semidiagrammatic, rugae not included.

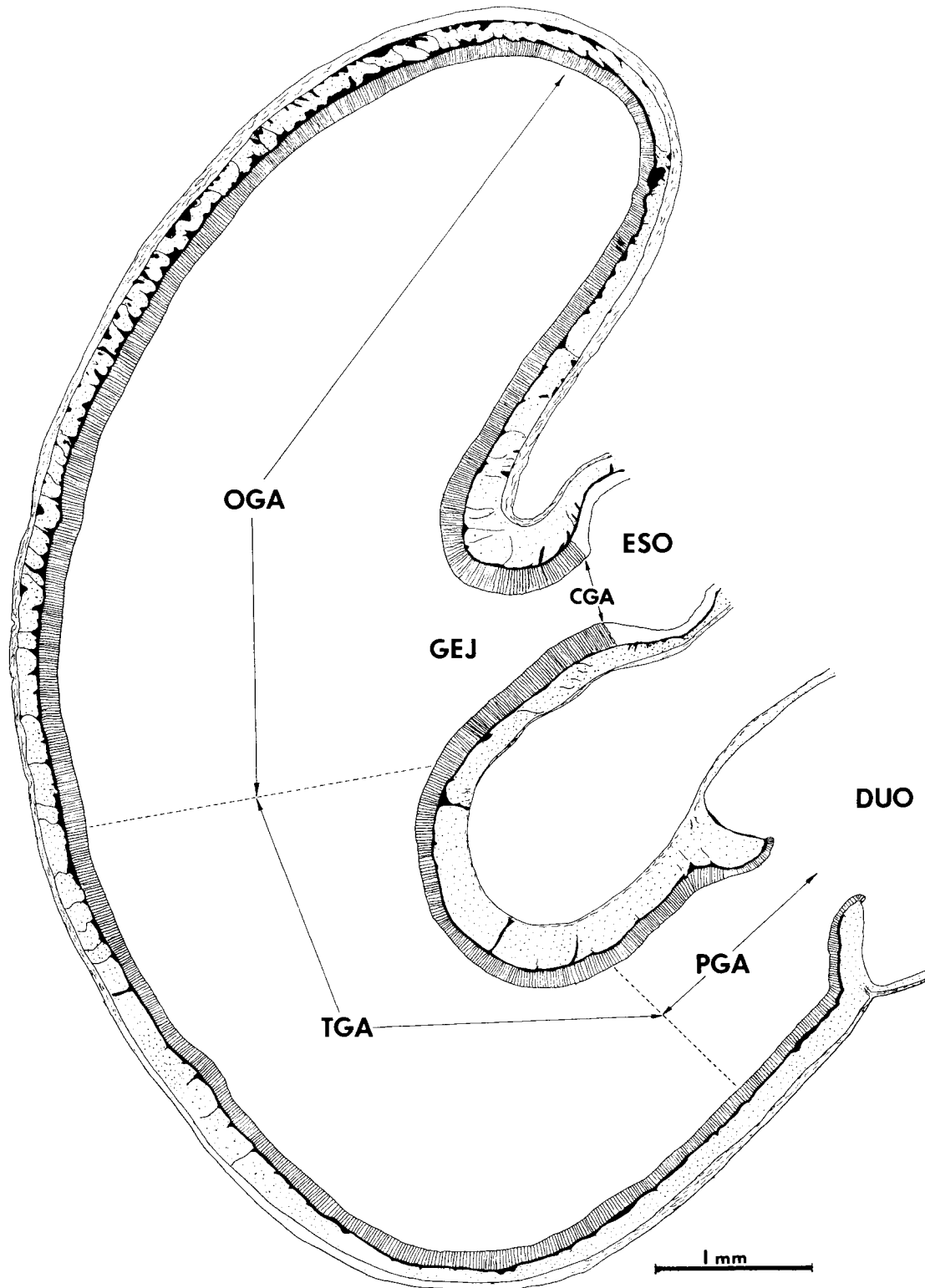


Figure 2. Sagittal section of stomach of *Myotis velifer*, dorsal view. Top of page represents the anterior. Abbreviations as in Figure 1. Semidiagrammatic, rugae not included.

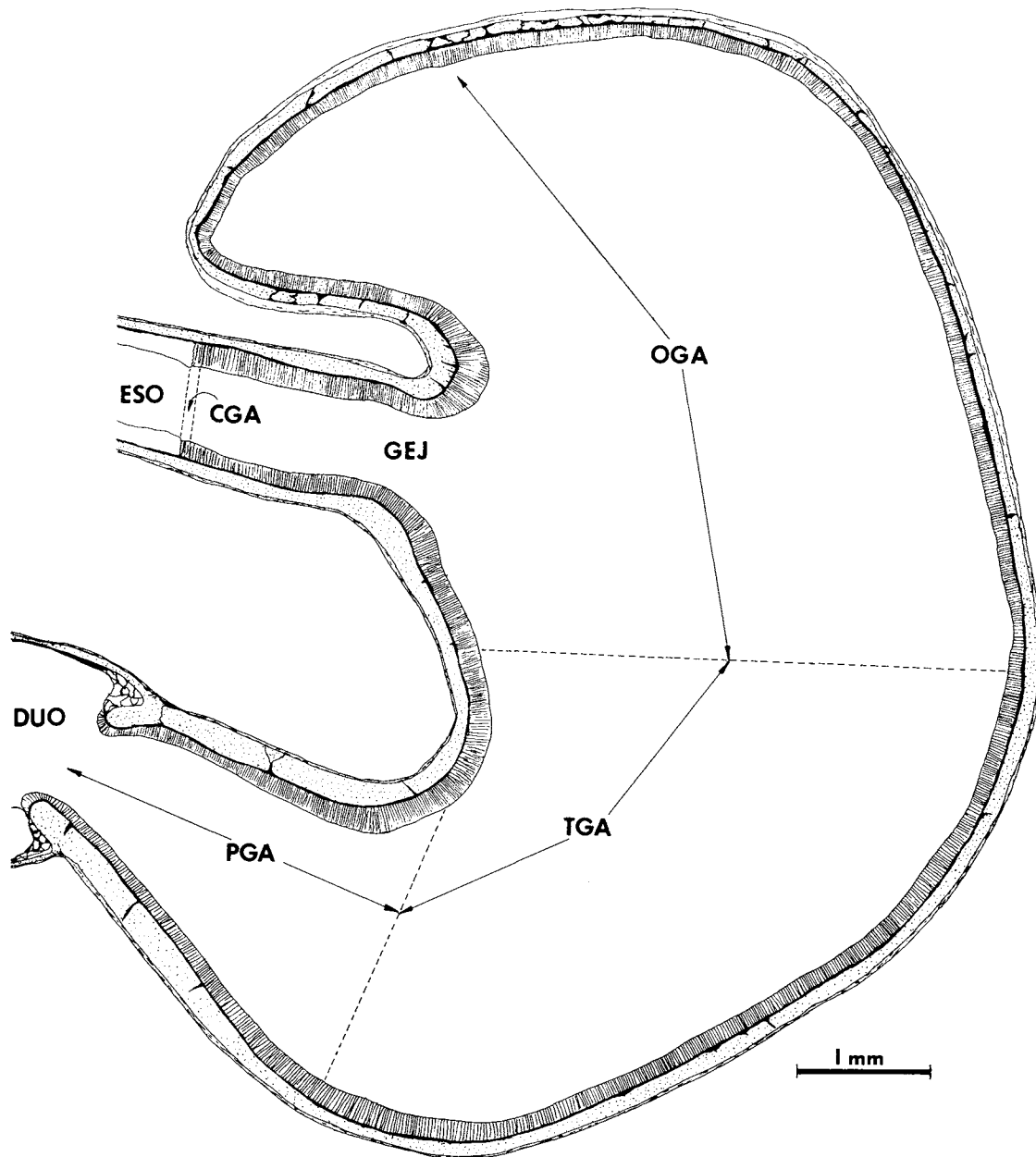


Figure 3. Sagittal section of stomach of *Antozous pallidus*, ventral view. Top of page represents the anterior. Abbreviations as in Figure 1. Semidiagrammatic, rugae not included.



Figure 4. Cross-section of stomach of Antrozous pallidus, showing rugus. TM, tunica mucosa; S, tunica submucosa; ME, tunica muscularis. Scale = 200 microns. Photomicrograph.

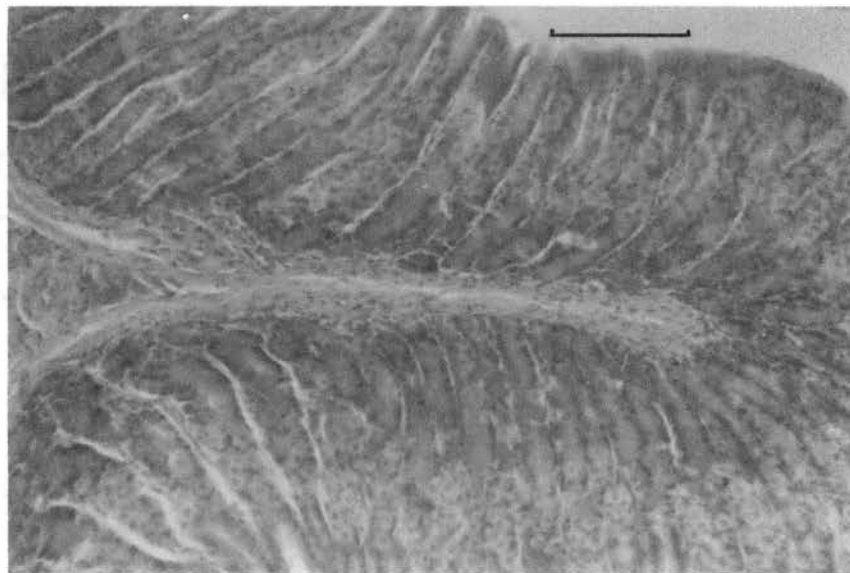


Figure 5. Cross-section of stomach of Antrozous pallidus, same rugus as in Figure 4, but at higher magnification. Note tubular oxyntic glands in tunica mucosa. Scale = 100 microns. Photomicrograph.

sections this portion of the stomach is distinguished by the presence of elastic fibers in the tunica muscularis. Elastic tissue is virtually absent from the tunica muscularis in the aboral half of the stomach.

The tunica muscularis is composed of two layers throughout most of the stomach. There is a third, incomplete inner layer in the form of smooth muscle bundles on both dorsal and ventral sides of the lesser curvature, arising from near the terminal portion of the esophagus, and bifurcating and extending aborally to the pyloric antrum where the two bundles anastomose with and contribute to the inner circular layer of the tunica muscularis. This inner layer is continuous with the inner circular layer of the esophagus.

The two complete layers of smooth muscle are disposed into an outer longitudinal layer and an inner circular layer. The outer longitudinal layer is generally the thinner of the two except in the fundic caecum and the greater curvature, where the two layers are subequal in thickness. The longitudinal layer is extremely thin along the lesser curvature. Also, in the elastic portion of the stomach the inner circular layer is composed of discrete bundles surrounded by areolar connective tissue, rather than being a continuous sheet. About midway along the greater curvature in Tadarida brasiliensis, but not in the two vesperilionids, in an area which wrinkles inwards when the stomach is empty (See Fig. 1).

Thickness of the tunica muscularis is quite variable. In T. brasiliensis it ranges from 40 microns (stretched) to 150 microns (relaxed) in the elastic portion, and from 150 microns to 200 microns in the pyloric portion. In Myotis velifer the tunica muscularis ranges from a maximum of 120 microns in the elastic portion to 300 microns in

the pyloric portion. The same regions in Antrozous pallidus measure 150 microns and 340 microns, respectively. Figures 1, 2, and 3 show the approximate thickness of these layers in the relaxed, empty stomach.

At the gastroduodenal junction the inner circular layer is greatly thickened to form the pyloric valve (See Figs. 6, 7, and 8). No structure similar to this is found at the gastroesophageal junction. All parts of the tunica muscularis are quite similar in all three species. Ganglia of the myenteric plexus of Auerbach are numerous throughout the stomach between the inner circular and outer longitudinal layers of muscle.

The tunica submucosa in these species appears to provide a supportive framework and cushion between the tunica muscularis and the tunica mucosa, and to be composed of the usual constituents of areolar connective tissue. Ganglia of Meissner's plexus are present, but rare. The submucosa of T. brasiliensis differs from that of M. velifer and A. pallidus in having very few elastic fibers.

Arterioles and venules are fairly abundant in the submucosa of all three species and are generally in and underlying the rugae. These vessels are continuous with smaller arterioles and venules which in turn form anastomosing capillary loops which proliferate throughout the lamina propria of the mucosa. Generally, vessels larger than arterioles and venules do not enter the mucosa. Lymph nodules and diffuse lymphoid tissue are sometimes found in the submucosa where no obvious pathological condition exists, but are more often associated with encysted nematodes.

The gastric mucosa of these species is composed of the typical components: surface epithelium of simple columnar mucous cells leading



Figure 6. Pyloric valve in Tadarida brasiliensis. PV, pyloric valve. Scale = 200 microns. Photomicrograph.

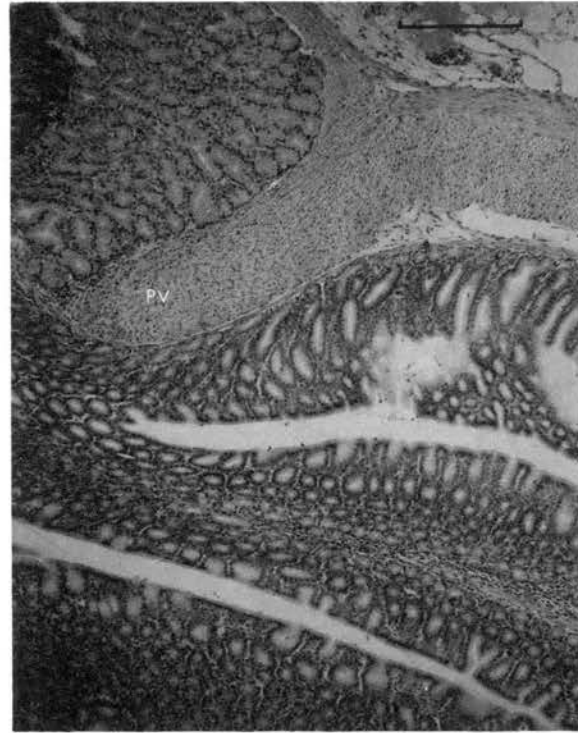


Figure 7. Pyloric valve in Myotis velifer. PV, pyloric valve. Scale = 200 microns. Photomicrograph.

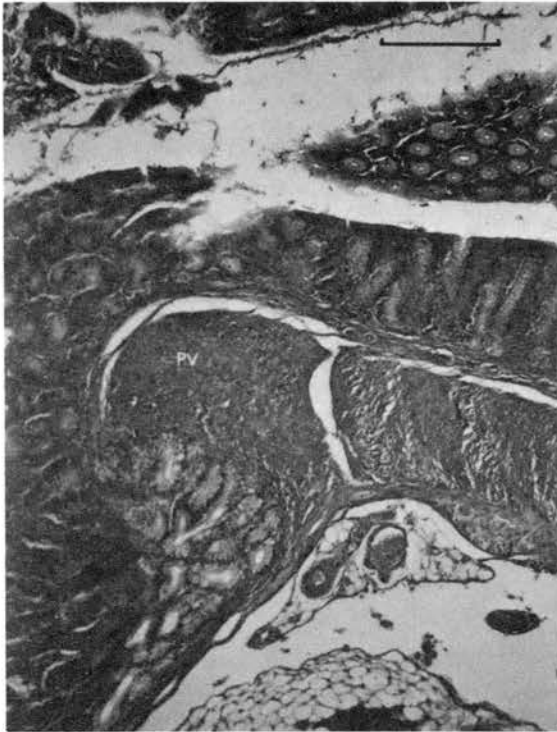


Figure 8. Pyloric valve in Antrozous pallidus. PV, pyloric valve. Scale = 200 microns. Photomicrograph.

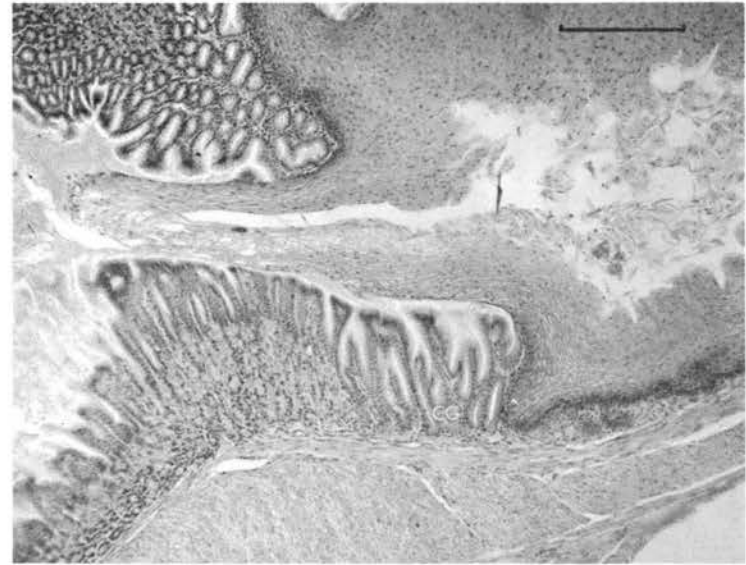


Figure 9. Gastroesophageal junction in Tadarida brasiliensis. CG, cardiac glands. Scale = 200 microns. Photomicrograph.

in most cases into gastric pits; tubular glands opening into the pits or onto the surface; glands imbedded in a cellular lamina propria; and a basally positioned lamina muscularis mucosae. The glandular mucosa is confined to the stomach in T. brasiliensis, the stratified squamous epithelium of the esophagus continuing all the way to the gastroesophageal junction where the transition from esophageal mucosa to cardiac glands is abrupt (See Fig. 9). In contrast, the esophageal mucosa of A. pallidus changes to typical gastric mucosa a few millimeters before forming the gastroesophageal junction. A similar condition to that in A. pallidus exists in M. velifer, but here the abrupt transition from esophageal to gastric mucosa is nearer the gastroesophageal junction, occurring only about one half millimeter crainad (See Fig. 10).

Four general types of glands occur in the gastric mucosa of these species: cardiac glands; fundic (oxyntic) glands; transitional glands; and pyloric glands. In T. brasiliensis (Figs. 1 and 9) the cardiac glands are found in the first 150-200 microns of the glandular mucosa surrounding the gastroesophageal orifice. In M. velifer (Figs. 2 and 10) and A. pallidus the cardiac glands are in the initial 150-200 microns of the glandular mucosa in the esophagus; the remaining glandular mucosa is like that found in the gastric fundus. In all three species the cardiac glands vary considerably in length (100-200 microns) and empty into pits of variable depth (75-100 microns). The entire lengths of these cardiac glands are composed of low columnar mucous neck cells. When stained by the aldehyde fuchsin-alcian blue technique, these cells appear bluish-purple, showing a positive reaction to both constituent stains. The pits into which the cardiac glands empty are lined with tall columnar mucous cells, typical of the surface epithelium

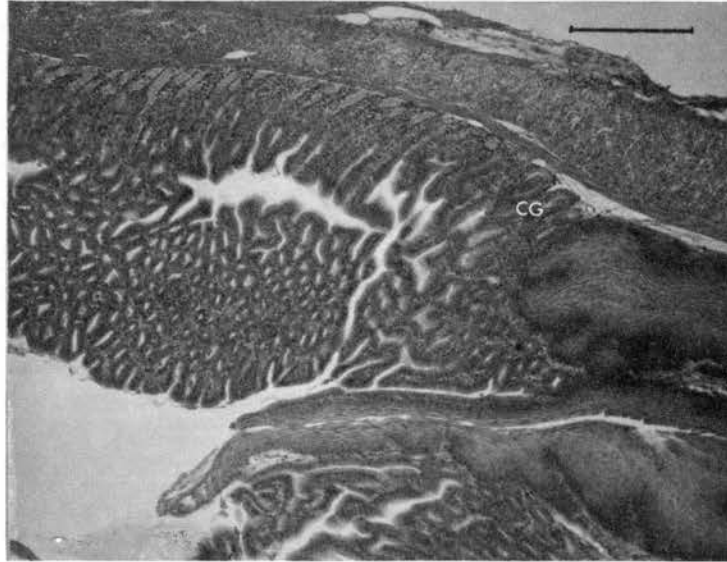


Figure 10. Esophagus of *Myotis velifer*, showing transition to glandular epithelium. The gastroesophageal junction is at the far left. CG, cardiac glands. Scale = 200 microns. Photomicrograph.

of the entire stomach. These show an affinity for the alcian-blue component only, and appear bright blue.

Most of the gastric mucosa of these species contain fundic or oxyntic glands. The oxyntic glands in the fundus proper (Figs. 11, 12, and 13) tend to be taller and less coiled than those in the terminal half of the fundic caecum (Figs. 14, 15, and 16). The large variation may be due in part to muscular activity, as there are a few solitary smooth muscle fibers in the lamina propria running perpendicularly to the surface and parallel to the long axis of the glands. All the oxyntic glands are tubular, some branching, and all are coiled to varying degrees near their bases.

The cross-section of the glandular mucosa displays three zones: a luminal zone composed of the gastric pits; a middle zone composed principally of the parietal cells with a few mucous neck cells and chief cells, and a basal zone composed principally of chief cells with a few mucous neck cells, parietal cells, and argentaffine cells. The argentaffine cells are quite rare. The shorter oxyntic glands of the fundic caecum, in contrast, contain only a few chief cells at the base of the glands, and otherwise are composed entirely of parietal and mucous neck cells. The longer oxyntic glands of the fundus proper have an abundance of chief cells. In M. velifer and T. brasiliensis the lower third of the gland is composed of chief cells whereas in A. pallidus the lower 1/2 to 3/4 of the gland contains them. The distribution of cell types in hibernating M. velifer is identical with that described for the active, fasting animal.

Throughout most of the oxyntic gland area in these three species, the glands are closely packed. There are, however, regions where the

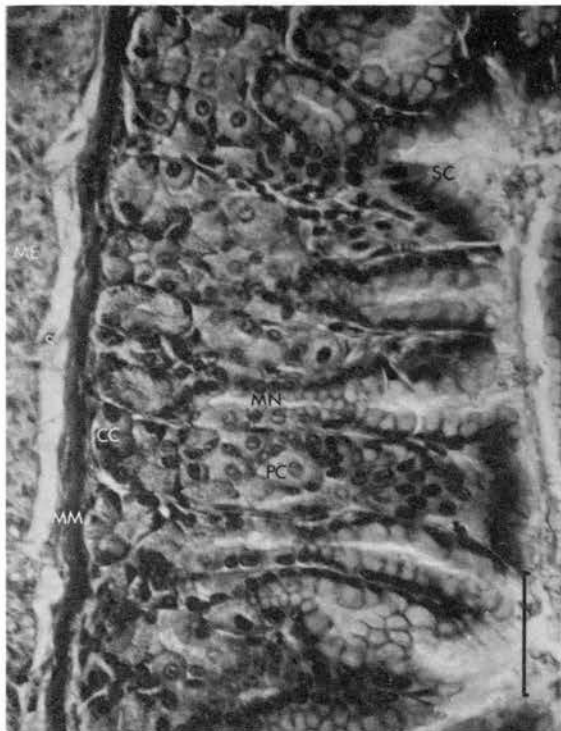


Figure 11. Oxyntic glands in fundus proper of stomach of *Tadarida brasiliensis*. CC, chief cells; MN, mucous neck cells; PC, parietal cells; MM, lamina muscularis mucosae; S, tunica submucosa; ME, tunica muscularis; SC, surface columnar cells, Scale = 50 microns. Photomicrograph.

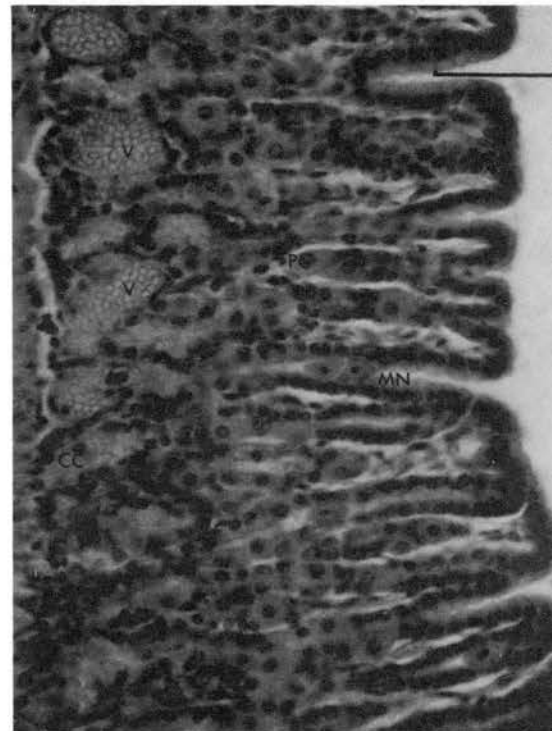


Figure 12. Oxyntic glands in fundus proper of stomach of *Myotis velifer*. V, venules; other abbreviations as in Figure 11. Scale = 50 microns. Photomicrograph.

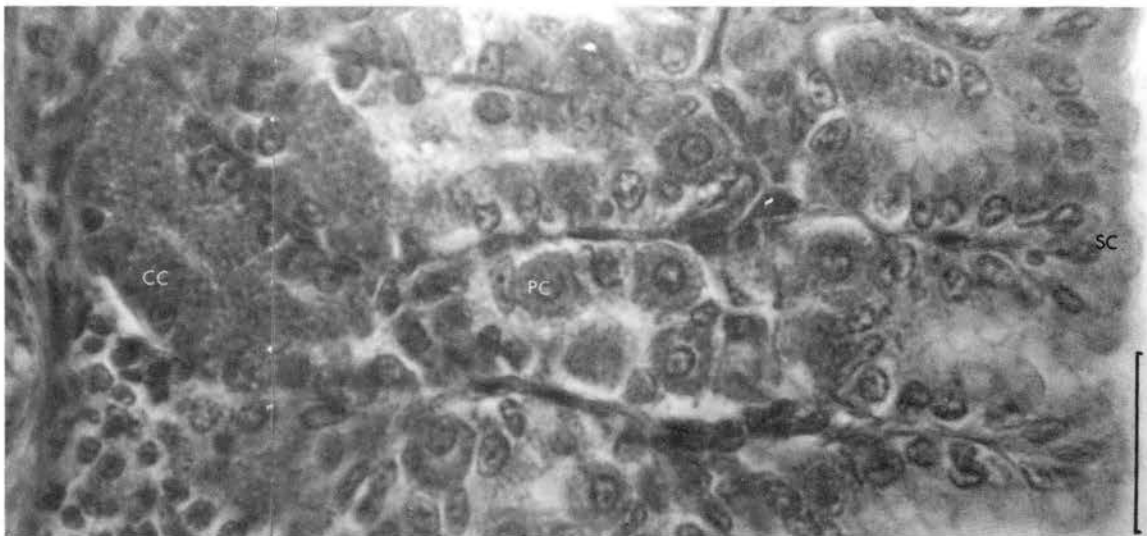


Figure 13. Oxyntic glands in fundus proper of stomach of Antrozous pallidus. Abbreviations as in Figure 11. Scale = 30 microns. Photomicrographs (composite).

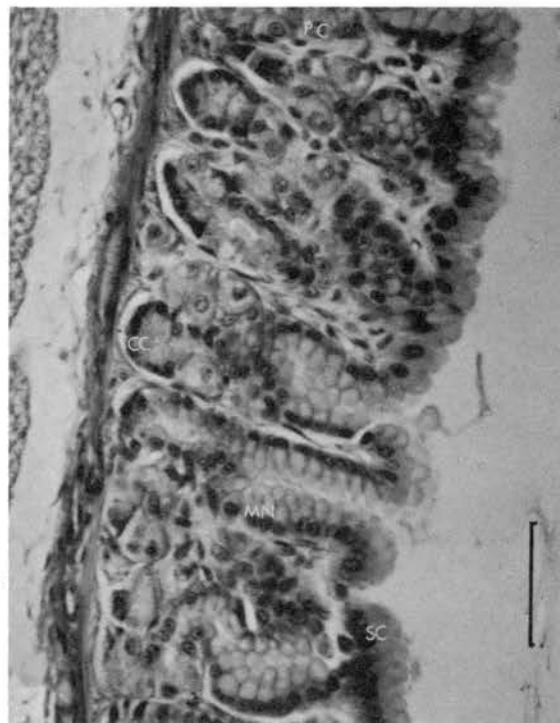


Figure 14. Oxyntic glands in caecum of stomach of Tadarida brasiliensis. Abbreviations as in Figure 11. Scale = 50 microns. Photomicrograph.

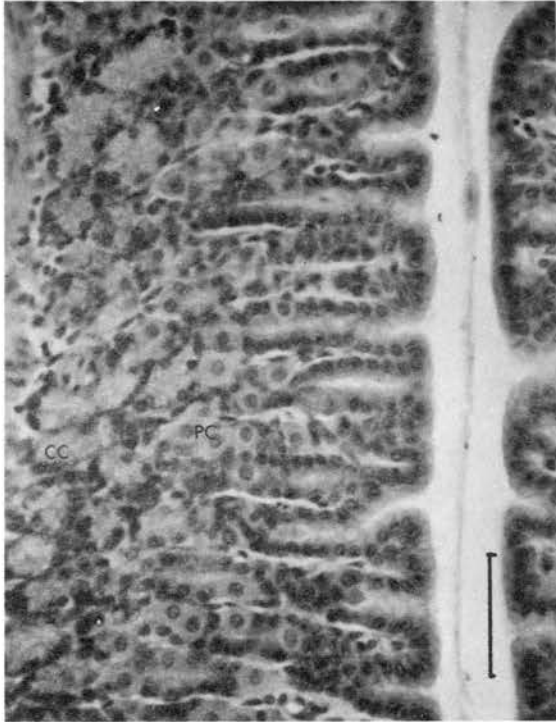


Figure 15. Oxyntic glands in caecum of stomach of Myotis velifer. Abbreviations as in Figure 11. Scale = 50 microns. Photomicrograph.

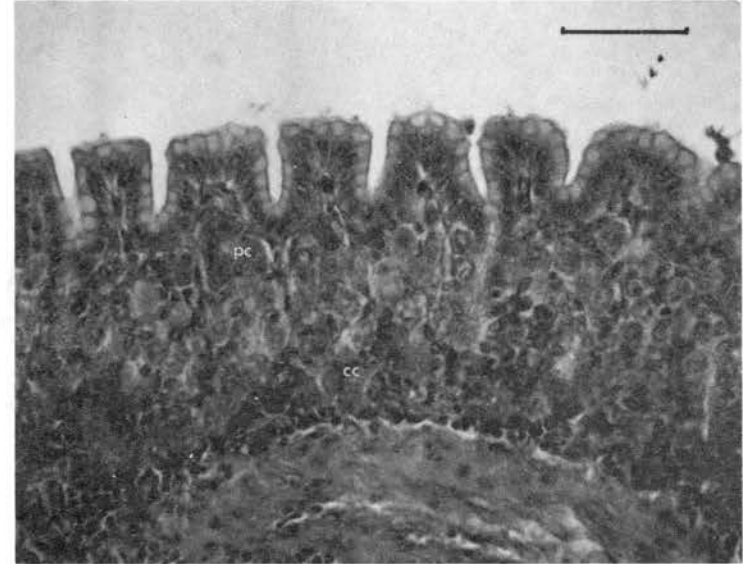


Figure 16. Oxyntic glands in caecum of stomach of Antrozous pallidus. Abbreviations as in Figure 11. Scale = 50 microns. Photomicrograph.

glands are more dispersed, separated in some instances by as much as 30 microns. There is no consistency as to the regions of the stomach exhibiting this condition, but it occurs more commonly in A. pallidus than in M. velifer and T. brasiliensis.

The transition from oxyntic glands to pyloric glands occupies an extremely broad zone in each of the three species. The first sign of transition is the abrupt disappearance of chief cells from the glands. The region of transition is characterized by glands composed primarily of parietal cells with a few mucous neck cells scattered throughout and an occasional large mucous gland cell (Reith et al. 1965) at the base (Figs. 17, 18, and 19). As the pyloric region is approached the parietal cells are gradually replaced by mucous neck cells and mucous gland cells. The transition area occupies roughly the angular portion of the stomach.

The pyloric glands occupy the short region between the aboral angular portion of the stomach and the posterior eminence of the pyloric valve. This cone-shaped pyloric region is quite short in M. velifer, being only slightly more than 1 mm. in length. The pyloric area is longer in T. brasiliensis than in M. velifer by a factor of almost 2. In A. pallidus the area is about three times longer than it is in M. velifer. Figures 1, 2, and 3 illustrate the delineations more precisely.

The pyloric glands (Figs. 20, 21, and 22) are quite similar in all three species, and resemble the cardiac glands in being entirely mucous in nature. They range in length from 100 to 200 microns, of which the gastric pits make up 50 to 100 microns. These glands are branched or unbranched tubes, and sometimes are coiled at their bases. Pyramidal

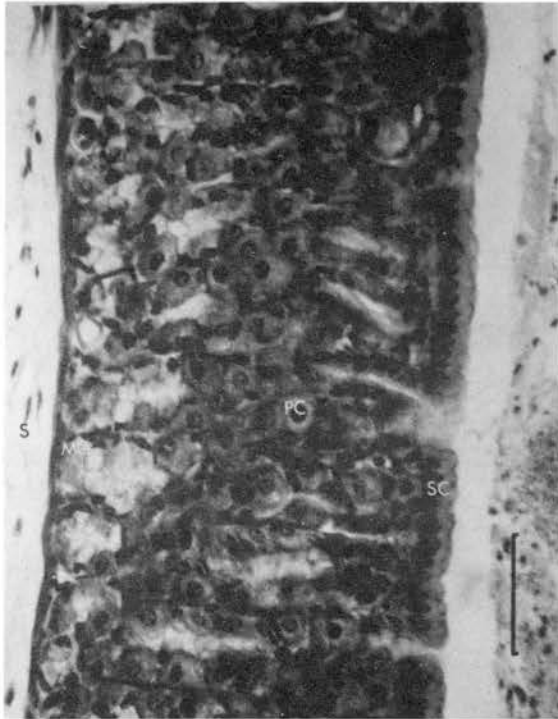


Figure 17. Transitional glands in stomach of Tadarida brasiliensis. MG, mucous gland cell; other abbreviations as in Figure 11. Scale = 50 microns. Photomicrograph.

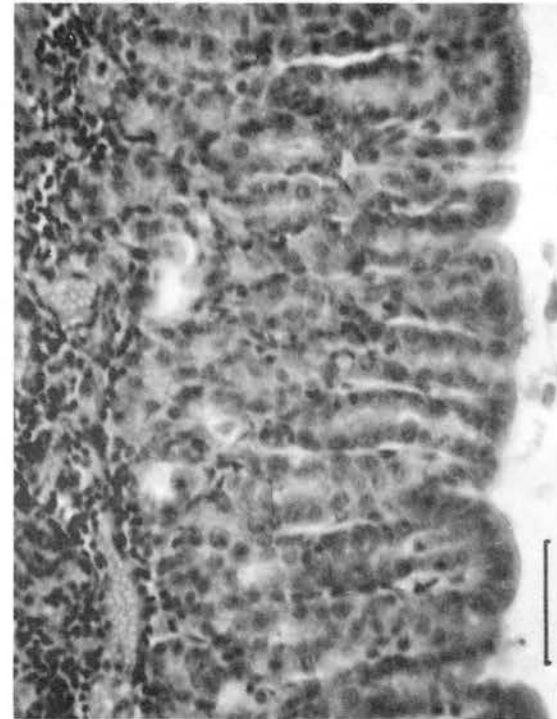


Figure 18. Transitional glands in stomach of Myotis velifer. Scale = 50 microns. Photomicrograph.

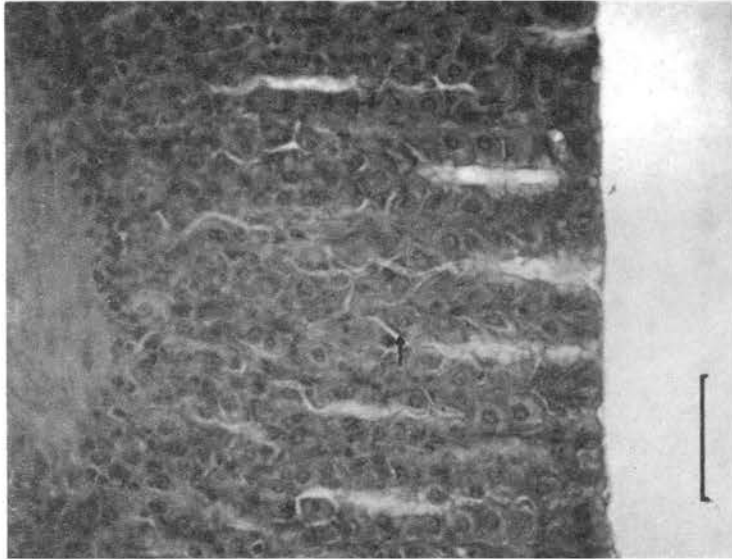


Figure 19. Transitional glands in stomach of Antrozous pallidus. Note predominance of parietal cells (Arrows) and lack of chief cells. Scale = 50 microns. Photomicrograph.

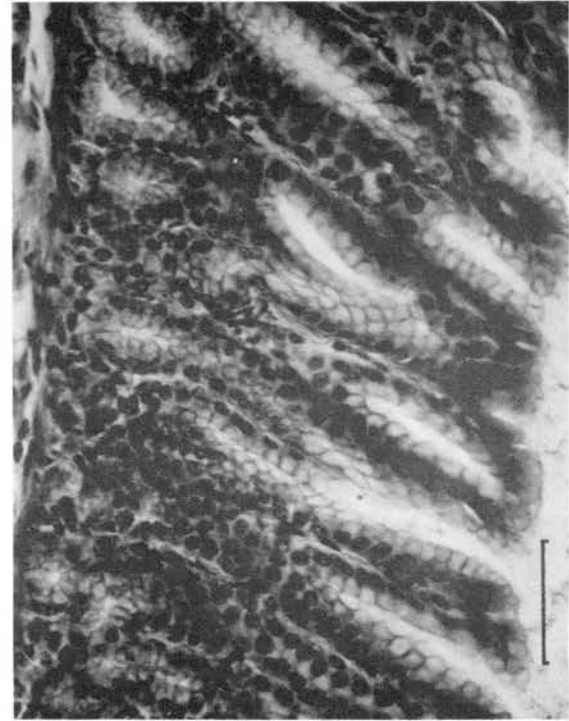


Figure 20. Pyloric glands in stomach of Tadarida brasiliensis. Note absence of chief and parietal cells. Scale = 50 microns. Photomicrograph.

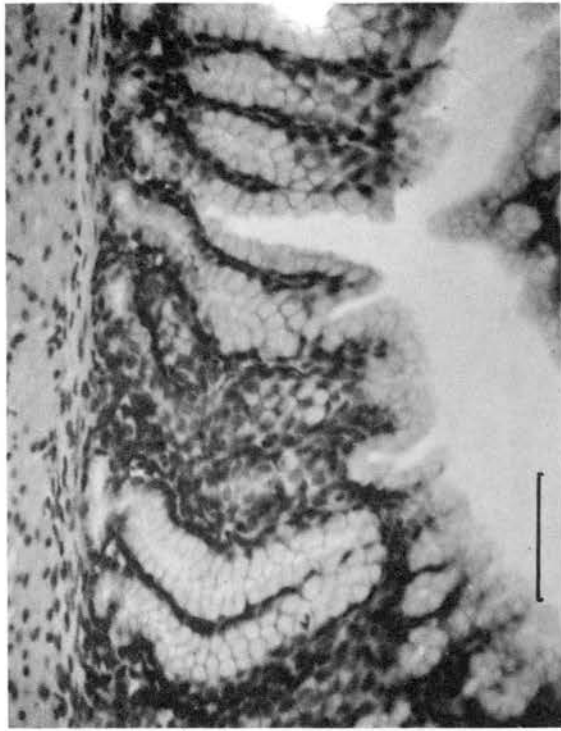


Figure 21. Pyloric glands in stomach of Myotis velifer. Note absence of chief and parietal cells. Scale = 50 microns. Photomicrograph.

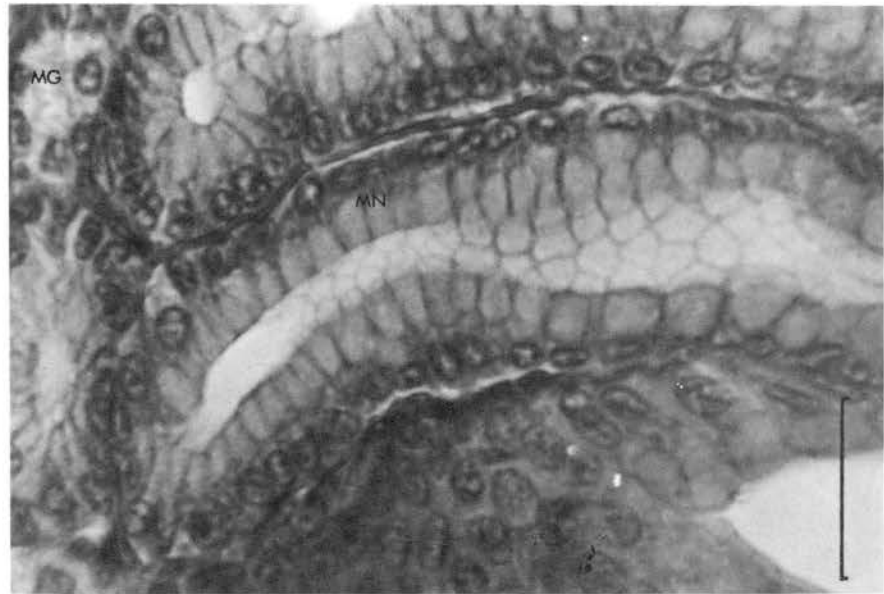


Figure 22. Pyloric glands in stomach of Antrozous pallidus. Note absence of chief and parietal cells. Note also coiled nature of the glands. MN, mucous neck cell; MG, mucous gland cell. Scale = 30 microns. Photomicrograph.

mucous gland cells are common in the basal portion.

Nectivore: Leptonycteris sanborni

The nectivorous stomach (Fig. 23) of L. sanborni differs from the simple type in the insectivores in being more globular or saccular. The ventral portion is somewhat more developed than the dorsal, which results in a much less symmetrical condition than in the insectivorous species. As in the insectivorous species, a fundic caecum is present.

The wall of the stomach of L. sanborni consists of the same four layers found in the insectivores. The tunica mucosa and tunica submucosa are thrown into numerous rugae which, rather than being longitudinally disposed, are short, branching, and anastomosing, thus imparting a honey-comb appearance to the mucosal surface. The folds tend to be effaced in the distended stomach.

As in the insectivorous species, the tunica muscularis is composed of two complete and a third incomplete layer of smooth muscle. The complete layers are the outer longitudinal and inner circular layers. The third layer is longitudinally disposed and lies internal to the inner circular layer on both sides of the lesser curvature, as in the insectivores. Qualitatively this innermost oblique layer seems to be equivalent to that found in the insectivorous species, although it is somewhat more extensive.

The thickness of the two complete layers varies throughout the stomach owing to their disposition in the form of bundles. The thickness of the inner circular layer is generally greater, varying from 30 microns to 125 microns. The thickness of the outer longitudinal layer rarely exceeds 50 microns and often is as thin as 20 microns. Elastic

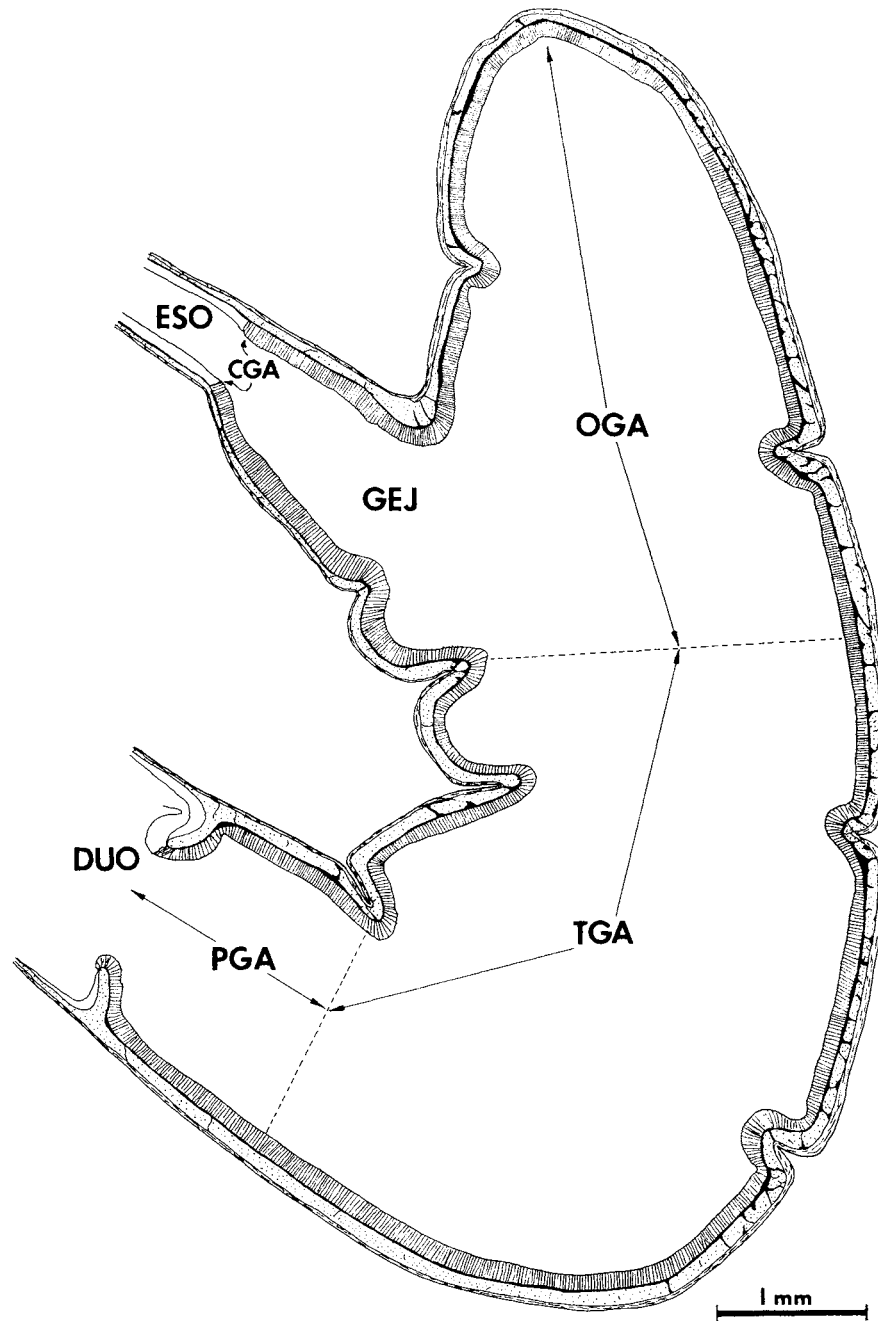


Figure 23. Sagittal section of stomach of *Leptonycteris sanborni*, ventral view. Top of page represents the anterior. Abbreviations as in Figure 1. Semidiagrammatic, rugae not included.

fibers are virtually absent from the tunica muscularis.

The inner circular layer of smooth muscle forms a pyloric valve at the gastroduodenal junction (Fig. 24). This structure is thinner than in the insectivorous species, where it is thick and rounded. As in the insectivorous species there is no gastroesophageal sphincter.

The submucosa in the stomach of L. sanborni is much like that described for T. brasiliensis, M. velifer, and A. pallidus. But, in the three specimens studied here, lymph nodules and diffuse lymphoid cells are much more numerous. Elastic fibers are virtually absent in the submucosa of L. sanborni, as noted also in T. brasiliensis, in contrast to the elastic walls of the other insectivorous species studied.

Arterioles and venules are abundant in the submucosa of L. sanborni. These vessels contribute qualitatively to the vascular network of the mucosa as in the insectivorous species. In L. sanborni, however, the mucosal vessels are more numerous and larger than in the species so far mentioned in this study.

The gastric mucosa consists of the surface epithelium of columnar mucous cells, gastric pits, tubular glands, lamina propria, and lamina muscularis mucosae. As in A. pallidus, the abrupt transition from esophageal stratified squamous epithelium to secretory columnar epithelium (Fig. 25) occurs more than a millimeter cranial to the gastroesophageal junction proper. At the transition, the esophagus abruptly expands to form a cone-shaped ampulla whose base forms the junction between stomach and esophagus. When empty, the luminal diameter of the esophagus is about 0.25 to 0.50 mm. and the widest part of the ampulla is 1.5 to 2.0 mm.

The four common types of glands are present in the gastric mucosa

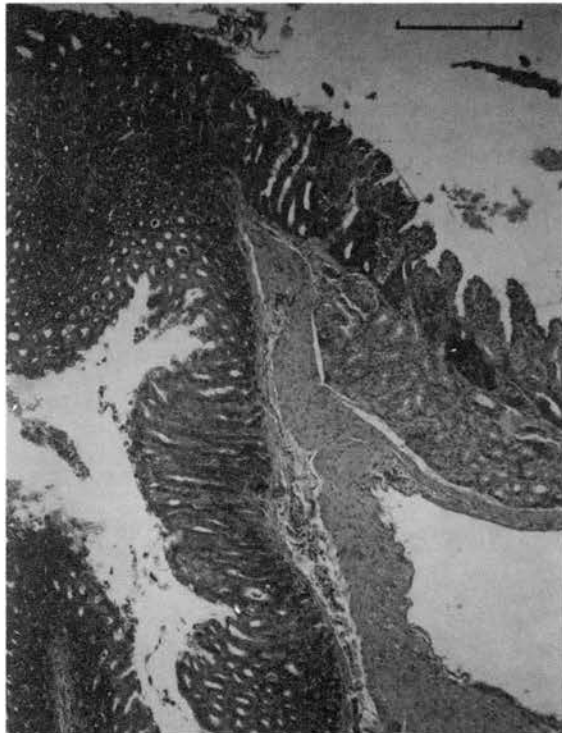


Figure 24. Pyloric valve in Leptoncyteris sanborni. PV, pyloric valve. Scale = 200 microns. Photomicrograph.

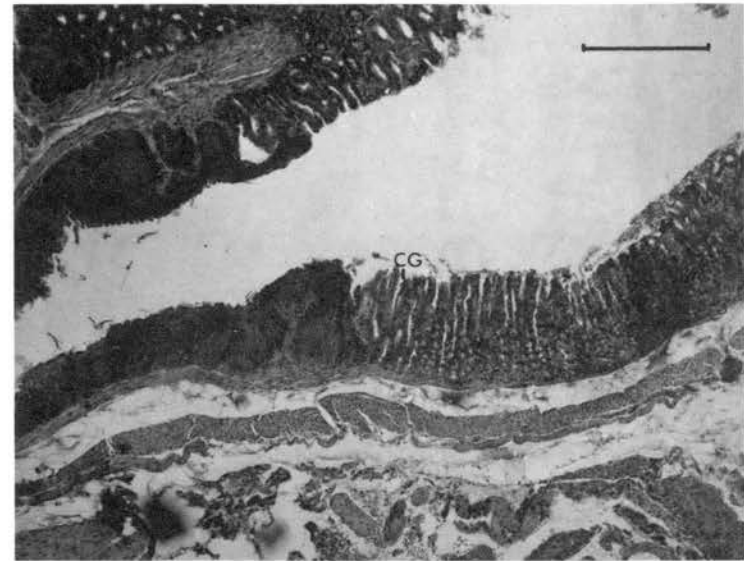


Figure 25. Initial portion of ampulla in terminal portion of esophagus in Leptoncyteris sanborni. Note transition to glandular epithelium and cardiac glands (CG). Scale = 200 microns. Photomicrograph.

of L. sanborni. The cardiac glands form the narrow band of transition from stratified squamous epithelium to glandular epithelium in the esophagus. These glands are 150 to 200 microns in length, including the gastric pits which are 50 to 75 microns in depth. The oxyntic glands (Fig. 26) occupy the ampulla and caecum. Transitional glands (Fig. 27) occupy a broad zone beginning slightly aboral to the gastroesophageal junction and ending a few millimeters short of the gastroduodenal junction. The pyloric glands (Fig. 28) occupy the region extending aborally from the transitional gland zone to the gastroduodenal junction.

The description of the cardiac glands of T. brasiliensis, M. velifer, and A. pallidus applies equally well to those of L. sanborni. The oxyntic glands in the ampulla differ somewhat from those in the caecum in being a bit deeper and narrower. Here again the variations may reflect variable mucosal thickness due in part to various states of contraction in smooth muscle cells within the lamina propria surrounding the glands. The oxyntic gland lengths vary from 185 to 325 microns including the gastric pits which are 75 to 135 microns in depth. Throughout the stomach the gastric pits tend to occupy half of the mucosa, although this may vary slightly. As in the insectivorous species the glands throughout the gastric mucosa are tubular, some being branched.

The oxyntic glands (Fig. 26) contain the cell types described previously, but their distribution within the gland is somewhat different. The parietal cells are fairly numerous and are distributed throughout the gland rather than being concentrated in the middle zone. Mucous neck cells are distributed throughout the gland. The chief cells are

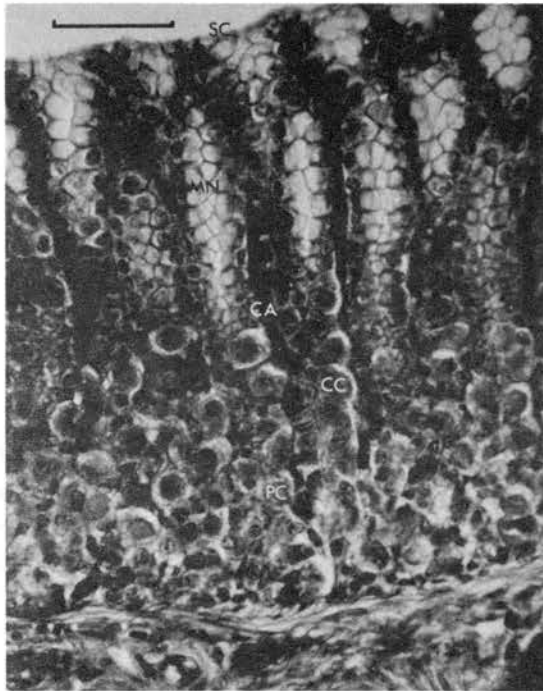


Figure 26. Oxyntic glands in caecum of stomach of Leptonycteris sanborni. CA, capillaries; other abbreviations as in Figure 11. Scale = 50 microns. Photomicrograph.

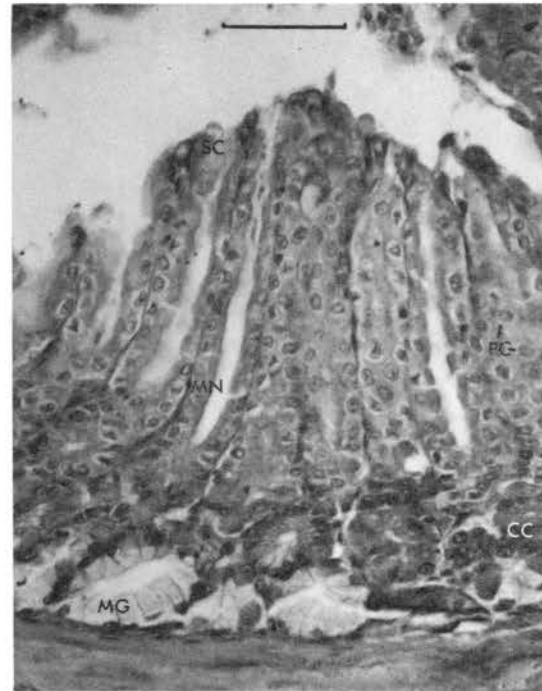


Figure 27. Transitional glands in aboral segment of fundus proper of stomach of Leptonycteris sanborni. Abbreviations as in Figures 11 and 17. Scale = 50 microns. Photomicrograph.

much less numerous throughout than in the insectivorous species, a few being found at the base of the gland mixed with mucous neck cells and parietal cells. Very occasionally, a few chief cells can be seen in the mid-portion of the gland. About midway between the gastroesophageal junction and the pylorus, the oxyntic glands give way to glands of the transitional variety (Fig. 27).

The glands in the transitional zone measure 175 to 225 microns including the gastric pits which are 60 to 125 microns in depth. These glands are distinguished more by the appearance of mucous gland cells than by the disappearance of chief cells, as occurs in the insectivorous species. The chief cells do not disappear abruptly, but can be seen in small numbers throughout the transitional zone. The mucous gland cells occupy the basal third of all of the glands both in the transition zone and in the pyloric glands of the aboral end of the stomach.

The pyloric glands are similar to those described for the three insectivorous species and appear as the parietal cells of the glands in the transition zone are gradually replaced by mucous neck cells. These glands measure from 160 to 300 microns in length, including the gastric pits which are 100 to 150 microns in depth. The delineations for the different glandular zones can be seen in Figure 23.

In the terminal portion of the pyloric gland area in one of the L. sanborni examined, several clusters of submucosal glands resembling the glands of Brunner are found. These glands empty by way of ducts into the lumen adjacent to the pylorus.

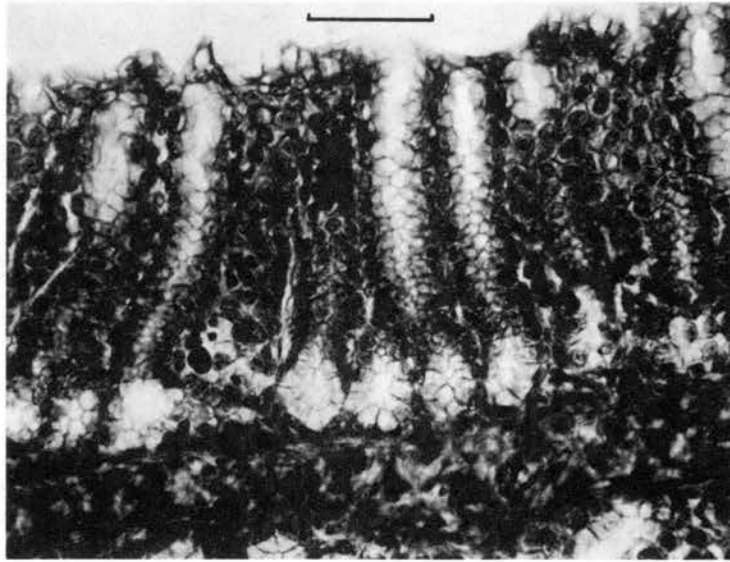


Figure 28. Pyloric glands in stomach of Leptonycteris sanborni. Scale = 50 microns. Photomicrograph.

Sanguivore: Desmodus rotundus

The stomach of D. rotundus (Fig. 29) is quite unlike those so far described in this study. A few millimeters to the left of the gastroesophageal junction, the tubular stomach bends sharply caudad. It then turns again sharply on itself after continuing several centimeters caudad ascending parallel to the descending portion to a point near the gastroesophageal junction where it again bends on itself to form a terminal pouch. The total lengths of two D. rotundus stomachs, one empty the other completely distended, are 6.2 cm. and 11.5 cm., respectively. The outside diameter of the empty, Bouin's-fixed stomach is fairly uniform throughout measuring about 2 mm. The full stomach varies considerably throughout its length from about 3 mm. to a maximum in the ascending portion of about 8 mm.

Folds of the tunica mucosa and tunica submucosa form numerous longitudinal and transverse, branching rugae. These rugae become effaced in the fully-distended stomach. The few rugae still remaining in what seems to be full distention may indicate a potential distention larger than that actually observed.

The tunica muscularis is composed of two layers throughout the stomach. The outer longitudinal and inner circular layers are represented by many longitudinal and circular bundles of smooth muscle, both surrounded by an abundance of connective tissue (Fig. 37). The proportions of muscle and connective tissue in the empty stomach are about equal. The muscle bundles measure 30 to 125 microns in diameter in the empty stomach and rarely exceed 40 microns in the distended stomach. The tunica muscularis does not exhibit elastic fibers when stained with aldehyde-fuchsin. Due to the loose-bundled nature of the tunica

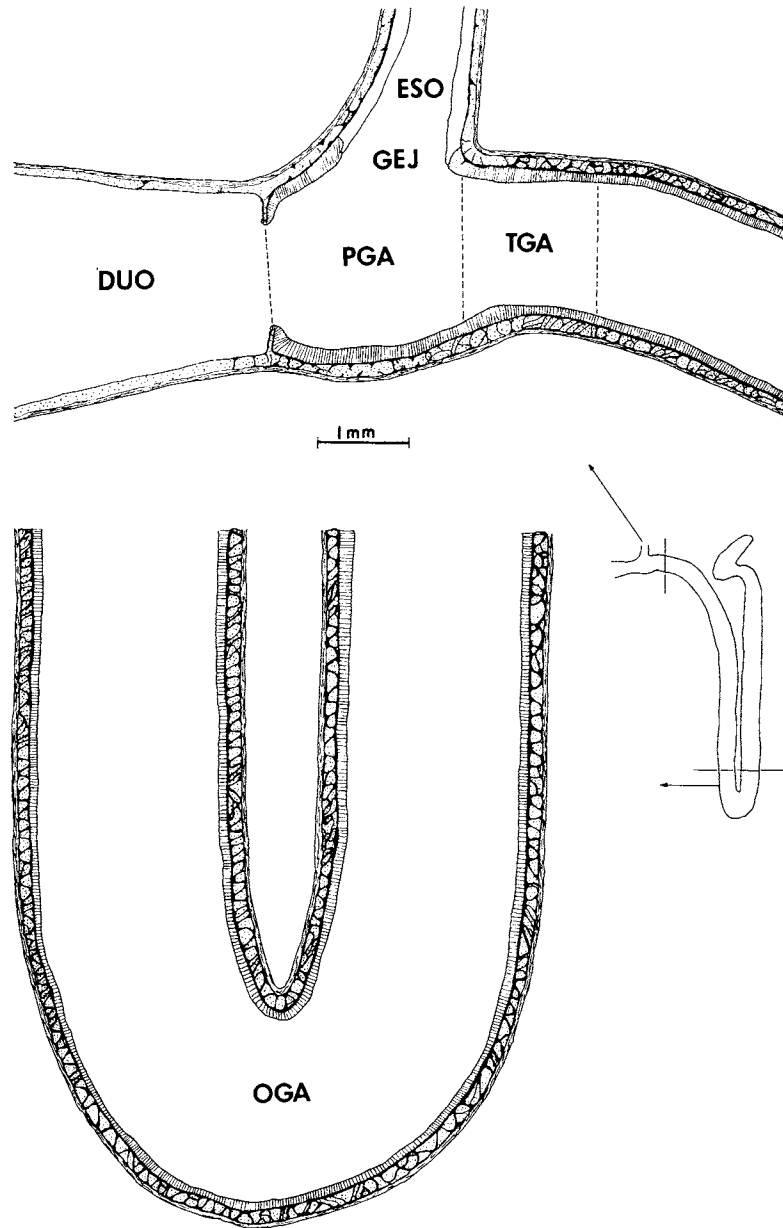


Figure 29. Sagittal section of stomach of *Desmodus rotundus*. Ventral view. Small figure to the right shows what segments have been drawn in greater detail. Abbreviations as in Figure 1. Semidiagrammatic.

muscularis it is difficult to determine whether there are two or three layers of muscle. The appearance of the muscularis in the fully distended stomach, however, indicates the presence of only two layers.

At the gastroduodenal junction (Fig. 30) the inner circular layer of muscle forms a very thin pyloric valve (Fig. 30), resembling more that of Leptonycteris sanborni than that of the insectivorous species. The gastroesophageal junction of D. rotundus lacks the sphincter seen in all of the other species studied.

The submucosa is composed of areolar connective tissue and contains many arterioles and venules which supply a rich network of capillaries in the mucosa. The submucosa is similar to Tadarida brasiliensis and L. sanborni in containing few elastic fibers.

As in T. brasiliensis, the gastric mucosa does not invade any part of the esophagus (Fig. 31). The tunica mucosa of the stomach contains glands of three general types: pyloric glands, transitional glands, and caecal glands. The short region between the esophagus and pyloric valve contains tubular glands of the pyloric type which are branched and for the most part not coiled. They measure about 200 microns in length and empty into short pits of about 35 microns. The pyloric glands (Figs. 30, 31, and 32) resemble the cardiac and pyloric glands of the other species considered in this study. The short duct or pit is composed of columnar mucous cells characteristic of the surface epithelium throughout the gastric mucosa. The cells below the pit are for the most part of the mucous type, although a few parietal and argent-affine cells can be seen occasionally. In the distended stomach these glands appear swollen, as though they were secreting against a pressure caused by the compact, dense material in the lumen. There are no

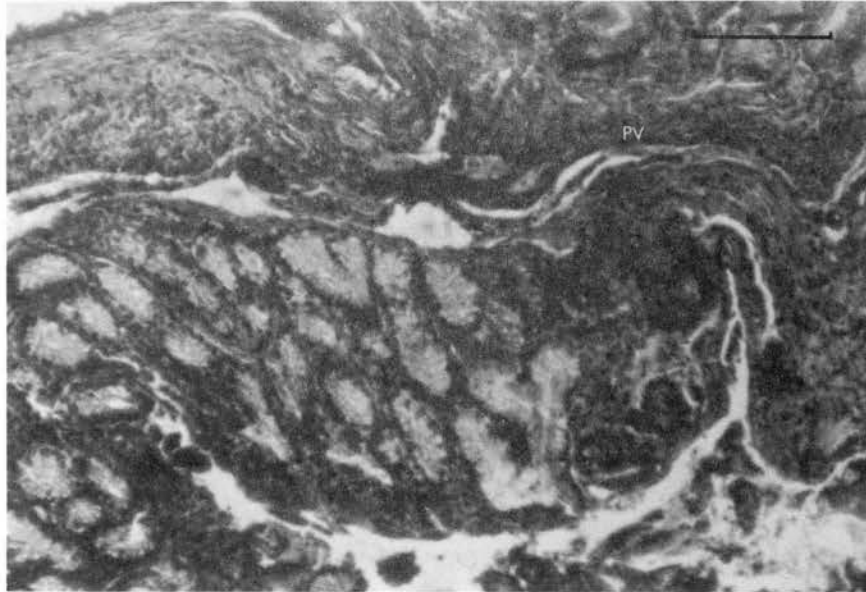


Figure 30. Pylorus in Desmodus rotundus. PV, pyloric valve. Scale = 100 microns. Photomicrograph.



Figure 31. Gastroesophageal junction in Desmodus rotundus. Note transition to glandular epithelium. Scale = 100 microns. Photomicrograph.

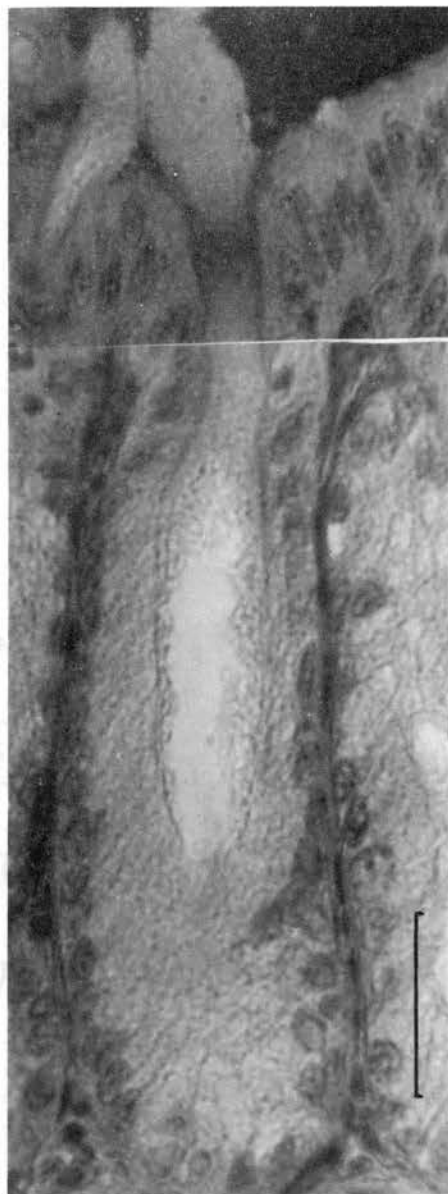


Figure 32. Pyloric gland in Desmodus rotundus. Scale = 30 microns. Photomicrograph.

features in the pyloric glands near the gastroesophageal junction (Fig. 31) that would characterize them as being different from the pyloric glands nearer the pyloric valve (Fig. 30).

The transitional glands (Fig. 33), which occupy the region extending about 1 mm. to the left of the gastroesophageal junction, are acinar and tubuloacinar glands containing the same cell components as the pyloric glands, plus a few chief cells. The acini are single for the most part and empty into the lumen by way of short, narrow ducts about 15 microns long (Fig. 36). The lumen of a duct, when seen from above, appears as a pore about 5 microns in diameter. These glands form a transition zone between the pyloric gland type and the caecal gland type.

Except for the short region containing the transitional glands, the caecum contains oxyntic glands which are simple acinar and tubuloacinar glands in which chief and parietal cells are found (Figs. 34, 35, and 36). These acini are 25 to 50 microns in diameter and empty by way of ducts similar to those described for the transitional glands. Tubular gastric glands of the type usually found in the mammalian stomach are completely absent from the caecum. The chief cells usually occupy the basal half of the acini and the parietal cells the luminal half. A few argentaffine cells are present in some acini.

Most of the parietal cells in the stomach of D. rotundus do not exhibit an intracellular canal, differing from those usually seen in the stomachs of the other bats included in this study. This condition may be caused secondarily by the methods utilized and should be more carefully studied. The cells also tend to be somewhat more polyhedral than oval.

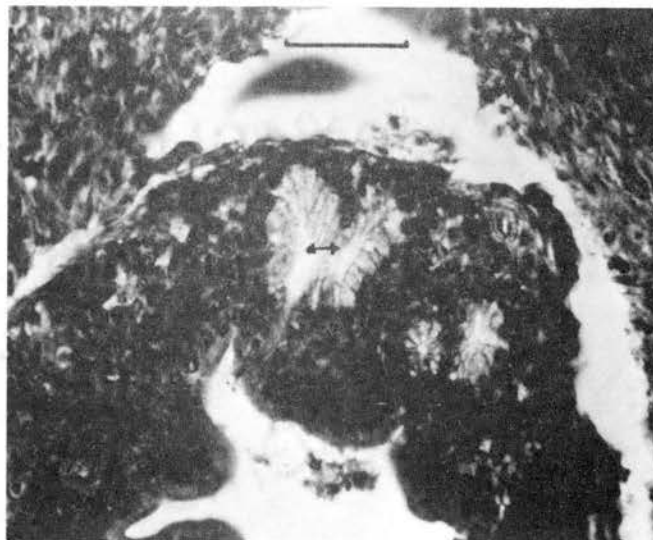


Figure 33. Transitional gland in Desmodus rotundus. Scale = 50 microns. Photomicrograph.

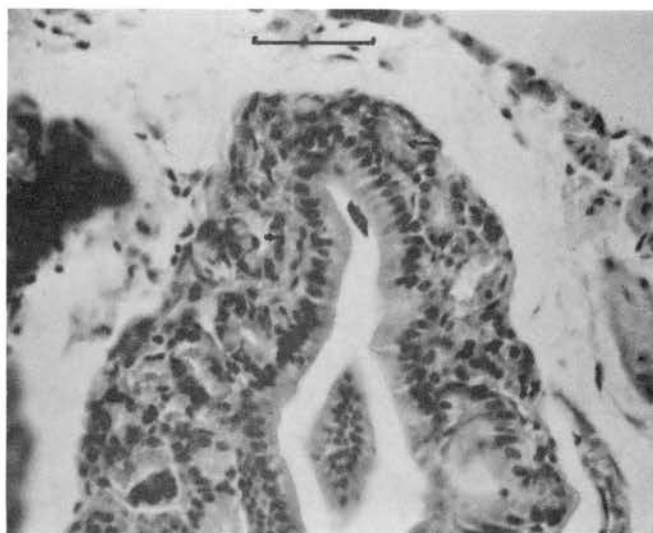


Figure 34. Oxyntic glands in caecum of stomach of Desmodus rotundus. Arrows, oxyntic gland acini. Scale = 50 microns. Photomicrograph.

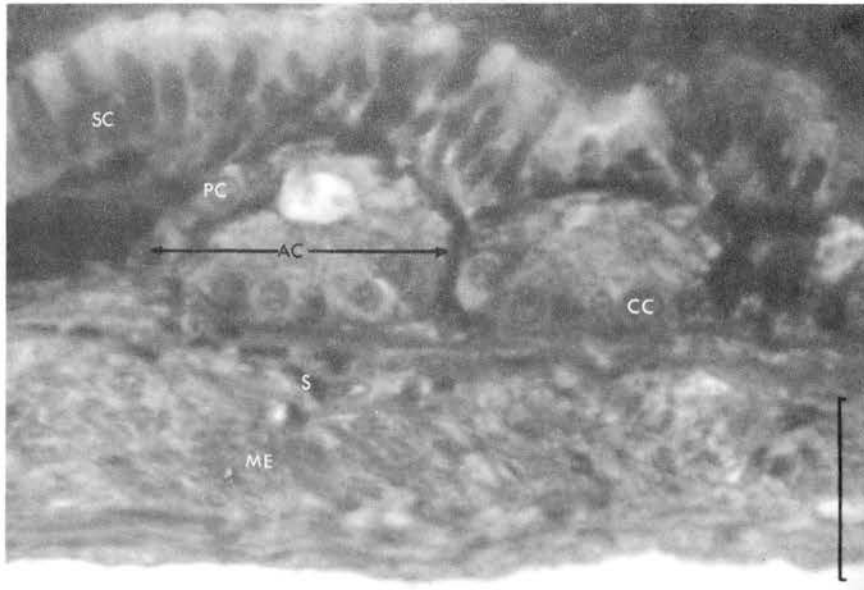


Figure 35. Acinus in caecum of stomach of Desmodus rotundus. AC, acinus; other abbreviations as in Figure 11. Scale = 30 microns. Photomicrograph.

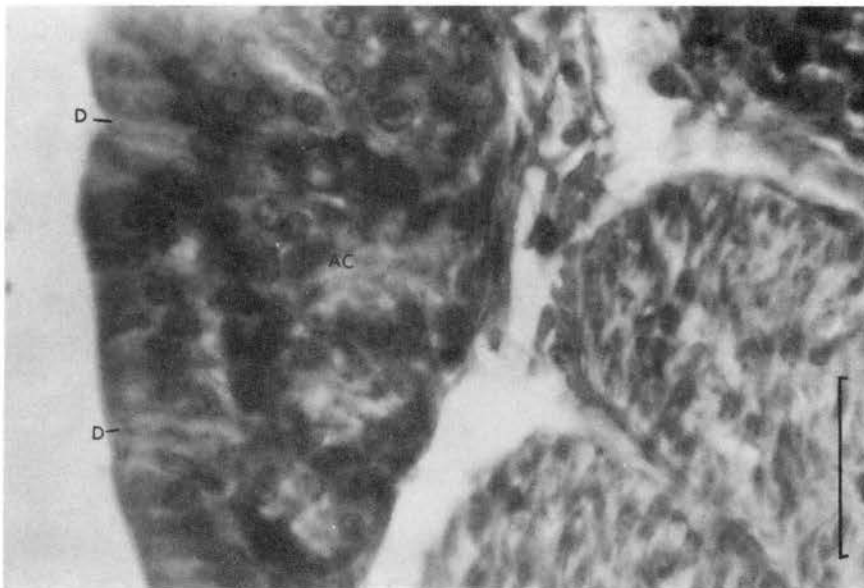


Figure 36. Ducts leading from acini in caecum of stomach of Desmodus rotundus. D, duct; AC, acinus. Scale = 30 microns. Photomicrograph.

The mucosa of the gastric caecum of D. rotundus is supplied with a vascular network (Fig. 37) that is unparalleled in any other species studied. The tunica propria appears to be an almost continuous vascular channel resulting in each acinus being bathed on all sides by blood.

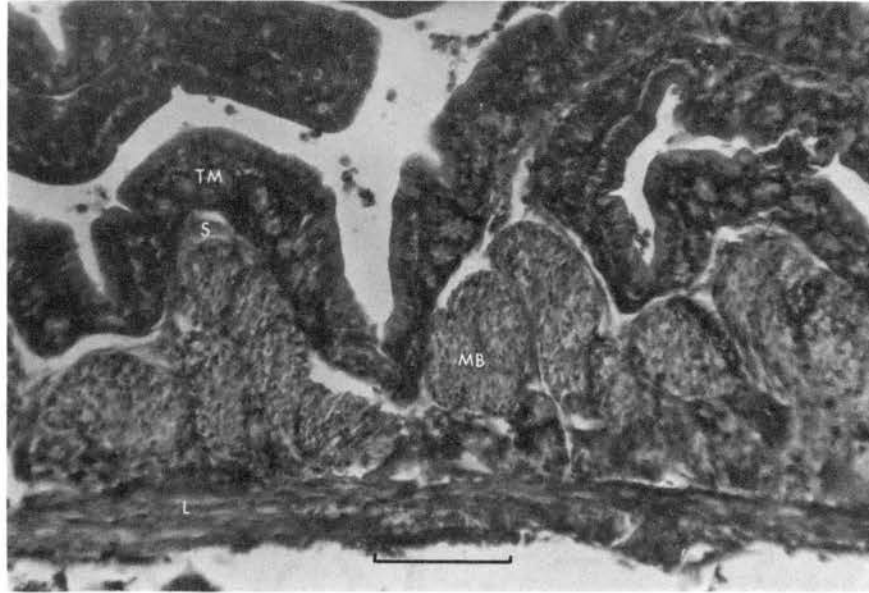


Figure 37. Longitudinal section through stomach of *Desmodus rotundus*. Note the long, thin rugae. MB, muscle bundle of inner circular layer of tunica muscularis; L, longitudinal layer of tunica muscularis; other abbreviations as in Figure 4. Scale = 100 microns. Photomicrograph.

CHAPTER IV

CONCLUSIONS

It is evident that differences in gastric histology occur among some bats. In the insectivorous vespertilionids and molossids, the gastric histology corresponds rather closely to the condition seen in the cat (Bowie, 1940) and humans (Berger, 1933). Here, chief and parietal cells are abundant in the gastric mucosa. This is not surprising, considering that the diets are rich in proteins. The gastric histology of Leptonycteris sanborni, a nectivore, is significantly different from that of the insectivorous species in the reduction of the number of chief cells in the mucosa. In addition, the stomach of L. sanborni is more saccular. These two factors, reduction in chief cells and increase in capacity, might be considered adaptations incident to a diet relatively less rich in proteins and higher in volume than in the insectivorous bats. The gastric histology of Desmodus rotundus exhibits the most striking differences. Here, the tubular type gland is all but lost and replaced by acinar and tubuloacinar glands. One can only speculate as to the advantages of this adaptation, but it might be related to the large proportions to which the stomach is filled during feeding. The swelling seen in the tubular pyloric glands in the fully distended stomach may indicate stress is being placed on the glands by the dense stomach content. Perhaps acinar glands are better able to withstand the stress of pressure than are tubular glands. The extreme vascularity

of this stomach may be related to the high water content of the food normally taken by the vampire, supplying an anatomical avenue for rapid water absorption and subsequent excretion via the kidneys, as suggested by Wimsatt and Guerriere (1962). These factors lead to a conclusion that gastric histology in bats is correlated to diet.

It should also be noted that the chief and parietal cells do not become involuted in hibernating Myotis velifer. This correlates with the observations and comments of Ito and Winchester (1963) on these cells in hibernating M. lucifugus. Involution of chief and parietal cells, which occurs in hibernating Spermophilis undulatus (Mayer and Bernick, 1957 and 1958) and Erinaceus (Carlier, 1893), apparently does not occur in hibernating Myotis.

These propositions are tentative, and suggest the need for more detailed physiological and anatomical studies. Analysis of the secretory products of the mucosa of all the species considered in this study should be made in order to evaluate the possible functions suggested by anatomical elements. Further studies of this type on a large number of species might prove very enlightening.

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